Fishery Resources of the Western Aleutians

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The fishery resources in the western Aleutian Islands are diverse, abundant, and heavily exploited, primarily by Japanese and Soviet fishermen. Seven groups make up the bulk of the current catch: salmon (sockeye, chum, and pink), king crabs, Pacific halibut, Pacific ocean perch, sablefish, walleye pollock, and Pacific cod. Three species of whales (sperm, fin, and sei) are also captured. The marine environment is highly productive and is relatively unaffected by man's activities other than fishing.

Prospects for continued or expanded fishery harvests vary according to species. Pink and chum salmon stocks will probably remain at about current levels. Sockeye stocks will probably recover somewhat from their present low levels if average environmental conditions prevail and international regulations are successful in controlling the high-seas catch. King crab harvests by U. S. fishermen should gradually increase as previously unexploited stocks are fished. Pacific halibut, sablefish, and Pacific ocean perch stocks and catches will probably continue at current low levels. Walleye pollock and Pacific cod catches will probably increase somewhat. Whale stocks will continue their precipitous decline, and their harvest will probably end within a few years as a consequence of conservation efforts and international treaties.

The fishery resources around Amchitka Island are abundant and diverse, but until recently man has used them to only a limited extent. Although the original Aleut inhabitants of Amchitka depended on the sea for most of their food, they had little impact on the fish stocks because fishing methods were primitive. Their refuse middens, formed during several milleniums of continuous occupation, consist almost entirely of the skeletal remains of marine fishes, mammals, and invertebrates (Desautels et al., 1970). The size of the original Aleut population is unknown, but all estimates are over 10,000, and nearly all the Aleutian Islands were inhabited; on Amchitka alone, 73 separate occupation sites have been identified (McCartney, Chap. 5, this volume). After the Aleutians were discovered by the Western World in the eighteenth century, the Aleut population dwindled to less than 1000 for the entire Aleutian chain. As a result, for the 100-year period between the mid-nineteenth and the mid-twentieth centuries, the fishery resources were disturbed very little by man.

In the 1950s fish stocks in the western Aleutians were exploited on a large scale on offshore or deepwater species that had not been available to the Aleuts. In 1952 Japan expanded the scope of its high-seas gill-net fishing for salmon, *Oncorhynchus* spp., from Asian waters to the western Aleutians, and in the early 1960s Japan and the Soviet Union sent enormous fleets of trawlers to the western Aleutians to fish virgin stocks of Pacific ocean perch, *Sebastes alutus*. During this same period both nations expanded their whaling fleets throughout the North Pacific Ocean.

Soviet or Japanese trawlers were frequently observed fishing off Amchitka during the Atomic Energy Commission (AEC) occupation of the island. Direct evidence of the magnitude of these Japanese and Soviet fisheries is the tremendous accumulation of derelict fishing gear on Amchitka's beaches (Fig. 1). In 1972 I surveyed 10,000 m (33,000 ft) of these beaches to provide a basis for estimating the total amount of fishing debris on the island. I estimated that at least 22,000 items made of synthetic materials were on the island beaches, including nearly 12 tons of discarded scraps of trawl web and 6600 salmon gill-net floats (Anonymous, 1973).

By 1971 the Soviet and Japanese fishing effort in the western Aleutians had declined, and only the Japanese high-seas salmon gill-net fishery was continuing at a level of effort comparable to the peak years in the 1960s. The stocks of Pacific ocean perch and whales had been so diminished by intensive fishing that they could no longer support the previous high levels of effort.

Although this relatively low fishing effort is continuing, the basic productivity of the seas in the western Aleutians is unimpaired, and it seems inevitable that additional species as well as remnant

Fig. 1—Japanese salmon gill-net fragment washed up on Amchitka Island beach.

or recovered stocks of previously fished species will again be exploited.

The fishery resources in the western Aleutians are now used only by Japan, the Soviet Union, and the United States. Other nations, however, may soon begin fishing there. South Korea has already done some exploratory fishing, and Poland, North Korea, West Germany, and the People's Republic of China have expressed interest in fishing in the area.

United States fisheries in the western Aleutians have been for Pacific halibut and crab, which have a high unit value. These U. S. fisheries have been far exceeded in intensity, total value, and geographic extent by the fisheries of Japan (Fig. 2) and the U.S.S.R. (Fig. 3), which concentrate on species with a low unit value. In 1972, for example, over 1300 Japanese and Soviet vessels were employed in fisheries off Alaska's coast (National Marine Fisheries Service, 1973). The situation is changing, however, because the target species sought by the foreign trawl fleets are being depleted and U. S. fishing is expanding to include previously unexploited crab stocks in the western Aleutians. Furthermore, as a result of changing economics and regulations, the U. S. fishing industry is exploring the feasibility of trawling on Alaska's continental shelf in competition with the foreign fleets.

So far there has been little direct competition between the United States and foreign fleets in the western Aleutians. Several international agreements restrict the foreign fleets to species and waters not fished by U. S. fishermen, whose catches come mostly from waters inside the 4.8-km (3-mile) territorial limit. Also, the United States has no distant-water trawl fleets, a reflection of the lack of economic incentives to the U. S. fishing industry under institutional and market conditions that have prevailed.

Discussion in this chapter is limited to the current status of commercially exploited fish and whale stocks around Amchitka. Other sections of this volume treat related topics, e.g., physical oceanography (McAlister and Favorite, Chap. 16), marine fish communities (Simenstad et al., Chap. 19), sea mammals (Abegglen, Chap. 20), and sea otters (Estes, Chap. 21).

The area of concern is arbitrarily defined as those waters between longitude 170°E and 170°W and latitude 50°N and 55°N, which coincides with the area designated as Aleutian area 5 by the International North Pacific Fisheries Commission (INPFC) for reporting catch statistics. Amchitka lies in about the center of this area (Figs. 2 and 3). The continental shelf to the east of Amchitka, including the Bering Sea and northeast Pacific Ocean, has very large stocks of fish and intensive fisheries, but they are not considered here.

Only the major species currently sought within the area of concern by U. S. and foreign fishermen are discussed here. These include sockeye salmon (*O. nerka*), chum salmon (*O. keta*), pink salmon (*O. gorbuscha*), coho salmon (*O. kisutch*), chinook salmon (*O. tshawytscha*), Pacific ocean perch, sablefish (*Anoplopoma fimbria*), walleye pollock (*Theragra chalcogramma*), Pacific cod (*Gadus macrocephalus*), Pacific halibut (*Hippoglossus stenolepis*), king crab (*Paralithodes camtschatica*), sperm whale (*Physeter catodon*), sei whale (*Balaenoptera borealis*), and fin whale (*B. physalus*).

Other commercial species in this area, which are not included in the discussion because they make up only a minor portion of the current catch, include tanner crab (*Chionoecetes tanneri*), Dungeness crab (*Cancer magister*), arrowtooth flounder (*Atheresthes stomias*), yellowfin sole (*Limanada aspera*), rock sole (*Lepidopsetta bilineata*), and flathead sole (*Hippoglossoides elassodon*).

There is no single source of statistics for all species caught in the western Aleutians, but I have included catches for the most recent year available (usually 1970 or 1971).

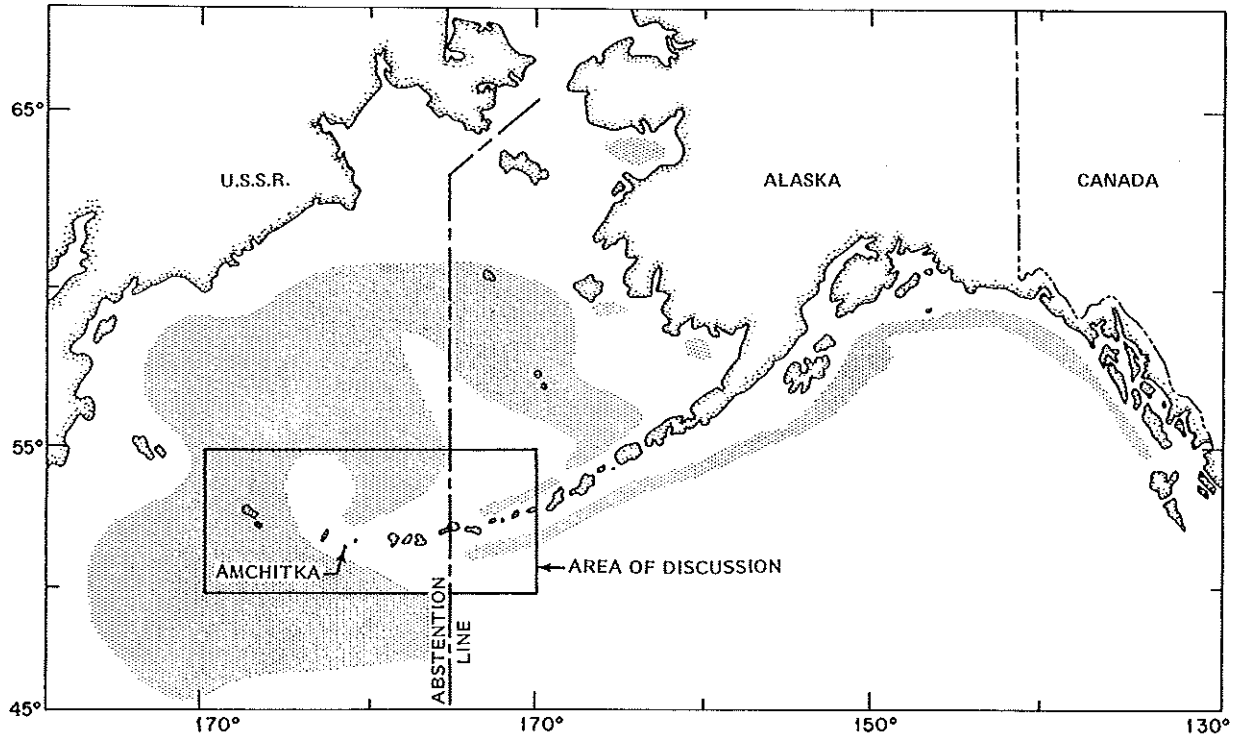

Fig. 2—Japanese fishing areas off Alaska, 1971 (excluding whales).

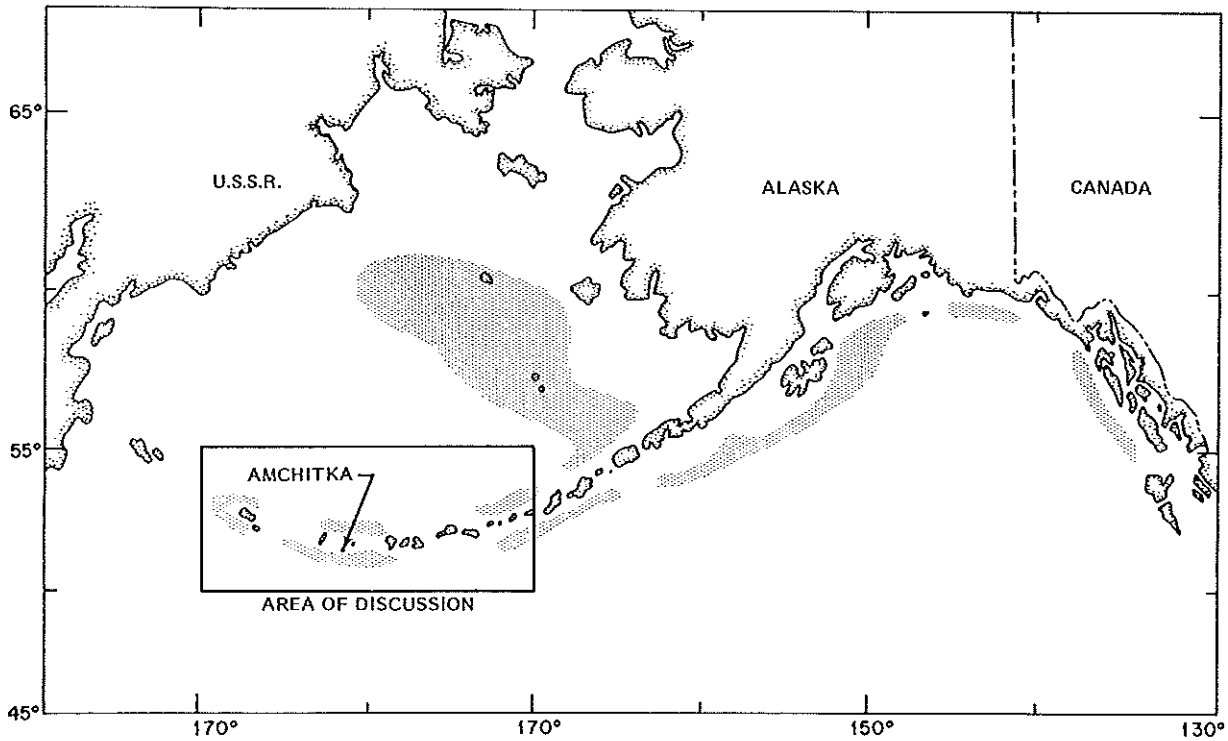

Fig. 3—Soviet fishing areas off Alaska, 1971 (excluding whales).

DATA SOURCES

Detailed information on the fishery resources in the immediate vicinity of Amchitka Island is scanty. Despite the limitations of available data, it is important to include in this volume a résumé of what we know or can infer about the fishery resources of the western Aleutians because they are potentially the most economically valuable component of the Amchitka marine ecosystem.

The only assessment of local resources was limited sampling of nearshore fish stocks by the University of Washington Fisheries Research Institute (FRI) during the AEC testing program. Although Japanese and Soviet scientists investigated some aspects of the fishery resources in the western Aleutians during their heavy exploitation of demersal fish stocks in the 1960s, most of the results of this research have not been published. In a discussion such as this, the published statistics are adequate to describe the general characteristics of the commercially exploited resources.

The best published sources of catch data are the INPFC, the National Marine Fisheries Service (NMFS), and the information exchanged annually since 1969 between the Soviet Union and the United States at bilateral agreement meetings.

Each year the INPFC publishes a statistical yearbook that tabulates by area and gear the weight of each species caught in the North Pacific Ocean and in the Bering Sea by Japan, the United States, and Canada. The INPFC also publishes the proceedings of annual meetings and bulletins describing research conducted by the three treaty nations on North Pacific fisheries.

The NMFS Division of Enforcement and Surveillance in Alaska publishes an annual summary of observations on patrols of foreign fishing fleets off the Alaska coast. These patrols are made by NMFS enforcement agents in cooperation with the U. S. Coast Guard. Their purpose is to enforce United States fishery laws and regulations, police fisheries subject to international agreements, and maintain surveillance of extra-treaty foreign fisheries. In 1971 the patrols covered about 145,000 km (90,000 miles) by ship and about 380,000 km (236,000 miles) by aircraft.

Several publications describe the general methods of operation of Japanese and Soviet fleets in the Gulf of Alaska and in the Bering Sea and the biology and life history of commercially exploited species, although none of these pertain specifically to the western Aleutian fisheries. The most comprehensive single source of general information is the study by Alverson, Pruter, and Ronholt (1964). These investigators describe the history and methods of fishing for demersal fishes by foreign and U. S. fishermen and discuss the geographic distribution, relative abundance, and biology of each species. A paper by Reeves (1973) provides similar but more current data for the Gulf of Alaska. Chitwood (1969) provides a concise history of Japanese, Soviet, and South Korean fisheries off Alaska through 1966 and describes fishing vessels, their numbers, and where they fish. Hitz (1970) gives detailed descriptions of vessels and fishing methods used by Soviet trawl fleets. Kasahara (1972) reviews Japanese distant-water fisheries throughout the world; he emphasizes the role of international agreements and predicts that the prospects for continued expansion are not bright. Hart (1973) is one of the most valuable general references for information on distribution and life history of Pacific Coast fishes. My discussions of individual species are drawn principally from these sources.

FISHERY RESOURCES

A caveat that applies to any discussion of abundance of ocean fish stocks is that it is seldom possible to directly and precisely determine the numbers or biomass of any species. Usually commercial fishery catch statistics provide the best basis for estimating relative abundance of a species in a particular area. Catches by Japanese fleets supply these data for the western Aleutians. Soviet catch statistics are not so useful as the Japanese statistics because they are not reported in as much detail and include only recent years. In using catch statistics as a measure of relative abundance, we must assume that the catch reflects actual abundance. This is obviously an imperfect procedure, but it is the best recourse available. It is also important to remember that stocks of species not currently sought by fishermen may be abundant but are not represented in proportion to their numbers in catch records.

The best single source of information for assessing the relative abundance of commercially sought fish in the western Aleutians (excluding salmon, crabs, and whales) is the series of INPFC Statistical Yearbooks, which contain summaries of Japanese catch statistics. In 1969 a new system of reporting catches was initiated. This system identified, for the first time, catches of each species for the western Aleutians specifically (Table 1). Before 1969 catches for the western Aleutians were combined with those from other areas to the east.

Despite the severe reduction of stocks, the catch of Pacific ocean perch is still greater than the catch of all other species combined.

Experimental research trawling by FRI from 1967 to 1972 provides insight into the condition

Table 1—Commercial Catch of Fish (Metric Tons) in the Western Aleutians by Japan and the U.S.S.R., 1969 to 1971

Nation and year	Pacific ocean perch	Sable-fish	Pacific halibut	Arrow-tooth flounder	Yellow-fin sole	Rock sole	Flathead sole	Walleye pollock	Pacific cod	Other
Japan										
1969*	15,597	1,673	330	65	20	2	2	512	222	2,558
1970*	13,650	1,247	351	288	9	2	11	179	284	2,002
1971†	14,664	2,766	387	44	1	1	16	622	432	3,928
U.S.S.R.‡										
1969§	23,172									1,453
1970	53,274							9,490		9,490
1971	7,190	170						2,535	1,653	1,322

*International North Pacific Fisheries Commission (1972a; 1973).
†Fishery Agency of Japan.
‡United States–U.S.S.R. Bilateral Scientific Meetings, 1970, 1971, and 1972.
§U.S.S.R. trawl fishery statistics for 1969, 1970, and 1971. Partial catch (does not include first quarter).

of fish stocks in the immediate vicinity of Amchitka and generally corroborates the relative abundance of species deduced from Japanese catches. The narrative summary by FRI of their catches from 1967 to 1972 (Simenstad et al., Chap. 19, this volume) states that bottom trawl catches ranged between 200 and 1000 fish per hour when dense schools of Pacific ocean perch, Pacific cod, or walleye pollock were encountered and that catch composition typically ranged from 40 to 900 Pacific ocean perch, 30 to 55 walleye pollock, 20 to 45 Pacific cod, 20 to 30 sculpins, 6 to 12 arrowtooth flounder, 6 to 7 rock sole, and 2 to 6 Pacific halibut per trawling hour.

Salmon

Five species of Pacific salmon occur in the western Aleutians as juveniles and maturing adults. They spawn in Asian and North American streams and intermingle in the western Aleutians in varying degrees during the 1 to 4 years they spend at sea.

The best source of information on the relative numbers of the five species in the western Aleutians is the catch records of Japanese fishing fleets. Table 2 shows the mother-ship catches of the Japanese high-seas fleet for each salmon species from 1952 to 1970. Although the effort has remained constant since 1962, the catches fluctuate widely because of annual variations in abundance of each species. The only data on salmon abundance in the immediate vicinity of Amchitka are FRI samples for 1969 and 1970 (International North Pacific Fisheries Commission, 1972b, Tables 8, 9, and 10). Kondo et al. (1965) provide a comprehensive review of ocean distribution and migration of salmon based on tag returns. All three sources indicate that sockeye and chum salmon predominate in most years in the western Aleutians and that pink salmon are third-most abundant. Coho and chinook salmon are present in insignificant numbers compared with the other three species.

Salmon in the western Aleutians originate from streams in both Asia and North America. Most chum salmon in the western Aleutians are from rivers in the U.S.S.R. and Japan (Shepard, Hartt, and Yonemori, 1968), and most sockeye salmon are from rivers in Bristol Bay, Alaska (Margolis et al., 1966; Bakkala, 1971). The abundance of pink salmon fluctuates greatly. During some years pink salmon of Asian origin predominate; in other years pink salmon from Alaska streams are most abundant (Neave, Ishida, and Murai, 1967). Pink salmon are the predominant species spawning in streams on Amchitka and other Aleutian Islands, but their numbers are relatively insignificant.

There is increasing evidence that many of the chinook salmon caught by the Japanese are from western Alaska rivers, such as the Yukon and Kuskokwim.

Fisheries. Only Japan fishes for salmon in the western Aleutian area. Kasahara (1972) reviews the history and development of this fishery, which began in its present form in 1952 with the signing of the International North Pacific Fisheries Convention by the United States, Canada, and Japan. This treaty requires Japan to abstain from fishing for salmon east of longitude 175°W and was believed to protect from the Japanese fishery most immature salmon originating from North American streams (Fig. 2). Subsequent research has shown that some North American stocks (mainly sockeye, but also some chums, pinks, and chinooks) migrate to the west of this abstention line, and since 1963 the United States and Canada have attempted, without success, to move the line farther west.

Table 2—Japanese Mother-Ship Salmon Fishery Catch* (Thousands of Fish), Longitude 160°E to 175°W

Year	Sockeye	Pink	Chum	Coho	Chinook
1952	738	698	629	24	1
1953	1,534	2,892	2,678	307	3
1954	3,382	2,698	8,254	675	57
1955	9,456	9,108	14,012	1,467	43
1956	8,702	6,589	15,316	3,393	117
1957	19,403	17,204	8,877	193	25
1958	10,708	7,859	14,048	3,106	38
1959	9,125	18,642	12,856	1,388	63
1960	12,879	1,826	10,517	862	180
1961	12,998	3,226	6,128	281	31
1962	10,590	1,011	6,372	1,531	122
1963	8,902	6,242	5,858	1,890	88
1964	7,097	2,198	8,640	3,533	410
1965	12,038	4,238	6,037	1,173	185
1966	7,254	2,457	8,562	466	208
1967	8,087	7,698	6,848	225	127
1968	6,373	3,609	8,107	805	362
1969	5,935	6,862	7,721	1,144	554
1970	6,944	1,573	9,639	180	437

*International North Pacific Fisheries Commission (1972c).

From 1962 through 1971 the Japanese fleet has consisted of 11 factory ships and 369 catcher boats. The salmon are caught in floating monofilament gill nets set off the sterns of the catcher boats (Fig. 4). The nets have a mesh size of about 120 mm stretch measure and are 5 m (16 ft) deep. When all the catcher boats are fishing, more than 5500 km (3400 miles) of net is fished daily because each catcher boat sets 15 linear kilometers of net each day. The catcher boats transfer each day's catch to a factory ship where the salmon are cleaned and frozen whole or canned. The processed catch is transported to Japan where it is marketed locally and throughout the world.

The fishery, which lasts from mid-May until July or August (Chitwood, 1969), starts south of the Aleutian Islands and moves progressively north toward Asia and North America to intercept mature adult salmon migrating toward parent spawning streams. The thousands of net floats and huge wads of derelict gill nets that have accumulated on Amchitka beaches provide striking evidence of this massive fishing effort.

Future Prospects. In 1973 and 1974 the valuable Bristol Bay sockeye salmon run declined to very low levels, apparently as a result of both the Japanese high-seas catch and adverse environmental conditions that caused unusually high mortality of juveniles in the Bristol Bay estuary and lakes. To reverse this decline, the United States has aggressively attempted to persuade Japan to curtail its high-seas fishing and has drastically curtailed its own catch. The present downward trend of sockeye salmon abundance will probably turn upward if environmental conditions during the fish's early sea life return to normal and international negotiations are successful in restricting catches on the high seas.

Chum and pink salmon seem to be maintaining their numbers better than sockeye. Barring the collapse of international fishery agreements, which limit to some extent the scope of Japanese high-seas fishing, the abundance of pink and chum salmon in the western Aleutians can be expected to continue at more or less the same levels as at present.

If other nations not party to the present fishery agreements between Japan, the United States, and Canada were to begin fishing, the unrestricted fishing could result in the decimation of present stocks of all salmon species.

King Crab

The king crab resource is the most significant present and potential fishery resource for U. S. fishermen in the western Aleutians. The precise size of this resource is undetermined, but it is substantial in localized areas. King crabs are not common at Amchitka. National Marine Fisheries Service biologist—divers saw a few juvenile king crabs during extensive underwater observations at Amchitka over the 5-year period 1969 to 1973, and biologists from FRI captured a few adults

Fig. 4—Japanese catcher boat hauling in salmon gill net. Note salmon on deck and small net astern of the gill net to retrieve salmon that fall out of gill net as it is being hauled aboard. (Photograph courtesy of NMFS Division of Enforcement and Surveillance.)

during the same period. *Lithodes aequispina,* a species similar to king crab, was captured by FRI in research trawls near Amchitka at an average rate of 4 to 9 per hour (Simenstad et al., Chap. 19, this volume).

Biology and Life History. King crabs occur along the entire North Pacific coast from northern Japan to British Columbia, usually on sand or mud bottoms in water depths to 400 m (1300 ft). The commercial fisheries are limited by law and international agreements to males only, which grow larger than females. King crab males may reach a weight of 11 kg (25 lb) and an age of 16 years, although the averages are much less. At Kodiak, Alaska, recent average weights of individual crabs in the catch have been about 3 kg (6 lb) (Haynes and Lehman, 1969). Both sexes mature at about 5 years of age. The fecundity of females ranges from 25,000 to 390,000 eggs (Haynes, 1968). The fertilized eggs are carried externally by the female for about 11 months and hatch in the spring just before molting and mating again. The larvae are planktonic and may be transported long distances by currents before settling to the bottom (Hebard, 1959; Haynes, 1974). Adults also migrate long distances by walking on the bottom. After they reach maturity, king crabs have few natural enemies.

Fisheries. The U. S. king crab fishery in the western Aleutians is concentrated east of Amchitka around Adak Island, but some exploratory fishing has been done around Kiska and Attu Islands. Significant commercial catches have been made on Petrel Bank, northeast of Semisopochnoi Island.

The Soviets and Japanese are prohibited from fishing for crabs in the western Aleutians under terms of bilateral agreements with the United States.

The U. S. fishermen catch king crabs in baited pots in waters to about 200 m (650 ft) deep. The

pots, which are about 2 m (6 ft) square and 1 m (3 ft) deep, are set on the bottom and attached by line to two buoys at the surface. The pots weigh about 150 kg (300 lb) and are hauled with a power winch. Crab vessels are 15 to 55 m (50 to 180 ft) long [average about 30 m (100 ft)]. The crabs are kept alive in tanks with circulating seawater until they are taken to a shore plant where they are butchered, cooked, and frozen. The U. S. catches west of longitude 172°W for the years 1969 to 1971 were as follows (Alaska Department of Fish and Game, 1972):

Year	Pounds	Kilograms
1969	18,040,000	8,182,800
1970	12,424,800	5,635,800
1971	25,828,100	11,715,400

Fishing is regulated by season and catch-quota restrictions, which vary from year to year.

Future Prospects. Crab fishing by U. S. fishermen on unexploited stocks in the western Aleutians is likely to increase.

Pacific Halibut

Pacific halibut occur on the continental shelf along the entire North Pacific coast from Japan to California in waters to 1100 m (3600 ft) deep (Bell and St.-Pierre, 1970). There is no reliable information on their distribution and abundance in the western Aleutians, but catches by research and commercial vessels indicate that Pacific halibut are present in low abundance throughout the area (Bernard E. Skud, International Pacific Halibut Commission, Seattle, Wash., personal communication). During the recent AEC occupation of Amchitka, sport fishing for Pacific halibut in Constantine Harbor was a popular pastime, and large Pacific halibut were sometimes hooked on baited setlines. The FRI personnel also caught some Pacific halibut near Amchitka with research fishing gear (Simenstad et al., Chap. 19, this volume).

Biology and Life History. Pacific halibut are among the largest fishes in the world. The North American record Pacific halibut [225 kg (495 lb)] was caught at Petersburg, Alaska. The average size of Pacific halibut in the U. S. commercial catch is about 15 kg (33 lb). Females mature later, live longer, and grow faster than males (Bell and St.-Pierre, 1970). Most large Pacific halibut are females. The females reach an age of more than 40 years, and males, about 30 years. The number of eggs produced is proportional to the weight of the fish, and large females may produce 3 million eggs annually. Pacific halibut migrate long distances; newly hatched young are sometimes carried thousands of kilometers from the spawning locations by currents, and tagged adults have been recovered as far as 3700 km (2300 miles) from the point of tagging (Bell, 1973). Pacific halibut are omnivorous but feed predominantly on other fish and crustaceans, including tanner and king crab.

Fisheries. Pacific halibut along the North American coast are exploited by the United States and Canada. The catch is regulated by the International Pacific Halibut Commission (IPHC). In addition, large numbers of juvenile Pacific halibut are incidentally captured off the Alaska coast by the Japanese and Soviets while trawling for other species. This catch has contributed to the recent declines in North American Pacific halibut stocks. Although Pacific halibut constitute only a small percentage of the total trawl catch, in aggregate, these trawl-caught Pacific halibut amount to a significant portion of the Pacific halibut resource in the Bering Sea. The IPHC has reduced the catch limits of the North American setline fishery, but the expected benefits have been negated by the growing incidental catch.

In the United States and Canadian fisheries, Pacific halibut are caught with baited hooks fastened to 1.5-m (5-ft) lengths of light line (gangions) attached at regular intervals to a heavy groundline (skate) lying on the sea bottom. Each skate (a unit of gear) is about 550 m (1800 ft) long and is anchored and marked by surface buoys at each end. The gear is pulled with a power winch after fishing for periods of a few hours to more than a day. The fish are cleaned immediately and transported to shore plants where they are frozen.

Pacific halibut from the western Aleutians constitute only a small part of the total United States–Canadian landings. The fishing intensity in this area varies greatly from year to year because of its distance from processing plants. The area is therefore attractive to fishermen only when areas to the east are closed to fishing. During recent years the catch in the western Aleutians ranged from 1 to 69 metric tons (Bernard E. Skud, International Pacific Halibut Commission, Seattle, WA., personal communication):

Year	Canada, metric tons	U. S., metric tons	Total, metric tons
1969	3	56	59
1970	38	31	69
1971	0	1	1
1972	9	16	25

Future Prospects. Because of the limited size of the stocks and the distance from processing plants, it is unlikely that Pacific halibut fishing in the western Aleutians will expand much beyond its present relatively low level.

Pacific Ocean Perch

Pacific ocean perch have been (and may still be) the most abundant fishery resource in the western Aleutians, but intensive fishing by fleets of Soviet and Japanese trawlers during the 1960s caused a precipitous decline in abundance. Chitwood (1969) summarizes the development of these fisheries.

Biology and Life History. Pacific ocean perch adults occur in dense schools throughout Alaska's continental shelf south of the Bering Strait at depths of 150 m (490 ft) to over 400 m (1300 ft), generally over rocky bottoms (Major and Shippen, 1970). During the first few weeks of life, the larvae are planktonic and drift with the currents. Since no verified collections of perch between the larval stage and year-old juveniles have ever been reported (Carlson and Haight, in press), the balance of their first year is unknown. Juveniles over the age of one year live in relatively shallow water [55 to 130 m (180 to 425 ft) deep]. In the fifth or sixth year of life, they mature and join adult offshore stocks in deeper water. They are long lived and slow growing, reaching a maximum age of about 30 years and a maximum size of about 45 cm (17.5 in.) and 2 kg (4.5 lb) (Alverson and Westrheim, 1961).

Juvenile Pacific ocean perch (1 to 5 years old) feed mainly on copepods and euphausiids. Young juveniles (1 to 2 years old) prefer copepods, and older juveniles (3 to 5 years old) prefer euphausiids (Carlson and Haight, in press).

Adults also feed on copepods and euphausiids but show a preference for euphausiids. Other larger food items, e.g., shrimp and squid, make up a significant part of their diet (Shalkin, 1964; Paraketsov, 1963; Lyubimova, 1965).

Fisheries. Pacific ocean perch in the western Aleutians are fished exclusively by the Soviets and Japanese. The history of the fishery encompasses a period of only a few years, i.e., from the first explorations of Pacific ocean perch stocks in the late 1950s by Soviet research vessels to one of the most massive fishing operations in history in the 1960s and to the present reduced level of effort. During that brief period the large virgin stocks of Pacific ocean perch in the Bering Sea and Gulf of Alaska were greatly reduced, and by 1968 only 39% of the original stock biomass remained (Quast, 1972). Quast's estimate was for the total North American Pacific ocean perch resource, but it is reasonable to assume that western Aleutian stocks of Pacific ocean perch have followed the overall pattern of decline. Published data are not available for catches of perch by Japan and the Soviet Union for specific areas over a series of years. The most useful data illustrating the rise and decline of Pacific ocean perch catches are Japanese statistics for the Bering Sea region, which includes the western Aleutians (International North Pacific Fisheries Commission, 1973, Table 32):

Year	Catch, metric tons	Year	Catch, metric tons
1961	13,002	1966	50,308
1962	12,449	1967	38,517
1963	17,257	1968	54,347
1964	43,750	1969	30,892
1965	47,648	1970	22,772

The Japanese and Soviets use the same fishing methods for Pacific ocean perch and other demersal fish. Schools of fish are first located by electronic hydroacoustic instruments, and then trawl nets are dragged through the water to intercept the schools. These schools contain predominantly Pacific ocean perch, but small numbers of other species are also caught. The catch is hauled aboard ship either over the side or over the stern (Fig. 5) and cleaned immediately (Fig. 6). Most are processed into frozen fillets. Nearly all fishing is now by large stern-ramp factory trawlers of 50 m (160 ft) to more than 100 m (320 ft) long (Figs. 7 and 8). These trawlers are completely self-sufficient, i.e., they are equipped to catch, process, and store the finished product until it is transferred to a refrigerated transport ship (Fig. 9) or until they return to the parent country. In the 1960s smaller trawlers were common, but the trend is toward larger ships.

Both Japan and the Soviet Union generally fish in summer (May–November) when Pacific ocean perch are more vulnerable to capture by trawling; in winter the perch are in deeper water (Gunderson, 1974). In 1971 between 1 and 6 Soviet trawlers and 2 and 10 Japanese trawlers operated in the western Aleutians (National Marine Fisheries Service, 1973).

Future Prospects. Because of the depleted condition of the stocks and because Pacific ocean perch grow very slowly, the present relatively low level of fishing effort will probably continue.

Sablefish

Sablefish are distributed throughout the North Pacific Ocean from California to Japan. In the

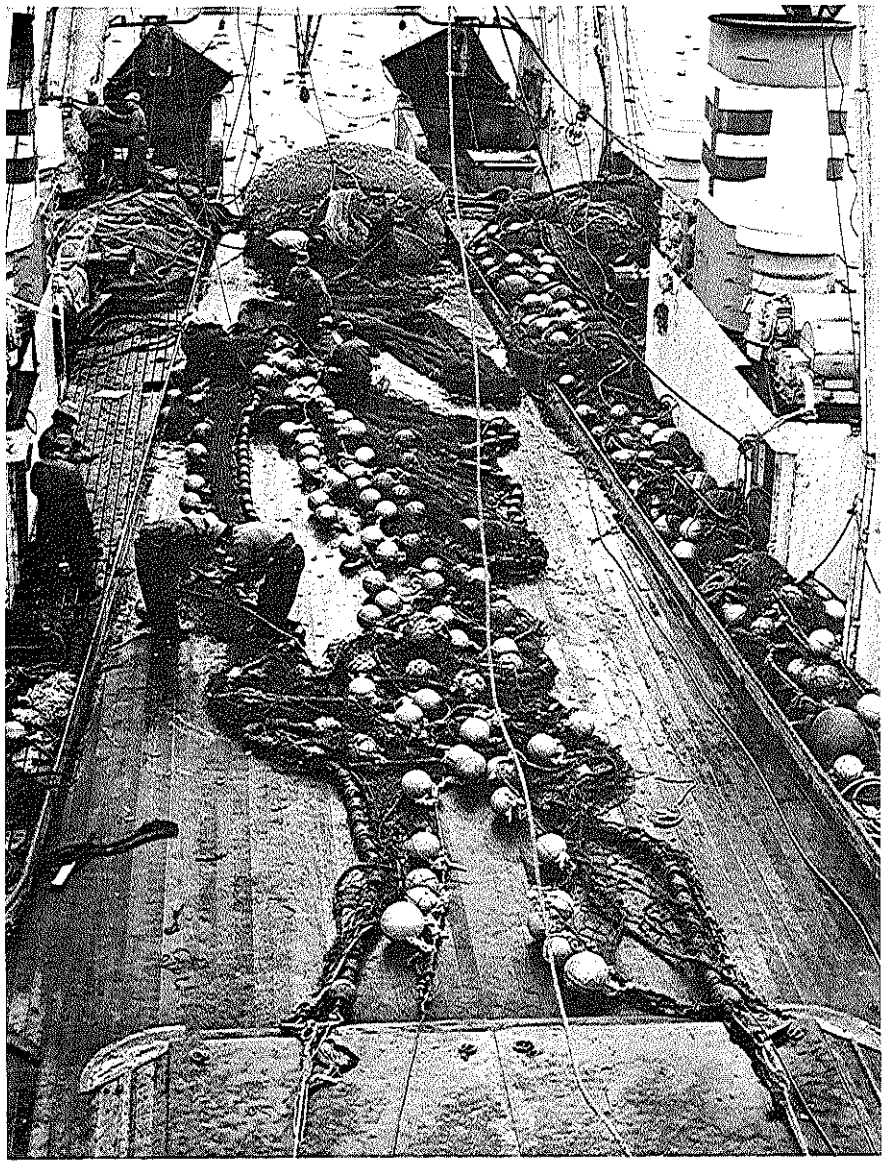

Fig. 5—Catch of 20 metric tons (44,000 lb) of ocean perch being hauled in over the stern ramp of a Japanese trawler. (Photograph courtesy of Jiro Nishimoto, National Marine Fisheries Service.)

Fig. 6—Japanese fisherman cleaning ocean perch aboard stern-ramp trawler. (Photograph courtesy of Jiro Nishimoto, National Marine Fisheries Service.)

Fig. 7—Japanese stern-ramp trawler *Taiyo Maru No. 81* at dock in Shimonoseki, Japan, before leaving on fishing voyage to Alaska waters. (Photograph courtesy of Jiro Nishimoto, National Marine Fisheries Service.)

Japanese catch in the western Aleutians, sablefish are second in abundance to Pacific ocean perch. They do not comprise as great a proportion of the total Soviet catch, presumably because the Soviets do not use longline gear (the most effective sablefish gear).* Sablefish were not common in catches by FRI in the immediate vicinity of Amchitka Island (Simenstad et al., Chap. 19, Table 3, this volume), but Kobayashi (1957) caught larval sablefish in the western Aleutians in July and August of 1955 and 1956.

Biology and Life History. Sablefish are known by the common name black cod in Alaska, but they are not taxonomically related to the true cods and bear only a superficial resemblance to them.

The following summary of what is known of sablefish distribution and biology is derived from Reeves (1973). Adult sablefish prefer deep water and are caught to depths of 530 fathoms (3200 ft); juveniles often occur in shallower waters (even intertidally). They reach maturity between 6 and 8 years of age and at 9 years are about 100 cm (39 in.) long and weigh about 18 kg (40 lb). Spawning takes place in deep water during the late winter, and the eggs and larvae are planktonic. Small immature fish frequent shallow bays and inlets during the late spring and early summer, often in the surface waters. Food items consist of Pacific herring (*Clupea harengus*), Pacific sand lance (*Ammodytes hexapterus*), and crustaceans. Tagging has shown that sablefish migrate long distances, e.g., from Alaskan waters to the Asian coast and from Puget Sound, Wash., to the Bering Sea. Sablefish apparently spawn in the western Aleutians because Kobayashi (1957) captured larval sablefish at nine locations in this area.

Fisheries. Sablefish are caught by Soviet and Japanese trawlers in the western Aleutians with the same gear and in the same areas as Pacific ocean perch. The Japanese also have a longline fishery specifically for sablefish. The longline gear is similar to that used by the U. S. and Canadian halibut fisheries (see the section on halibut). From 1969 to 1971, between 20 and 50% of the Japanese catch of sablefish in the western Aleutians was by longline.

*U. S.–U.S.S.R. Bilateral Scientific Meeting, 1972; U.S.S.R. trawl fishery statistics for 1971.

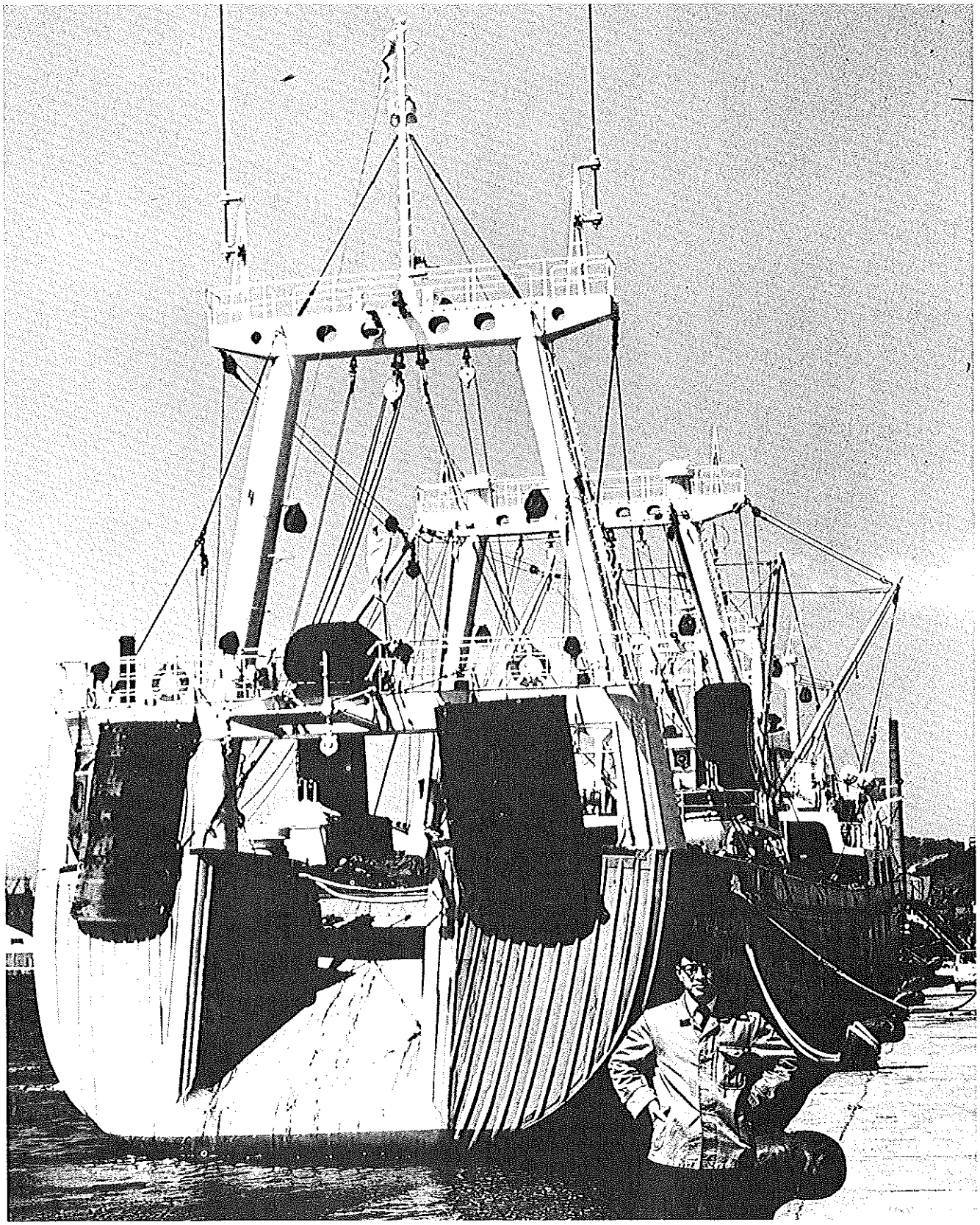

Fig. 8—Stern-ramp trawler *Taiyo Maru No. 81.* Complex superstructure and rigging is used to set and haul the trawl net and manipulate the gear after it comes aboard. (Photograph courtesy of Jiro Nishimoto, National Marine Fisheries Service.)

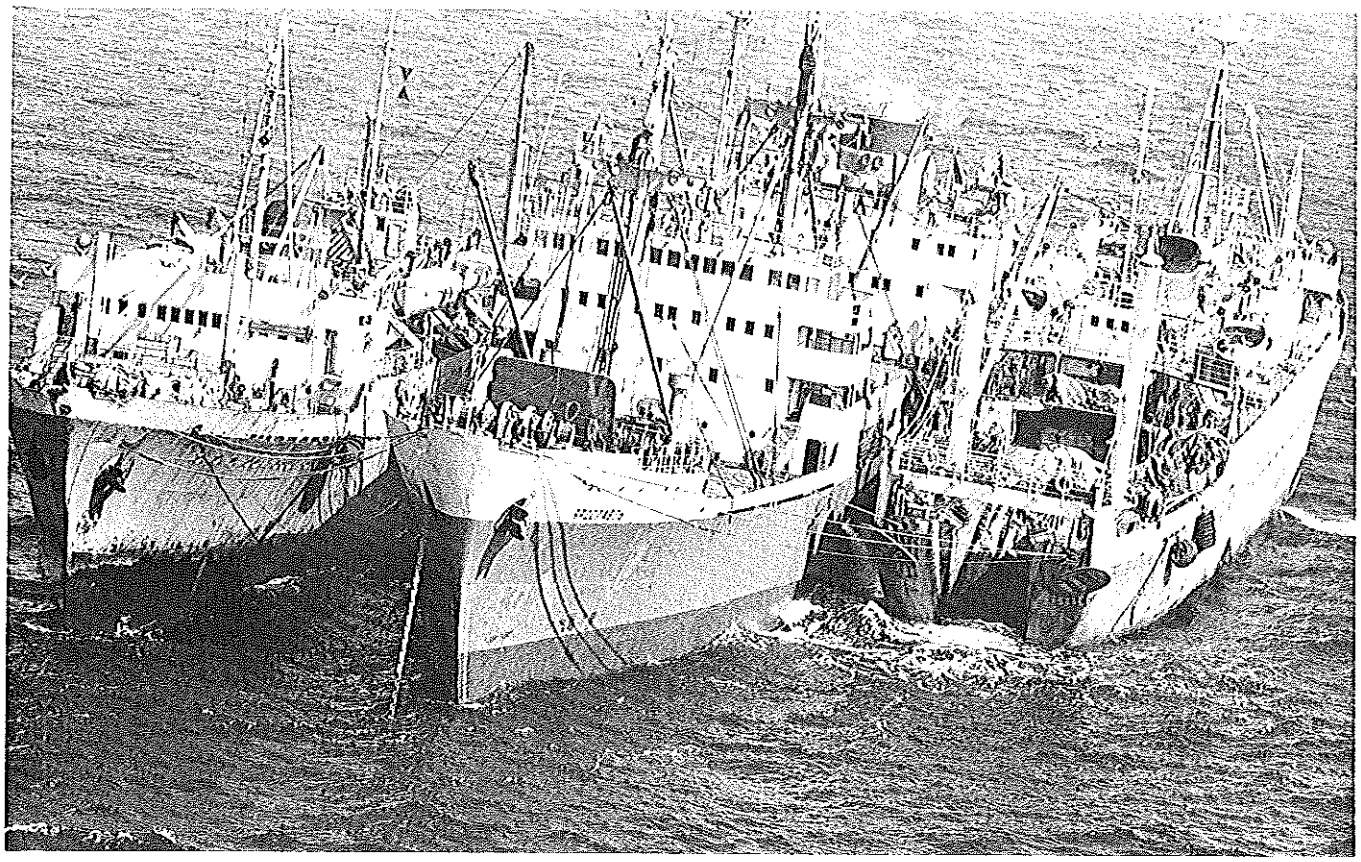

Fig. 9—Soviet refrigerated transport anchored in Aleutian waters while transferring fish products from stern-ramp trawlers. The transport is about 130 m (430 ft) long, and the two trawlers are about 85 m (280 ft) long. (Photograph courtesy of NMFS Division of Enforcement and Surveillance.)

Sablefish are a highly esteemed food fish in Japan. They are usually marketed filleted and frozen, but their fine texture and high oil content also make them a superior salted or smoked product.

Future Prospects. The catch of sablefish in the western Aleutians will probably continue at about the same level. Most will continue to be caught incidentally by fishermen trawling for other species, such as Pacific ocean perch.

Walleye Pollock

Walleye pollock (also known as Alaska pollock and Pacific pollock) were, until recently, the only remaining large unexploited stocks of fish off the North American continental shelf (Kasahara, 1961). The Japanese catch of pollock in the eastern Bering Sea region increased from 24,000 metric tons in 1961 to more than 1,200,000 metric tons in 1970 (International North Pacific Fisheries Commission, 1973, Table 32). Pollock are apparently abundant around Amchitka (Simenstad et al., Chap. 19, Table 3, this volume). Soviet and Japanese trawlers are switching to pollock as a prime target species (Kasahara, 1972; National Marine Fisheries Service, 1973), although Pacific ocean perch still predominate in western Aleutian trawl catches (Table 1). This recent shift of emphasis to pollock is primarily a consequence of depletion of other species and of new developments in food technology, which have generated a heavy demand for minced pollock to use in making surimi, a fish paste that is blended with other food products (Miyauchi, Kudo, and Patushnik, 1973). Previously the demand for pollock as human food was slight in both the Soviet Union and Japan.

Biology and Life History. Temperature apparently determines where pollock occur (Kasahara, 1961). They are caught at all depths where the water temperature is between 0 and 10°C. Pollock mature when 3 or 4 years old and form dense schools during spawning migrations in winter and spring. The eggs are planktonic, and the young hatch in about 12 days. Pollock commonly reach an age of 8 years, but some reach an age of 15 years and a weight of 18 kg (40 lb). The primary foods are planktonic crustaceans, mostly euphausiids, although shrimp and fish are also

important. The diet varies in different geographic areas and is probably determined by the availability of food.

Fisheries. Walleye pollock are caught mostly by large stern-ramp Japanese and Soviet trawlers with the same type of gear as is used for Pacific ocean perch. In 1971 Japanese trawlers caught 622 metric tons of pollock in the western Aleutians, and Soviet trawlers caught 2535 metric tons in the same area (Table 1).

Future Prospects. Future prospects are uncertain. Although the pollock catch and demand are increasing, there is evidence in the eastern Bering Sea, where the largest catches off Alaska are made, that catch per unit of fishing effort is dropping and the bulk of the catch increasingly comprises young and immature fish (Pruter, 1973). The Bering Sea situation may be different from that of the western Aleutians, however, and there appear to be substantial stocks of pollock that have only begun to be exploited. Therefore it is likely that catches near Amchitka will increase.

Pacific Cod

One of the earliest commercial fisheries in Alaska was for Pacific cod. Stocks in the Aleutian Islands and Bering Sea were first exploited commercially in 1864, and their great abundance was first noted and recorded by a Russian navigator in 1765 (Cobb, 1916; 1927). The catch by U. S. fishermen reached its maximum in the early part of the twentieth century; in most years between 1905 and 1925, the average catches were between 2.5 and 3.9 million fish (Kasahara, 1961). Pacific cod fishing by U. S. fishermen has been at a low level off Alaska for many years because of the lack of U. S. market demands. Pacific cod are still widely distributed and abundant on Alaska's continental shelf, and the present stocks are virtually unexploited. They are apparently abundant around Amchitka in offshore waters (Isakson, Simenstad, and Burgner, 1971). Several dead Pacific cod were found washed ashore on Amchitka after the Cannikin explosion.

Biology and Life History. Pacific cod live near the bottom at depths to 400 m (1300 ft) around the entire North Pacific rim from California to Honshu, Japan (Kasahara, 1961). They apparently migrate to shallow inshore areas in summer and to deeper offshore areas in winter; these movements are related to temperature. Females have between 1.4 and 6.4 million eggs; they may reach a maximum weight of about 18 kg (40 lb) after 15 years of growth, although size, age, and fecundity vary widely. They feed on a variety of invertebrates and fish.

Fisheries. Pacific cod in the western Aleutians are caught incidentally by Soviet and Japanese trawl fleets and by Japanese longliners fishing for sablefish. Soviet catches are greater than Japanese catches; e.g., in 1971 the Soviets caught an estimated 1653 metric tons of Pacific cod in the western Aleutians whereas the Japanese landed only 432 metric tons. Pacific cod are filleted and frozen and are considered a delicacy.

Future Prospects. The catch of Pacific cod in the western Aleutians is likely to increase as other target species decline in abundance because the large stocks are still only lightly exploited.

Whales

Many aspects of the biology and distribution of whales are poorly known despite more than 100 years of worldwide exploitation. There is consequently little information about whale stocks around Amchitka. Between 1968 and 1973 whales were occasionally sighted from shore by personnel at Amchitka, but their species was not verified. Several dead sperm whales washed ashore on Amchitka during the AEC occupation.

Mackintosh (1965) and Slijper (1962) are two of the best sources of general information on whales and the whaling industry. Nishiwaki (1966) describes the distribution and migration of whales in the North Pacific Ocean on the basis of the kill by the Japanese whaling industry between 1945 and 1962. In the Rat Islands area (which includes Amchitka), more sperm whales (*Physeter catodon*) were taken than any other species, but blue whales (*Balaenoptera musculus*), humpback whales (*Megaptera novaeangliae*), fin whales (*Balaenoptera physalus*), and sei whales (*Balaenoptera borealis*) were also taken. Presumably these five species are still present, although the killing of blue and humpback whales is now prohibited, and their occurrence is no longer reflected in whaling statistics.

Biology and Life History. Only the three species of whales still hunted and occurring in the Aleutians (sperm, fin, and sei) are discussed.

The sperm whale is a toothed whale that reaches a length of 18 m (60 ft). Sperm whales are polygamous, and the males are much larger than the females. Their distribution is worldwide except for polar regions. Several species of squid are their primary food.

In the northern hemisphere the fin whale, a baleen whale, reaches a length of 24 m and is second in size only to the nearly extinct blue whale. Fin whales are monogamous, as are all baleen whales. Their distribution is worldwide; in

Alaska waters their distribution extends into the Arctic Ocean in summer. They are filter feeders, straining planktonic crustaceans and small fishes from the water by horny bristled plates (baleen) that are attached to the roof of the mouth. A large fin whale may have as many as 400 of these plates spaced about half an inch apart on each side of the upper jaw (Mackintosh, 1965).

Sei whales are relatively small baleen whales that reach a maximum length of 15 m (50 ft). Because of their low oil content, they were not harvested to any extent until recent years when stocks of the larger species of whales were reduced to the extent that hunting them became uneconomical. They are widely distributed in subarctic waters throughout the world and are common in Aleutian waters (Nishiwaki, 1966).

Fisheries. Japan and the U.S.S.R. are the only nations that now hunt whales commercially in the Gulf of Alaska and in the Bering Sea. A severe worldwide decline in numbers of whales as a result of excessive killing and consequent restriction of the kill by the International Whaling Commission are responsible for the present limited extent of the whaling industry. In 1971 the Japanese had 3 North Pacific Ocean fleets with 26 killer vessels; the Soviets operated 2 factory ships and 28 killer vessels (National Marine Fisheries Service, 1973). Table 3 shows the Japanese and Soviet pelagic whale kill for 1969 to 1971 in all North Pacific Ocean waters. Sperm whales make up the majority of the kill (Nishiwaki, 1966). The whaling season occurs from May to October, and hunting takes place far offshore. In 1971 no whales are believed to have been taken near Alaska by the Soviets, and only 622 whales, or 13%, of the Japanese kill was from Alaska waters (National Marine Fisheries Service, 1973).

Table 3—Japanese and Soviet North Pacific Ocean Whale Kill, 1969 to 1971*

Nation and year	Sperm	Sei	Fin
Japan			
1969	3000	3591	576
1970	2700	3235	518
1971	1803	2431	542
U.S.S.R			
1969	8211	1091	593
1970	8585	782	412
1971	5525	296	190

*From National Marine Fisheries Service (1973).

After the whale is hauled aboard the factory ship, the entire whale is converted to food or industrial products. Sperm whale oil is used only for industrial oils, whereas much of the oil of baleen whales is used for edible products, especially margarine. The meat of all species is used for human and pet food; that of baleen whales is similar to beef in palatability.

Future Prospects. The numbers of whales taken each year will probably continue to decline because of restrictive regulations to prevent further reduction of the stocks. Further, world opinion is mobilizing against harvest of any whales. For these reasons the high-seas whaling industry will probably come to an end within a few years.

[Author's Comments]

Since the foregoing was prepared, the outlook for future foreign exploitation of fishery resources in the western Aleutians has been complicated by the probability of unilateral action by the United States extending its fishery jurisdiction from 12 miles to 200 miles offshore. Legislation has passed both houses of Congress, and the President is expected to sign the ultimate bill, which is likely to become effective by mid-1977.

Except for salmon and whales, most of the other currently exploited fishery stocks of the western Aleutians are within 200 miles of land. What action will be taken with regard to these fishery resources and what the effect of this action will be is difficult to predict.

REFERENCES

Alaska Department of Fish and Game, 1972, 1971 Alaska Catch and Production Commercial Fisheries Statistics, Statistical Leaflet 23.

Alverson, D. L., A. T. Pruter, and L. L. Ronholt, 1964, A Study of Demersal Fishes and Fisheries of the North Western Pacific Ocean, H. R. MacMillan Lectures in Fisheries, University of British Columbia.

——, and S. J. Westrheim, 1961, A Review of the Taxonomy and Biology of the Pacific Ocean Perch and Its Fishery, *Rapp. P.-v Reun., Cons. Int. Explor. Mer.*, 150: 12-27.

Anonymous, 1973, NMFS Finds Tons of Plastic Debris on Alaskan Island, *NOAA Week*, 4(March): 1.

Bakkala, R. G., 1971, Distribution and Migration of Immature Sockeye Salmon Taken by U. S. Research Vessels with Gillnets in Offshore Waters, 1956–1967, in International North Pacific Fisheries Commission Bulletin 27.

Bell, F. H., 1973, The Pacific Halibut—A Managed Resource, in A Review of the Oceanography and Renewable Resources of the Northern Gulf of Alaska, D. H. Rosenberg (Ed.), pp. 361-409, Institute of Marine Science, University of Alaska, Report R72-23 (Sea Grant Report 73-3).

——, and G. St.-Pierre, 1970, The Pacific Halibut, International Pacific Halibut Commission, Technical Report 6.

Carlson, H. Richard, and Richard E. Haight, in press, Juvenile Life of Pacific Ocean Perch, *Sebastes alutus*, in Coastal Fiords of Southeastern Alaska: Their Environment, Growth, Food Habits, and Schooling Behavior, Transactions of the American Fisheries Society.

Chitwood, P. E., 1969, *Japanese, Soviet, and South Korean Fisheries off Alaska, Development and History Through 1966,* U. S. Fish and Wildlife Service, Circular 310.

Cobb, J. N., 1927, Pacific Cod Fisheries, Report of the U. S. Commissioner of Fisheries, 1926, Appendix 7, pp. 385-499. (Doc. 1014).

——, 1916, Pacific Cod Fisheries, Report of the U. S. Commissioner of Fisheries, 1916, Appendix 4, pp. 5-111. (Doc. 803).

Desautels, R. J., A. J. McCurdy, J. D. Flynn, and R. R. Ellis, 1970, Archaeological Report, Amchitka Island, Alaska, 1969–1970, USAEC Report TID-25481.

Gunderson, D. R., 1974, Availability, Size Composition, Age Composition, and Growth Characteristics of Pacific Ocean Perch (*Sebastes alutus*) off the Northern Washington Coast During 1967–1972, *J. Fish. Res. Board Can.*, 31: 21-34.

Hart, J. L., 1973, *Pacific Fishes of Canada,* Fisheries Research Board of Canada, Bulletin 180.

Haynes, Evan B., 1974, *Distribution and Relative Abundance of Larvae of King Crab,* Paralithodes camtschatica, *in the Southeastern Bering Sea, 1969–1970,* U. S. National Marine Fisheries Service, Fishery Bulletin 72, pp. 804-812.

——, and C. Lehman, 1969, Minutes of the Second Alaskan Shellfish Conference, Alaska Department of Fish and Game, Information Leaflet 135.

——, 1968, Relation of Fecundity and Egg Length to Carapace Length in the King Crab, *Paralithodes camtschatica, Proc. Nat. Shellfish Ass.*, 58: 60-62.

Hebard, J. F., 1959, *Currents in Southeastern Bering Sea and Possible Effects Upon King Crab Larvae,* U. S. Fish and Wildlife Service, Special Scientific Report—Fisheries No. 293.

Hitz, C. R., 1970, *Operation of the Soviet Trawl Fleet off the Washington Coasts During 1966 and 1967,* U. S. Fish and Wildlife Service, Circular 332, pp. 53-75.

International North Pacific Fisheries Commission, 1973, *Statistical Yearbook 1971.*

——, 1972a, *Statistical Yearbook 1970.*

——, 1972b, Annual report 1970.

——, 1972c, Annual report 1971.

Isakson, J. S., C. A. Simenstad, and R. L. Burgner, 1971, Fish Communities and Food Chains in the Amchitka Area, *BioScience,* 21: 666-670.

Kasahara, H., 1972, Japanese Distant-Water Fisheries: A Review, *Fish. Bull.*, 70: 227-282.

——, 1961, Fisheries Resources of the North Pacific Ocean, Pt. 1, H. R. MacMillan Lectures in Fisheries, pp. 1-135, University of British Columbia, Vancouver.

Kobayashi, K., 1957, Larvae and Youngs (Sic) of the Sablefish, *Anoplopoma fimbria* (Pallas), from the Sea near the Aleutian Islands, *Bull. Japan. Soc. Sci. Fish.*, 23(8): 376 (abstract only).

Kondo, H., Y. Hirano, N. Nakayama, and M. Miyake, 1965, Offshore Distribution and Migration of Pacific Salmon (Genus *Oncorhynchus*) Based on Tagging Studies (1958–1961), International North Pacific Fisheries Commission, Bulletin 171.

Lyubimova, T. G., 1965, The Main Stages of the Life Cycle of Pacific Ocean Perch (*Sebastes alutus* G.) in the Gulf of Alaska, in *Soviet Fisheries Investigation in the Northeast Pacific,* Part IV, pp. 85-111.

Mackintosh, N. A., 1965, *The Stocks of Whales,* Fishing News (Books), Ltd.

Major, R. L., and H. H. Shippen, 1970, Synopsis of Biological Data on Pacific Ocean Perch, *Sebastodes alutus,* FAO Species Synopsis No. 79, Circular 347, U. S. Department of Commerce, Washington, D. C.

Margolis, L., F. C. Cleaver, Y. Fukuda, and H. Godfrey, 1966, *Salmon of the North Pacific Ocean,* Pt. 6, Sockeye Salmon in Offshore Waters, International North Pacific Fisheries Commission, Bulletin 20.

Miyauchi, D., G. Kudo, and M. Patushnik, 1973, Surimi—A Semi-Processed Wet Fish Protein, *Mar. Fish. Rev.*, 35(12): 7-9.

National Marine Fisheries Service, 1973, Foreign Fishing Activities, Bering Sea and Gulf of Alaska, 1971, Enforcement and Surveillance Division, Juneau, Alaska.

Neave, F., T. Ishida, and S. Murai, 1967, *Salmon of the North Pacific Ocean,* Pt. 7, Pink Salmon in Offshore Waters, International North Pacific Fisheries Commission, Bulletin 22.

Nishiwaki, M., 1966, Distribution and Migration of the Larger Cetaceans in the North Pacific as Shown by Japanese Whaling Results, in *Whales, Dolphins, and Porpoises,* Kenneth S. Norris (Ed.), pp. 171-191, University of California Press, Berkeley.

Paraketsov, I. A., 1963, On the Biology of *Sebastodes alutus* in the Bering Sea, in *Soviet Fisheries Investigation in the Northeast Pacific,* Part I, pp. 319-327. Translated by Israel Program for Scientific Translations (1968), Report TT 67-51203.

Pruter, A. T., 1973, Development and Present Status of Bottomfish Resources in the Bering Sea, *J. Fish. Res. Board Can.*, 30: 2373-2385.

Quast, J. C., 1972, Reduction in Stocks of the Pacific Ocean Perch, an Important Demersal Fish off Alaska, *Trans. Amer. Fish. Soc.*, 101: 64-74.

Reeves, J. E., 1973, Groundfish of the Gulf of Alaska, in A Review of the Oceanography and Renewable Resources of the Northern Gulf of Alaska, D. H. Rosenberg (Ed.), pp. 411-455, Institute of Marine Science, University of Alaska, Report R72-23 (Sea Grant Report 73-3).

Shepard, M. P., A. C. Hartt, and T. Yonemori, 1968, *Salmon of the North Pacific Ocean,* Pt. 8, Chum Salmon in Offshore Waters, International North Pacific Fisheries Commission, Bulletin 25.

Skalkin, V. A., 1964, The Feeding of Ocean Perch in the Bering Sea, in *Soviet Fisheries Investigation in the Northeast Pacific,* Part II, pp. 159-174.

Slijper, E. J., 1962, *Whales,* Basic Books, Inc., New York.

16

Oceanography

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Circulation near Amchitka Island is influenced by complex patterns of exchange and mixing between the North Pacific Ocean and Bering Sea waters in the passes of the Aleutian Islands, resulting in wide variations in physical, chemical, and biological conditions seasonally, and also over short geographic distances. Strong westward flow in the Alaskan Stream south of Amchitka Island brings water of 2 to 4°C into the area in winter, ameliorating sea and air temperatures and inhibiting the development of extensive shore ice. During spring and summer, coastal turbulence reduces thermal stratification in the surface layer, and inshore water temperatures are 1 to 4°C lower than in the offshore oceanic regimes. Zooplankton are typical subarctic Pacific forms. Zooplankton volumes in the 0- to 150-m surface layer increased roughly one order of magnitude from winter to summer. Nutrients do not appear to be limiting for phytoplankton growth.

The bulk of oceanographic research has taken place in those areas of the ocean which present the most enticing lure to man. This attraction most often takes the form of a bountiful fishing ground or an economical practical sea route. Research data on the large circulations of water in and between the Bering Sea and the North Pacific Ocean have accumulated mainly in conjunction with the expansion of the area's fisheries and are only now beginning to include detailed information on circulation in the passes of the Aleutian Islands and in the nearshore waters of the individual islands.

The Aleutian–Commander Island arc divides the Bering Sea from the North Pacific Ocean along a stretch of 1500 km. The arc is submerged in 39 places, forming passes and straits, but only 14 of these have an area greater than 1 km^2 or a sill depth deeper than 200 m. The series of passes among the Aleutian Islands is unique; the shallow sills connecting many of the islands block the free exchange of intermediate and deep water between the Bering Sea and the North Pacific Ocean. The deepest pass in the Aleutian portion of the island arc is Amchitka Pass, which has a sill depth greater than 1000 m. Because of exchange through this pass, the oceanography of the Amchitka Island area is related to offshore areas in both the North Pacific Ocean to the south and the Bering Sea to the north.

PHYSICAL OCEANOGRAPHY

Subarctic Pacific Circulation

The subarctic Pacific region of the North Pacific Ocean is defined as bounded on the north by Bering Strait, the land constriction at the entrance to the Arctic Ocean, and on the south at about 40°N by a change in vertical water structure. The southern edge, where marked temperature inversions that are characteristic of surface dilution and winter cooling end and marked salinity inversions that are characteristic of net surface evaporation begin, is generally referred to as the subarctic–subtropic boundary and for convenience is specifically denoted by the 34 ‰ isohaline in the surface layer (Fig. 1). The predominant oceanic feature of the region is the large cyclonic subarctic gyre. Formed by a merging of currents off Japan and driven by local winds, water in the gyre moves eastward across the North Pacific Ocean and sweeps around the Gulf of Alaska and northward into and around the Bering Sea. Oceanographic conditions in this region were extensively reviewed by Favorite, Dodimead, and Nasu (1976). Only a summary is presented here.

Southward flow (Oyashio) along the northeastern coast of Japan and northward flow (Kuroshio) along the southeastern coast of Japan converge, mix, and turn eastward across the North

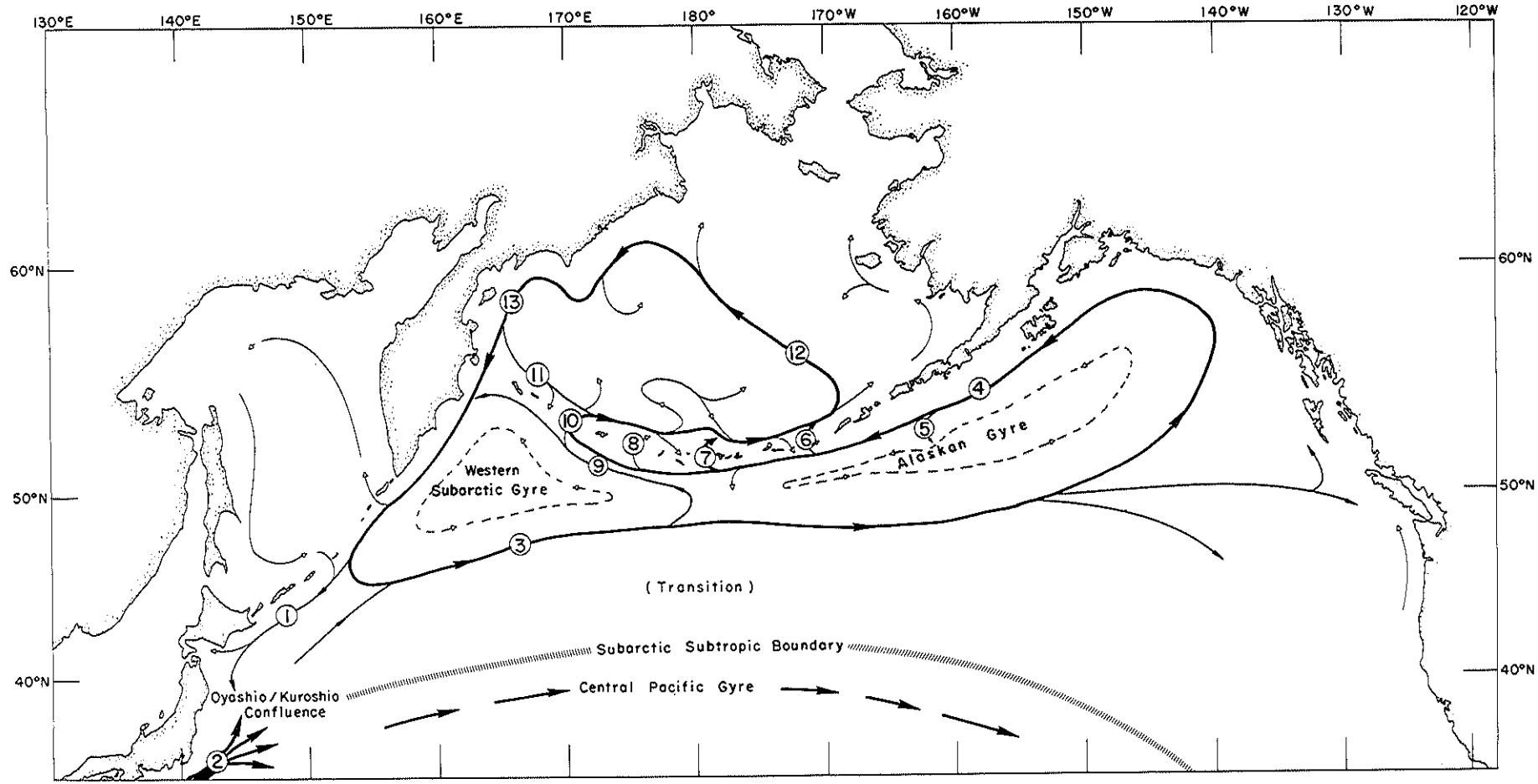

Fig. 1—Subarctic Pacific region showing basic subarctic gyre and associated currents: 1, Oyashio; 2, Kuroshio; 3, subarctic; 4, Alaskan Stream; 5, Aleutian; 6, Amukta; 7, Amchitka; 8, Buldir; 9, West subarctic; 10, Near; 11, Commander; 12, Transverse; and 13, East Kamchatka.

Pacific Ocean, forming a transition zone between the cold dilute subarctic waters and the warm saline subtropic waters. Although the demarcation of these two flows is sharp and abrupt in the western part of the ocean, it becomes gradually more diffuse as stirring, advection, and diffusion occur during the transpacific travel and characteristic broad, weak, boundary currents occur at the eastern side. Net inflow at the western side of the ocean from the confluence of the Kuroshio and Oyashio as well as other factors, such as deep flow, precipitation, and river runoff, is balanced by a net discharge southward at the eastern side of the ocean in the area of the divergence of the Subarctic Current. The northward flow at the eastern side into the Gulf of Alaska is largely constrained by the Alaskan coast to turn southwestward out along the Alaska Peninsula as the Alaskan Stream. Exchanges with the Bering Sea occur at the northern edge of the Alaskan Stream (Favorite, 1967) at the various openings in the Aleutian–Commander Island arc from 165°W to 170°E. These exchanges occur to various levels, depending on sill depths of the passes, which generally increase in depth to the west. Of the approximately 40 passes, those of major significance to flow are Unimak, 165 to 177°W, 60-m depth (although shallow, this is the first major opening into the Bering Sea); Amukta, 170 to 172°W, 430 m; Amchitka, 178°W to 179°E, 1155 m; Buldir, 176 to 174°E, 640 m; Near, 172 to 169°E, 2000 m; and Kamchatka, 163 to 155°E, 4420 m. The major component of surface flow sweeps westward along the south coast of Amchitka Island and turns northward into the Bering Sea through Near Strait, east of the Commander Ridge. This flow impinges on the Near Current in the vicinity of 170°E and turns northward into the Bering Sea; westward flow, below the sill depth of Near Strait (2000 m), continues along the south side of the Aleutian–Commander Island arc to 166°E, merging with but underriding westward flow in the West Subarctic Current, and then turns northward into the Bering Sea through Kamchatka Strait. North of Near Strait the northward flow merges with the eastward flow, the Commander Current, along the north side of the island arc, and the combined flow subsequently diverges, sending one branch northward along the west side of the Olyutorskiy Ridge and the other eastward around Bowers Ridge into the southeastern part of the central basin where it is joined by the Amchitka and Amukta branches of the Alaskan Stream. A frontal zone occurring at the western edge of the continental shelf in the eastern Bering Sea indicates that the main flow, the Transverse Current, turns northward following the continental slope and then southwestward along the Siberian coast. At Cape Olyutorskiy a southward branch forms an eddy in the northern Bering Sea, but the main flow continues southwestward and completes the overall cyclonic circulation in the Bering Sea. The East Kamchatka Current continues southwestward along the coast, completing the circulation around the subarctic gyre.

At least 3 to 4 years would be required for a hypothetical surface-water parcel to pass around the periphery of this gyre. Drift-bottle studies (Favorite and Fisk, 1971) indicate that about 2 years are required to traverse the southern boundary, several months to circuit the Gulf of Alaska, less than a year to exit the Bering Sea, and several months to move southward along the Kuril Islands. During this traverse the parcel (and thus any planktonic biota associated with it, assuming confinement in the surface layer and neglecting vertical movements associated with diel and seasonal vertical migrations) would be exposed to a wide range of environmental conditions, e.g., maximum temperatures of 20°C occurring off Japan and minimum temperatures of −2°C in the northern Bering Sea. Numerous subsidiary gyres and eddies can, of course, cause considerable departures from the overall basic cyclonic flow.

Flow in the Aleutian Area

Several methods for the measurement of flow and currents are available. The most direct but most difficult is direct observation. Not only are the problems of positioning and measurement formidable but also net currents tend to be small; thus the net currents may be masked by large turbulent velocities, which make point estimates of currents ambiguous. Other methods are to infer currents and flow from drift-bottle observations, distributions of properties, observed density fields (geostrophic currents), and requirements of continuity of flow. All these methods have been used to some extent to describe the flow through the passes of the Aleutian Islands.

Favorite (1974) used a convenient grouping for the passes, dividing them into east, central, and west pass groups and Commander–Near and Kamchatka Straits (Fig. 2); 99.9% of the area of the openings through the island arc is contained in these five major pass groups (Table 1). Amchitka Pass, in the central Aleutian group, is the only pass east of 172°E that exceeds 1000 m in depth, and only in Kamchatka Strait do depths exceed 2000 m. The major currents through these openings, as indicated in the previous section, are the Amukta, Amchitka, Buldir, Near, and Commander Currents; the source of these flows is largely the

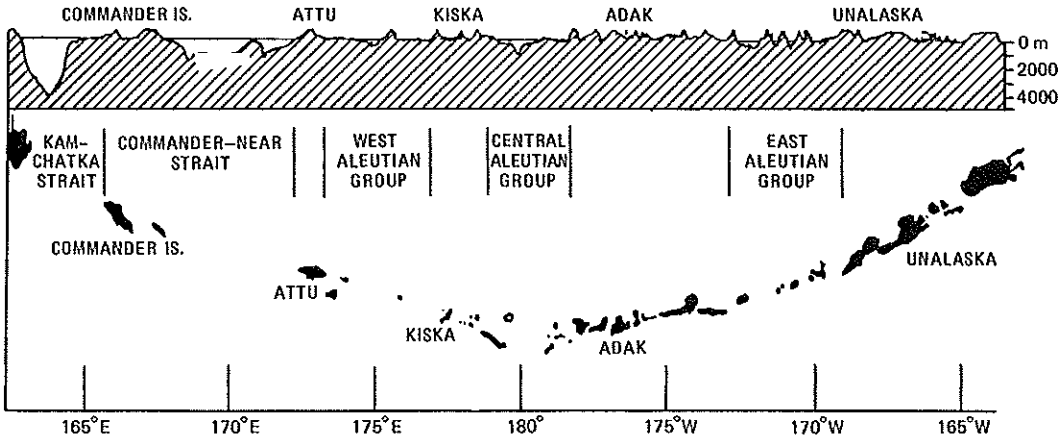

Fig. 2—Vertical profile of all openings through the Aleutian–Commander Island arc and selective groupings of major ones.

Table 1—Depth and Area of the Major Openings in the Aleutian–Commander Island Arc

General opening	Pass/Strait	Depth, m	Area, km^2
East Aleutian group	Unimak	60	0.9
	Samalga	200	3.9
	Chuginadak	210	1.0
	Herbert	275	4.8
	Yunaska	457	6.6
	Amukta	430	19.3
	Seguam	165	2.1
			38.6
Central Aleutian group	Tanaga	235	3.6
	Amchitka	1155	45.7
			49.3
West Aleutian group	Kiska	110	6.8
	Buldir	640	28.0
	Semichi	105	1.7
			36.5
Commander–Near Strait	Near	2000	239.0
	Commander	105	3.5
			242.5
Kamchatka Strait		4420	335.2
		Total area	702.2

Alaskan Stream. This boundary current has speeds of 50 to 100 cm/sec, and, although distributions of water properties around the head of the Gulf of Alaska at times may indicate some lack of continuity in flow in the surface layer, continuity always exists below 300 m. Normally the Coriolis forces on the westward flow in the Alaskan Stream would result in an elevation of the sea surface shoreward and a tendency for the water to not only hug the coastline but also to veer to the right (northward) through any openings in the island arc; however, this is not always the case. An appreciable component of flow in the upper 200 to 300 m is southward (the Aleutian Current), closing circulation in the surface layer of the Alaskan gyre. At times inshore countercurrents with speeds in excess of 10 cm/sec occur along the continental slope, but the continuity of such flows is poorly documented—these eastward flows may be associated with large eddies in the Alaskan Stream.

Thomson (1972) described conditions that may cause instabilities and separation of the flow from the coast.

Although the dominant flow in the passes is tidal, there is increasing evidence that eddies exist which encompass major island clusters and require both north and south flows through the passes. Records of direct-current measurements in the Aleutian passes by the U. S. Coast and Geodetic Survey commenced in 1934 with data collected near Unimak Pass, and these data are of considerable value in describing maximum tidal velocities. However, estimates of nontidal components of these measurements are of questionable value because of the limited time scale used in the measurements. Of the 18 records, 5 were of only 1-day duration; 13 other measurements taken from 1934 to 1946 covered periods of 2 to 8 days.

Reed (1971) analyzed 25 surface tidal-flow records from radio current meters suspended from buoys anchored in various passes for intervals of over 4 days during 1949 to 1956. Northerly and southerly net flows were recorded at some locations although at different times. Problems are encountered in such observations when the movement of the vessel or buoy may be greater than the flow. This was clearly demonstrated by observations recorded aboard the U. S. Coast and Geodetic Survey vessel *Surveyor* in Amchitka Pass (51°35′N, 180°) in the late spring of 1963 when precise positioning at 15-min intervals indicated vessel speed as great as 85 cm/sec at anchor. The direct-current observations from the Amchitka area are considered in detail in a later section.

Eight drift-bottle experiments were made between 1957 and 1972 in the Aleutian area (Favorite, 1974). Releases of bottles well south of the Aleutian Islands from a merchant ship of opportunity in the fall of 1964 implied a northerly drift from five of seven release locations southward of Adak Island, several recoveries being made on Attu Island (the affinity of Attu Island for drift bottles released from all directions was also reflected in recoveries of bottles released from the research vessel *George B. Kelez* during an oceanographic cruise in the winter of 1966). One bottle released south of Amchitka Island in 1964 was recovered on the Pribilof Islands. Two bottles released north of Amchitka Pass in 1971 were recovered on the Pribilof Islands (Favorite and Ingraham, 1972), but bottles released to the north and south of this location were recovered on Amchitka Island (Favorite and Ingraham, 1973). In general, drift-bottle recoveries have reflected flow implied by the distribution of water properties.

A number of authors have examined the density and wind-stress fields in the Aleutian area in an attempt to ascertain the water exchange between the North Pacific Ocean and the Bering Sea. Arsen'ev (1967) summarized oceanographic conditions in the Bering Sea in an exhaustive analysis of station data prior to 1959. He considered the Commander–Near Strait as the most significant source of flow into the Bering Sea (4.4 Sv),* whereas only 0.7 Sv occurred through the western groups; no net exchange was considered to occur in the eastern Aleutian passes. These transports appear derived from a reference depth of 3000 db, and it is also apparent that, except for a deep inflow in Kamchatka Strait, almost the entire flow into the Bering Sea was derived from the Alaskan Stream (Table 2). On the basis of continuity of the Alaskan Stream, Favorite (1974) summarized flow into the Bering Sea. Mean annual transport of 12.5 Sv in the Alaskan Stream south of Adak Island was obtained with 4000 db (about 4000 m) as a reference level. Because only Kamchatka Strait is deeper than 2000 m, 1.5 Sv of this flow reaches this westernmost passage. Favorite found no net exchange in the western or eastern Aleutian passes. Of the 11 Sv above 2000 db, 4 Sv is lost through the central Aleutian passes, 3 Sv is gained across the southern boundary, and 10 Sv flows northward through the Commander–Near Strait west of Attu Island. The result is a net annual flow of 14 Sv into the Bering Sea. This result falls between the transport values of 8.0 Sv proposed by Batalin (1964) and 19.5 Sv proposed by Arsen'ev (1967).

Table 2—Flow (Sv) Through Aleutian–Commander Island Arc

Pass	Transport out of Bering Sea	Transport into Bering Sea	
	Arsen'ev	Arsen'ev	Favorite
Kamchatka	18.4		
Commander–Near		14.4	10.0
Western Aleutian group		0.7	0
Central Aleutian group		4.4	4.0
Total	18.4*	19.5	14.0

*1.1 Sv loss through Bering Strait.

WINTER DATA 1968

Observations of temperature, salinity, and selected chemical properties were conducted in

*Sv = Sverdrup = 1×10^6 m^3/sec.

January–March 1968 in support of the AEC Supplemental Test Site Program on Amchitka Island (Fig. 3). These data permit a description of the marine environment in the vicinity of Amchitka Island.

A brief drogue and dye current study was conducted in February 1968 (McAlister et al., 1968). One 10-m parachute drogue was set in the channel north of Amchitka Island and followed for 5 hr, during which time it moved counterclockwise at 25 to 40 cm/sec. Additional drogue studies were undertaken south of Adak Island in the summer of 1969 (Favorite, Ingraham, and Fisk, 1972). These studies again indicated the strong tidal component of current in this area and the great difficulty of attempting to derive meaningful net current values from a limited program of direct current measurements.

Temperature

Surface temperatures in the North Pacific Ocean are normally lowest during March when winter convective overturn forms an isothermal layer that may extend from the surface to 100 m. The coldest surface temperature (2.7°C) was observed in the western portion of the study area. The warmest water (3.4 to 3.7°C) was also relatively low in salinity and characteristic of water transported westward by the Alaskan Stream. Water in the island passes, intermediate in temperature (3.0 to 3.2°C), represents a mixture of the warm Alaskan Stream water with cooler water from the Bering Sea. Near the shore Alaskan Stream water occurred as a core of warm water with a maximum temperature of 3.8°C between 150 and 400 m (see Fig. 6). Although inversions and layering were frequent, continuity of the core structure through Amchitka Pass indicated a net northward flow of Alaskan Stream water. Below about 500 m the temperatures decreased gradually with depth, and the vertical distribution of temperature was similar in structure to salinity.

Salinity

Considerable freshwater runoff enters the coastal area of the Gulf of Alaska and is advected westward south of the Aleutian Islands by the Alaskan Stream into the western North Pacific

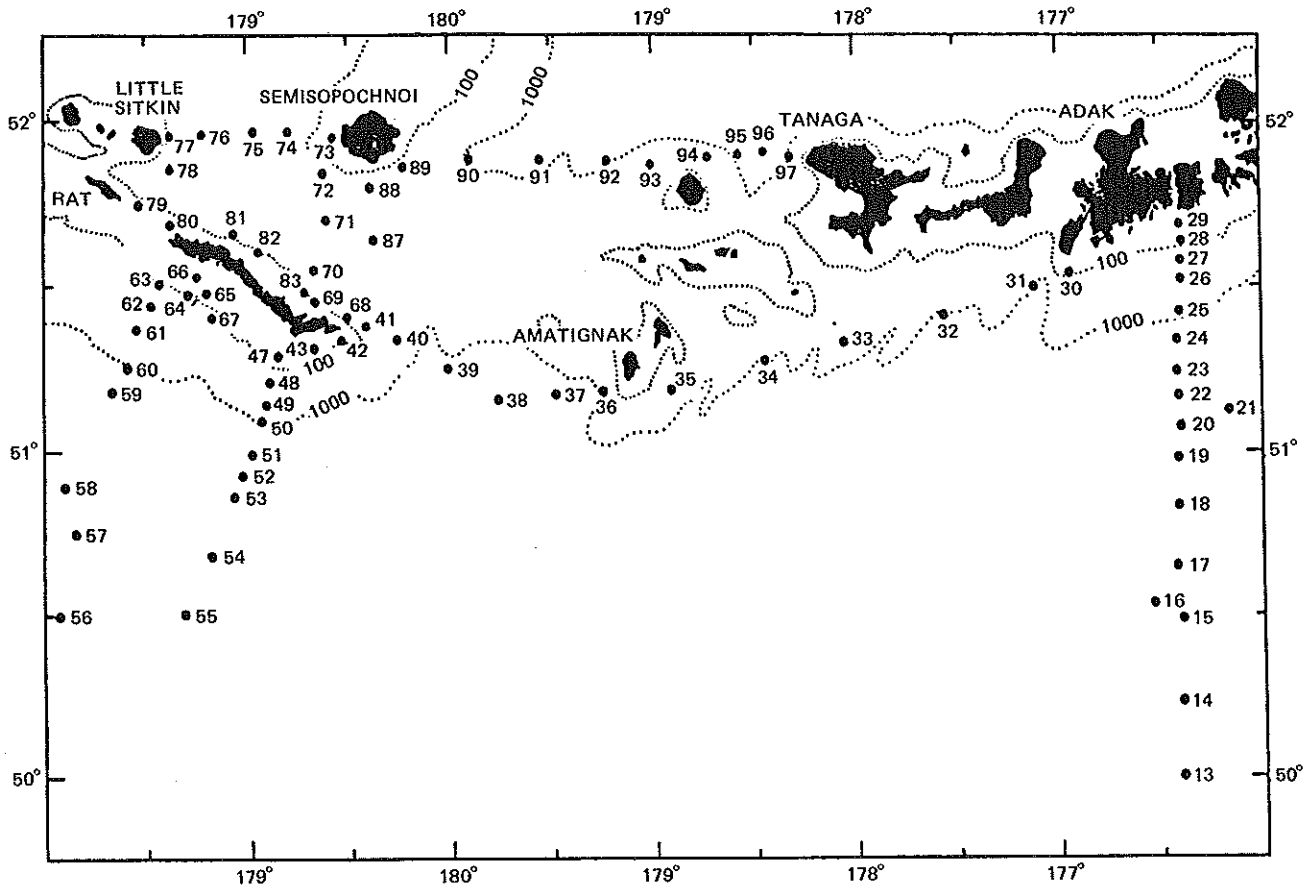

Fig. 3—Locations of oceanographic stations during Amchitka study, January–March 1968 (Research Vessel *George B. Kelez*).

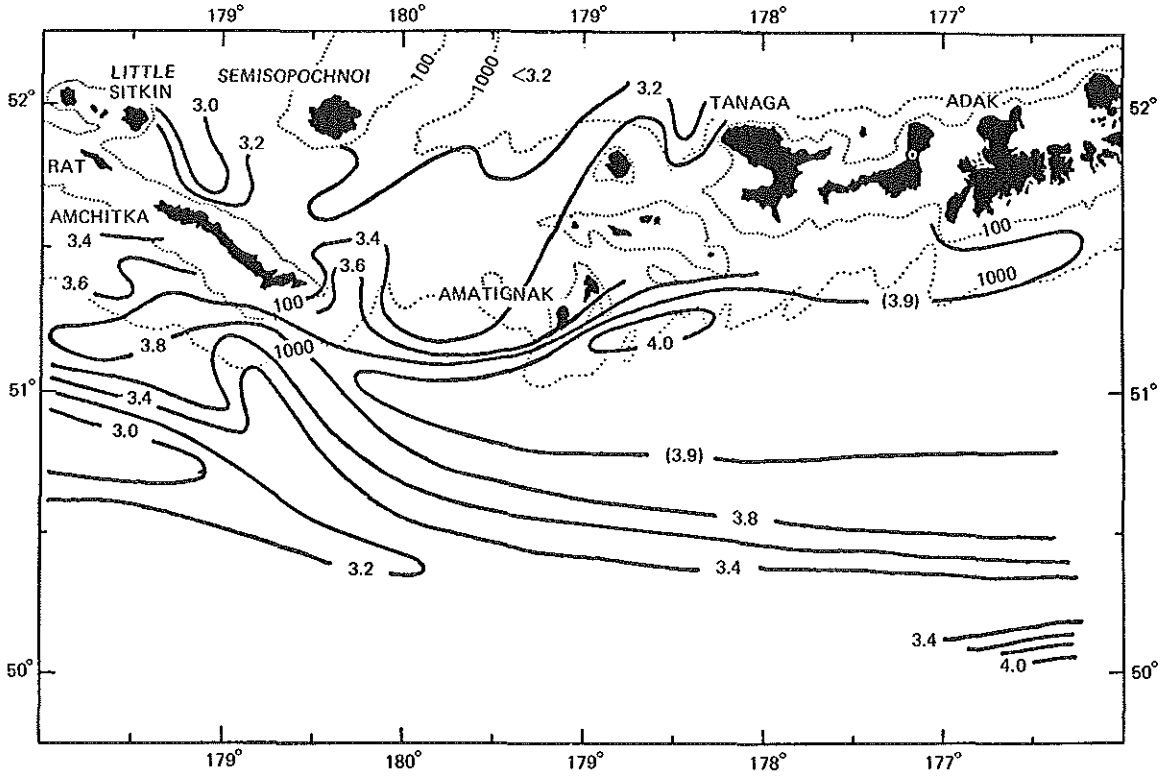

Fig. 4—Temperature distribution on sigma-t surface = 26.5 (100- and 1000-fathom isobaths shown).

Ocean. Sharp fronts and eddies form at the confluence of the Gulf of Alaska water and the more saline Bering Sea water that is usually present at the Aleutian Passes west of Unimak Island. This feature is present even during winter when runoff to the Gulf of Alaska is diminished by freezing and when seasonal overturn causes mixing of surface water with more saline water to depths of about 100 m. At the axis of the westward flow is a tongue of dilute water (< 32.8 ‰). Bering Sea water (characteristically > 33.0 ‰) was not found south of the entrance to Amchitka Pass. Offshore, North Pacific water had a slightly higher salinity (~32.9 ‰) than Alaskan Stream water.

Salinity increased with depth; the most rapid change occurred in the well-developed halocline between 100 and 300 m. South of the island arc, characteristic ridging of salinity and temperature was seen at all sections. The sharpest halocline was well offshore at about 50°30′N. Although surface dilution in the Alaskan Stream would be expected to enhance a strong coastal halocline, the halocline was less developed toward shore and weakest in the turbulent passes where high-salinity water of the Bering Sea was mixed in the surface layer.

Density

The distribution of density, calculated from the observed temperature and salinity, was dominated by and generally similar to the distribution of salinity. The greatest stability occurred well offshore with intermediate stability in the Alaskan Stream and the weak to neutral stability in the Aleutian passes.

Water masses mix most easily along sigma-t (equal-density) surfaces. The distribution of temperature on a sigma-t surface indicates the extent of horizontal mixing and suggests movement of water masses at various depths. South of Adak Island the temperature distributions on the sigma-t = 26.5 surfaces showed tongue-like extensions westward toward Amchitka Island (Fig. 4). These extensions represented a westward advection at depth of relatively warm water by the Alaskan Stream from its source in the Gulf of Alaska. At shallow depths, which are influenced by seasonal overturn (0 to 100 m), the coldest water was south of Amchitka Island near 51°N, and water of intermediate temperature occurred north of Amchitka Pass in the Bering Sea. At depths greater than 150 m (sigma-t = 26.0 to 26.5), the coldest water was in the Bering Sea, and water of intermediate temperature occurred south of Amchitka Island. This reversal of temperature gradient with depth suggests that the warmer water of the Gulf of Alaska and the Alaskan Stream had mixed northward into the Bering Sea; at shallow depth, below sill depths, however, horizontal mixing is restricted by the barrier at the island arc.

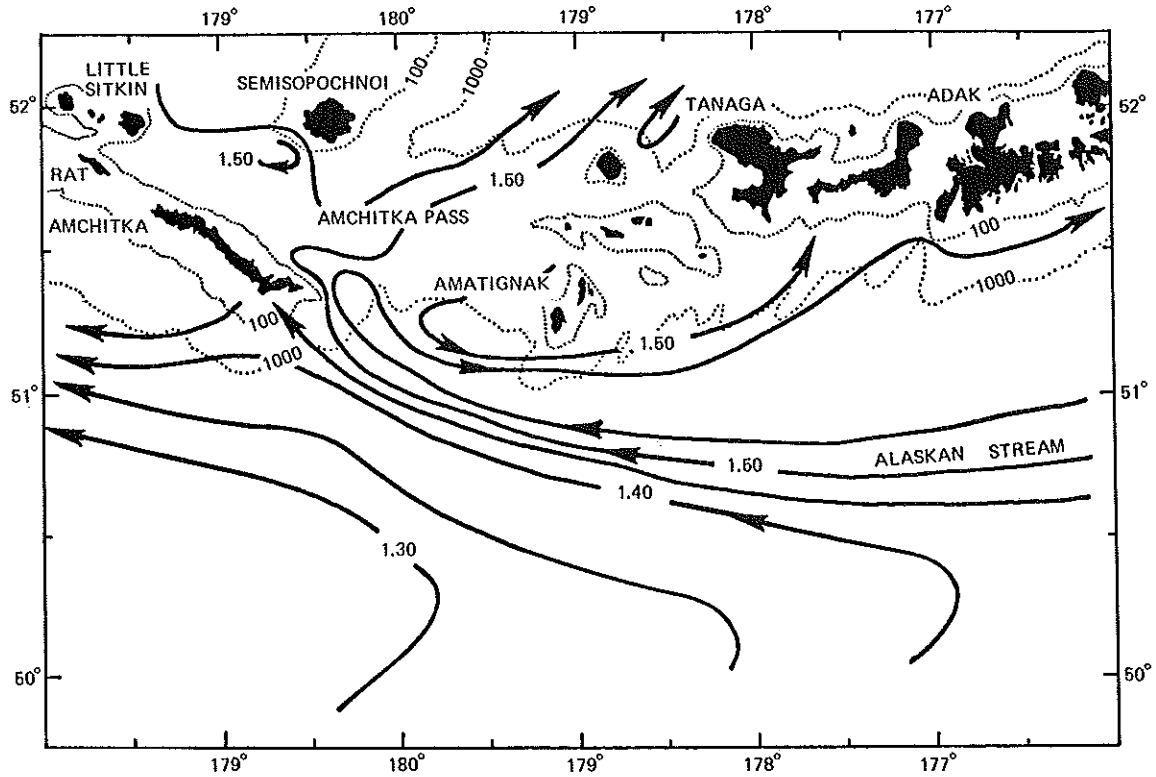

Fig. 5—Geopotential topography (dynamic meters referred to 1500 decibars) indicating surface flow.

Flow

Except for north–south tidal excursions through the shallow openings in the island arc (and probable shelf waves), westward flow south of the Andreanof Islands follows the general zonal trend of isobaths from 172°W to Amchitka Pass where an irregular bathymetry is encountered. Considerable mixing results which is due not only to flow funneling through channels between the islands lining the eastern side of the pass but also to the impingement of eastward and southward flow from the Bering Sea at the western side of the pass. Roughly 20 to 30% of the flow in the Alaskan Stream moves northward through Amchitka Pass, and Amchitka Island appears to be near the critical focal point where this divergence occurs (Fig. 5). East of Amchitka Island an eastward countercurrent occurred seaward of the edge of the continental shelf.

Flow through Amchitka Pass is extremely complex at all depths. North–south vertical sections through Amchitka Pass indicated a northerly current on the east side of the pass and one flowing to the south on the west side at a depth as determined from the distribution of properties (Fig. 6). Relative to 1500 db, a net northward transport of 5×10^6 Sv was observed flowing into the Bering Sea. This transport can be compared with the average annual figure of 4×10^6 Sv given by Favorite (1974). The flow was highly turbulent; geostrophic velocities in eddies were calculated in excess of 40 cm/sec and may have been two or three times this value for periods of short duration.

A series of direct-current observations were made from the vessel *Surveyor* at 51°35′N, 179°57′E (about 40 km northeast of the eastern end of Amchitka Island in about 1900 m of water) on June 3 to 6, 1963. A plot of directions and speeds at 10, 100, 200, and 300 m recorded each hour (commencing alternately at 10 m and at 300 m) indicate the complexity of flow evident in a data series for June 5 (Fig. 7). Isolated, abrupt, brief deviations from the direction of mean surface flow from 0 to 300 m occurred at 10 m; at 10 and 100 m; at 100 and 200 m; and at 100 and 300 m at various intervals. An extended period of flow (0400 to 1100 hr) with a consistently uniform easterly direction, opposite the offshore flow in the Alaskan Stream, was also indicated near this same location in the 1968 data (see Fig. 5). Velocities at all levels varied from about 25 to about 50 cm/sec, rarely in phase or with a specific relation to increasing depth; in fact, in several instances maximum velocities occurred at 300 m.

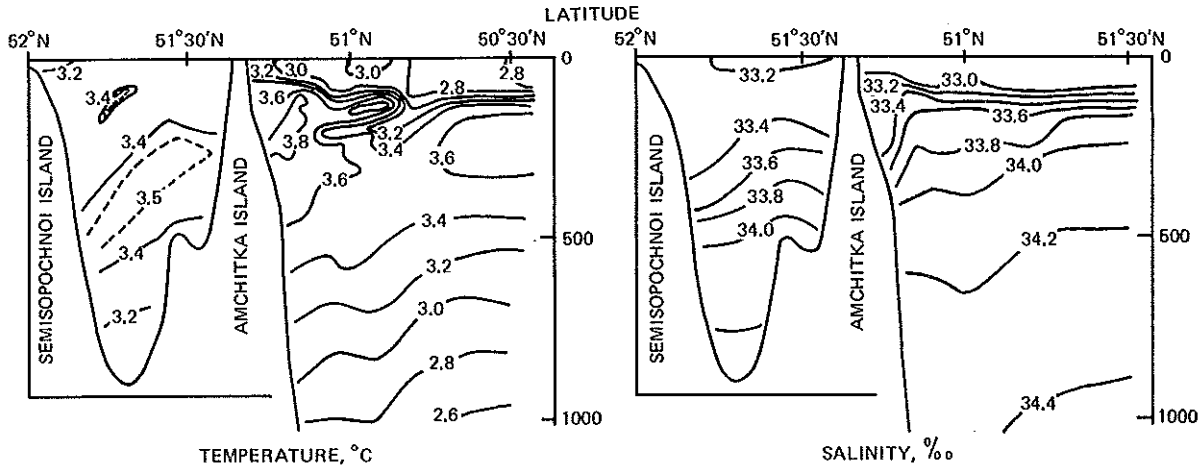

Fig. 6—Vertical sections of temperature and salinity from Semisopochnoi Island to 50°30′N.

GEOCHEMISTRY

Although temperature and salinity data are reasonably complete, geochemistry data for the Amchitka area are fragmentary even though such data could be informative not only as baseline information but also from a descriptive oceanography standpoint. The equilibrium between the saturation of CO_2 in surface water with respect to atmospheric CO_2 has great potential for explaining variations in the surface environment that are not evident from the distributions of temperature and salinity that reflect primarily large-scale physical processes. However, the analytical methods are complex, and only limited observations are available (Park, Gordon, and Alvarez-Borrego, 1974). If exchange with the atmosphere is restricted, cooling produces a decrease in the partial pressure of CO_2 and warming the opposite effect. Although photosynthesis by marine plants has the greatest effect on the reduction of CO_2, several factors can contribute to supersaturation compared to atmospheric CO_2, such as biochemical oxidation, addition of CO_2-rich river waters, increase in the depth of the surface mixed layer, upwelling of CO_2-rich subsurface waters, and upward divergence of deep water in cyclonic gyres. Although considerably more information is required to determine the individual effects of these processes, high variability in relative carbon dioxide concentrations between air and surface seawater exists in data from closely spaced stations in Amukta Pass near 171°W (Kelley, Longerich, and Hood, 1971). These data again reflect the intensity of turbulent processes near the passes. Nevertheless, Gordon et al. (1973) indicated that in late summer generally slightly supersaturated conditions occur all along the Aleutian chain, whereas CO_2 concentrations in the central Bering Sea are undersaturated by over 60 ppm.

Geochemical studies conducted in February 1968 provided an information base on the concentration of major and trace elements and aided, where possible, in describing the general circulation in the vicinity of Amchitka Island. In addition to salinity and temperature, determinations were made of pH and magnesium, calcium, silicate, phosphate, strontium, and heavier metal ions (zinc, manganese, nickel, iron, and copper) (Table 3 and Fig. 8). The distributions are generally consistent with the circulation described on the basis of temperature and salinity distribution, and the scatter of values in the passes north of Amchitka (Fig. 8) suggests the strong mixing and movement of water through the Aleutian passes; offshore values are relatively uniform.

BIOLOGICAL OCEANOGRAPHY

Although relatively few biological observations in the immediate area of Amchitka Island have been made, both the Bering Sea and the North Pacific Ocean are regions of major fisheries and have an extended history of biological investigations.

McRoy, Goering, and Shiels (1972) discussed the work on primary productivity; Sanger (1974) reviewed the available data and obtained a value of 415 mg C m^{-2} day^{-1} as a best estimate of summer primary production in the Bering Sea. A schematic food chain for the Bering Sea area in summer (defined as June through November) shows examples of species representative of the kinds of organisms that would reasonably be expected to occur at several trophic levels (Fig. 9). Calculations

(Text continues on page 344.)

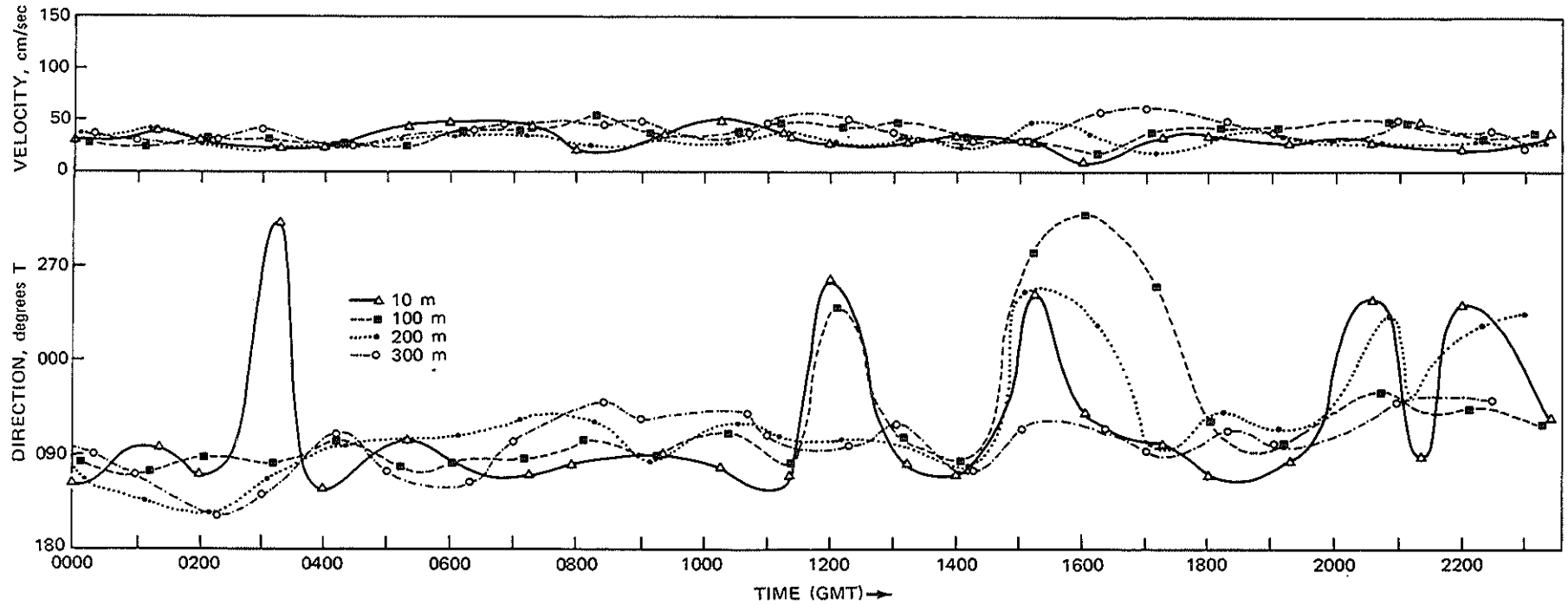

Fig. 7—Direct current measurements at 51°35′N, 179°57′E on June 5, 1963 (USCGS *Surveyor*).

Table 3—Chemical Analysis of Water Samples

Master station	Geochemistry station	Depth, m	Temperature, °C	Salinity, ‰	Chlorosity (Chl)	pH (in situ temp.)	Silicate silicon, μg-at/liter	Magnesium, g/liter	(Mg/Chl) × 10^{-2}	Calcium, g/liter	(Ca/Chl) × 10^{-2}	Strontium, mg/liter	(Sr/Chl) × 10^{-4}	Nickel, μg/liter	Iron, μg/liter	Copper, μg/liter	Zinc, μg/liter
1	1	2	4.7	32.681	18.51	7.88	25.4	1.54	8.32	0.527	2.85	5.29	2.86	1.2	0.9	11	
2	2	2	4.4	32.628	18.49	7.93	28.9	1.50	8.11	0.473	2.56	5.29	2.86	1.6	<0.1	13	
3	3	2	3.99	32.678	18.51	7.84	30.3	1.50	8.10	0.459	2.48	5.29	2.86	0.3	<0.1	5	
4	4	2	3.82	32.666	18.50	7.81	31.5	1.54	8.32	0.461	2.49	5.22	2.82	0.2	<0.1	7	
5	5	2	3.58	32.711	18.52	7.84	31.9	1.48	7.99	0.458	2.47	5.34	2.88	3.8	0.8	11	
6	6	2	3.71	32.657	18.50	7.81	30.8	1.42	7.68	0.450	2.43	5.33	2.88	1.2	0.9	10	
7	7	2	3.61	32.695	18.52	7.81	30.7	1.52	8.21	0.458	2.47	5.29	2.86	<0.1	1.9	5	
8	8	2	3.58	32.560	18.44	7.83	26.6	1.60	8.68	0.455	2.47	5.31	2.88	0.3	<0.1	8	
9	9	2	3.62	32.378	18.34	7.84	25.5	1.46	7.96	0.452	2.46	5.22	2.85	0.2	1.1	10	
10	10	2	3.63	32.438	18.37	7.85	29.7	1.52	8.27	0.453	2.47	5.31	2.89	0.2	1.0	9	
11	11	2	4.20	32.846	18.61	7.82		1.68	9.03	0.512	2.75	5.29	2.84	0.1	0.1	9	
12	12	2	3.8	32.726	18.54	7.72	39.7	1.48	7.98	0.472	2.55	5.22	2.82	0.1	0.9	10	13.7
13	13	2	3.65	32.921	18.65	7.78	42.4	1.50	8.04	0.469	2.51	5.22	2.80	0.1	1.0	8	3.0
	19	2	3.58	32.751	18.55	7.75	44.9	1.50	8.09	0.467	2.52	5.34	2.88	0.1	0.7	7	10.9
	18	1050	2.97	34.291	19.45	7.42	137.0	1.56	8.02	0.480	2.47	5.44	2.80	0.5	0.4	10	21.2
16	14	2	3.72	32.878	18.63	7.78	42.4	1.46	7.84	0.460	2.47	5.31	2.85				5.8
17	17	2	3.72	32.656	18.50	7.81	33.3	1.46	7.89	0.463	2.50	5.34	2.87	0.7	<0.1	5	9.4
21	15	2	3.75	32.686	18.52	7.94	35.8	1.48	7.99	0.460	2.48	5.29	2.86	1.8	0.8	10	13.0
26	16	2	3.58	32.82	18.59	7.77	43.9	1.58	8.50	0.460	2.47	5.31	2.86	0.6	0.8	8	11.7
32	20	2	3.61	32.651	18.59	7.77	38.3	1.44	7.79	0.450	2.43	5.34	2.89	0.3	0.2	12	12.4
34	21	2	3.45	32.841	18.60	7.68	47.6	1.50	8.06	0.456	2.45	5.29	2.84	0.1	<0.1	7	8.7
39	39	2	3.20	32.250	18.26		56.0	1.38	7.56	0.444	2.43	4.81	2.63	0.9	2.4	1	3.2
41	38	2	3.13	33.030	18.71		45.0	1.38	7.38	0.447	2.39	4.98	2.66	0.8	3.6	2	3.2
43	22	2	3.38	33.139	18.78	7.58	65.6	1.50	7.99	0.462	2.46	5.44	2.90	0.4	5.7	10	5.3
47	35	2	3.26	32.782	18.57	7.77	56.3	1.28	6.89	0.411	2.21	4.88	2.63	1.9	5.3		5.6
50	33	2	2.86	32.904	18.64	7.77	42.5	1.46	7.83	0.437	2.34	5.49	2.95	<0.1	0.8	12	4.6
	34	2000	2.09	34.559	19.60	7.64	160.0	1.48	7.55	0.469	2.39	5.44	2.78	0.8	5.4	11	19.8
55	31	2	2.82	32.90	18.64	7.76	55.5	1.48	7.94	0.443	2.38	5.26	2.82	0.1	1.0	9	8.9
	32	495	3.31	34.227	19.41	7.35	120.5	1.44	7.42	0.474	2.44	5.34	2.75	0.4	1.5	13	12.3
56	30	2	2.80	32.964	18.67	7.73	55.7	1.42	7.61	0.468	2.51	5.34	2.86	0.1	0.8	10	4.2
59	28	2	3.33	32.845	18.60	7.77	47.3	1.40	7.53	0.451	2.42	5.39	2.90	0.1	1.5	11	8.3
	29	150	3.76	33.565	19.02	7.56	84.1	1.50	7.89	0.459	2.41	5.16	2.71	0.3	1.6	9	12.2
63	27	2	3.02	32.996	18.69	7.75	55.7	1.44	7.70	0.454	2.43	5.26	2.81	0.3	1.6	12	11.3
67	36	2	3.15	32.841	18.60	7.69	39.3	1.48	7.96	0.482	2.59	5.19	2.79	1.3	6.2	2	1.6
	37	110	3.75	33.507	18.99		47.8	1.04	5.48	0.323	1.70	4.03	2.12	0.8	2.2	1	5.6
69	42	2	3.27	33.195	18.81		57.2	1.14	6.06	0.407	2.16	5.29	2.81	0.5	3.8		6.4
	43	170	3.35	33.342	18.89		59.3	1.08	5.72	0.439	2.32	5.03	2.66	3.6	4.9	1	1.6
71	23	2	3.45	33.186	18.80	7.68	69.7	1.48	7.87	0.465	2.47	5.34	2.84	0.7	1.4	9	9.0
75	25	2	3.14	33.250	18.84	7.64	77.3	1.50	7.96	0.460	2.44	5.44	2.89	0.4	3.3	11	11.0
	24	590	3.31	34.085	19.33	7.41	151.5	1.52	7.86	0.492	2.55	5.31	2.75	0.5	2.7	10	18.6
80	26	2	3.20	33.012	18.70	7.69	63.3	1.46	7.81	0.446	2.39	5.31	2.84	0.4	0.9	11	13.3
82	40	2	3.00	33.199	18.81		49.0	1.26	6.70	0.418	2.22	4.81	2.56	0.8	5.6	1	8.0
	41	405	3.50	33.836	19.18		75.9	1.00	5.21	0.397	2.00	4.76	2.48	1.9	2.8		7.2
86	44	2	2.80	33.06	18.73		61.5	1.14	6.09	0.463	2.47	5.13	2.74	1.7	5.7		25.8
93	45	2	3.35	33.253	18.84		61.5	1.20	6.37	0.489	2.60	5.24	2.78	1.1	2.2	1	10.9

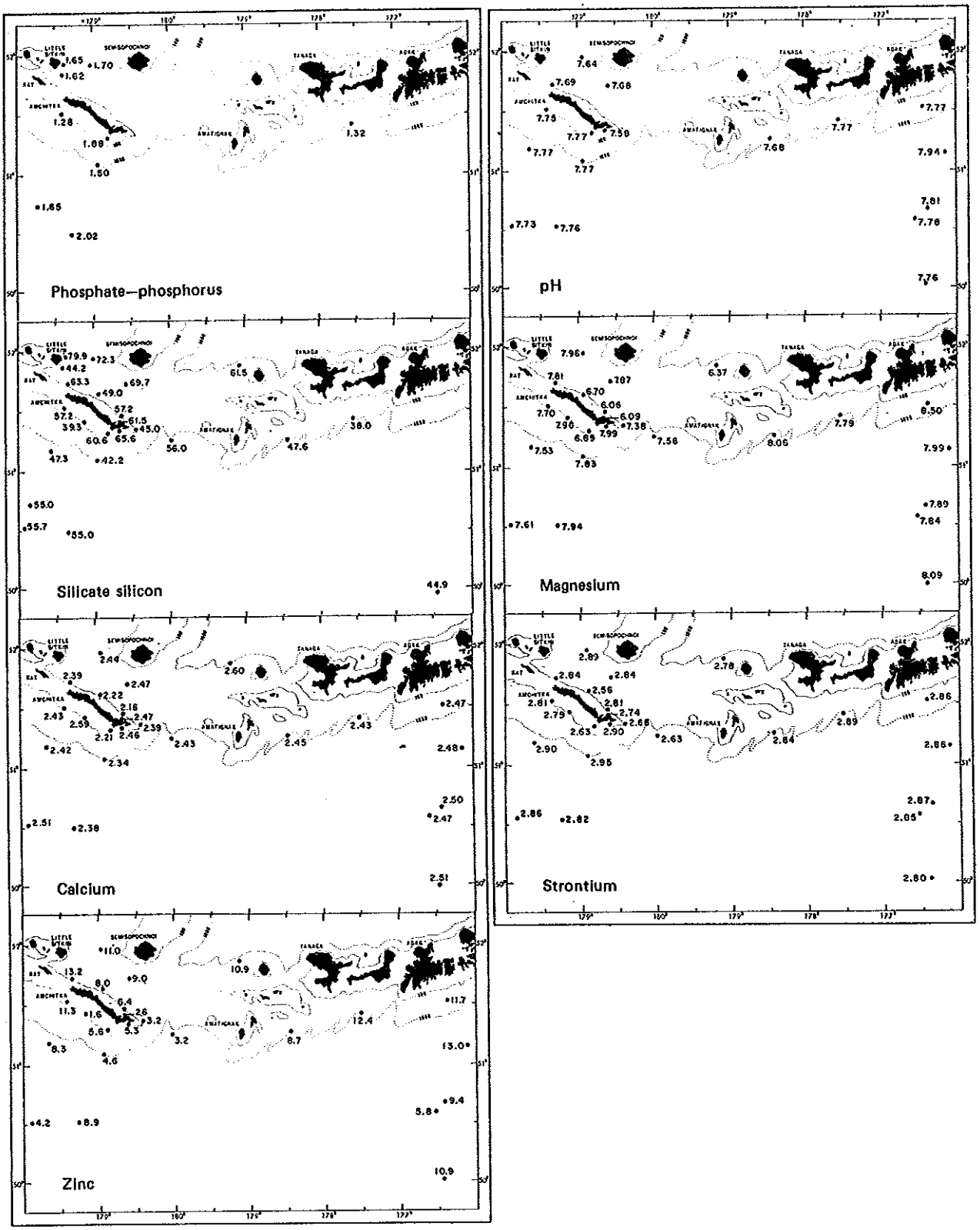

Fig. 8—Surface distributions of phosphate—phosphorus (μg-at/liter), pH (in situ temperature), silicate silicon (μg-at/liter), magnesium (Mg/Chl) × 10^{-2}, calcium (g/liter) and (Ca/Chl) × 10^{-2}, strontium (Sr/Chl) × 10^{-4}, and metals reported as zinc (μg/liter).

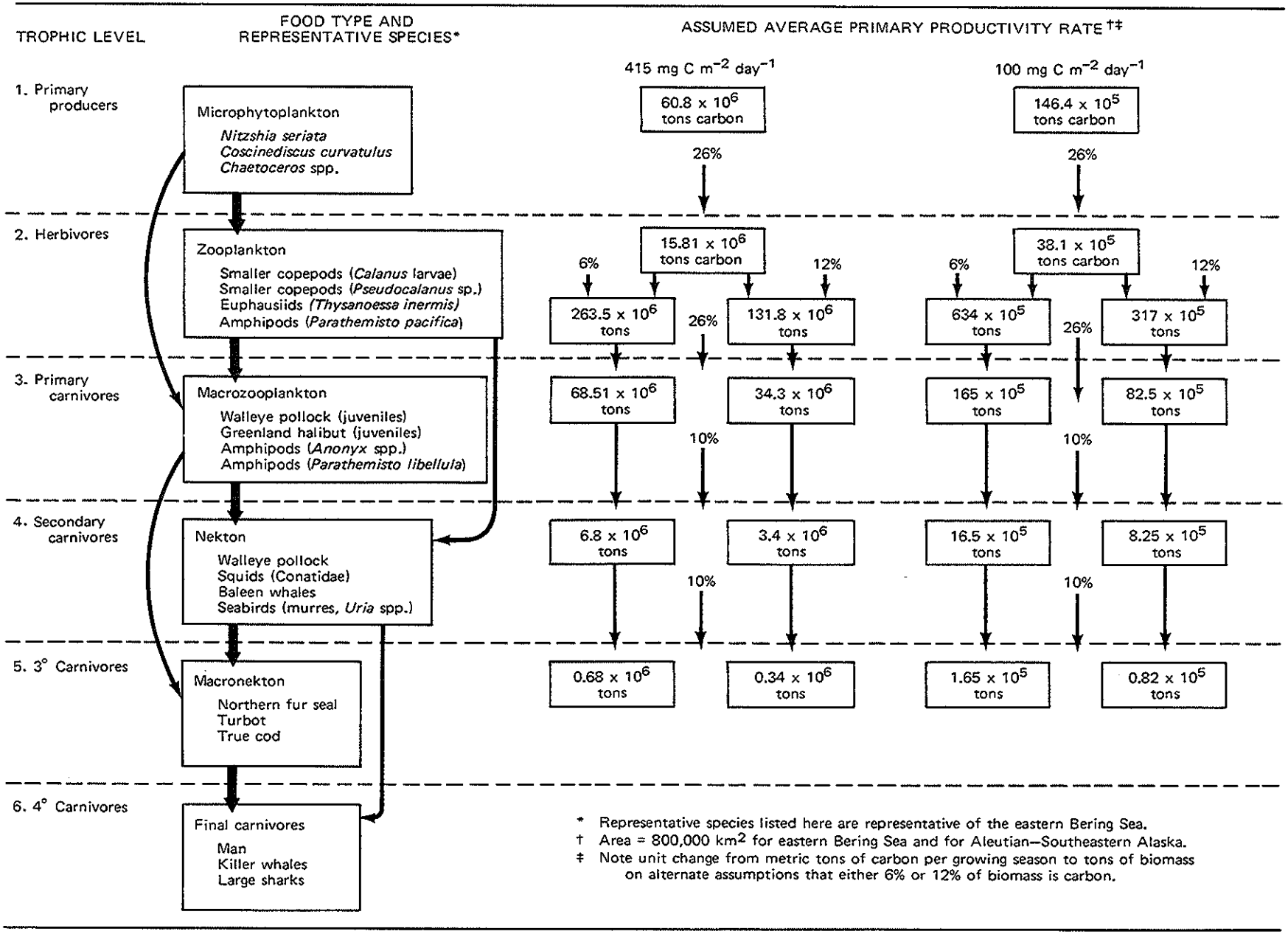

Fig. 9—Schematic of food chain and estimates of production for the Bering Sea area, June–November.

are also shown for an average daily primary production rate of 100 mg C m^{-2} day^{-1}, which is more representative of estimated productivity in the North Pacific Ocean south of the island arc.

As part of the investigations on North Pacific Ocean and Bering Sea fisheries, the U. S. National Marine Fisheries Service conducted a series of investigations near Adak Island in the central Aleutians starting in 1957 which provided background data for investigations on primary productivity and zooplankton distribution. Observations in 1968 included measurements of primary productivity (carbon isotope method), chlorophyl *a* for standing phytoplankton stock, and other environmental variables, including incoming solar radiation. Zooplankton samples were analyzed for standing stock and for relative importance and distribution of the major zooplanktonic groups.

Primary Productivity

Motoda and Kawamura (1961) reported primary productivity from measurements taken about 80 km north and east of Amchitka Island during the summer of 1960. Although only surface values were obtained, productivity in the euphotic zone appeared to be several times higher in summer than in winter. Koblents-Mishke (1965) summarized measurements of primary productivity in the Pacific Ocean and estimated average daily production throughout the year in the Aleutian area to be 100 to 150 mg C m^{-2} day^{-1}. The most comprehensive study of primary productivity in the Bering Sea is by Taniguchi (1969), who noted variations in primary production ranging from 160 to 630 mg C m^{-2} day^{-1}. Larrance (1971) and McAlister et al. (1968) report extensively on productivity for the Aleutian area and subarctic waters south of the Aleutians. High productivity ranging from 350 to 460 mg C m^{-2} day^{-1} in March and as high as 2400 mg C m^{-2} day^{-1} for spring and summer was measured near Adak on the Bering Sea side. Observations in January and February 1967 (McAlister et al., 1970) south of the Aleutian Islands (162°W) showed much lower values, averaging 87 mg C m^{-2} day^{-1}. These results are summarized in Table 4.

During the Amchitka observations of February 1968, productivity was measured at seven stations (McAlister et al., 1968) by the ^{14}C method of Steemann Nielsen (1952). Duplicate experimental bottles were held in an incubator with circulating seawater to provide ambient water temperature. The bottles were covered with neutral-light filters to simulate light intensities at the sample depths and were exposed to daylight. Each experiment lasted one-half day, from sunrise to local apparent noon or from local apparent noon to sunset. Chlorophyl *a* and nutrient concentration were also measured at these stations (McAlister et al., 1968).

Observed concentrations of chlorophyl *a* ranged between 0 and 0.44 mg/m^3. The wide fluctuations of chlorophyl *a* and nutrients in the surface layer indicated that the phytoplankton were not evenly distributed in the surface layer and suggested large-scale turbulence. A single dominant subsurface maximum of chlorophyl *a* occurred within the mixed layer when the layer did not extend to 100 m. Where the mixed layer extended below 100 m, chlorophyl *a* displayed several maximums and minimums, none of which were distinctly dominant. The highest (14.5 mg/m^2) and lowest (3.8 mg/m^2) values (summed through the euphotic zone) of chlorophyl *a* were found at stations on the continental shelf south of Amchitka. The mean of chlorophyl *a* values was 9.0 mg/m^2. The values of chlorophyl *a* did not differ significantly between offshore stations and those closer to shore. Mean productivity for all stations was 76 mg C m^{-2} day^{-1}. The offshore stations averaged 102 mg C m^{-2} day^{-1}.

All nutrient levels measured are adequate for phytoplankton growth. The regulating ecological factor appears to be light. Typically, light energy in higher latitude temperate zones is inadequate during winter to sustain an increase in phytoplankton populations. A comparison of the potential for production among stations was made assuming light as a limiting factor. Values calculated were generally similar at all stations, suggesting that, with equivalent light and standing stocks, the environment at the various stations will support about the same production.

Zooplankton

Zooplankton in the Subarctic Pacific Region are extremely important in the diet of baleen whales, the young of nearly all fishes, and some adult fish. Table 5 contains a fairly complete but not exhaustive list of dominant forms. Zooplankton studies have been made in the northwest North Pacific Ocean and adjacent seas by scientists from the Union of Soviet Socialist Republics (Heinrich, 1961; Bogorov and Vinogradov, 1968) and the United States (Aron, 1962). The biomass of zooplankton in the northwest Pacific Ocean during the spring and summer has been reported as 100 to 200 g/1000 m^3 (NORPAC Committee, 1960), 100 to 500 g/1000 m^3 (Bogorov, Beklemishev, and Vinogradov, 1961), and 100 to 2000 g/1000 m^3 (Bogorov and Vinogradov, 1968). Aron (1962) found that near the Aleutian Islands ten times more macrozooplankton were found in some samples than in others taken short distances away;

Table 4—Recent Estimates of Primary Production in the Water Column for Oceanic Waters Contiguous to Alaska (^{14}C method)*

Region	Daily rate, mg C m^{-2} day^{-1}	Dates	Source
Bering Sea			
Bering Strait	4100	June 1969	McRoy et al. (1972)
Eastern Bering Sea	21	February 1970	McRoy et al. (1972)
Aleutian area			
Unimak Pass area	243	June 1968 and 1970	McRoy et al. (1972)
	87	January–February 1967	McAlister et al. (1970)
Amchitka Island area	38 to 45	February 1968	McAlister et al. (1968)
Adak Island coast	686	June–July 1967	Larrance (1971)
	581	August 1967	
	404	September 1966	
Adak Bay	350 to 460	March 1966	Larrance (1971)
	840 to 2400	Late spring–summer	
Central subarctic domain			
Subarctic waters south to Adak Island	133	February	Larrance (1971, Fig. 5, p. 604)
	325	March	
	280	May	
	327	June	
	250	July	
	207	August	
	240	September	

*Adapted from Sanger (1974).

large catches were obtained preferentially in areas of high stability in the water column.

Zooplankton samples were collected with a Pacific Oceanic Group (POG) net at 35 night stations in February 1968. Two replicate tows, 5 to 10 min apart, were made at each station. Vertical tows from 150 to 0 m were made at each station, depth permitting, and were retrieved at a rate of 2 m/sec. Total time required to retrieve 150 m of cable was 75 ± 3 sec. Where the depth of the bottom did not permit tows to 150 m, shallow tows were made by lowering the net to approximately 6 m above the bottom. The rate of retrieval for shallow tows was also 2 m/sec. Geographic position, date, time of tow, depth range, and meter revolutions obtained from a flowmeter located at the side of the net mouth were recorded for all collections. Samples were preserved at sea in 5% Formalin.

Displacement volumes were measured, and taxonomic groups were sorted and counted at the Northwest Fisheries Center, National Marine Fisheries Service, Seattle. Samples were subdivided for taxonomic enumeration into subsamples of 300 to 500 animals. Most subsamples were $\frac{1}{8}$ splits but ranged from $\frac{1}{4}$ to $\frac{1}{16}$ of a sample. The total numbers of organisms were counted in six samples (4, 28, 36, 38, 54, and 68) as a check on the accuracy of subsampling.

Zooplankton volume near Amchitka Island ranged from 9.6 to 107 ml/1000 m^3 with a mean of 40.7. Data from the U. S. National Marine Fisheries Service cruises in 1966 and 1967 indicated volume values in the Alaskan Stream south of Adak Island which ranged from 10 to 70 ml/1000 m^3 in winter to 400 to 500 ml/1000 m^3 in summer. Thus zooplankton volume in the area south of the Aleutian Islands may change seasonally by an order of magnitude. Values for displacement volume of replicate samples varied as much as 166%. This variation is probably due to a patchy distribution of zooplankton and again represents effects of large- and medium-scale turbulence.

Numerically, copepods dominated the zooplankton, contributing 85.2% to the samples; other main zooplankton groups are shown in Table 6. Analysis of variance showed a significant variation ($p < 0.05$) in abundance between stations for all groups except ostracods. The maximum variation in biomass (9.6 to 107 ml/1000 m^3) was observed across the Alaskan Stream south of Amchitka. Biomass was lowest near the center of the Alaskan Stream but increased near its northern and southern boundaries (Fig. 10). Southward of this flow, the abundance of all organisms was relatively low except for euphausiids and amphipods. Total abundance of zooplankton organisms followed a distributional pattern similar to the total biomass except

Table 5—Dominant Species of Zooplankton

Subclass: Copepoda
- Order: Calanoida
  - Family: Calanidae
    - Genus and Species:
      - *Calanus plumchrus*
      - *Calanus cristatus*
      - *Calanus marshallae*
      - *Calanus glacialis*
  - Family: Eucalanidae
    - Genus and Species:
      - *Eucalanus bungii*
      - *Eucalanus californicus*
      - *Eucalanus elongatus hyalinus*
  - Family: Paracalanidae
    - Genus and Species:
      - *Paracalanus parvus*
  - Family: Pseudocalanidae
    - Genus and Species:
      - *Pseudocalanus minutus*
      - *Clausocalanus arcuicornis*
      - *Clausocalanus pergens*
      - *Ctenocalanus vanus*
  - Family: Aetideidae
    - Genus and Species:
      - *Aetideus pacificus*
      - *Gaetanus armiger*
  - Family: Euchaetidae
    - Genus and Species:
      - *Pareuchaeta elongata*
  - Family: Scolecithricidae
    - Genus and Species:
      - *Scolecithricella minor*
  - Family: Metridiidae
    - Genus and Species:
      - *Metridia lucens*
      - *Pleuromamma abdominalis*
  - Family: Centropagidae
    - Genus and Species:
      - *Centropages abdominalis*
  - Family: Lucicutiidae
    - Genus and Species:
      - *Lucicutia flavicornis*
  - Family: Candaciidae
    - Genus and Species:
      - *Candacia columbiae*
      - *Candacia bipinnata*
  - Family: Acartiidae
    - Genus and Species:
      - *Acartia clausi*
      - *Acartia longiremis*
- Order: Cyclopoida
  - Family: Oithonidae
    - Genus and Species:
      - *Oithona helgolandica*
      - *Oithona spinirostris*
      - *Oithona* sp.
  - Family: Oncaeidae
    - Genus and Species:
      - *Oncaea media*
- Order: Harpacticoida
  - Family: Ectinosomidae
    - Genus and Species:
      - *Microsetella norvegica*

Subclass: Malacostraca
- Order: Euphausiacea
  - Family: Euphausiidae
    - Genus and Species:
      - *Euphausia pacifica*
      - *Euphausia gibboides*
      - *Thysanoessa gregaria*
      - *Thysanoessa inermis*
      - *Thysanoessa inspinata*
      - *Thysanoessa longipes*
      - *Thysanoessa spinifera*
      - *Tessarabrachion oculatus*
      - *Nematoscelis difficilis*
      - *Nematobrachion flexipes*
      - *Stylocheiron maximum*
- Order: Amphipoda
  - Suborder: Gammaridae
    - Family: Lysianassidae
      - Genus and Species:
        - *Cyphocaris challengeri*
  - Suborder: Hyperiidae
    - Tribe: Physocephalata
      - Family: Vibiliidae
        - Genus and Species:
          - *Vibilia australis*
      - Family: Hyperiidae
        - Genus and Species:
          - *Hyperia medusarum*
          - *Hyperoche mediterranea*
          - *Parathemisto pacifica*
      - Family: Anchylomeridae
        - Genus and Species:
          - *Primno macropa*
      - Family: Lycaeidae
        - Genus and Species:
          - *Tryphaena malmii*
      - Family: *Oxycephalidae*
        - Genus and Species:
          - *Streetsia challengeri*

Phylum Chaetognatha (Tokioka classification)
- Class: Sagittoidea
  - Order: Phragmophora
    - Family: Eukrohniidae
      - Genus and Species:
        - *Eukrohnia hamata*
  - Order: Aphragmophora
    - Family: Sagittidae
      - Genus and Species:
        - *Parasagitta elegans*
        - *Flaccisagitta scrippsae*

in the nearshore waters south of Amchitka Island where biomass was high and total abundance low. Except for pteropods and amphipods, all taxonomic groups were most abundant at the boundaries of the Alaskan Stream. Distribution patterns for select zooplankton are shown in Figs. 11 to 18.

The general north–south distributional patterns of biomass may be summarized as follows:

low north of Amchitka Island in waters of Bering Sea origin; high in nearshore waters south of Amchitka Island; high near the northern boundary of the Alaskan Stream, decreasing in the axis of flow and increasing near the southern boundary; and low south of the Alaskan Stream.

Table 6—Percent Composition of Zooplankton Volume

Item	Percentage	Item	Percentage
Copepods	85.2	Euphausiids	1.5
Chaetognaths	5.2	Pteropods	1.0
Amphipods	2.4	Ostracods	0.9
Cnidarians	1.8	Remaining zooplankton	0.4
Larvaceans	1.6		

eastward flow to the north of the island arc. Second, the island is adjacent to a major passage, Amchitka Pass, through which north–south excursions override and penetrate well into the east–west flows. Third, it is situated at the junction of the Alaskan and western subarctic gyres, the former having a predominant southward flow and the latter a predominant northward flow in this area. Finally, it is at the southernmost part of the island arc; thus flows along bathymetric contours are subject to different geophysical effects east and west of the island.

There is no evidence of local upwelling; thus chemical nutrients must be advected laterally into

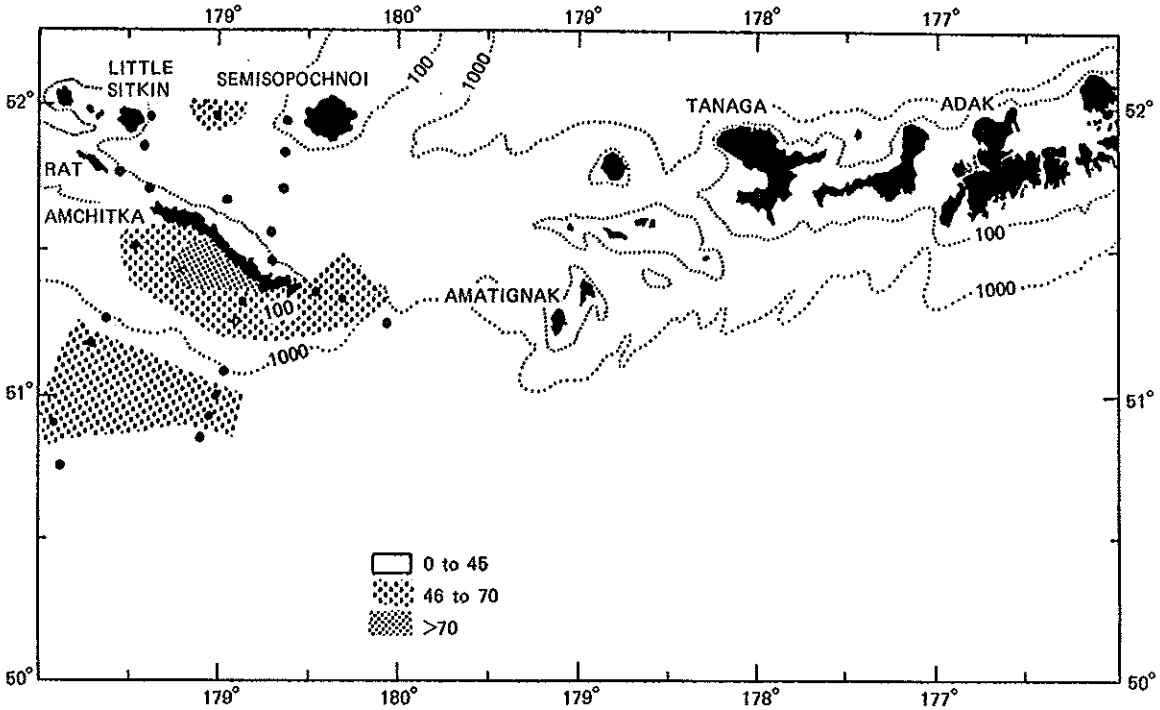

Fig. 10—Zooplankton volume in oceanic and coastal waters (ml per 1000 m^3).

CONCLUSIONS

Although broad easterly currents (Kuroshio and Subarctic Currents) dominate flow in the central North Pacific Ocean, the circulation near Amchitka Island is directly influenced by the complex patterns of exchange and mixing between North Pacific Ocean and Bering Sea waters in the passes of the Aleutian Islands. A number of factors contribute to the turbulent flow regime characteristic of the area around Amchitka Island. First, the island is located in what may be considered a shear zone between the westward flow to the south and the area. Nevertheless, concentrations are not limiting primarily because of turbulent mixing and stirring along the island arc. As a result of turbulence, there is a 1 to 4°C decrease in surface temperatures in the coastal regime compared to offshore oceanic conditions which is usually manifested as a temperature frontal zone near the northern boundary of the Alaskan Stream.

The general biological characteristics and processes are similar to those found throughout the Subarctic Pacific Region. The wide variations from station to station are characteristic of large-scale turbulence; maximum concentrations of organisms

(Text continues on page 352.)

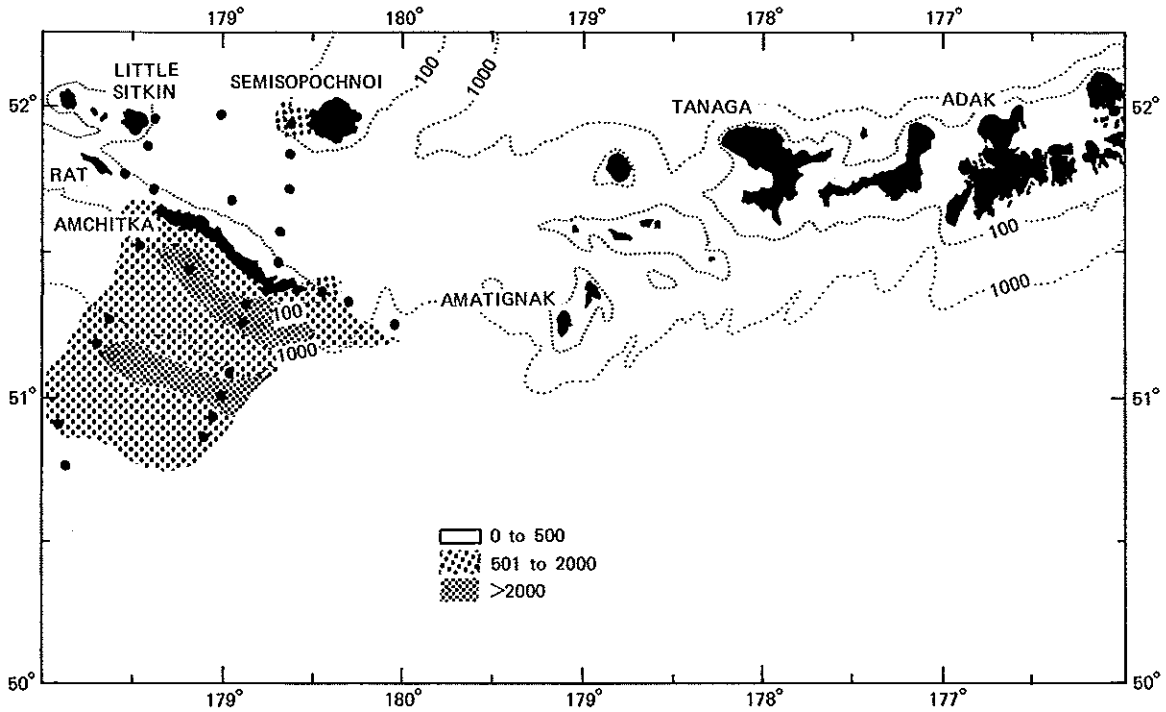

Fig. 11—Estimated abundance of cnidarians per 1000 m^3 of water, oceanic and coastal waters.

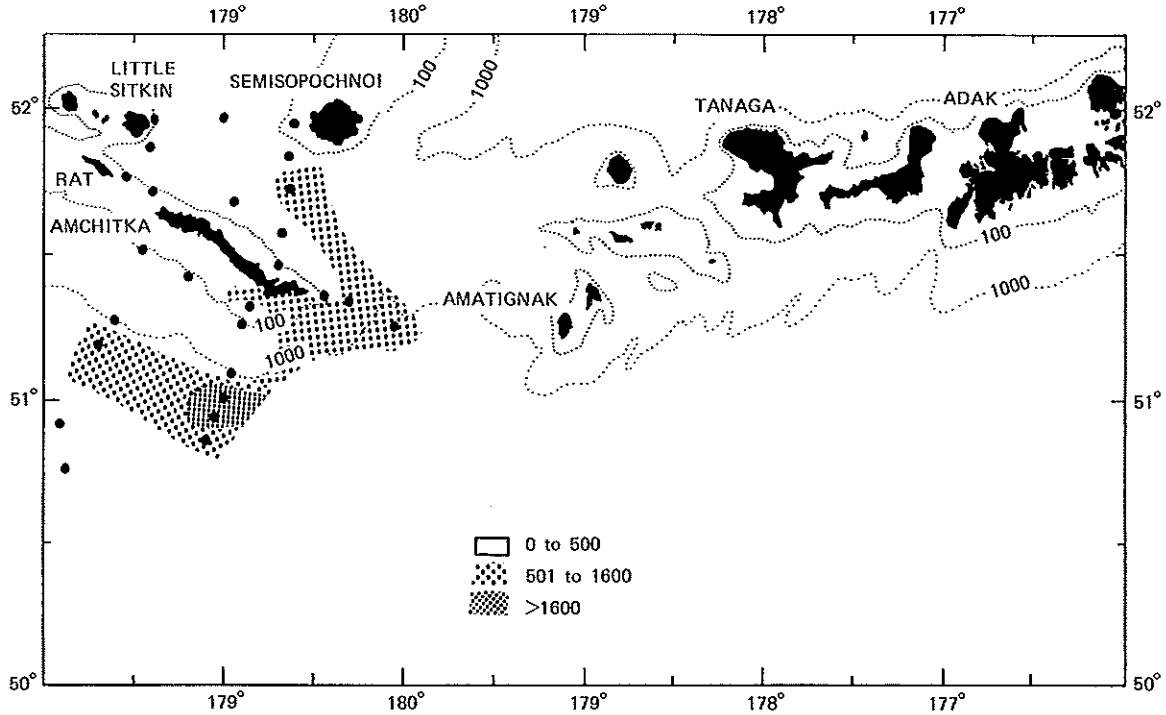

Fig. 12—Estimated abundance of ostracods per 1000 m^3 of water, oceanic and coastal waters.

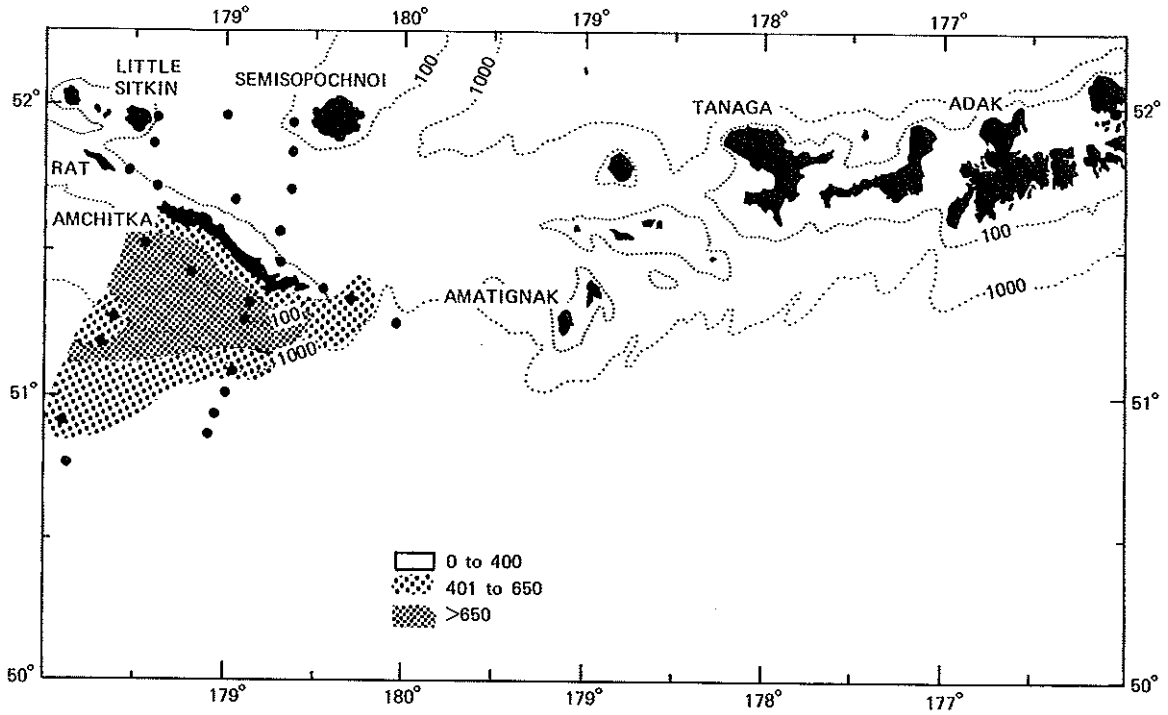

Fig. 13—Estimated abundance of pteropods per 1000 m^3 of water, oceanic and coastal waters.

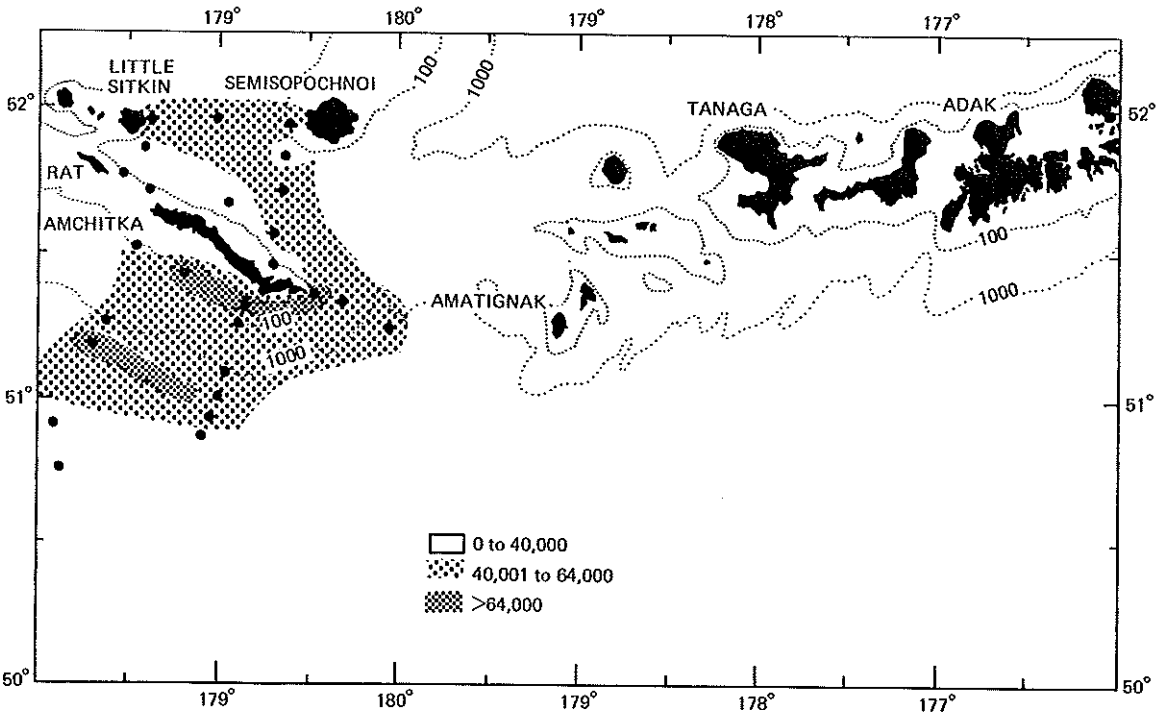

Fig. 14—Estimated abundance of copepods per 1000 m^3 of water, oceanic and coastal waters.

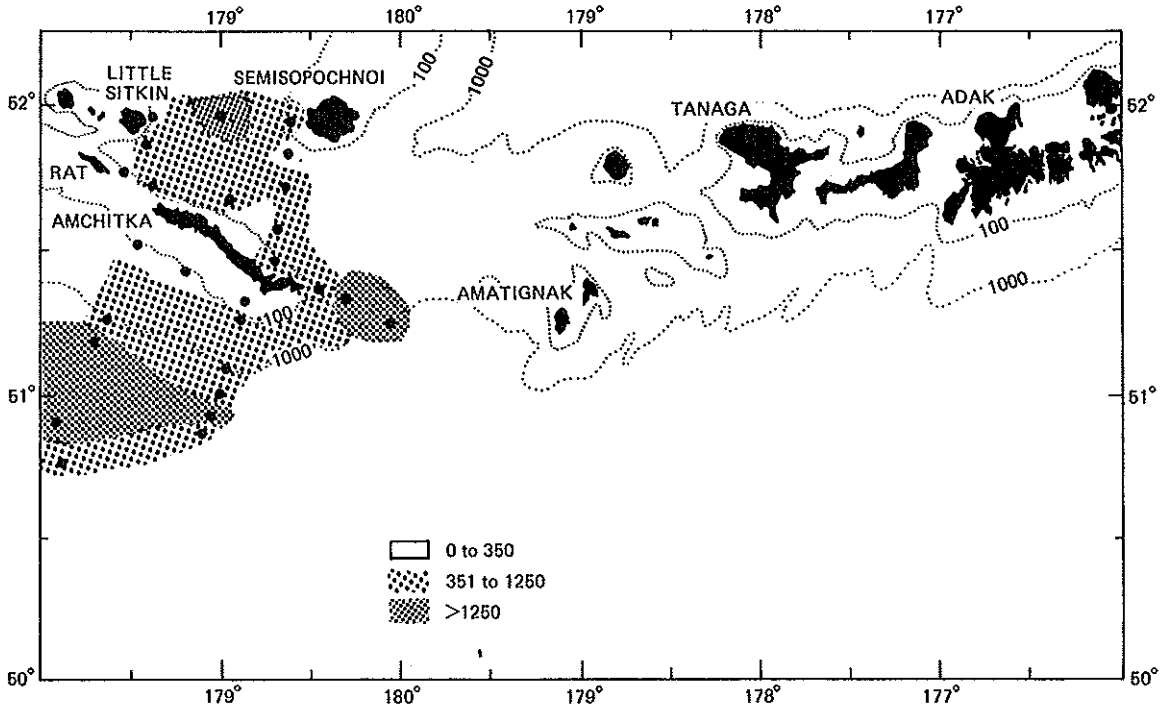

Fig. 15—Estimated abundance of euphausiids per 1000 m^3 of water, oceanic and coastal waters.

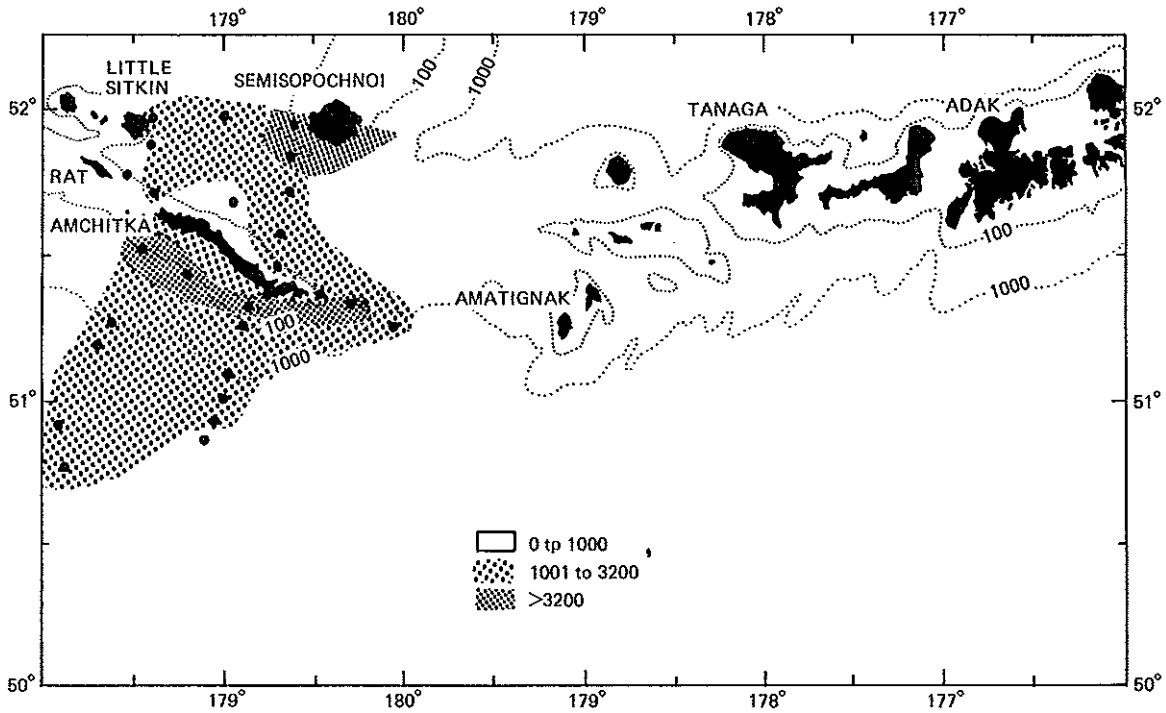

Fig. 16—Estimated abundance of chaetognaths per 1000 m^3 of water, oceanic and coastal waters.

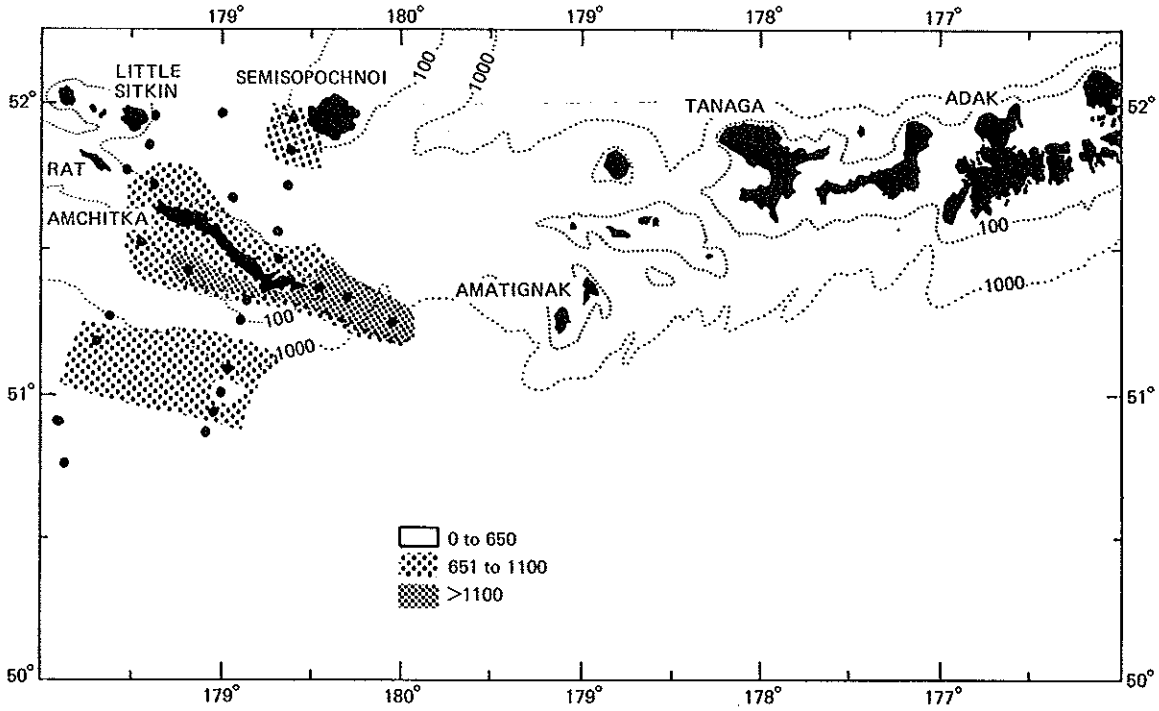

Fig. 17—Estimated abundance of larvaceans per 1000 m^3 of water, oceanic and coastal waters.

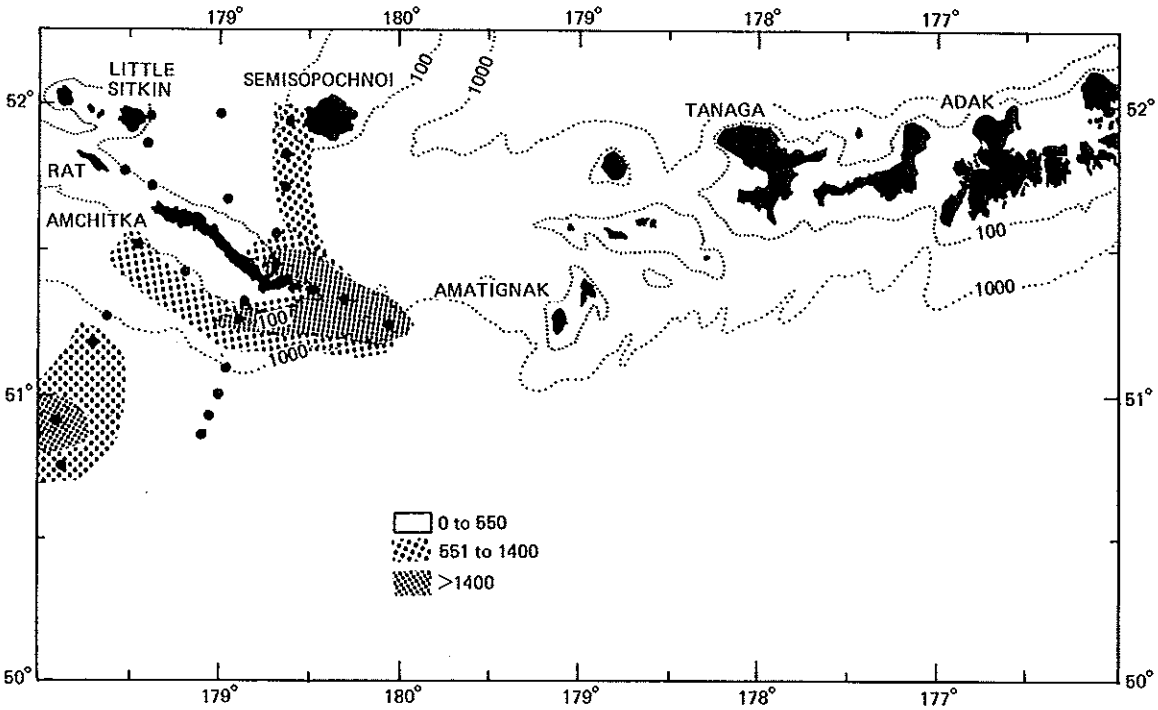

Fig. 18—Estimated abundance of amphipods per 1000 m^3 of water, oceanic and coastal waters.

are associated with fronts between water masses, lowering of temperature, and erosion of vertical stability. Violent movements associated with the inshore turbulent regime affect primary production directly as well as the movement and concentrations of zooplankton herbivores.

REFERENCES

Aron, W., 1962, The Distribution of Animals in the Eastern North Pacific and Its Relationship to Physical and Chemical Conditions, *J. Fish. Res. Board. Can.*, 19: 271-314.

Arsen'ev, V. S., 1967, Techeniya i vodnye masey Beringova morya (Currents and Water Masses of the Bering Sea). Izd. "Nauka," Moscow (in Russian, English summary). (Translated in 1968 by National Marine Fisheries Service, Northwest Fisheries Center, Seattle, Wash.)

Batalin, A. M., 1964, On the Water Exchange Between the Bering Sea and the Pacific Ocean (in Russia). *Tr. VNIRO*, 49: 7-16. (Translated in 1968 in Soviet Fisheries Investigations in the Northeastern Pacific, Part 2, pp. 1-12, Report TT 67-51024.)

Bogorov, V. G., K. V. Beklemishev, and M. E. Vinogradov, 1961, The Distribution of Plankton in the Pacific Ocean and Its Relation to Geographical Zonation, in *Pacific Basin Geography*, J. L. Gressitt (Ed.), 10th Pacific Science Congress, Honolulu, Hawaii, 1961, University of Hawaii Press.

——, and M. E. Vinogradov, 1968, Distribution of Zooplankton in the Kurile–Kamchatka Region of the Pacific Ocean, U. S. Naval Oceanographic Office, Translation 336. [Translated from *Trans. Inst. Okeanol., Akad. Nauk SSSR*, 34: 60-84 (1960).]

Favorite, F., 1974, On Flow into Bering Sea Through Aleutian Islands Passes, in *Oceanography of the Bering Sea*, Institute of Marine Sciences Occasional Bull. No. 2, D. W. Hood and E. J. Kelley (Eds.), pp. 3-37, University of Alaska, Fairbanks.

——, 1967, *The Alaskan Stream*, International North Pacific Fisheries Commission, Bulletin 21, pp. 1-20.

——, and Donald Fisk, 1971, Drift Bottle Experiments in the North Pacific Ocean and Bering Sea: 1957–60, 1962, 1966 and 1970, U. S. Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Data Report 67 (on microfiche).

——, and W. J. Ingraham, Jr., 1973, International North Pacific Fisheries Commission, Annual Report 1971, pp. 89-97.

——, and W. J. Ingraham, Jr., 1972, Influence of Bowers Ridge on Circulation in Bering Sea and Influence of Amchitka Branch, Alaskan Stream on Migration Paths of Sockeye Salmon, in *Biological Oceanography of the Northern North Pacific Ocean*, A. Y. Takenouti et al. (Eds.), pp. 13-29, Idemitsu Shoten, Tokyo.

——, A. J. Dodimead, and K. Nasu, 1976, Oceanography of the Subarctic Pacific Region, 1960-71, International North Pacific Fisheries Commission, Bulletin No. 33.

——, W. J. Ingraham, Jr., and D. M. Fisk, 1972, Oceanography, International North Pacific Fisheries Commission, Annual Report 1970, pp. 90-98.

Gordon, L. I., J. J. Kelley, D. W. Hood, and P. K. Park, 1973, Carbon Dioxide Partial Pressures in the North Pacific Surface Waters. 2: General Late Summer Distribution, *Mar. Chem.*, 1: 191-198.

Heinrich, A. K., 1961, Seasonal Phenomena in Plankton of the World Ocean, Report TT 63-19929. (Translated from *Trans. Inst. Oceanol.*, 51: 57-81.)

Kelley, J. J., L. L. Longerich, and D. W. Hood, 1971, Measurements of Carbon Dioxide in Northern Sea (Progress Report to Office of Naval Research, Washington, D. C.), Institute of Marine Sciences, University of Alaska, Fairbanks.

Koblents-Mishke, O. I., 1965, The Value of Primary Productivity in the Pacific Ocean, *Oceanology (USSR)* (English Translation), 5(2): 104-116.

Larrance, J. D., 1971, Primary Production in the Mid-Subarctic Pacific Region, 1966–68, *Fish. Bull. U. S.*, 69(3): 595-613.

McAlister, W. B., W. J. Ingraham, Jr., D. Day, and J. Larrance, 1970, Oceanography, International North Pacific Fisheries Commission, Annual Report 1968, pp. 90-101.

——, C. Mahnken, R. C. Clark, Jr., W. J. Ingraham, J. Larrance, and D. Day, 1968, Amchitka Bioenvironmental Program. Oceanography and Marine Ecology in the Vicinity of Amchitka Island, USAEC Report BMI-171-112, Battelle Memorial Institute.

McRoy, C. P., J. J. Goering, and W. E. Shiels, 1972, Studies of Primary Production in the Eastern Bering Sea, in *Biological Oceanography of the Northern North Pacific Ocean*, A. Y. Takenouti et al. (Eds.), pp. 199-216, Idemitsu Shoten, Tokyo.

Motoda, S., and T. Kawamura, 1961, Data on Phytoplankton Photosynthetic Activity, in The "Oshoru Maru" Cruise 46 to the Bering Sea and North Pacific in June–August 1960, *Data Rec. Oceanogr. Observ. Explor. Fish (Hokkaido)*, 5: 142-165.

NORPAC Committee, 1960, *Oceanic Observations of the Pacific, 1955*, Vol. 2, The Norpac Data, University of California Press and University of Tokyo Press, Berkeley and Tokyo.

Park, P. K., L. I. Gordon, and S. Alvarez-Borrego, 1974, The Carbon Dioxide System of the Bering Sea, in *Oceanography of the Bering Sea*, D. W. Hood and E. J. Kelley (Eds.), Institute of Marine Sciences Occasional Publication No. 2, pp. 107-147, University of Alaska, Fairbanks.

Reed, R. K., 1971, Nontidal Flow in the Aleutian Island Passes, *Deep-Sea Res.*, 18(3): 371-372.

Sanger, G. A., 1974, A Preliminary Look at Marine Mammal Food Chain Relationships in Alaskan Waters, Northwest Fisheries Research Center Processed Report, National Marine Fisheries Service, Seattle.

Steemann Nielsen, E., 1952, The Use of Radio-Active Carbon (C^{14}) for Measuring Organic Production in the Sea, *J. Cons., Cons. Perma. Int. Explor. Mer.*, 18(2): 117-140.

Taniguchi, A., 1969, Regional Variations of Surface Primary Production in the Bering Sea in Summer and Vertical Stability of Water Affecting the Production, *Bull. Fac. Fish., Hokkaido Univ.*, 20: 169-179.

Thomson, R. E., 1972, On the Alaskan Stream; *J. Phys. Oceanogr.*, 2(4): 363-371.

Tsuruta, A., 1963, Distribution of Plankton and Its Characteristics in the Oceanic Fishing Grounds, with Special Reference to Their Relation to Fishery, *J. Shimonoseki Univ. Fish.*, 12(1): 13-214 (in Japanese, English summary).

17

Ecology of Marine Algae*

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The rocky shores of Amchitka Island are densely carpeted by marine algal communities, which, beyond the coast exposed by the tides, are characterized by extensive floating kelp beds. An unusual feature of the intertidal area of the southeastern third of the island is the occurrence of wide, often extremely flat, rock benches at about mean tide level.

The littoral region is characterized by a supralittoral fringe area with Prasiola, Rhodochorton, *and* Porphyra–Ulothrix *zones and a midlittoral area with* Fucus, Hedophyllum, *and* Alaria *zones. Many species distributions are strongly influenced by the benches, being correlated with horizontal distance perpendicular to the shore. The presence of* Hedophyllum *and* Fucus *zones indicates more protected conditions than might have been expected. It is suggested that the bench topography and offshore kelp beds provide an exposure gradient across the intertidal area. The sublittoral fringe is characterized by a zone of* Laminaria longipes. *Most littoral algae occur throughout the year but exhibit growth in the spring and summer. The* Porphyra–Ulothrix *zone and the* Halosaccion *association appear in spring and reach a peak of development in the summer. Plots in the intertidal region denuded of all organisms exhibited colonization by a sequence of diatoms and filamentous algae, leafy green algae, and, last, larger red and brown algae. Initial settlement was seasonal and occurred fastest in exposed areas at low levels. The removal of only the kelp canopy gave similar results, but colonization occurred more quickly and was influenced by the remaining understory vegetation.*

The most conspicuous element of the sublittoral flora is Alaria fistulosa, *which forms the extensive floating kelp beds. Down to 20-m (66-ft) depth, the bottom is densely covered with species in the genera* Laminaria, Alaria, Cymathere, Agarum, *and* Thalassiophyllum. *A third level of vegetation is formed by populations of* Ptilota, Hypophyllum, Cirrulicarpus, *and* Constantinea. *Finally, crustose coralline algae, particularly* Clathromorphum nereostratum, *and the green alga* Codium ritteri *dominate rocky bottoms below 20 m (66 ft). The predation of the sea otter on invertebrate herbivores is undoubtedly a major factor in the formation of such dense algal communities.*

The Milrow nuclear test affected about 4 ha (10 acres) of littoral vegetation when an uplift of about 12 cm (5 in.) occurred on an intertidal rock bench. Mortality was extensive in the upper portions of all zones 6 months after the disturbance, and significant changes were still occurring when last observed, 3½ years after Milrow. The Cannikin nuclear test resulted in uplifting up to a maximum of 1 m (3 ft). Mortality of littoral vegetation was severe along 1.9 km (1.2 miles) of coast, including areas with 0.5 to 1 m of uplift. Moderate mortality was observed along an additional 1.5 km (1 mile) of coast, and mortality was detectable along a further 2.7 km (1.7 miles) of coast. Significant changes in vegetation were reported to be occurring nearly 3 years after Cannikin. A normal littoral vegetation will eventually return to both the Milrow- and Cannikin-disturbed areas. The lifting of some rock benches above the midlittoral area as a result of the Cannikin test has resulted in a significant permanent reduction in area available to most littoral species.

The benthic marine algae, commonly known as seaweeds, grow luxuriantly around the rocky coasts of Amchitka Island. These plants form a conspicuous covering on rocks uncovered by low tides. Floating kelp beds, consisting of plants that are attached to the rocky bottom, occupy large areas of the ocean surface surrounding the island. As primary producers these kelp plants are a major source of food for primary consuming organisms, particularly marine invertebrates.

The history of phycological research in the North Pacific Ocean and our studies of the physical environment, the structure of marine algal communities, biological interactions, and the effects of underground nuclear testing on the algal communities of Amchitka Island are reviewed in this chapter.

HISTORICAL REVIEW

Until 1967, the starting point for studies reported in this chapter, the Aleutian marine algae were practically unknown. Therefore the floristic

*All sections of this chapter except the section "Colonization Studies" were written by Lebednik.

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relationships of the Amchitka algal flora are best obtained by reviewing the literature of surrounding areas of the North Pacific Ocean. A comprehensive review of the Russian literature is given because most of the articles are practically unknown or unavailable in North America.

Aleutian Islands

The first publication on marine algae from the Aleutian Islands (Mertens, 1829) resulted from the expedition of the Russian ships *Seniavin* and *Moller*, which were under the command of Lütke. The famous "Illustrationes Algarum" (Postels and Ruprecht, 1840) presented the full treatment of the marine algae collected on this expedition by Postels, Mertens, and Kastalsky. In the Aleutian Islands marine algae were collected at Unalaska Island only. Further records of Aleutian marine algae, again limited to Unalaska Island, were published by Setchell and Gardner (1903). Algal specimens from the western Aleutian Islands, including the first collections from Atka, Amchitka, and Agattu Islands, were gathered by Kobayashi from May to August 1931 and were reported on by Okamura (1933). Brief comments on the marine and land plant communities of the Aleutian Islands were made by Tatewaki and Kobayashi (1934). Field work was conducted by Tatewaki in 1929 on Attu, Amchitka, and Atka Islands and by Kobayashi in 1931 on Attu, Amchitka, Atka, Umnak, and Unalaska Islands. The account of the marine vegetation, comprising 21 species of marine algae, includes no details on localities; thus it is impossible to determine on which islands each species was observed. Collections of marine algae from Attu, Shemya, Adak, and Unimak Islands were made in 1960 as part of a large study of the North Pacific algal distributions by Scagel (1962; 1963). These collections, deposited in the Phycological Herbarium of the University of British Columbia, were later used by students and associates of Scagel in monographic studies of the genera *Hedophyllum* (Widdowson, 1965), *Laminaria* (Druehl, 1968), *Alaria* (Widdowson, 1971a; 1971b), *Porphyra* (Conway et al., 1976), and *Ulva* (Tanner, in preparation). Druehl (1970) discussed the distribution of the Laminariales in the North Pacific Ocean. Only three species of marine algae had been reported from Amchitka Island prior to our studies.

Several other publications, although not dealing directly with the Aleutian Islands, are important either taxonomically or geographically in studies of the marine algae of Amchitka Island. Probably the most pertinent of these are the publications of Kjellman (1889) on the algae of the Bering Sea and Guryanova (1935), Kardakova-Prezhentsova (1938), and E. Zinova* (1940) on the marine algae of the Commander Islands.

The publication by Kjellman (1889) resulted from collections made on the *Vega* expedition in the Bering Sea from July 20 to Aug. 19, 1879. These collections were made at St. Lawrence Bay and Konyam Bay on the Chukotski Peninsula, Union of Soviet Socialist Republics; Port Clarence, on the Seward Peninsula, Alaska; and Bering Island, one of the Commander Islands. This work is still an important taxonomic reference, and it is the only work in which the distribution of the marine algae of the Bering Sea is treated comprehensively.

Guryanova (1935) discussed the history of scientific research, geology, climate, oceanography, and biology of the Commander Islands and made extensive observations on the marine algal vegetation of Bering Island from November 1930 to June 1931. The distribution of marine plants and animals on Bering Island, although treated in detail, was not studied with quantitative methods. A more detailed study of the distribution of the seaweeds of the Commander Islands was undertaken by Kardakova-Prezhentsova from 1928 to 1932 (Kardakova-Prezhentsova, 1938). A comprehensive list, containing 174 species of marine algae collected at the Commander Islands from 1871 to 1932, was compiled by E. Zinova (1940).

Eastern Bering Sea

Several short papers have dealt with marine algae from the eastern Bering Sea. Setchell (1899) published a short list of marine algae collected at the Pribilof Islands and Chihara (1967) reported on some marine algae collected at Cape Thompson, Alaska. From Izembek Lagoon, on the north coast of the Alaska Peninsula opposite Cold Bay, McRoy (1968) collected the Eurasian alga *Fucus inflatus* f. *latifrons* and Biebl (1970; 1972) studied the temperature resistance of a few local algal species.

Pacific North America

Research on marine algae east of the Alaska Peninsula, along the Pacific North American coast, has resulted in many publications. The importance of these studies to the Amchitka flora is generally

*Spelled E. S. Sinova as transliterated on the original publications. This spelling is generally used in the phycological literature. To conform with transliteration standards now accepted, we have spelled her name with a "Z" in this paper. So that this author will not be confused with A. D. Zinova, a niece, who also published on marine algae, the first initial is used in citations throughout this chapter.

inversely related to their distance from the Aleutian Islands. The Harriman Alaska Expedition collected 207 species of marine algae at Victoria, British Columbia, and at several localities along the southern coast of Alaska as far west as the Shumagin Islands (Saunders, 1901). Scagel's annotated list of marine algae of British Columbia and northern Washington (Scagel, 1957) has recently been superseded by his monograph of the Chlorophyceae (Scagel, 1966) and revised lists and keys for the Phaeophyceae (Widdowson, 1973) and Rhodophyceae (Widdowson, 1975) which cover the same geographical area. These publications contain information on many species that occur in the Aleutian Islands. A guide to the literature and distributions of Pacific benthic algae, including Alaska, was published by Dawson (1961). Johansen (1971) reported on the effects of the Alaska earthquake of 1964 on intertidal benthic algae in Prince William Sound. Although the littoral marine algae were destroyed in some localities, 120 taxa of macroalgae were collected, and 17 of these represented new records for the area.

Russian Studies

Bibliographies of the Russian literature on marine algae published from 1900 to 1940 have been compiled by Gaĭdukov (1901), Elenkin and Ol' (1929; 1935; 1950a; 1950b), Gollerbakh et al. (1966), and Krasavina (1968). A taxonomic cross-index to these bibliographies, spanning the years 1737 to 1960, was compiled by Gollerbakh and Krasavina (1971). A short history of Pacific Russian scientific investigations was given by Komarov (1962). Nearly all the Russian taxonomic studies on marine algae have been carried out at the Komarov Botanical Institute in Leningrad (St. Petersburg in the older literature) by Elena S. Zinova and later by her niece, Anna D. Zinova. A history of the Institute in English was recently published (Shetler, 1967).

Eastern Kamchatka

The earliest records of marine algae from Kamchatka (Komarov, 1962) appear to have been those of Gmelin (1768), which were based on specimens that had accumulated at the Imperial Academy in St. Petersburg. Gmelin classified into the Linnean algal genera *Fucus* and *Ulva*, fifteen species from Kamchatka that were collected in part by Steller and "Kraschenninikow." Most of the later studies on marine algae on this coast took place in Avachinskaya Bay. The first of these studies was carried out in 1908 and 1909 as part of the Kamchatka Expedition of F. P. Ryabushinski. Savich" (1914) described the algal vegetation in the bay. The taxonomy of Savich"s specimens was determined by Voronikhin (1914). The area was studied again in 1929 and 1930 by a zoological expedition, and the algal specimens were described by E. Zinova (1933). A few species in the red algal family Delesseriaceae were also recently described from the area (A. Zinova, 1965). In northeastern Kamchatka, eight marine algae were collected by Takayama in August 1923 at Korf (Baron Korfe), on the northwest coast of Korf Zaliv (Okamura, 1928). The littoral and sublittoral algae from Anadyrskiy Bay were described by Vinogradova (1973a; 1973b). A study of the littoral and sublittoral algae of Karaginskiy Island was carried out in 1930 (Kongiser, 1933). Further studies of marine algae from southeastern Kamchatka included an expanded list of species (E. Zinova, 1954a) and a detailed description of littoral zonation (Spasskiĭ, 1961).

Kurile Islands

An extensive account in English of the marine algae of the Kurile Islands was published by the Japanese phycologist Nagai (1940; 1941). Subsequently several Russian papers have been published. The distribution of the fauna and flora of the littoral region of the Kurile Islands was described by Kusakin (1961). Several taxonomic papers have also appeared that are based on specimens of Laminariaceae (Gusarova and Petrov, 1970; 1972) and various red and brown algae (Gusarova, 1972).

Okhotsk Sea

The first major paper on the marine algae of the Okhotsk Sea was the classical phycological treatise "Tange des Ochotskischen Meeres" (Ruprecht, 1851). This work was based on specimens that had accumulated in the herbarium of the Imperial Academy of St. Petersburg since Gmelin's time. Most of these specimens had been collected in 1807 by Redovski (a few possibly also by Steller) in the eastern Okhotsk Sea and later by Middendorff in the Shantar Islands. In this work, which is rare and generally unavailable in North America, 57 species of algae were reported. A more detailed study of the Shantar Islands algal flora was made by E. Zinova (1930). A brief description of the littoral zonation of the Okhotsk Sea was given by Ushakov (1951). From 1905 to 1945 the southern portion of Sakhalin Island, which separates the Okhotsk Sea from the Sea of Japan, was under the jurisdiction of Japan. During this period

extensive studies of marine algae were conducted by various Japanese workers, and a total of 182 species were recorded from the area (Tokida, 1954). Taxonomic papers on *Laminaria* (Petrov and Vozzhinskaya, 1970; A. Zinova, 1964; 1969), *Cystoseira* (Petrov, 1966), *Sargassum* (Petrov, 1968), *Rhodymenia* (Blinova and A. Zinova, 1967), and *Rhodoglossum* (Perestenko, 1967) were published. Vozzhinskaya (1960b) described some endophytic algae. The comprehensive Russian paper on the algae of the Okhotsk Sea (E. Zinova, 1954b) has also been further augmented by papers covering several algal groups (Blinova, 1968; Blinova and Gusarova, 1970; Vozzhinskaya, 1960a; 1964a; 1965a; 1967; Vozzhinskaya and Vishnevskaya, 1968).

Ecological studies of marine algae, dealing mainly with distributions, associations, and biomass, have also been carried out in the Okhotsk Sea. The distribution of a few littoral algae was described by Ushakov (1951). In 1954 and 1955 an extensive study of the littoral and sublittoral marine algae of Sakhalin Island was carried out by the Far Eastern Coastal Expedition of the Institute of Oceanology (Shchapova, Mokievskiĭ, and Pasternak, 1957; Shchapova and Vozzhinskaya, 1960; Vozzhinskaya, 1964b). In the littoral region quantitative samples were taken along transects, and in the sublittoral region qualitative samples were obtained by grabs, trawls, and diving. The results of these studies are available in English (Shchapova and Vozzhinskaya, 1960; Vozzhinskaya, 1964b). Littoral and sublittoral community studies were carrried out in the northern Sea of Okhotsk, along the western coast of Kamchatka, by Vozzhinskaya (1965b) and Vozzhinskaya and Blinova (1970). The marine vegetation of the Shantar Ostrovov was discussed by Vozzhinskaya and Selitskaya (1970b). Finally, the distribution and biomass throughout the Okhotsk Sea was described by Vozzhinskaya and Selitskaya (1970a).

Phytogeography

Several Russian papers have dealt with phytogeography in which more than one of the above geographical regions have been discussed. Shchapova (1946) discussed the distribution of some Phaeophyceae in the Pacific Ocean, and later (Shchapova, 1948) she considered the distribution of the Laminariales at greater length. The marine algal resources of the Soviet Union from the point of view of utilization were compared by Kireeva (1965). Finally, phytogeographical changes of littoral biota from the Bering Sea to Sunda Strait were discussed by Mokievskiĭ (1967).

Japanese Studies

The literature on Japanese marine algae is too extensive to review here. A recent book on this subject (Tokida and Hirose, 1975) gives a good review of Japanese ecological work. Taniguti (1962) gives an extensive account in English of phytosociological studies that he carried out in the littoral region along the entire Japanese coastline. Other important papers are in the numerous publications of various Japanese universities and the *Bulletin of Japanese Society of Phycology* (sic).

The preceding review illustrates the extensive research that has been carried out on marine algae in the North Pacific Ocean and also points out the lack of information from the Aleutian Islands. We hope that our studies will partially fill this gap in our knowledge of North Pacific marine algae.

Amchitka Studies

Beginning in 1967, F. C. Weinmann made extensive collections of marine algae around Amchitka. He also studied the distributions and community structure of littoral algae along two transects, one on the Pacific Ocean coast (Makarius Bay,* designated T-1) and one on the Bering Sea coast (Square Bay, designated T-2). (See Geological Survey map in the pocket at the back of this volume.) The results of these transect studies constituted a master's thesis (Weinmann, 1968) and a Battelle Columbus Laboratories publication (Weinmann, 1969). Photogrammetry was used in continued study of Weinmann's transects, and a third transect at Rifle Range Point (designated T-3) was established in 1969 (Burgner et al., 1969). A summary of results to 1969 was reported at a Symposium on Amchitka Bioenvironmental Studies held at the 21st Annual Meeting of the American Institute of Biological Sciences and was subsequently published (Lebednik, Weinmann, and Norris, 1971).

Extensive analysis of the T-3 transect and comparison of algal weight and cover relationships (Burgner et al., 1971), continued sampling at the T-1 and T-2 transects (Burgner and Nakatani, 1972; Nakatani et al., 1973), and denudation of plots of selected algae (Nakatani et al., 1973; Palmisano, 1975) were three additional studies completed at Amchitka. Effects of the Milrow underground nuclear test on marine algae were reported by Burgner, Isakson, and Lebednik (1970), Lebednik (1973), Nakatani et al. (1973), and Nakatani and Burgner (1974). The effects of

*Also known as St. Makarius Bay.

Table 1—Sampling Dates of Transects and Test-Effects Study Areas

Date	T-1*	T-2*	T-3*	IA-1*	IA-2*	IA-3*	Coastal walk*	Colonization studies (3 areas)*
†March to April 1968	W	W						
†May 1968	O	O						
August 1968	P	P						
March 1969	P	P						
May 3 to 7, 1969			P, W					
June 1969	P	P						
Oct. 2, 1969 (Milrow test)								
Apr. 21, 1970				P				
May 21, 1970				P				
August 1970					P	P		
September 1970				P				
December 1970	P	P						
March 1971				P				P
May 1971								P
July 1971				P	P	P	O	P
August 1971								P
September 1971								P
October 1971				P	P	P		
Nov. 6, 1971 (Cannikin test)								P
December 1971				P	P	P		
February 1972	P	P		P	P	P		P
April 1972	P	P		P	P	P	O	P
June 1972	P	P		P	P	P		P
August 1972	P	P		P	P	P		P
October 1972	P	P		P	P	P		P
December 1972								P
April 1973	P	P		P	P	P	O	P
August 1973	P	P		P	P	P		
‡May 1974					P	P		
‡August 1974					P	P		

*P, photographic sample; W, dry-weight sample; and O, visual observations.
†Samples taken by F. C. Weinmann.
‡Samples taken by FRI staff; reported in Kirkwood (1974; 1975).

the Cannikin test were reported by Nakatani et al. (1973) and Nakatani and Burgner (1974). From August 1968 to August 1973, the preceding studies were conducted by Lebednik. The experimental denudation studies were conducted by Palmisano (1975). Subsequent observations of Milrow and Cannikin effects as reported in Kirkwood (1974; 1975) were made by other FRI investigators. The littoral sampling program is summarized in Table 1.

From the beginning of the marine algal studies, it was apparent that many poorly known and undescribed species were common in the Amchitka flora and that a comprehensive taxonomic study would produce a valuable contribution to our knowledge of the marine algal flora of the North Pacific Ocean. In 1968, R. E. Norris, F. C. Weinmann, and M. J. Wynne agreed to undertake a taxonomic study of all the macroscopic algae of Amchitka. Subsequently Lebednik joined the project and undertook taxonomic studies of the coralline algae. Weinmann continued his graduate career elsewhere. Extensive collections were made for this taxonomic study in the littoral and sublittoral regions from 1967 through 1973.

In the first contributions to this study, Wynne described the Delesseriaceae (Wynne, 1970a; 1975), Bonnemaisoniaceae (Wynne, 1970b), and *Porphyra* species of Amchitka (Wynne, 1972), all members of the red algae. An ecological study on algal canopy interactions in the sublittoral region was reported by Dayton (1975).

A number of later papers have been based, in part, on collections made at Amchitka. Wynne (1971) merged the brown algal genera *Analipus* and *Heterochordaria*. Lebednik presented a monographic treatment of the coralline genera *Clathromorphum* and *Mesophyllum* on the Pacific Coast of North America (Lebednik, 1974; 1975; 1977) and an evolutionary scheme for the Corallinaceae and Cryptonemiales (Lebednik, in press, a; in press,

c). The algal communities of the Aleutian Islands were reported by Lebednik (in press, b). Live material of crustose red algae collected on Amchitka and sent to the laboratory of Dr. J. West contributed data for three papers dealing with hybridization and development in culture (Polanshek, 1975; Polanshek and West, 1976; DeCew and West, in press).

Three genera and eight species of red algae from Amchitka have been newly described in the preceding papers.* Table 2 is a list of species identified to date. The taxonomic studies are continuing, and we hope that the entire macroscopic algal flora will be described in future publications.

PHYSICAL FEATURES OF THE ENVIRONMENT

The topography of the Amchitka littoral region, which is important in the determination of the distribution of littoral algae, is unusual and deserves description. An aerial view of a segment of coastline at low tide (Fig. 1) shows two extensive rocky flats (B), dissected by large channels (C), bordered landward by boulder strands and separated by a sandy beach and the mouths of two streams (S). Such stream mouths usually indicate a sand or gravel trough (T) projecting seaward through and beyond the littoral rock flats (Powers, Coats, and Nelson, 1960; Lebednik, Weinmann, and Norris, 1971). The littoral rocky areas are mainly characterized by a feature termed rock benches (Powers et al., 1960), intertidal platforms (Morris, 1971), or strandflats (Everett, Chap. 8, this volume). At Bird Cape, at East Cape, at some other promontories, and in the northwest third of the island these benches are lacking, but, in the southeastern third of Amchitka, they are a dominant feature, occurring where there is a bedrock of permeable fine-grained breccia (L. M. Gard, personal communication; Powers et al., 1960). Sand, cobble, or boulder strands, which are mostly associated with stream mouths, occur for short intervals.

Figure 2 is an idealized schematic section through a segment of coast where an intertidal bench is present. The landward margin is commonly a sheer cliff 20 to 30 m (60 to 100 ft) high surmounted by a mantle of tundra. At the foot of the cliff, huge blocks of cliff fragments and isolated sea stacks arise out of a beach of well-rounded gravel or cobbles. These blocks and stack bases as well as the larger boulders and cobbles and sometimes the cliff face itself constitute the substrate for supralittoral fringe populations of *Porphyra, Prasiola, Bangia,* and *Ulothrix*. Midlittoral vegetation begins at the abrupt transition from gravel beach (frequently enriched by great piles of drift algae) to rock bench covered by silt as much as 5 cm (2 in.) thick which is stabilized by several sabellid polychaete species (Fig. 3). In the winter this silt blanket may be eroded away, exposing a rock surface sparsely occupied by the crustose coralline alga, *Clathromorphum circumscriptum*. Frequently this area is lower than the seaward portion of the bench; consequently seawater may cover the rock bench at low tide. This depressed area is referred to as the moat.

The greatest fraction of the littoral region is occupied by the next seaward component, the emergent intertidal rock benchflat (Figs. 1 and 2). The midlittoral vegetation reaches its greatest development here and is readily accessible; most of our research was conducted in this area. The benchflat lies approximately at mean sea level, varying 2 to 3 m (7 to 10 ft) above and below. Powers et al. (1960) report the bench width to be about 15 m (50 ft) on the average, with an occasional segment as wide as 400 m (1300 ft). This bench area is topographically diverse. It may be an extremely flat surface with a pure stand of a single algal species or it may be a surface undulating a meter or more in height and with a diverse vegetation. Cobble-lined channels (Fig. 1), usually connected with the sea even at low tide, may dissect the surface, and local depressions may form tide pools (but tide pools are uncommon along the whole coastline). Both channels and tide pools have a vegetation that is mostly sublittoral in composition. A microtopographical feature of significance is the occurrence of small or large masses of harder rock 5 to 100 cm (2 to 40 in.) in diameter that project above the plane of the softer breccia. Often an isolated clump of *Fucus distichus* on the bench will mark the presence of one of these protruding rocks. The final feature, common but not present on all benches, is an elevated ridge or rampart on the seaward edge of the bench (Fig. 2). The rampart is typically 1 to 2 m (2 to 7 ft) higher than the bench and tends to have an irregular outline with small tide pools in depressions. Within a small distance along its length, a rampart may show a wide range of littoral algal species as well as a sharp difference between species on the exposed seaward face and the protected landward face, the former being the most exposed habitat of the bench region.

*The new genus *Mikamiella* Wynne has been proposed but not validly published (Wynne, 1975).

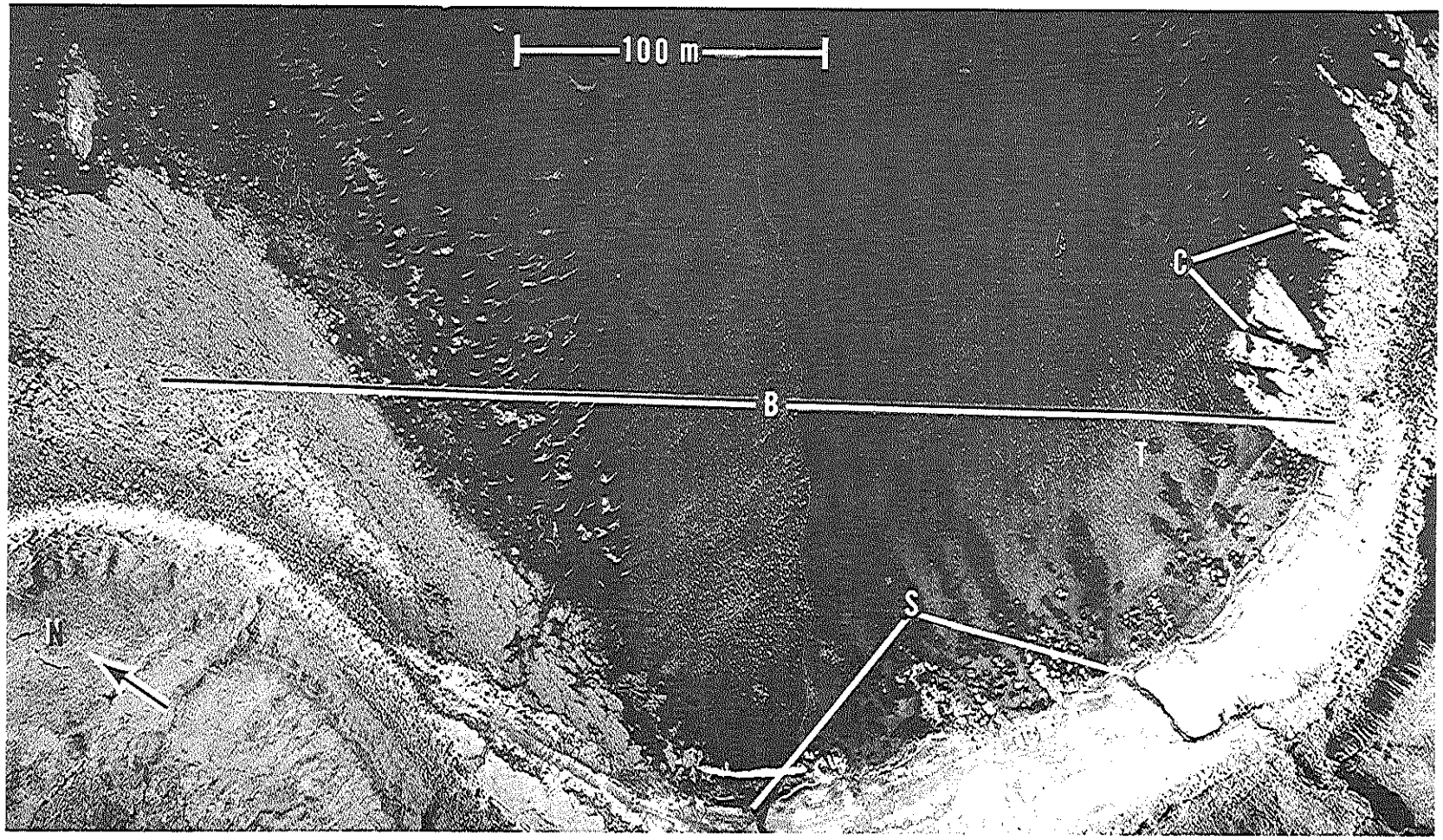

Fig. 1—Aerial photograph of a portion of the Bering Sea coastline studied on July 21, 1971. (Photograph taken on Sept. 2, 1971, by Battelle Memorial Institute).

Table 2—Marine Algae of Amchitka Island, Alaska, as of June 1973

Phylum Chlorophycophyta
- Order Ulotrichales
  - *Enteromorpha* sp.
  - *Monostroma arcticum* Wittrock
  - *Monostroma fuscum* (P. et R.) Wittrock
  - *Ulothrix flacca* (Dillwyn) Thuret
  - *Ulva lactuca* L.
  - *Ulva* sp.
- Order Schizogoniales
  - *Prasiola borealis* Reed
  - *Rosenvingiella* sp.
- Order Cladophorales
  - *Chaetomorpha melagonium* (Weber et Mohr) Kütz.
  - *Cladophora* sp.
  - *Lola lubrica* (S. et G.) A. et G. Hamel
  - *Spongomorpha spinescens* Kütz.
- Order Chlorococcales
  - *Codiolum petrocelidis* Kuckuck
- Order Codiales
  - *Codium ritteri* Setch. et Gardn.
  - *Halicystis* sp.

Phylum Phaeophycophyta
- Order Ectocarpales
  - *Ectocarpus tomentosus* (Hudson) Lyngb.
  - *Pylaiella littoralis* (L.) Kjellman
  - *Ralfsia fungiformis* (Gunnerus) Setch. et Gardn.
- Order Chordariales
  - *Analipus filiformis* (Harvey) Papenf.
  - *Analipus japonicus* (Harv.) Wynne
  - *Chordaria flagelliformis* (Müll.) C. Ag.
  - *Leathesia difformis* (L.) Areschoug
- Order Desmarestiales
  - *Desmarestia intermedia* P. et R.
- Order Dictyosiphonales
  - *Coilodesme bulligera* Stroemfelt
  - *Coilodesme fucicola* (Yendo) Nagai
  - *Dictyosiphon foeniculaceus* (Hudson) Greville
  - *Petalonia fascia* (Lyngb.) Link
  - *Scytosiphon lomentaria* (Lyngb.) Link
  - *Soranthera ulvoidea* P. et R.
- Order Laminariales
  - *Agarum cribrosum* Bory
  - *Alaria crispa* Kjellman
  - *Alaria fistulosa* P. et R.
  - *Alaria praelonga* Kjellman
  - *Alaria pylaii* (Bory) Greville
  - *Cymathere triplicata* (P. et R.) J. Ag.
  - *Fucus distichus* L.
  - *Hedophyllum sessile* (C. Ag.) Setch.
  - *Laminaria dentigera* Kjellman
  - *Laminaria groenlandica* Rosenvinge
  - *Laminaria longipes* Bory
  - *Laminaria yezoensis* Miyabe
  - *Nereocystis luetkeana* (Mert.) P. et R.*
  - *Thalassiophyllum clathrus* (Gmelin) P. et R.

Phylum Rhodophycophyta
- Order Bangiales
  - *Bangia fuscopurpurea* (Dillw.) Lyngb.
  - *Porphyra amplissima* (Kjellman) Setchell et Hus
  - *Porphyra ochotensis* Nagai
  - *Porphyra perforata* J. Ag.
  - *Porphyra pseudolinearis* Ueda
  - *Porphyra purpurea* (Roth) C. Ag.
  - *Porphyra tasa* (Yendo) Ueda
  - *Porphyra umbilicalis* (L.) J. Ag.
  - *Porphyra variegata* (Kjellman) Hus
  - *Porphyra yezoensis* Ueda
  - *Porphyrella gardneri* Smith et Hollenb.
- Order Nemaliales
  - *Pleuroblepharis japonica* (Okam.) Wynne
  - *Rhodochorton purpureum* (Lightfoot) Rosenv.
- Order Cryptonemiales
  - *Bossiella cretacea* (P. et R.) Johansen
  - *Callophyllis flabellulata* Harvey
  - *Cirrulicarpus gmelini* (Grunow) Tokida et Masaki
  - *Clathromorphum circumscriptum* (Stroemf.) Fosl.
  - *Clathromorphum compactum* (Kjellm.) Fosl.
  - *Clathromorphum loculosum* (Kjellm.) Fosl.
  - *Clathromorphum nereostratum* Lebednik
  - *Clathromorphum reclinatum* (Fosl.) Adey
  - *Constantinea rosa-marina* (Gmelin) P. et R.
  - *Corallina pilulifera* P. et R.
  - *Corallina vancouveriensis* Yendo
  - *Dumontia simplex* Cotton
  - *Endocladia muricata* (P. et R.) J. Ag.
  - *Gloiopeltis furcata* (P. et R.) J. Ag.
  - *Halymenia* sp.
  - *Hildenbrandia prototypus* Nardo
  - *Lithophyllum* spp.
  - *Lithothamnium* spp.
  - *Mesophyllum aleuticum* Lebednik
- Order Gigartinales
  - *Ahnfeltia plicata* (Hudson) Fries
  - *Gigartina pacifica* (Kjellman) Tokida
  - *Iridaea cornucopiae* P. et R.
  - *Petrocelis franciscana* S. et G.
  - *Petrocelis middendorffii* (Ruprecht) Kjellman
  - *Platoma* sp.
  - *Rhodoglossum pulchra* (Kützing) Setch. et Gardn.
  - *Turnerella* sp.
- Order Rhodymeniales
  - *Halosaccion glandiforme* (Gmelin) Ruprecht
  - *Rhodymenia palmata* (L.) Greville
- Order Ceramiales
  - *Amplisiphonia pacifica* Hollenberg
  - *Antithamnion floccossum* (Müller) Kleen
  - *Antithamnion shimamuranum* Nagai
  - *Asterocolax hypophyllophila* Wynne
  - *Callithamnion californicum* Gardner
  - *Callithamnion* sp.
  - *Ceramium* sp.
  - *Heterosiphonia* sp.
  - *Hymenena ruthenica* (P. et R.) Zinova
  - *Hypophyllum dentatum* Wynne
  - *Hypophyllum ruprechtianum* Zinova
  - *Laingia aleutica* Wynne
  - *Membranoptera serrata* (P. et R.) Zinova
  - *Membranoptera setchellii* Gardner
  - *Membranoptera spinulosa* (Rupr.) Zinova
  - *Microcladia borealis* Ruprecht
  - *Myriogramme kjellmanianum* Zinova
  - *Nienburgia prolifera* Wynne
  - *Odonthalia floccosa* (Esper) Falkenberg
  - *Pantoneura juergensii* (J. Ag.) Kylin
  - *Phycodrys amchitkensis* Wynne
  - *Phycodrys riggii* (Gardner)
  - *Platythamnion* sp.
  - *Polysiphonia pacifica* Hollenberg
  - *Polysiphonia* sp.
  - *Pterosiphonia gardneri* Hollenberg
  - *Pterosiphonia* sp.
  - *Ptilota asplenioides* (Esper) C. Ag.
  - *Ptilota filicina* (Farlow) J. Ag.
  - *Tokidadendron bullata* (Gardner) Wynne
  - *Yendonia crassifolia* (Rupr.) Kylin
  - *Zinovaea acanthocarpa* Wynne

*This species was found only in drift on beaches and was never found attached to rocks in the Amchitka coastal area.

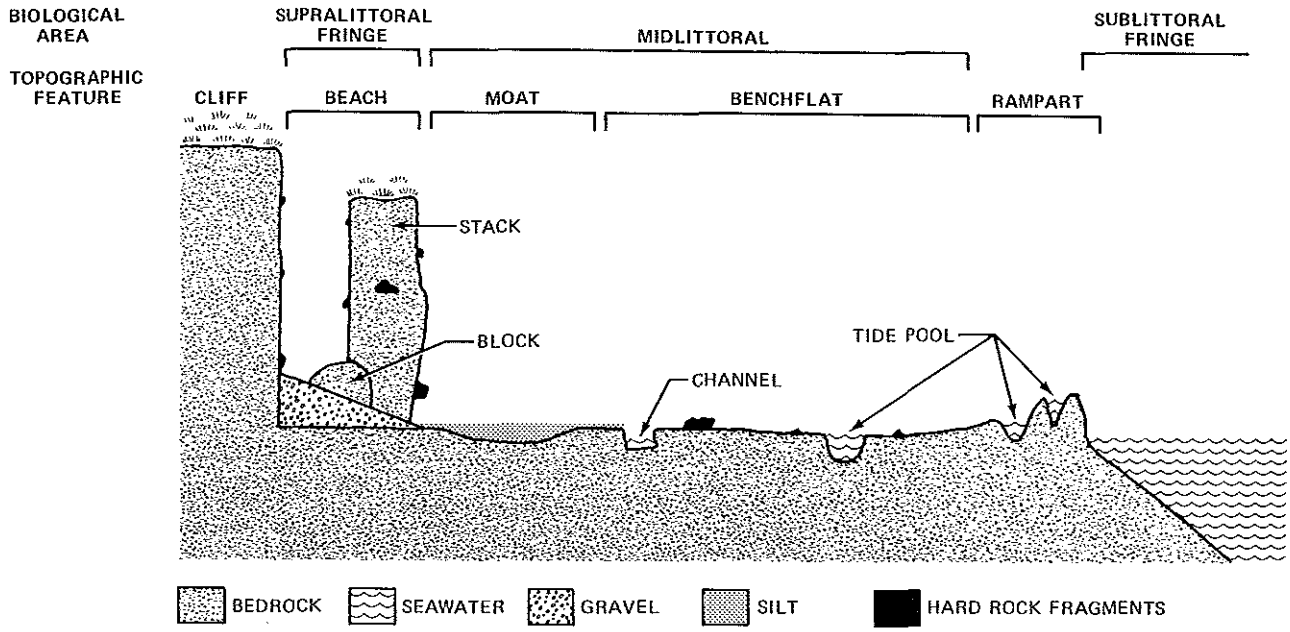

Fig. 2—Schematic diagram of topographic features and biological regions of a typical intertidal bench.

Figure 4 shows schematically the relationship of wave action (exposure*) to the bench configuration. At low tide wave fronts (1) approaching the bench break solely along the seaward face of the rampart (2). As the sea level rises, water flows over the rampart onto the benchflat (3), resulting in currents shoreward across the benchflat and in the channels. Approaching the moat (4), these currents turn and run parallel to the shore, finally emptying into sand troughs on either side of the bench (5). At high tide waves plunge over the then submerged rampart and dissipate most of their energy there. Ordinarily, only unidirectional flow occurs over the benchflat at high tide, and in some localities the moat area appears to be a river of seawater. Only during storms do waves reach and break on the beach or on the cliff itself. Even under these conditions there is little or no plunging action over the benchflat because of the uniformity of water depth. Of all the components of the rock bench, the rampart has the greatest exposure. Tidal phenomena are discussed elsewhere in this book. According to the tide tables, the tides alternate from diurnal in the spring phase to mixed semidiurnal in the neap phase, and the maximum tidal range is just over 2 m (O'Clair, Chap. 18, this volume). The lowest tides occur in June at about 1100 (BST) and in December at about 0100 (National Ocean Survey, 1971). Weinmann (1969) indicated that the low tide on any day may be about 1 hr later than predicted. During our studies at fixed points in the intertidal area, we found that the lowest tide within a spring tide cycle often occurred about 1 to 3 days later than predicted. There are also large irregular deviations from the

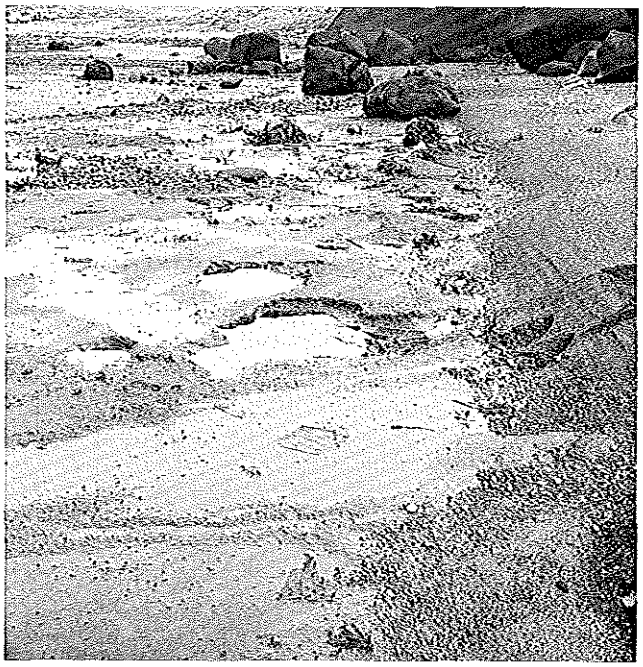

Fig. 3—View of the moat area of an intertidal bench at Duck Cove (IA-1) on Aug. 26, 1973.

*The term exposure as used in this chapter refers to exposure to wave action.

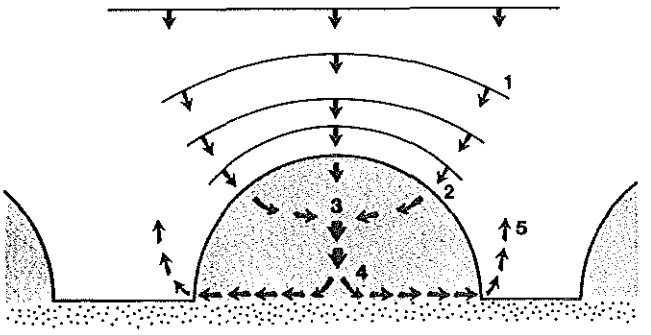

Fig. 4—Schematic diagram of wave exposure in relation to an intertidal bench. (See text for explanation of diagram.) [From P. A. Lebednik, F. C. Weinmann, and R. E. Norris, *BioScience*, 21: 657(1971).]

predicted tides from day to day. We have seen areas completely covered with seawater throughout one day, and the next day they would be uncovered even though the predicted tide heights were identical and there was little wave action. Nearshore currents are generally gentle except at Bird Cape and East Cape.

Armstrong (1971; Chap. 4, this volume) describes the island's climate in detail. We consider here those factors of particular importance to littoral algae. Record high and low temperatures recorded at Amchitka during 1943 through 1948 were +18.3°C and −10.0°C, whereas extreme mean daily high and low temperatures were +10.6°C and −2.2°C, respectively. Perhaps most critical to littoral algae is the occasional coincidence of low tides with temperature extremes. In the comparison of maximum and minimum mean daily temperatures at various times of the year with times of predicted low tides, two such periods appear possible: an air temperature of about +9°C near noon in August coinciding with water at the −61-cm (−2.0-ft) level and an air temperature of −0.3°C near midnight in January above water at the −39.6-cm (−1.3-ft) level. The former is about equivalent to seawater temperatures at that season and would not appear to be critical, but the latter extreme, besides being more than 4° below ambient sea temperatures, is below the freezing point and may represent a critical stress factor for littoral organisms. Indeed, we have seen ice forming on emersed seaweed and surface freezing of pools during nighttime winter low tides.

Desiccation as well as temperature stress may occur in summer months when low tides coincide with clear skies and calm seas. Since clear skies and calm seas are rare at Amchitka (Burgner et al., 1969; Armstrong, 1971; Chap. 4, this volume), these conditions occur infrequently.

Wave exposure depends on local winds and the incoming swell from distant sources. The lowest mean monthly wind speed of 13.8 knots occurs in July. Wind speeds and durations significantly greater than this occur in the fall, blowing from the southwest sector (Armstrong, 1971; Chap. 4, this volume). The Pacific Ocean coast receives swells of a greater wavelength than the Bering Sea coast owing to the greater fetch in that direction, but no data on swell frequency are available. The Bering Sea coast has smaller swells than the Pacific Ocean coast, and heavy wave action is less often observed. In the evaluation of the degree of exposure, caution must be exercised because bench topography strongly influences exposure of the intertidal area.

Seawater conditions are of great importance to sublittoral communities. In the surrounding offshore surface waters, winter conditions are about 3°C temperature and 33 ‰ (parts per thousand) salinity (McAlister, 1971; McAlister and Favorite, Chap. 16, this volume); in summer they are about 6°C temperature and 30 ‰ salinity (Burgner et al., 1968). There is no sharp thermocline at any season above 30-m (100-ft) depth, the limit of our collecting activities. In numerous profiles taken in August 1967, neither salinity nor temperature changed more than one unit from the surface to 114-m (374-ft) depth (Burgner et al., 1968). At the shore seawater temperatures ranged from a minimum of 2°C in winter to a maximum of about 8°C on the Bering Sea coast and 10°C on the Pacific Ocean coast in summer. Thus the annual range of temperature is only 8°C at maximum.

Turbidity of water is an important limiting factor in the determination of the maximum depth of sublittoral algal communities. Although no measurements are available, it can be said that the water surrounding Amchitka Island is one of the least turbid waters in high northern latitudes. It is probably nearly comparable to the extremely clear waters reported for tropical areas. The best indication of water clarity is the depth distribution of the algal communities themselves.

The composition of offshore bottom substrates varies widely around Amchitka. Sand, ledge, gravel, and cobble bottoms, in approximate order of frequency, may be found on either side of the island. In all cases, down to depths reached by scuba diving [about 30 m (100 ft)], these substrates are clean of fine detrital deposits. No true mud bottoms were observed in numerous dives around the island.

LITTORAL ZONATION

Along rocky coastlines the distribution of marine organisms uncovered at low tide is extremely complex and depends on many factors

(Lewis, 1964). A major factor influencing distribution, aside from the tidal regime, is the degree of exposure (opposite of protected or sheltered). In highly exposed areas on the open coast, so-called intertidal marine organisms may extend well above the theoretical upper limits of the tides, indicating that the distribution of these organisms cannot be defined by a single physical factor, such as tidal levels. However, the extensive literature on this subject (see Lewis, 1964, for a review of the literature) indicates that marine organisms on most rocky coastlines of the world are observed in zones or belts (". . . horizontally extensive, biotically distinct . . ." groupings of organisms, Doty, 1957) that are arranged one above the other in a pattern of zonation. Many systems of terminology have been used to describe and classify the zonation of rocky shores. It is generally agreed that the organisms themselves best define the zones, and in this chapter we have adopted the schemes of Stephenson and Stephenson (1949) and Lewis (1964) with slight modification (see Table 3). The littoral region (littoral zone of Lewis) extends from the upper limit of the lichen (*Verrucaria*) zone down to the upper limit of *Laminaria* (*L. longipes* at Amchitka). The sublittoral region (sublittoral zone of Lewis) has as its upper limit the top of the *Laminaria* population, and its lower limit for the algae is defined as the greatest depth at which benthic algae occur. The littoral region is usually divided into an upper supralittoral fringe area (Stephenson and Stephenson, 1949; littoral fringe of Lewis, 1964) and a lower midlittoral area (midlittoral zone of Stephenson and Stephenson, 1949; eulittoral zone of Lewis, 1964).

The boundary between the supralittoral fringe and midlittoral areas is usually defined at the upper limit of barnacles (Stephenson and Stephenson, 1949). Because barnacles are rare at Amchitka and do not form a distinct zone there, we have assigned the boundary between these two areas to the upper limit of *Fucus distichus*. In this chapter no attempt is made to formally subdivide the sublittoral region. For convenience, the portion of the sublittoral region exposed by the lowest tides is referred to as the sublittoral fringe (infralittoral fringe of Stephenson and Stephenson, 1949). In the supralittoral fringe and midlittoral areas, zones of limited vertical extent, each usually dominated by a single species, are observed in a consistent vertical sequence (zonation) over large horizontal distances of coastline. In the midlittoral area, where the greatest number of littoral species and the most complex zonation occur, a further breakdown of zones into *associations* is possible. In this chapter an association refers to an area that is locally dominated by a single species but does not necessarily have horizontal contiguity. Thus, within the *Hedophyllum* zone one can recognize several associations (including the *Hedophyllum* association), each of which is named according to the dominant alga.

It is generally agreed that the application of these terms is often arbitrary and that the implication of discrete zones and associations will not hold up to close examination of littoral communities. Despite these drawbacks, apparently no better system is available at present with which one can compare the general features of littoral zonation of a particular locality with those of another area.

Table 3—Classification Scheme and Approximate Elevations Above Mean Lower Low Water of the Littoral Vegetation of Amchitka Island*

Region	Area	Zone	Association	Elevation, cm
Littoral	Supralittoral fringe	*Prasiola*		185 to 230
		Rhodochorton		125 to 190
		Porphyra–Ulothrix		75 to 140
	Midlittoral	*Fucus*		10 to 80
		Hedophyllum	*Ulva*, *Analipus*, *Corallina*, *Halosaccion*, *Hedophyllum*, *Iridaea*	0 to 15
		Alaria		5 to 15
Sublittoral	Sublittoral fringe	*Laminaria*		0 to –300

*Modified from Weinmann (1969).

The classification of zones and associations as used in this chapter is intended solely as a general framework that we hope will enable the reader to visualize the major features of the marine vegetation at Amchitka.

Methods

Weinmann's objective was to make an initial description of algal distribution in the littoral region (Weinmann, 1969). In March and April 1968, he established one transect at Makarius Bay on the Pacific Ocean coast (T-1) and another at Square Bay on the Bering Sea coast (T-2). Species distributions in the supralittoral fringe were recorded by visual observation and in the midlittoral area and the sublittoral fringe by the removal of adjacent 90- by 20-cm samples of algae along the entire transect line. The abundance of each species was measured by dry-weight analysis of each sample. The abundance of crustose coralline algae was estimated in percent cover values. Associations were studied by placing 35- by 35-cm or 20- by 20-cm quadrats in the vicinity of the transect (but not within the dry-weight samples) and estimating the percent cover with the use of the Braun–Blanquet method (den Hartog, 1959).

The transects established by Weinmann were easily accessible yet sufficiently distant from the planned nuclear test that it was thought possible to use them for two further purposes: (1) To study the seasonal changes in littoral species and (2) as controls for any test effects that might be detected in other areas. For these studies the sample areas could not be disturbed; so a photographic sampling frame (Fig. 5) was designed to sample a 0.25-m^2 quadrat by means of an underwater camera accompanied by a strobe. A photograph and notes for each plot were taken in the field. In the laboratory the 6- by 6-cm color transparencies were viewed with a hand magnifier over a light box with a clear plastic grid, and the percent cover of each species was determined quantitatively. Since it was necessary that the plants remain undisturbed, the composition and percent cover of the understory vegetation could not be determined with this technique.

The plots were originally located by measuring distances from a base-line point, but later, because of the problems in measuring, each plot was marked by nailing polypropylene rope flags into the soft breccia bedrock.

In an attempt to correlate the photographic sampling method with dry-weight values, a third transect (T-3) at Rifle Range Point was sampled in May 1969 with the use of both methods. This transect, which was studied by Lebednik, was not resampled. The sampling dates of all marine algal studies are given in Table 1.

Description of Algal Zones and Associations

The zonation and floristic composition of the littoral region were studied by Weinmann (1969) at Makarius Bay on the Pacific Ocean coast and Square Bay on the Bering Sea coast. The following description is based on his study.

Seven zones, each denoted by the dominant species in it, have been characterized at Amchitka (Table 3). In areas at Amchitka with steep slopes, the general vertical relationship holds, but flat topography tends to blur the distinction between adjacent zones. Horizontally, the upper three zones are discontinuous, depending on the presence of suitable substrate and exposure conditions. Some of these zones are present only at certain seasons of the year.

Only qualitative data were obtained in the supralittoral fringe area. Inconspicuous, but sometimes occupying large areas, each zone of the

Fig. 5—Photographic sampling apparatus used for quantitative intertidal studies.

supralittoral fringe consists of a very few species adapted to the stress conditions of the high littoral environment. Thus only one association can be recognized in each of these zones.

The highest zone is characterized by the macroscopic alga *Prasiola borealis*, a species found throughout the cold waters of the North Pacific. It occurs on the tops of large boulders, the sides of sea stacks, and on high areas of the rampart on rock benches. A luxuriant green carpet of this species may be conspicuous on promontories where sea birds alight and provide a habitat rich in nutrients. In places maritime lichens and small nearly invisible blue-green algae may occur with this species.

Rhodochorton purpureum, the species characterizing the next lower zone, occurs only in shaded or semishaded areas. This habitat preference limits its distribution to sea cliffs that are exposed at least intermittently to salt spray. Typically, this species can be found in caves or below overhanging rock on vertical faces, such as at Rifle Range Point, but occasionally it may be found in the open, especially where suitable conditions occur with a north or east aspect. The vertical distribution of the species begins about 40 cm (16 in.) above, and may extend to as much as 340 cm (134 in.) above, the highest local *Fucus distichus* plants. An undetermined species of *Cladophora* sometimes occupies as much as 25% of the area in the *Rhodochorton* zone, and *Ulothrix flacca* occurs sparsely in the lower portion of the zone. This zone seems to occur more frequently along the Bering Sea coastline than on the Pacific Ocean coastline, a fact that may be attributed to the north aspect or to the less-well-developed benches and consequent increase in exposure on that side of the island.

Immediately below the *Rhodochorton* zone in elevation but much more widespread is the *Porphyra–Ulothrix* zone. Species of these genera are dominant components of the vegetation on the boulder shores that are common on the Bering Sea coast (Fig. 6) as well as at high cliff, stack, and rampart locations. *Bangia fuscopurpurea* occurs sporadically in this zone. The *Porphyra* species usually have their lower limit somewhat above the *Fucus* zone, leaving a band sparsely occupied by *Ulothrix flacca*. All but one of the *Porphyra* species (probably *P. pseudolinearis*) occur only in this zone. *P. pseudolinearis*, a species that attains lengths of 50 to 80 cm (20 to 31 in.), is commonly found on cobbles in the moat area of rock benches as well as in the upper portion of the *Fucus* zone.

The upper limit of the midlittoral region is defined as the upper limit at which *Fucus distichus* is found. At Amchitka its preferred habitat is on the top of boulders in the beach or moat areas and in the lower zones on harder portions of the rock that project from the benchflat (Fig. 7). The *Fucus* zone occupies a vertical range of about 70 cm (28 in.). There are distinctly more species recorded in this zone than in the *Porphyra–Ulothrix* zone next above it (Fig. 8). *Pylaiella littoralis*, an epiphyte, is commonly found on mature *F. distichus* plants around the island. As Table 4 indicates, several species that occur in and characterize associations at lower levels also occur within the *Fucus* zone, but they rarely form associations at this level. Only *Iridaea cornucopiae*, *Ulva lactuca*, and *Gigartina pacifica* occur with a percent constancy greater than 50%.

The second zone-characterizing canopy species of the midlittoral region is *Hedophyllum sessile*. This is the major zone occurring on the benchflat area. *H. sessile* does not appear to be adapted to exposed conditions. Its preferred habitat is on the very flat benches at the appropriate level where it may reach biomass values of 12.2 kg/m^2 wet weight. On benchflats with a rolling topography, it occurs in depressions with little standing water (Fig. 9). The Amchitka plants have blades that lack bullation, but they have a large, continuous, more or less bowl-shaped morphology. In exposed areas, especially on the Bering Sea coast and on vertical ledges, there may be no *Hedophyllum* between the *Fucus* and the lower lying *Alaria* or *Laminaria* zones. In these situations the understory associations are conspicuous. The *Hedophyllum* zone has the greatest number of species of all the intertidal zones (Fig. 8).

Six associations can be recognized within the *Hedophyllum* zone (Table 4): *Ulva*, *Analipus*, *Corallina*, *Halosaccion*, *Hedophyllum*, and *Iridaea*.

Fig. 6—*Porphyra–Ulothrix* zone on the Bering Sea coast, July 20, 1971.

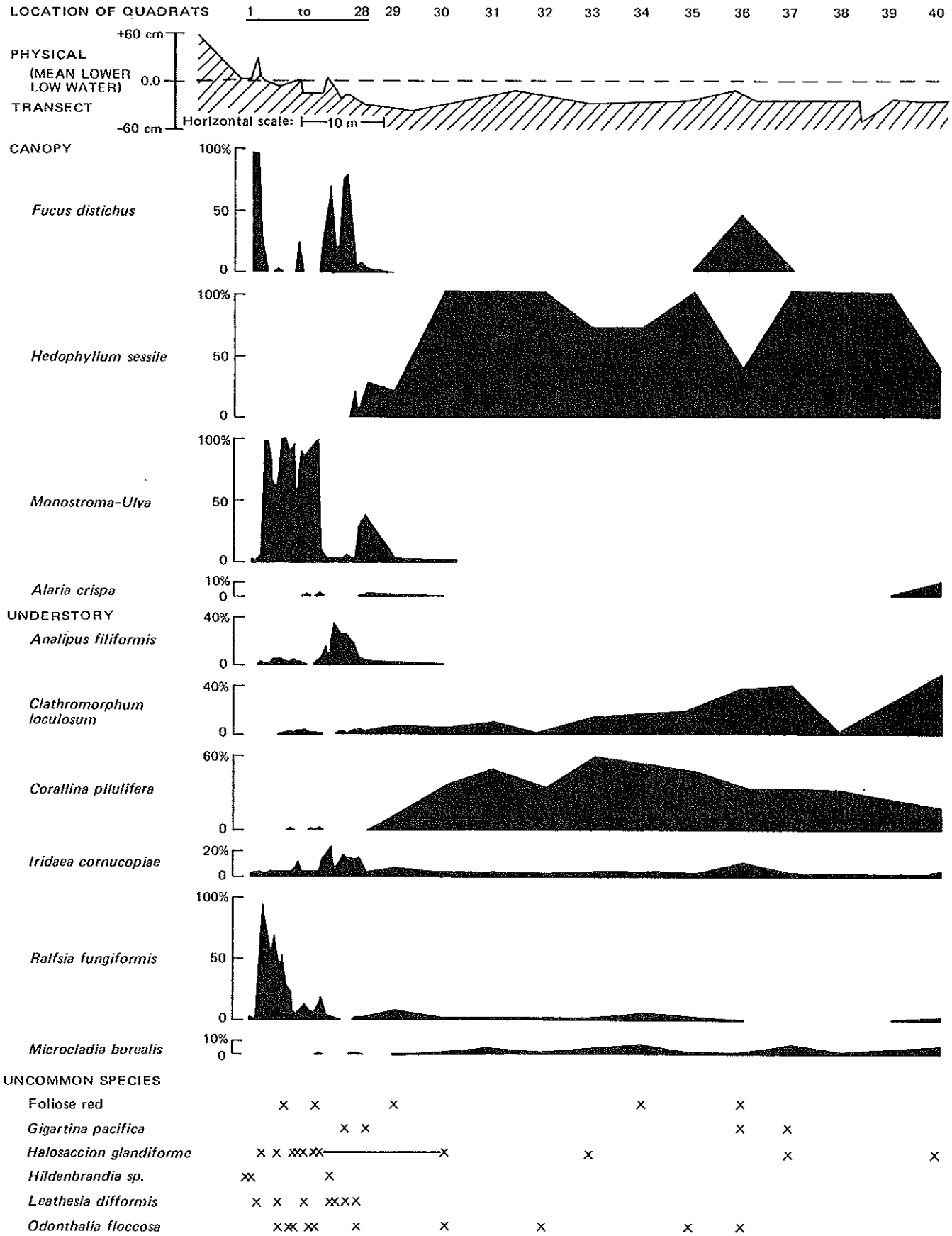

Fig. 7—Species composition and percent cover at the T-3 transect.

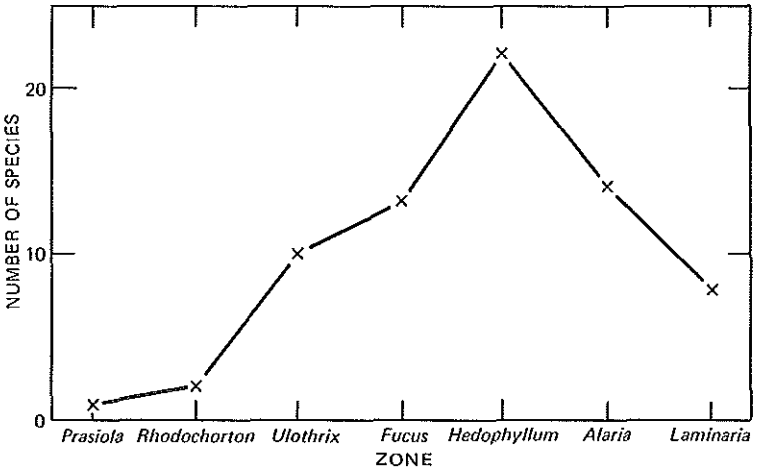

Fig. 8—Number of algal species (excluding blue-green and unicellular species) reported within the major algal zones at Amchitka.

Fig. 9—Shoreward *Hedophyllum* zone in Makarius Bay. Plot 2 of the T-1 transect is located on top of the boulder in the rear.

The *Analipus* association usually occurs on boulders just below the *Fucus* zone and never extends out far along the benchflat. Most of the year it is recognizable only as an extensive holdfast system, but in May the upright fertile fronds make this species more noticeable (Wynne, 1971). *Ulva lactuca, Iridaea cornucopiae,* and *Halosaccion glandiforme* are commonly associated species.

Corallina pilulifera commonly occurs over the benchflat from below the *Fucus* zone to the outer portion of the benchflat but forms an association (together with *Clathromorphum loculosum* and *C. circumscriptum*) only on extremely flat areas on the bench. Except for *Clathromorphum loculosum* and *C. circumscriptum,* only *Halosaccion glandiforme* occurs in this association with a percent constancy greater than 50%.

Halosaccion glandiforme is one of the most conspicuous of the association-characterizing species. It occurs in all the associations of the

Table 4—Percent Constancy Values of Algal Species in Littoral Algal Zones and Associations of Amchitka*

Zone:	*Fucus*	*Hedophyllum*						*Alaria*	*Laminaria*
Association		*Ulva*	*Analipus*	*Corallina pilulifera*	*Halosaccion glandiforme*	*Hedophyllum*	*Iridaea*		
Species									
Ahnfeltia plicata		10						14	
Alaria crispa				20		10		100	8
Analipus filiformis	10		100		40		50		
Bossiella cretacea									8
Coilodesme bulligera		40							
Corallina pilulifera	30	10	11	100	50	100	20		
Corallina vancouveriensis								86	67
Cladophora sp.							10		
Fucus distichus	100		22		30		10		
Gigartina pacifica	60	10		20	30	10	20	28	
Halosaccion glandiforme	40	20	56	50	100	30	100	28	
Halymenia	10	20				40	10		
Hedophyllum sessile					20	100	40	14	
Hildenbrandia	20								
Iridaea cornucopiae	70	50	56	40	80	70	100	71	
Laminaria longipes				20		20		43	100
Microcladia borealis		20		10	40	20	20		
Odonthalia floccosa	10	50				20		43	
Petrocelis middendorffii	20		11		20		20	14	
Ptilota asplenioides									17
Ptilota filicina				10		20		43	50
Ralfsia fungiformis	20	10	22	10		20	10	43	
Rhodymenia palmata			11		40	10			
Tokidadendron bullata						20		14	8
Ulva sp.	50	100	89		60	30	50		
Encrusting corallines	30	40	11	60	20	80	30	86	100
Total No. species in each association		12	10	10	12	16	14		
Total No. species in each zone	13				22			14	8

*From Weinmann (1969).

midlittoral zones and has an average percent constancy of 53%. The most important of the associated genera are *Corallina, Iridaea,* and *Ulva.*

The *Hedophyllum* association has the greatest number of species (16) in it, but outside its association *H. sessile* occurs only in the *Halosaccion* and *Iridaea* associations of the *Hedophyllum* zone, and in no case does it occur with greater than 40% constancy. *Halosaccion glandiforme* is often associated with *Hedophyllum*, and encrusting coralline algae and *Iridaea* also occur frequently in this association. The *Hedophyllum* association occurs over a small vertical range (Weinmann, 1969), but, since this frequently coincides with the level of the benchflat, it covers extensive areas (Fig. 7).

Iridaea cornucopiae is the most frequent species throughout all the associations of the intertidal region (average percent constancy of 67%), and the *Iridaea* association is second only to the *Hedophyllum* association in the number of species present in it (14). Since this species is dark or frequently black and since it grows low against the rock, *I. cornucopiae* is not nearly as conspicuous as *H. glandiforme,* yet it occurs with a greater abundance overall.

The *Ulva* association is found primarily in the upper part of the *Hedophyllum* zone. Weinmann (1969) found *U. lactuca* common during May through September in shallow tide pools just below the *Fucus* zone. Scattered plants of *U. lactuca* can be found in any part of the benchflat at most times of the year, but the species appears to be most abundant in the moat area (Burgner et al., 1969; 1971) (Figs. 3 and 7). The species most commonly found with *U. lactuca* in this association are *I. cornucopiae* and *Odonthalia floccosa.*

The Pacific coast intertidal benches of Amchitka demonstrate that some of these species, given appropriate conditions, can form nearly pure stands on particular benchflats. Figure 7 shows an abundance profile for a transect at Rifle Range Point indicating extensive dominance by *H. sessile. Corallina pilulifera* also sometimes occupies extensive benchflat areas nearly to the exclusion of all other algal species.

The presence of a distinct *Alaria* zone along the Bering Sea coast may be correlated with the lack of *Hedophyllum.* When *Alaria crispa* and *Hedophyllum sessile* occur together, *A. crispa* generally occupies the more seaward portion but may grade slowly into the *Hedophyllum* zone. The association analysis (Table 4) shows that *A. crispa* occurs in insignificant frequencies in other associations, but a high number of species (14) occur in association with it. *A. crispa* was not present on the Pacific coast transect in 1968 (Weinmann, 1969), but we found this species there from 1969 to our final visit in 1973.

On the outer face of the rampart, plants of various *Alaria* species form an association in the most exposed area of the bench (Fig. 10). Morphologically these plants differ from those of the benchflat in that they have tufts of thick linear sporophylls; from each tuft protrudes a short ragged main lamina, the whole being reminiscent of small *Postelsia palmaeformis* plants seen in similar habitats along the west coast of North America. These plants frequently have their upper limit above that of the *Fucus distichus* plants on the landward portion of the bench.

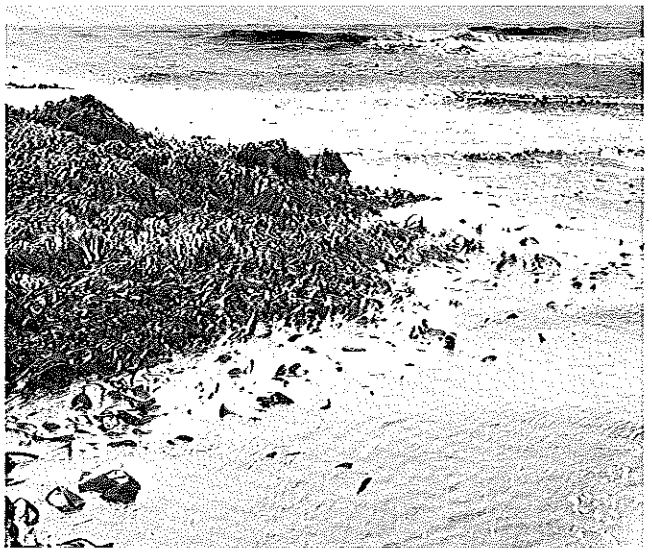

Fig. 10—Rampart area of an intertidal bench at Rifle Range Point dominated by *Alaria* sp.

The lowest zone of the intertidal area is that characterized by *Laminaria longipes.* This sublittoral fringe species occupies large areas of rock down to −3 or −5 m (−10 or −15 ft), thus constituting a transition species between the littoral and sublittoral regions. Most of the species associated with this zone are sublittoral species at the upper limit of their ranges, and the number of species found in this zone (8) is fewer than that in the three previous zones. Regardless of exposure or bench topography, *L. longipes* appears to be fairly consistent in occupying ledges from about mean lower low water downward. Unlike all the other canopy-forming kelps at Amchitka, which form a single stipe from a limited holdfast, *L. longipes* grows by means of a prostrate branching stipe that produces numerous upright stipes and blades (Markham, 1972).

Sublittoral fringe vegetation is found in channels (Fig. 1) cutting through the bench and in deep tide pools (which are rare) on the bench. In one sense much of the benchflat could be considered a tide pool since at low tide seawater stands up to a few centimeters deep in many undrained depressions. However, only littoral species are present in these shallow depressions. The rare deep tide pools have an abundance of *Thalassiophyllum clathrus, Ptilota* spp., *Cymathere triplicata,* and other sublittoral species in them. *L. longipes* is only occasionally seen in tide pools.

Tatewaki and Kobayashi (1934) recognized three associations (apparently comparable to our zones) in the littoral belt of the Aleutian Islands: (1) *Alaria–Hedophyllum–Laminaria,* (2) *Halosaccion glandiforme,* and (3) *Fucus evanescens.* The first association includes our *Laminaria longipes* and *Hedophyllum sessile* zones. The recognition of a separate *H. glandiforme* zone probably resulted from the fact that their observations were made only in the summer when this species is most conspicuous.

When the distributions of the major littoral species are plotted against distance on the benchflat perpendicular to the shoreline (Figs. 7 and 11), the distribution of the zones is not strictly correlated with elevation. This result is surprising because the primary control over the distribution of intertidal organisms is usually thought to be exerted by some tidal factor or factors (Doty, 1946). No biological interactions, such as herbivory, can account for the particular case at hand. Our explanation is that bench topography and offshore kelp beds modify wave action so that there is a gradient of exposure across the intertidal benches which gives an effect similar to that of protected versus exposed coastlines but on a much

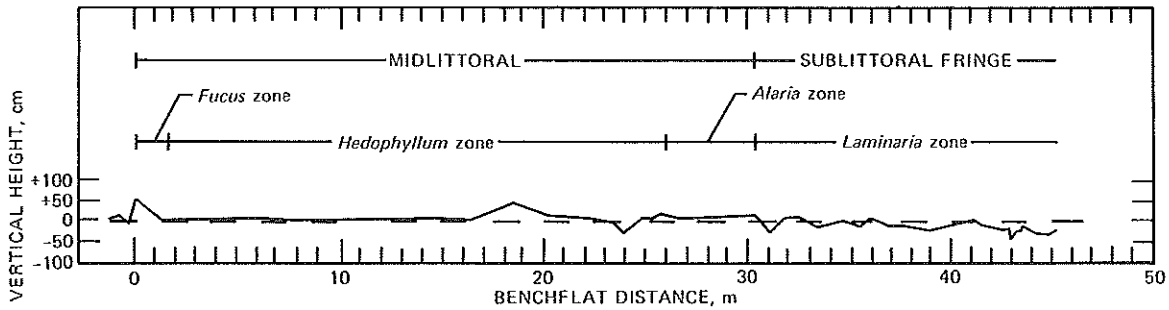

Fig. 11—Schematic diagram of the major zones on the Square Bay transect (T-2).

smaller scale (Weinmann, 1969; Lebednik et al., 1971). This is perhaps the most unusual feature of the littoral flora at Amchitka.

Seasonal and Annual Variation

The only observations of seasonal variation of species in the supralittoral fringe are the comments of Weinmann (1969) that *Ulothrix flacca* and *Porphyra pseudolinearis* reached a peak of abundance in March and April. Only a few *Porphyra* plants could be seen in May, and by August–September the zone was nearly absent.

A preliminary account of seasonal variation in the midlittoral area was given by Lebednik et al. (1971). The following data are from a more complete study in which frequencies of the major species occurring in the midlittoral and sublittoral fringe areas from February 1972 to August 1973 were recorded. These data are shown in Tables 5 and 6.

As shown in the tables, the frequency of *Fucus distichus* changed little on the T-1 transect, but an increase was seen in late summer 1972 on T-2. Data from one plot of the T-2 transect show that cover values of *Fucus distichus* remained high throughout the year, but they had a tendency to peak in June–August. This is shown more graphically in tracings of *Fucus distichus* plants from photographs of a plot on the T-1 transect from February 1972 to August 1973 (Fig. 12). *Fucus* sporelings probably settled on the hard rock fragment (indicated by the dashed line in A) in the summer of 1971. During 1972 significant growth occurred, increasing the percent cover from 3.1% in February to 28.1% by October. Surprisingly, significant growth occurred during the winter so that by April 1973 cover had increased to 49.3%, although the growth in winter was certainly smaller than that in summer. Also, the receptacles (stippled in Fig. 12) were more conspicuous and more developed in late summer than in winter. The final value of 73.6% cover measured in August 1973 probably represented the maximum development of these plants.

At Amchitka *Hedophyllum sessile* develops very large entire blades without bullation or longitudinal splitting, and most plants persist from year to year. Widdowson (1965) concluded that bullation is primarily caused by exposure to sunlight and splitting is due to exposure. The lack of bullation or longitudinal splitting at Amchitka is consistent with his hypothesis. Clear skies are rarely present (see sky cover in Armstrong, Chap. 4, this volume), and *H. sessile* appears to be restricted to relatively protected localities on Amchitka. Colorless marginal zones were observed on *H. sessile* plants in February, becoming most evident in April of each year; presumably this represented the time of spore release in these plants. The frequency of *H. sessile* was constant at T-1 but started to increase in April 1973 on T-2. Overall, the abundance of *H. sessile* appeared to remain constant, but cover probably increased slightly owing to growth in summer.

Analipus spp. holdfasts are present year round, but upright fertile (spore-bearing) fronds are produced in May (Weinmann, 1969; Wynne, 1971). We believe that the apparent summer decrease in frequency of occurrence of this species, as shown in Tables 5 and 6, does not reflect an actual decrease in population but is due to the covering of plants by summer growth of canopy species.

Corallina pilulifera exhibited some late winter–early spring die-off on T-1 but none on T-2. Some of the variations in frequency of *C. pilulifera* were due to the occasional covering of some plants by nearby kelp fronds.

Halosaccion glandiforme and *Porphyra* spp. are annuals and show the most conspicuous seasonal changes in abundance of all littoral species. Nevertheless, frequencies of *H. glandiforme* were fairly constant at T-1 and T-2 (Tables 5 and 6). The percent cover values of *H. glandiforme* for five plots at T-2 are given in Fig. 13. This species showed a peak in cover in August and a minimum

Table 5—Frequency of Occurrence of Common Species in 18 0.25-m^2 Plots at T-1 from February 1972 Through August 1973

Species	Feb. 1972	April 1972	June 1972	Aug. 1972	Oct. 1972	Apr. 1973	Aug. 1973
Alaria crispa	6	7	7	6	6	9	6
Analipus filiformis	3	3		1		2	
Clathromorphum circumscriptum	1	2		1	1	1	1
Corallina pilulifera (live)	4	4	3	3	4	4	4
Corallina pilulifera (dead)	1	3	1			1	
Fucus distichus	4	5	4	5	5	5	5
Halosaccion glandiforme	5	5	5	5	5	5	5
Hedophyllum sessile	12	11	12	13	12	12	13
Iridaea cornucopiae	6	5	4	5	5	5	5
Laminaria longipes	4	4	3	3	5	5	5
Ulva sp.	3	4	3	2	5	5	3

Table 6—Frequency of Occurrence of Common Species in 24 0.24-m^2 Plots at T-2 from February 1972 Through August 1973

Species	Feb. 1972	April 1972	June 1972	Aug. 1972	Oct. 1972	Apr. 1973	Aug. 1973
Alaria crispa	10	11	9	10	11	16	15
Analipus filiformis	1	3				2	1
Clathromorphum circumscriptum (live)	7	6	7	3	8	6	6
Clathromorphum circumscriptum (dead)	2	4	3	3	5	1	1
Corallina pilulifera (live)	5	5	4	1	4	5	3
Fucus distichus	3	4	5	7	7	6	6
Halosaccion glandiforme	4	8	7	7	8	7	7
Hedophyllum sessile	3	2	3	4	3	5	6
Iridaea cornucopiae	9	9	8	8	8	8	8
Laminaria longipes	7	6	6*	6	7	6	4
Ulva sp.	7	6	4	8	7	9	8

*Dead plants were found with a frequency of 4 in this sample.

in winter, probably February–March. In agreement with Weinmann (1969), we observed that the increase in cover was due to the growth of new upright thalli in early summer, although a few plants survived for two summers.

Iridaea cornucopiae has a perennial crustose base that produces upright blades each year in early spring. The frequency of this species (Tables 5 and 6) was remarkably constant throughout the year. Figure 14 shows that the cover of the species (based on the upright blades because the crusts are impossible to distinguish in the photographs) peaked in early summer and declined thereafter as the blades became fertile and disintegrated in the process of releasing spores.

Ulva lactuca showed a great deal of irregularity in its frequency of occurrence. This is a species characteristic of the moat area of the benchflat, an area of annual deposition and removal of silt. This factor contributes to a strong seasonal variation in cover.

Another species common in moat areas, *Clathromorphum circumscriptum*, also shows a great deal of variability in frequency of occurrence. This species is a slow-growing crustose coralline alga, and seasonal variability in cover would not be expected. However, the percent cover on four plots at T-2 showed definite seasonal variation and die-off (Fig. 15). This undoubtedly resulted from the removal of silt by storms and uncovering of plants in winter and buildup of silt and burying of plants in summer. As shown by the peak in dead cover in Fig. 18, some summer mortality occurred in the population, but some plants survived and continued growing the following winter.

Alaria crispa sporelings appear in the spring, and growth continues throughout the summer. A slight increase in frequency was seen in the spring of 1972. An even greater increase in frequency was recorded in the spring of 1973, when *A. crispa* was also exceptionally abundant in other midlittoral areas we visited. This was the only instance we recognized of a definite annual variation in this species' abundance at Amchitka. Because *Alaria* plants are strap-shaped, attached at one end and usually much larger than a 0.25-m^2 quadrat,

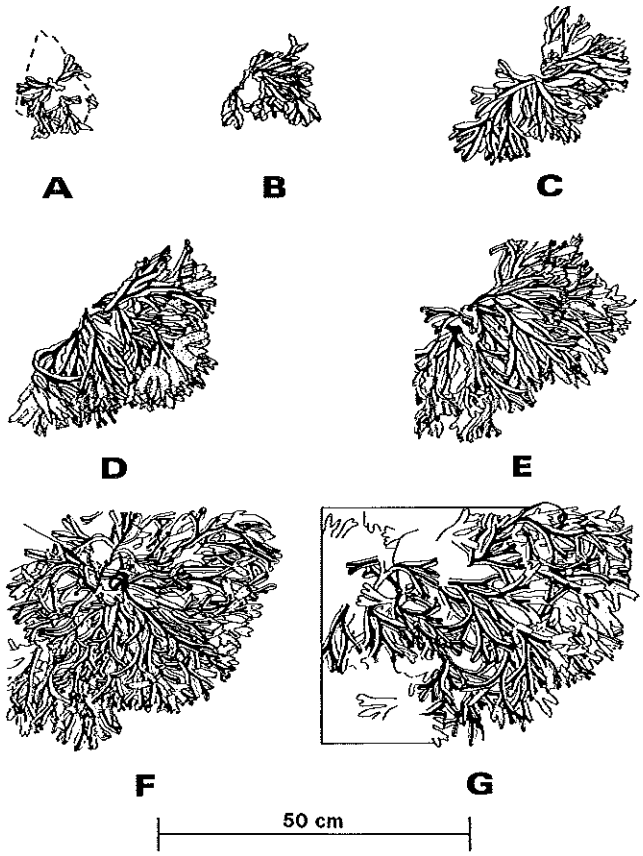

Fig. 12—Growth and reproduction of *Fucus distichus* plants on plot 7 of the T-1 (Makarius Bay) transect. A, Feb. 22, 1972; B, Apr. 15, 1972; C, June 10, 1972; D, Aug. 20, 1972; E, Oct. 22, 1972; F, Apr. 5, 1973; G, Aug. 25, 1973. Stippled portions are receptacles; the dashed line in "A" indicates the outline of a hard volcanic rock fragment on which the plants were growing.

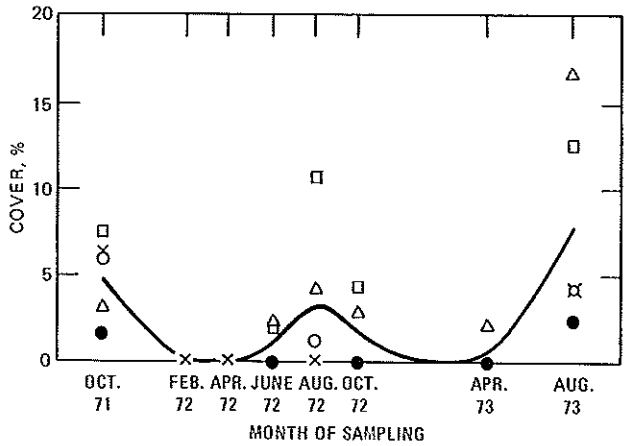

Fig. 13—Percent cover of *Halosaccion glandiforme* on the T-2 transect from October 1971 to August 1973. ●, plot 3. X, plot 4. ○, plot 8. □, plot 9. △, plot 11. Species cover too small to measure accurately is assigned a value of 0.1%.

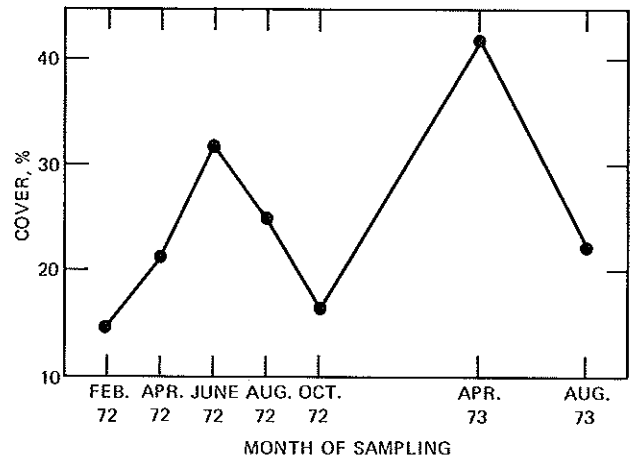

Fig. 14—Percent cover of *Iridaea cornucopiae* on plot 3, T-1 transect, from February 1972 to August 1973.

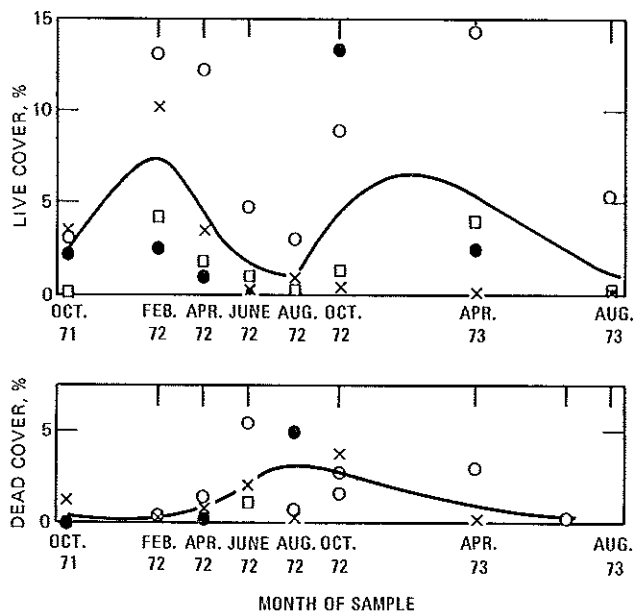

Fig. 15—Percent cover of live and dead *Clathromorphum circumscriptum* on the T-2 transect from October 1971 to August 1973. ●, plot 2. X, plot 3. ○, plot 4. □, plot 9. Species cover too small to measure accurately is assigned a value of 0.1%.

abundance data from the transects are poor measures of growth and recruitment.

Generally *Laminaria longipes* exhibits no seasonal change in its populations. There were occasional dead patches, sometimes over a meter in diameter, within otherwise healthy areas of the species (Fig. 16). This phenomenon caused a decline in frequency on T-2 as seen in 1973, although visual observations indicated that in the zone as a whole die-off was more extensive in June 1972 (J. Isakson, personal communication). The

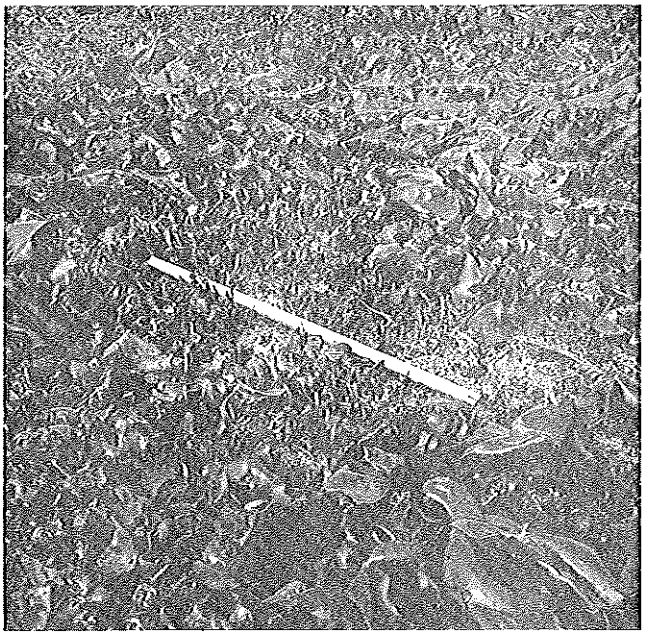

Fig. 16—Dead patches of *Laminaria longipes* at Duck Cove near IA-1, Aug. 26, 1973 (meter stick in one patch).

Fig. 17—Reproductive *Laminaria longipes* on plot 22 of the T-2 transect, April 1972. The photograph is of a 0.5- by 0.5-m (1½- by 1½-ft) area. Reproductive areas that have released spores are conspicuous as white margins on blades.

release of zoospores results in marginal linear colorless patches on the fronds (Fig. 17), which are most conspicuous in April each year. This reproductive process is apparently not related to the mortality mentioned because in the later case holdfasts, stipes, and meristematic areas degenerate and the blades are lost completely.

Comparison with Other Regions

There are many inherent problems in the comparison of studies of zonation from different parts of the North Pacific Ocean with our studies at Amchitka. Aside from any real differences that may exist, different application of vegetation terms may be found in different countries and even between workers within one country. Misidentification of species or other taxonomic problems may strongly influence the apparent similarities or differences between two studies (particularly in the older literature where recent taxonomic changes might make comparison with present species names very misleading). Finally, one must ask how representative of an entire geographic region a particular study is. These problems can be reduced somewhat by concentrating on species that are conspicuously and consistently dominant either as a zone or as an association, are easily identified, and/or are known to be characteristic of particular environmental conditions.

Kardakova-Prezhentsova (1938) made a detailed study of the littoral region of the Commander Islands. She found a zonation pattern very similar, if not identical, to that at Amchitka. The supralittoral zone was characterized by *Urospora penicilliformis, Bangia fuscopurpurea, Porphyra* sp. (all winter species), and *Prasiola borealis*. The principal species of the upper littoral zone (comparable to the midlittoral *Fucus* zone at Amchitka) were *Fucus distichus* (as *F. evanescens**), *Gloiopeltis furcata, Monostroma grevillei,* and *Analipus japonicus.*† The occurrence in this zone of *Chordaria flagelliformis*, an arctic species, suggests a slightly colder environment than at Amchitka. The medium littoral zone of Kardakova-Prezhentsova is equivalent to both the *Hedophyllum* and *Alaria* zones at Amchitka. This difference probably reflects a matter of opinion rather than a significant difference in zonation because *Alaria* is seasonal and does not form a zone everywhere at Amchitka. The major species of the medium littoral zone at the Commander Islands were *Alaria lanceolata, Hedophyllum sessile* [as *H. subsessile*, see Widdowson (1965)], *Rhodomela larix*, and *Fucus distichus*. The lower littoral zone at the Commander Islands (comparable to the sublittoral fringe *Laminaria* zone at Amchitka) was dominated by *Laminaria longipes, L. dentigera, Thalassiophyllum*

**Fucus evanescens* is now recognized as a subspecies of *F. distichus* (Powell, 1957).

†For synonyms used in the literature (*Chordaria abietina* and *Heterochordaria abietina*), see Wynne (1971).

clathrus, Codium adherens (probably *Codium ritteri*), and *Pterosiphonia bipinnata*. Except for the absence of the *Halosaccion glandiforme* and *Iridaea cornucopiae* associations, the preceding description of zonation at the Commander Islands agrees very well with the results of our studies at Amchitka.

Spasskiĭ (1961) reported on the littoral zonation of southeastern Kamchatka. In the supralittoral region, two "horizons" were distinguished: (1) An upper first horizon of *Rhodochorton purpureum* and *Bangia fuscopurpurea* and (2) a lower second horizon of *Rhizoclonium riparium*. These horizons are probably comparable to the *Rhodochorton* and *Porphyra–Ulothrix* zones, respectively, of the supralittoral fringe at Amchitka. Spasskiĭ recognized three horizons in the littoral region which were, from top to bottom: (1) *Gloiopeltis coliformis*, (2) *Analipus japonicus, Chordaria flagelliformis*, and (3) *Corallina* and various Rhodophyceae and Laminariales. *Fucus distichus, Porphyra perforata, Ulva lactuca, Laminaria longipes*, and three species of *Alaria* were also present in the littoral region but were apparently not sufficiently abundant to establish zones or associations. The geographical distribution of *Hedophyllum sessile* does not extend beyond the Commander Islands (Kardakova-Prezhentsova, 1938; Widdowson, 1965).

The littoral zonation of the Kurile Islands was studied by Nagai (1940; 1941). In the northern Kurile Islands, he recognized a cold-water flora that he named the "upper boreal district." Within this district three formations were recognized in the littoral vegetation: (1) An upper *Fucus distichus* formation (including *Halosaccion saccatum, Ulva fenestrata, Porphyra* spp., *Iridaea cornucopiae, Ulothrix pseudoflacca, Analipus japonicus*, and *Corallina pilulifera*), (2) a lower *Alaria angustata* formation, and (3) a *Laminaria longipes* formation. Thus it would appear that the zonation of littoral algae in the Kurile Islands is more similar to that of the Commander and Aleutian Islands than that of the southeastern coast of Kamchatka. Only the midlittoral *Hedophyllum* zone was not observed in the Kurile Islands.

Considerably less affinity in littoral zonation is seen on the east coast of Hokkaido. The main "belts" recognized by Taniguti (1962) were, from top to bottom: *Porphyra pseudocrassa, Pelvetia wrightii, Fucus distichus*, and *Laminaria longipedalis*. In exposed localities *Pelvetia* and *Fucus* were replaced by *Analipus japonicus* and *Iridaea cornucopiae* (as *Iridophycus*). *Corallina pilulifera* was also present. The presence of a distinctly southern element, *Sargassum*, signals a transition to a warmer water flora elsewhere on Hokkaido.

The littoral zonation of Sakhalin Island in the Okhotsk Sea was recently studied by Vozzhinskaya (1964b). On the southern coasts of the island, the supralittoral area was dominated by *Gloiopeltis capillaris*, which was often associated with *Porphyra* sp. and *Urospora* sp. The littoral region was characterized by three horizons (comparable to the midlittoral zones of Amchitka), which were, from top to bottom: (1) *Analipus japonicus*, (2) *Corallina pilulifera* and *Iridaea cornucopiae* (*Fucus* in protected localities), and (3) *Chordaria magellanica* and *Laminaria japonica*. The occurrence of *Sargassum* on the southern coasts once again indicates a transition to a warmer water flora.

From the comparison of the above studies with our study of Amchitka, one can conclude that the littoral zonation of the Commander Islands is nearly identical with that of Amchitka. The vegetation of the Kurile Islands is generally similar, but that of southeastern Kamchatka is less similar. Finally, the islands of Hokkaido and Sakhalin bridge the transition to a distinctly warmer water flora.

Practically no studies have been made of littoral zonation in the northern Bering Sea, which precludes a review of the arctic affinities of the Amchitka flora.

Along the west coast of North America, surprisingly few descriptive studies of littoral zonation have been done. Rigg and Miller (1949) reported on studies of littoral zonation at Neah Bay, on the Strait of Juan de Fuca. They distinguished seven zones in the littoral region, which were, from top to bottom: (1) *Ralfsia–Prasiola*, (2) *Endocladia–Gigartina*, (3) *Postelsia*, (4) *Halosaccion glandiforme*, (5) *Alaria*, (6) *Lessoniopsis*, and (7) *Laminaria andersonii*. The first zone occurred in their "splash zone" (comparable to the supralittoral fringe area of Amchitka). The second zone straddled the splash zone and the "upper intertidal zone," the latter including zones 3 and 4 (comparable to the *Fucus* and *Hedophyllum* zones of Amchitka). The "lower intertidal zone" of Rigg and Miller included zones 5 and 6, and zone 7 was classified the "demersal zone." Zones 6 and 7 appear to be comparable to the *Laminaria longipes* zone at Amchitka. Both *Fucus distichus* and *Hedophyllum sessile* occurred in abundance in the more protected areas studied by Rigg and Miller.

The above review indicates the variation of classification schemes as used by different workers in various parts of the North Pacific Ocean. The presence or absence of the large kelp species in the midlittoral area appears to have the greatest influence on littoral zonation schemes adopted by various authors. In contrast, the supralittoral fringe area can be recognized in most localities by the

presence of characteristic genera (*Prasiola, Porphyra, Ulothrix,* and *Bangia*) of wide geographical distribution and with a strong seasonal difference in abundance. The sublittoral fringe area is characterized in exposed localities by a dominance of kelps with massive holdfasts and strap-shaped blades.

According to some authors (Taniguti, 1962; Vozzhinskaya, 1964b) *Fucus* occurs in abundance only in relatively protected areas. The same distribution appears to characterize *Hedophyllum sessile* (Rigg and Miller, 1949). The morphology of *Hedophyllum* plants at Amchitka (smooth entire blades) also indicates a relatively protected environment (see Widdowson, 1965). These facts correlate with the idea presented above that the rock-bench topography provides an exposure gradient so that zonation of an exposed type is observed on the promontories and outer bench areas, whereas a more protected zonation pattern, including extensive *Hedophyllum* and *Fucus* zones and a diverse flora, characterizes the benchflat area.

COLONIZATION STUDIES

Denudation experiments and studies of subsequent colonization have been suggested as a means of understanding the factors influencing the zonation of littoral algae (Chapman, 1943). Such studies have been conducted in Hawaii (Neal, 1930), California (Northcraft, 1948), Washington (Dayton, 1971), England (Kitching, 1937; Rees, 1940), South Africa (Bokenham, 1938), and elsewhere. No such experiments had been performed in the Aleutian Islands prior to our studies. Starting in 1971 Palmisano (1975) conducted denudation experiments at Amchitka to delineate these factors and to aid in predicting the effects of nuclear testing on littoral algal communities. In these experiments either the entire community or the canopy only was removed from permanently marked plots, and the subsequent colonization was recorded.

Methods

So that differences in colonization due to exposure could be accounted for, plots were established at sheltered (Makarius Bay), intermediate (Duck Cove), and exposed (Rifle Range Pt.) areas. These plots were completely independent of the T-1, T-2, and T-3 transects. Local differences in colonization in the midlittoral area were studied by establishing plots in pure stands (associations) of the following species: *Alaria crispa, Hedophyllum sessile, Corallina vancouveriensis,* and *Halosaccion glandiforme*. In the sublittoral fringe area, plots were established in the *Laminaria longipes* association. Not all associations were sampled at each locality (see Table 7). Seasonal differences were studied by clearing plots in some areas at nearly bimonthly intervals from March 1971 to December 1972 and in April 1973 (see Table 1). Two types of manipulation (each on separate plots) were used: (1) Total denudation of rock surface by the removal of all organisms and (2) removal of the canopy species only by selective cutting of stipes.

For a study of colonization on newly denuded rock, 1-m^2 areas of *L. longipes, A. crispa,* and *Hedophyllum sessile* and 0.25-m^2 areas of *Corallina vancouveriensis* and *Halosaccion glandiforme* were cleared with a shovel, putty knife, and wire brush. Each area was burned twice with a 1 : 1

Table 7—Summarized Descriptions of Plots Established for Denudation and Canopy-Removal Studies at Amchitka from March 1971 to April 1973

Species	Number of plots	Zone	Location	Manipulation
Laminaria longipes	22*	*Laminaria*	Makarius Bay	Rock denuded
Laminaria longipes	16*	*Laminaria*	Makarius Bay	Canopy removal
Hedophyllum sessile	18*	*Hedophyllum*	Makarius Bay	Rock denuded
Halosaccion glandiforme	16†	*Hedophyllum*	Makarius Bay	Rock denuded
Corallina vancouveriensis	14†	*Alaria*	Rifle Range Point	Rock denuded
Alaria crispa	18*	*Alaria*	Duck Cove	Rock denuded
Alaria crispa	12*	*Alaria*	Duck Cove	Canopy removal
Hedophyllum sessile	16*	*Hedophyllum*	Duck Cove	Canopy removal
Hedophyllum sessile	4*	*Hedophyllum*	Makarius Bay	Canopy removal
Corallina vancouveriensis	18†	*Alaria*	Duck Cove	Rock denuded

*1-m^2 plots (1 by 1 m).
†0.25-m^2 plots (0.5 by 0.5 m).

mixture of fuel oil and white (unleaded) gasoline. For an evaluation of the effects of canopy removal on colonization, the blades and stipes of *L. longipes, A. crispa,* and *Hedophyllum sessile* were removed with a wire cutter in 1-m^2 areas (Table 7).

All plants and animals were removed from a 50-cm(20-in.)-wide strip around each plot to minimize physical disturbance from adjacent algae during surge at high tide and from grazing by benthic invertebrate herbivores (sea urchins, limpets, and chitons). One disturbed plot and one undisturbed control plot were established for each study area.

So that study areas could be located and identified, one corner of each was marked with a 0.3-m length of cord secured with a concrete nail and a numbered washer. Each 1-m^2 area was divided into four contiguous 0.25-m^2 plots that were delineated with concrete nails and identified with a numbered piece of survey flagging. Each 0.25-m^2 area was further marked by an additional concrete nail and numbered washer placed in the corner diagonally away from the cord.

Data were collected from all study areas (experimentally disturbed and control plots) at nearly bimonthly intervals from March 1971 to December 1972, in April 1973, and in August 1973. At each time each 0.25-m^2 plot was photographed during low tide, and species composition and percent cover were determined for algae on that plot. The photographic sampling frame described in the section Littoral Zonation was used, but the photographs were taken with a 35-mm camera.

Results and Discussion

The sequence of algal species observed on denuded rock benches at Amchitka was (1) diatoms and filamentous brown and green algae; (2) ulvoids, i.e., small leafy green algae (*Ulva lactuca* and *Monostroma* spp.); and (3) macrophytic red and brown algae (*Iridaea cornucopiae, Halosaccion glandiforme, Hedophyllum sessile, Alaria crispa, Fucus distichus, Corallina vancouveriensis, Laminaria longipes*, etc.) (see Table 8). Succession observed in areas where the canopy was removed was similar to that indicated earlier, but the rate was faster (Table 9), primarily because they received a lower level of experimental disturbance. In the canopy-removal studies, only *Laminaria* exhibited vegetative growth from its holdfasts, a site of meristematic tissue in this kelp. *Alaria* and *Hedophyllum* plants did not regenerate because their meristematic region occurs in their blades. *Hedophyllum* settled in all areas where the canopy was removed, but *Alaria* settled only in the *Laminaria* zone. For *Alaria* to settle, bare substratum, which was more plentiful in the *Laminaria* zone than in the *Hedophyllum* zone or its own, is required.

Others have noted similar successional patterns (Wilson, 1925; Bokenham, 1938; Northcraft, 1948; Southward, 1956; Dayton, 1971). Bokenham, Northcraft, and Dayton have described various groups of colonizing algae. In general, these are (1) pioneer species (diatoms); (2) fast-growing annuals (ulvoids and *Halosaccion*); (3) fast-growing perennials (*Hedophyllum* and *Alaria*); (4) slow-growing perennials (*Laminaria* and *Corallina*); (5) canopy-producing species, i.e., those which are most successful in competition for light (*Hedophyllum* and *Laminaria*); (6) obligatory understory species, i.e., those which require a canopy to survive or are more often subtidal (coralline algae); and (7) fugitive species, i.e., those which exist in disturbed areas or on the fringes of communities

Table 8—Optimum Algal Colonization Schedule Observed on Denuded Rock Surfaces at Amchitka Island, Alaska, from March 1971 to August 1973

Alga	Season of settlement	Optimum clearing time for rapid recolonization	Period of time before alga is observed	Time to attain at least 75% coverage
Diatoms*	All	All	Within 1 month	1 month
Ulvoids*	All	All	2 to 4 months	2 to 4 months
*Iridaea**	Fall and winter	Summer and fall	2 to 4 months	†
Halosaccion	Summer and fall	Fall	4 months	6 months
Hedophyllum	Spring and summer	Fall and winter	4 to 6 months	1 year
Alaria	Winter	Summer and fall	4 to 6 months	4 to 6 months
*Fucus**	Summer and fall	Spring and summer	6 to 8 months	14 to 16 months
Corallina	Spring and summer‡	Fall and winter‡	6 to 8 months‡	†
Laminaria	Fall and winter‡	Winter‡	8 to 10 months‡	†

*Settlement did not occur in its own zone.
†Cover never exceeded 18% (see Table 10).
‡Little information is available.

Table 9—Optimum Algal Colonization Schedule Observed in Canopy-Removal Areas at Amchitka Island, Alaska, from March 1971 to August 1973

Alga	Season of settlement	Optimum clearing time for rapid colonization	Period of time before alga is observed	Time to attain at least 75% coverage
Diatoms*	All	All	Within 1 month	†
Ulvoids*	All	All	2 months	2 to 4 months
*Iridaea**	All	All	2 months	†
*Halosaccion**	Spring, summer, and fall	Spring, summer, and fall	1 month	†
Hedophyllum	Spring, summer, and fall	Summer, fall, and winter	2 to 4 months	11 months
*Alaria**	Fall and winter	Summer and fall	2 to 4 months	10 to 12 months
*Fucus**	Summer, fall, and winter	Spring, summer, and fall	4 to 6 months	†
Corallina	‡	‡	‡	†
Laminaria	Fall and winter §	Fall and winter §	2 months §	7 to 9 months §

*Settlement did not occur in its own zone.
†Cover never exceeded 62% (see Table 11).
‡Little information is available.
§Colonization was by vegetative growth.

(*Porphyra* and ulvoids). This last category, suggested by Dayton (1971), is so broadly defined that it could include diatoms, ulvoids, *Halosaccion*, or even *Alaria* at Amchitka.

Most algae that colonized disturbed study areas at Amchitka settled in broader vertical expanses and in more diverse exposures than they normally occupy (Tables 10 and 11). At the indicated exposures to wave action and heights above sea level, the following algae were the most abundant: Diatoms, in all exposures and at all levels; ulvoids, in all areas except those most exposed to wave action; *Halosaccion*, at higher levels in areas of little or intermediate exposure; *Hedophyllum*, in protected areas at lower and intermediate levels; *Alaria*, at lower levels and in exposed areas; *Laminaria*, at lower levels at all exposures; and *Corallina*, in exposed areas at intermediate and lower levels. In general, initial settlement rate was faster in exposed areas at lower levels than in protected areas at higher levels.

Diatoms and ulvoids settled on denuded rock surfaces during all seasons. Their year-round reproductive ability enabled them to occur whenever space was available. All other algae settled on denuded rock during specified seasons (Table 8) when their spores were available. In areas where the canopy was removed, settlement of most species occurred almost throughout the entire year (Table 9). Again this was correlated with the low level of experimental disturbance.

Diatoms persisted for 1 to 8 months after settling, and ulvoids persisted for 5 to 15 months after replacing the diatoms. Peak densities of the ulvoids occurred in summer on areas disturbed in winter.

Species whose stands were denuded started to colonize their original areas immediately after diatoms and ulvoids disappeared, but only if the area was cleared just before the season when their spores were released and settled, which was inferred from the subsequent appearance of sporelings (see Table 8 for the optimum time period). If a species was cleared too early or too late relative to the time its propagules settled, then any species whose propagules were settling when the diatoms and ulvoids disappeared occupied the area. Thus a *Hedophyllum* plot cleared in December (early winter) was replaced by *Hedophyllum*, and a *Halosaccion* plot cleared then recovered to *Halosaccion*. However, a *Laminaria* plot cleared in the fall contained *Alaria* by spring, and a *Halosaccion* plot cleared in spring contained *Fucus* the following year.

Three of the five species whose stands were denuded and two of the three whose canopies were removed persisted and increased their percent cover when they settled in their own zones. The areas that did not contain at least 80% of the original algal species at the end of our study in April 1973 were the *Laminaria* and *Corallina* denuded areas and the *Alaria* canopy-removal areas. A low reproductive potential may have been responsible for the sparse settling of *Laminaria longipes*. Laboratory experiments (Markham, 1972) indicated little sexual reproduction by this kelp. At Amchitka colonization by *L. longipes* occurred primarily by vegetative growth. As stated

above, the lack of bare substratum probably prevented settlement of *Alaria* in areas where the canopy was removed. *Alaria* and *Hedophyllum* did invade other areas, especially the *Laminaria* plots, and large percent cover values were recorded for these species at the end of the study. Algae that settled outside their normal area will not persist there indefinitely, but it is not known how long it will take the original climax vegetation to establish itself.

Causes of Intertidal Zonation

The results of the colonization studies can now be related to the physical and biological features of the Amchitka environment and can be used to understand the dynamic aspects of the present littoral zonation. Competitive success may be influenced by physical features of the habitat and by biological interactions. Some of the physical stresses typical of littoral communities appear to be relatively ameliorated at Amchitka.

For example, low temperatures, with little seasonal fluctuation, high humidity, and low levels of direct insolation, provide favorable conditions for desiccation-sensitive littoral algae. Other physical stresses, i.e., wave shock and abrasion, also appear to be reduced, as shown by the abundance of species characteristic of protected environments. This protection is due to a reduction in wave action caused by the sheltering effect of offshore kelp beds and by the topography of the intertidal rock benches. Herbivory, an important biological factor in littoral communities, is reduced owing to the reduction of the major herbivores by intensive sea otter predation (Palmisano and Estes, Chap. 22, this volume). The relatively low levels of physical and biological stresses result in a relatively simple system in which the important interactions are probably confined to direct competition for space among algal colonizers.

Each of the species studied in the denudation experiments is a dominant in the Amchitka littoral region and comprises either a zone or an associa-

Table 10—Maximum Percent Cover Attained at Any Time by Intertidal Algae in Five Different Denuded Rock Study Areas at Amchitka Island, Alaska, from March 1971 to August 1973

	Percent cover in denuded rock areas					
					Corallina	
Algae	*Laminaria* at Makarius Bay	*Alaria* at Duck Cove	*Hedophyllum* at Makarius Bay	*Halosaccion* at Makarius Bay	at Rifle Range Point	at Duck Cove
Diatoms	100	100	100	100	100	90
Ulva lactuca	100	100	100	100	20	82
Iridaea cornucopiae	18	T*	12	11		T
Halosaccion glandiforme	29	13	66	100†	5	95
Hedophyllum sessile	100	58	100			
Alaria crispa	98	100	90	T	100	25
Fucus distichus	89	27	6	75		1
Corallina vancouveriensis	T		T		10	1
Laminaria longipes	3		T			
Filamentous brown	10	100			85	90
Filamentous green	22	79			T	70
Spongomorpha sp.	T		T	T	30	41
Gigartina pacifica	T		T			T
Porphyra spp.	18	T	58	T	5	14
Rhodymenia palmata	36	T	7	11	90	90
Microcladia borealis			T			T
Tokidadendron bullata	T		T		T	
Dumontia simplex	25	8				T
Foliose red‡	35	11	4		2	
Crustose coralline	T	T	T		T	T
Analipus spp.	9	2		T		T
Scytosiphon lomentaria		13	T	T		T
Leathesia difformis			T			
Petalonia fascia	70		8			7
Cymathere triplicata§	11					

*T, trace, <1%.
†Circled values indicate the dominant species prior to denudation.
‡Unidentified red alga.
§Upper sublittoral alga.

Table 11—Maximum Percent Cover Attained at Any Time by Intertidal Algae in Three Different Canopy-Removal Study Areas at Amchitka Island, Alaska, from March 1971 to August 1973

Algae	Percent cover in canopy-removal area		
	Laminaria at Makarius Bay	*Hedophyllum* at Duck Cove	*Alaria* at Duck Cove
Diatoms	14	56	
Ulva lactuca	78	55	79
Iridaea cornucopiae	5	49	13
Halosaccion glandiforme	39	62	2
Hedophyllum sessile	100	100*	36
Alaria crispa	100	3	T†
Fucus distichus	T	35	T
Corallina pilulifera	2	5	5
Laminaria longipes‡	80		
Filamentous brown	T		
Spongomorpha sp.		T	
Gigartina pacifica	T	T	T
Porphyra spp.	1	T	2
Odonthalia floccosa		T	
Rhodymenia palmata	9	1	T
Microcladia borealis		35	T
Tokidadendron bullata	T	1	
Dumontia simplex		14	4
Foliose red§	7	14	14
Crustose coralline	5	9	
Analipus spp.		T	T
Scytosiphon lomentaria			T
Leathesia difformis			T
Cymathere triplicata¶	T		

*Circled values indicate the dominant species prior to denudation.
†T, trace, <1%.
‡Vegetative growth.
§Unidentified red alga.
¶Upper sublittoral alga.

tion. The attributes of these species, which may give them a competitive advantage, can now be considered in view of the results of the colonization studies.

Laminaria species, principally *L. longipes*, characterize a zone in the sublittoral fringe area. A secure holdfast system, round stipes, and long narrow blades may allow them to occupy more exposed areas, but their apparent inability to withstand desiccation probably restricts them to this region of extensive spray. Their dense canopy excludes most other algae except crustose coralline algae from occupying their zone as understory species. The colonization experiments indicate that, when disturbed, *Laminaria longipes* is slow to return unless holdfasts remain from which vegetative growth can take place.

Alaria species, principally *A. crispa*, characterize the next higher zone. Their disk-like firmly attached holdfasts and long flat stipes and blades probably enable them to occupy exposed areas, but the flatness of these blades and stipes may not withstand wave exposure as well as the round stipes and thin blades of *Laminaria* spp. *Alaria* spp. normally occur in areas of slowly receding tides and where there is wave splash. They settle during winter (a season when few species settle) and grow rapidly, both of which characteristics appear to be competitively advantageous. *Alaria*'s dense canopy (and possibly the whiplash effect of their blades) may also help in the competition for space.

Corallina species, particularly *C. pilulifera*, occur throughout the *Hedophyllum* zone, at times in sufficient density to characterize an association within that zone. Their small size and secure holdfasts make them usually an understory species. Their environmental tolerance is apparently quite wide, but they are slow to return when disturbed.

Hedophyllum sessile is a canopy species of sufficient dominance to characterize an association and a zone of its own, the zone that covers most of the middle intertidal bench (Figs. 7 and 11). A weak holdfast, the lack of a stipe, and a large inflexible blade probably exclude *H. sessile* from

the exposed outer edge of the bench but are likely not disadvantageous on the protected middle regions. The colonization experiments indicate that it is a vigorous competitor that quickly recovers from disturbance.

Halosaccion glandiforme is an understory species of the middle bench. Its ability to retain seawater in its thallus during low tide possibly helps it to tolerate desiccation and to occur at high intertidal levels. It may be helped in competition for space by the fact that its spores settle at all times of the year except winter.

Iridaea cornucopiae also characterizes an association within the *Hedophyllum* zone. A perennial alga, it outcompetes *H. glandiforme* (an annual) at higher levels by permanently occupying space and presumably prevents *H. glandiforme* spores from surviving. *I. cornucopiae* occurs in slight depressions that tend to accumulate silt, and thus this tolerance to silt may enable it to outcompete other algae in this area.

The ulvoids, *Ulva lactuca* and *Monostroma* spp., are abundant probably as a result of their spores being available and settling year round.

Fucus distichus characterizes the highest of the midlittoral zones. It not only withstands desiccation well but also it may actually require it. Johnson et al. (1974) showed that *F. distichus* reaches maximum photosynthesis after some degree of drying. It may be absent from lower zones because of increased exposure there (Southward, 1956) and because it requires high light intensities (Gail, 1918) that would be absent under the kelp canopies of lower zones.

Not all species of littoral algae at Amchitka occur in distinct vertical zones. Some species occur in seemingly random places on the intertidal bench or outside their normal location. This suggests the existence of favorable microhabitats or of naturally occurring disturbances that permit their temporary presence.

SUBLITTORAL COMMUNITIES

As emphasized by Wynne (1970a), the statement by Ruprecht (1851, p. 97) that coasts of the Bering Sea are depauperate of algae is "grossly inaccurate." Nowhere is this more evident than in the sublittoral communities. Powers et al. (1960) commented that the floating kelp beds are dense enough to impede transit of small boats. These beds are formed by a single species, *Alaria fistulosa* (Fig. 18). This is the largest species in the genus and is distributed from the southern Kurile Islands to southeast Alaska (Widdowson, 1971a). At Amchitka we saw plants with blades over a meter

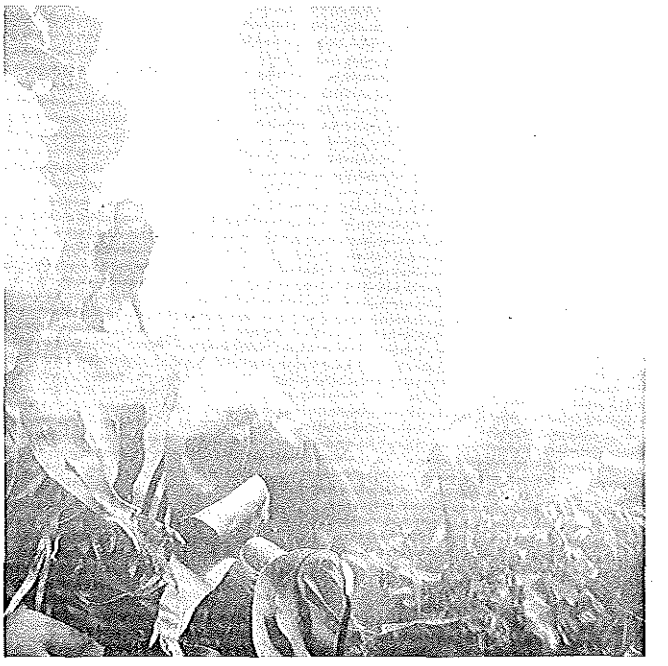

Fig. 18—Underwater photograph of the kelp bed at −10 m (−33 ft) near Kirilof Point on Apr. 23, 1972. A dense lower canopy of *Laminaria groenlandica* (broad blades, lower foreground) and a few plants of *Alaria fistulosa* floating toward the surface (upper background) are visible.

in width. We made no measurements of the length of plants owing to collection problems, but we observed that the densest beds occur in water of 5- to 15-m (16- to 46-ft) depth, where by late summer blades of plants often are over 10 m (33 ft) long along the surface. The reports of total blade lengths up to 25 m (82 ft) (Setchell and Gardner, 1903) should be considered minimum for large plants in late summer. At the lowest tides of the year, a few of the shallowest *A. fistulosa* plants may be emersed on seaward-sloping rock benches not dominated by other kelps, but it cannot be considered an intertidal species. The deepest plants were observed at about 20-m (66-ft) water depth. On the shallow Pacific coast, beds may be seen several kilometers offshore. These beds have a great damping effect on waves. In moderate seas, there is usually only gentle surging on a coast behind these beds. This is probably a major reason for the relatively protected aspect of the littoral communities at Amchitka.

As seen at the surface, *A. fistulosa* beds are small in winter, but by late summer they reach a peak of density, and much of the nearshore area is covered. This change results from the growth of individual plants, at least some of which persist through the winter. It is also brought about by an increase in population size in the spring. Since we

did not conduct a tagging study, the longevity and population turnover of these plants were not determined. Most of the population may be annual with few plants remaining throughout the winter; however, winter storms may break off the floating fronds but leave the holdfasts intact to produce new blades the following spring. Other species of *Alaria* are perennial and have a peak of summer growth (Widdowson, 1971a).

Specimens of *Nereocystis luetkeana*, the well-known floating kelp of the West Coast of the United States, are commonly found drifted onto the beaches of Amchitka and a few have been found tangled in offshore kelp beds, but no attached *Nereocystis* plants have been observed at Amchitka. The same situation occurs in the Commander Islands (Kardakova-Prezhentsova, 1938). These plants must drift along the Alaska Stream current from the westernmost point of its known distribution, Unalaska Island (Druehl, 1970), or from points still farther east.*

Beginning with the *Laminaria longipes* population on the intertidal bench and extending down to about 20-m (66-ft) depth, there is a continuous cover of the solid-rock bottom by various kelp species (Fig. 19). In some areas *L. longipes* extends in beds down to about 3-m (10-ft) depth. In other areas and extending down to depths of 10 m (33 ft) or more, *L. dentigera, L. groenlandica, L. yezoensis, Alaria* sp., and *Thalassiophyllum clathrus* make up the dense kelp canopy. *Cymathere triplicata* is present on boulders in shallow water, and *Agarum cribrosum* occurs with increasing frequency until it dominates the solid-rock substrate at about 20-m (66-ft) depth.

The morphology of some of these kelps, with long 50- to 100-cm (20- to 40-in.) stipes, allows for a dense understory of a rich red algal flora (Weinmann, 1969). Notable among the species are *Ptilota asplenioides, P. filicina, Hypophyllum ruprechtianum, Cirrulicarpus gmelini,* and *Constantinea rosa-marina.*

Finally, the very lowest of the floral elements is that of the crustose species, particularly *Codium ritteri, Lithothamnium* spp., *Mesophyllum aleuticum*, and *Clathromorphum* spp. This element begins at the lower edge of the *Laminaria longipes* beds and extends far below the kelp cover to well over 30 m (98 ft). At these depths, the limit of our scuba diving effort, *Clathromorphum nereostratum* dominated the bottom, and its lower limit has not been ascertained.

Observations of marine algal populations in sublittoral plots at 5- and 9-m (16- and 30-ft) depths 9 months after selective removal of the dominant kelps indicated that strong competitive interactions influence algal distributions in these populations (Dayton, 1975). Predation by sea otters on algal herbivores has been suggested as the major reason for the dense algal populations in the Amchitka sublittoral region. Dayton concluded that the larger *Laminaria* species are competitive dominants and that *Alaria fistulosa* behaves as a fugitive species. He suggested that the removal of *Laminaria* spp. by wave shock in shallow areas and selective grazing by sea urchins in deep areas explain the general distribution of kelp species in sublittoral communities at Amchitka (see Palmisano and Estes, Chap. 22, this volume).

Fig. 19—Underwater photograph of the shallow kelp bed at −1 to −2 m (−3 to −7 ft) near Kirilof Point on Apr. 23, 1972. *Laminaria longipes* (upper) and *Thalassiophyllum clathrus* (lower right) are dominant. The broad blade in the center is probably *Laminaria yezoensis.*

PHYTOGEOGRAPHY AND FLORISTICS

Lebednik et al. (1971) examined the geographical distributions of the marine algae identified from Amchitka up to 1970. Each species was classified into one or more of the following groups: endemic; western North Pacific; eastern North Pacific; and Arctic—Atlantic. The percentages of the total number of species within each group are shown in Table 12, which indicates that the Amchitka flora has strong affinities to the three major surrounding regions. Whether the "endemic"

*However, E. S. Zinova (1940) stated that *Nereocystis* plants were found attached in the Commander Islands.

Table 12—Floristic Affinities of the Amchitka Marine Algal Flora Expressed as Percentages of the Total Number of Amchitka Species (69) Reported from Surrounding Regions*

Percent	Region
22.8	Atlantic–Arctic coasts
49.3	Western North Pacific coasts
39.2	Eastern North Pacific coasts
10.1	Endemic to Bering Sea islands (including Aleutians)

*Based on species identified as of 1970 (some species occur in two or three regions).

species are truly limited in distribution or are not known elsewhere because of lack of comparable collections, especially in the sublittoral region, cannot be deduced at this time.

Wynne (1972) found that three of the nine species of *Porphyra* found on Amchitka have a circumboreal distribution. The other *Porphyra* species showed affinities both to the Japanese flora and to the American flora, in agreement with the overall distributions reported by Lebednik et al. (1971). We have not attempted to reexamine the overall floral affinities of the Amchitka marine algae using the expanded list of 117 species now known from the island (see Table 2) because of the difficulty of assessing the identifications in the older literature and of the application of recent taxonomic changes to wide geographical areas. Many algal groups have not received critical taxonomic attention. There is a great need for systematic studies that include collections from the Asiatic and North American coasts as well as from the Aleutian Islands. Following these studies it will be possible to make more definitive statements concerning the floristic affinities of the Amchitka flora.

Wynne (1970a) showed that the development at Amchitka of the Delesseriaceae, order Ceramiales, is diverse. Of the 16 species recognized from Amchitka, 6 were newly described* and 1 was placed in a new genus, *Zinovaea*. Wynne (1970b) also described another new genus, *Pleuroblepharis*, in the family Bonnemaisoneaceae, order Nemaliales.

The taxonomy and distributions of the coralline genera *Clathromorphum* and *Mesophyllum* were examined by Lebednik (1973). Of the species occurring at Amchitka, *C. circumscriptum* and *C. compactum* occur in the North Pacific Ocean northward from Hokkaido, Japan (Adey, Masaki, and Akioka, 1976), and Baranof Island, Alaska. Both extend into the Arctic and North Atlantic Oceans. *Clathromorphum loculosum* is known only from the northern Bering Sea, Commander and Aleutian Islands, and southward to Baranof Island, Alaska. The epiphyte *C. reclinatum* occurs widely in the North Pacific Ocean, from Hokkaido and Sakhalin in the west to southern California in the east. Two new species were described from Amchitka: (1) *C. nereostratum*, a massive plant covering large areas of the Amchitka sublittoral region, and (2) *Mesophyllum aleuticum*, one of two species in the genus to be found at Amchitka (the second species is not yet named and is still under study). *C. nereostratum* is known from the Aleutian and Kurile Islands, and *M. aleuticum* has been collected at the Alaska Peninsula as well as in the Aleutians. It was concluded that the center of distribution of *Clathromorphum* (which was based on concentration of number of species) is in the Aleutian Islands. These initial taxonomic studies suggest that, when the Amchitka collections of other groups of marine algae are studied in detail, more new species and genera are likely to be described.

EFFECTS OF UNDERGROUND TESTING ON MARINE ALGAE

The Milrow and Cannikin tests affected littoral communities principally by permanently uplifting coastal areas. The mortality and subsequent recovery of littoral vegetation were studied in these disturbed areas.

Methods

The effects of the Milrow test were studied by 0.25-m^2 quadrats straddling a fault line at Duck Cove on the Pacific Ocean coast (IA-1). The effects of the Cannikin test were studied by placing 51 plots (8 of the original 40 were destroyed and 11 were established after the test) in the major species associations in two areas (IA-2 and IA-3) on the Bering Sea coast. All these plots were permanently marked and photographically sampled as described earlier for T-1 and T-2. In addition, 15.4 km (10 miles) of Bering Sea coast, centered approximately at IA-2, was surveyed by visual observation at low tide once before the Cannikin test and twice afterward.

Milrow-Affected Areas

Lebednik (1973) reported the effects of the nuclear test Milrow, which caused a fault shift

**Asterocolax hypophyllophila, Hypophyllum dentatum, Laingia aleutica, Neinburgia prolifera, Phycodrys amchitkensis,* and *Zinovaea acanthocarpa* (see also footnote, p.358).

resulting in an uplift of about 12 cm (5 in.) of an intertidal area (Fig. 20) of about 4 ha (10 acres) on the Pacific Ocean coast. The uplift caused die-off in certain algal populations, especially those of the *Hedophyllum* zone. Twenty-five species were observed in plots on the uplifted portion of the bench. Seventeen of these species were so infrequent or sporadic that any possible effects could not be deduced in their populations. Of the eight most frequent species for which effects could be observed, five showed mortality attributable to the uplifting, one (*Fucus distichus*) increased significantly in frequency, and the remaining species exhibited little change in frequency (Fig. 21). Most die-off occurred in the first 6 months after the test. Lebednik (1973) concluded: "The rather rapid and extensive die-off suggests that the populations affected were vertically close to their upper physiological limits before the uplifting. . . ." Continued sampling of the area indicates a gradual shift of algal species. Three and one-half years after the test (in early 1973), major increases in the *Fucus* and *Alaria crispa* populations were still occurring in 64% of the plots (Nakatani and Burgner, 1974). This confirms Lebednik's (1973) prediction that the die-off in the *Hedophyllum* zone would be followed by formation of a *Fucus* zone. There is no doubt that a stable algal community will eventually be established.

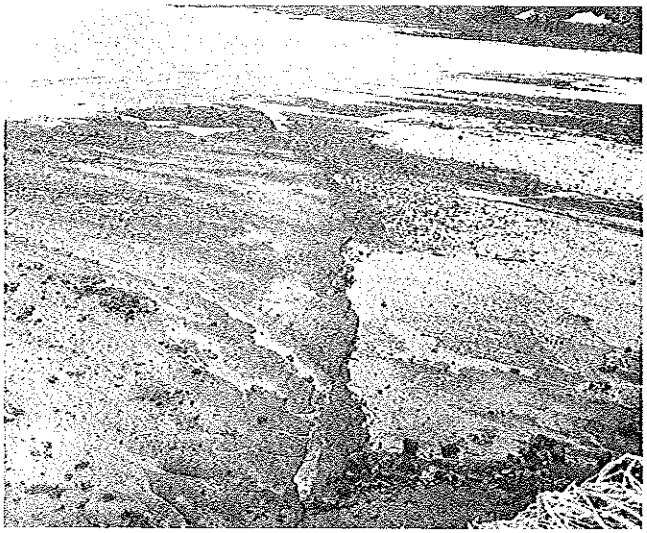

Fig. 20—View of the IA-1 area at Duck Cove. The fault runs across the center of the intertidal bench. To the left the bench was uplifted; to the right no elevation change occurred. Photograph was taken on Mar. 29, 1971, at a −30-cm (−12-in.) low tide.

Cannikin-Affected Areas

The 1971 Cannikin test caused an uplift of as much as a meter along the Bering Sea coast. Two areas with fixed plots (IA-2 and IA-3, see Fig. 26) were located in the area most affected by the test. An average uplift of 91 cm (36 in.) occurred in the IA-2 study area (Nakatani et al., 1973; 1974). An indication of the damage caused is given in Fig. 22, which shows a portion of the IA-2 area. The upper photograph was taken in August 1970 (15 months before Cannikin), at which time the rock bench in the foreground was completely covered by *Halosaccion glandiforme, Rhodymenia palmata,* and *Corallina* spp. The surge channel at the center was dominated by *Alaria crispa* and *Laminaria longipes,* and, between this area and the sea stack, a varied vegetation of *Hedophyllum sessile* and *Laminaria longipes* was dominant in low pools. The lower photograph was taken in April 1973 during an equivalent low tide. More rock was exposed both in the surge channel and in reefs behind the stack. A great deal of rockfall from both the stack and the adjacent sea cliff had buried some intertidal areas, including three study plots. Of greater significance was the complete lack of algal vegetation on the rock benches. In the surge channel the algae that had settled since Cannikin were limited to areas below the 1970 low-water line, and the only other vegetation visible was on the offshore reefs behind the sea stack.

Following the uplifting, *Iridaea cornucopiae* was the first species to show conspicuous mortality. By April 1973 all the 20 surviving plots (5 more had been buried by rockfalls), which preshot were representative of the entire vertical range of intertidal vegetation, were devoid of algae except for a few *Porphyra* sp. and green algal plants. Total destruction of littoral vegetation also occurred in other areas with comparable uplifting (Nakatani and Burgner, 1974).

At IA-2 the sublittoral region, including the sublittoral fringe, was lifted to a new level, and a new littoral vegetation is expected to develop. The shallow sublittoral fringe is one of the most difficult areas to sample because it is mostly underwater even during low tides, and knowledge of the sublittoral communities occurring there has been limited (Weinmann, 1969). The uplifting of Cannikin allowed observations of these communities. At the IA-2 area a large portion of the kelp community was occupied by three *Laminaria* species: (1) *L. longipes*, (2) *L. groenlandica*, and (3) *L. yezoensis*. *Thalassiophyllum clathrus* was present in some localities, and *Alaria fistulosa*, which forms the extensive offshore floating kelp beds fringing the island, was abundant on one rock bench at the lowest level exposed by the uplift. These species and their associated flora, except for *Laminaria longipes*, wherever they had been lifted into the intertidal area, were dead by April 1973.

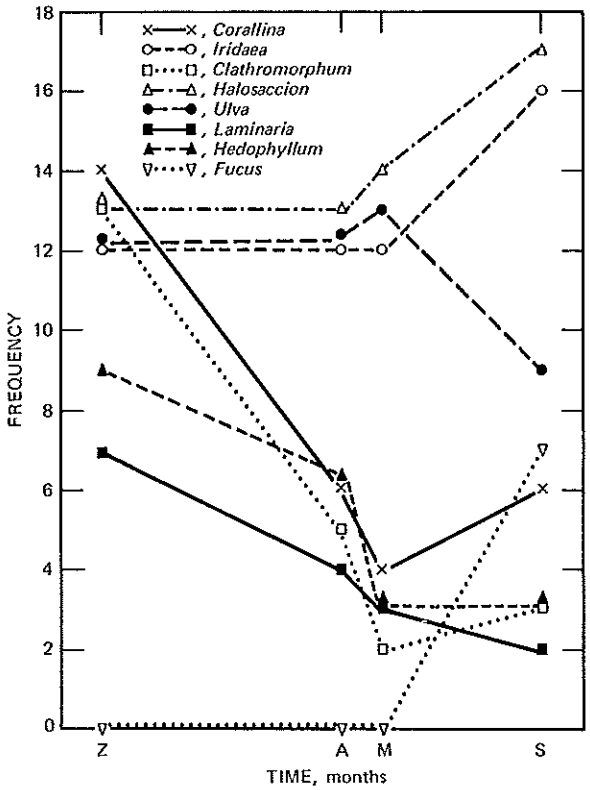

Fig. 21—Summary of frequencies of the eight most frequent species (except *Analipus filiformis*) on the uplifted plots at IA-1 in 1970. Z, deduced pretest pattern. A, April. M, May. S, September. [From P. A. Lebednik, *Marine Biology*, 20: 201 (1973).]

New plots were established at IA-2 after Cannikin in four types of habitat: (1) High outer bench, (2) surge channel basin, (3) newly exposed rock, and (4) low outer bench.

Two plots in the first habitat were located on the outer portion of the intertidal bench at a relatively high level. This was an area exposed to heavy wave action; the pretest vegetation was characteristic of the lower levels. The reaction of *Laminaria longipes* at a relatively protected plot (Fig. 23) is compared with that of a more exposed population (Fig. 24). In vegetation the plots were identical initially and followed generally the same pattern of decrease in cover. However, some plants remained alive 2 months longer on the more exposed plot, and the remains of dead plants were still visible 17 months after Cannikin. The exposure conditions have changed because the outer vertical face of the bench is well above mean lower low water and does not allow wave splash on the bench top as it did pre-Cannikin except during the highest tides. Should any new vegetation develop on these plots, there should be a significant difference between the two.

Two new plots were established in the bottom of a surge channel basin where the stable substrate is large boulders. In both plots the pre-Cannikin vegetation was dominated by a tall dense canopy of *Laminaria yezoensis*, beneath which was a dense stand of *L. longipes*, covering most of the rock. Although the entire *L. yezoensis* population died,

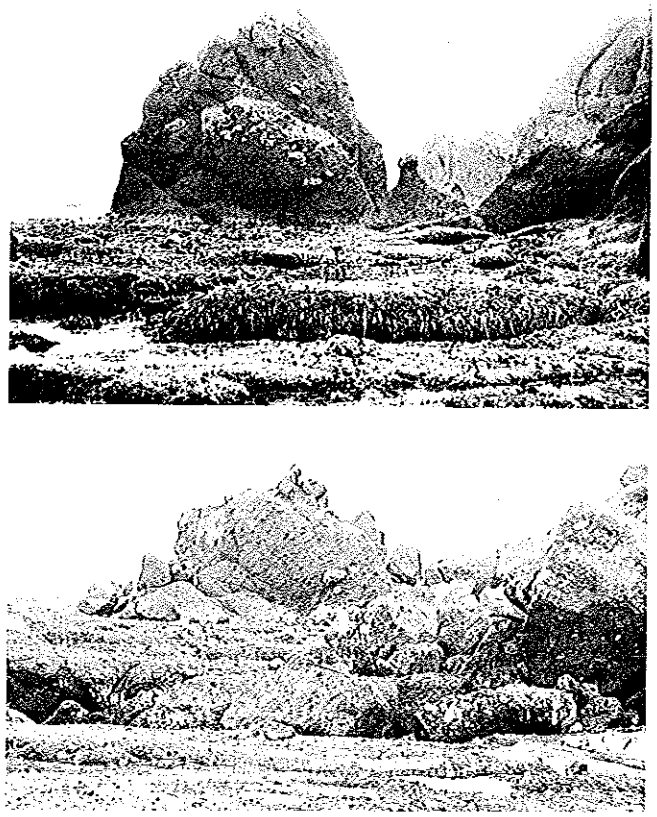

Fig. 22—View eastward at IA-2 in August 1970 (upper) pre-Cannikin and April 1973 (lower) post-Cannikin.

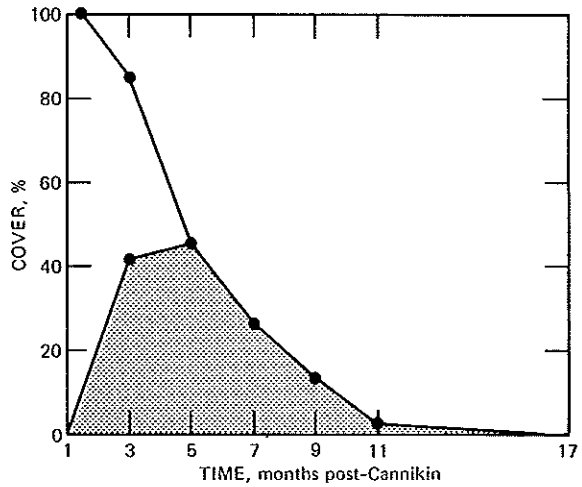

Fig. 23—Percent cover of *Laminaria longipes* versus time at IA-2 (dead cover of *L. longipes* indicated by shading), December 1971 to April 1973. Preshot elevation, 34.3 cm (14 in.); postshot, 122.1 cm (48 in.); uplift, 87.8 cm (35 in.).

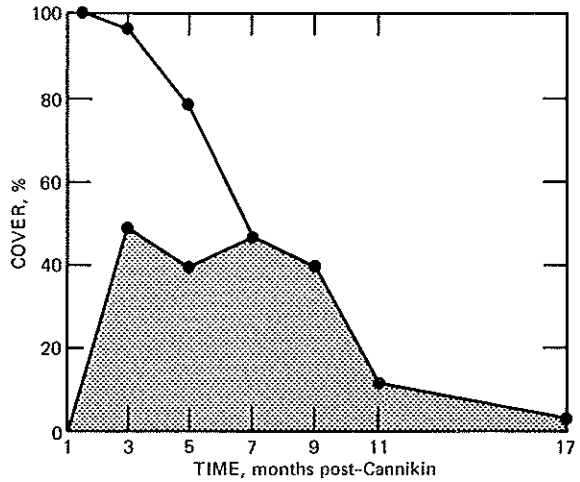

Fig. 24—Percent cover of *Laminaria longipes* versus time at IA-2 (dead cover of *L. longipes* indicated by shading), December 1971 to April 1973. Preshot elevation, +58.3 cm (23 in.); postshot, +153.2 cm (60 in.); uplift, 94.9 cm (37 in.).

L. longipes, which initially showed some die-off, began to recover in August 1972 (9 months after Cannikin), as illustrated in Fig. 25. *Laminaria longipes* normally occurs in the sublittoral fringe, and its survival here is consistent with the present elevation of these plots.

Succession on newly exposed rock surfaces was studied in three plots. Two of them were on the vertical surface that formed the outer face of the pre-Cannikin intertidal bench and one was on the horizontal surface of a large rock boulder immediately seaward of the other two. All these plots showed a similar pattern of colonization. Three

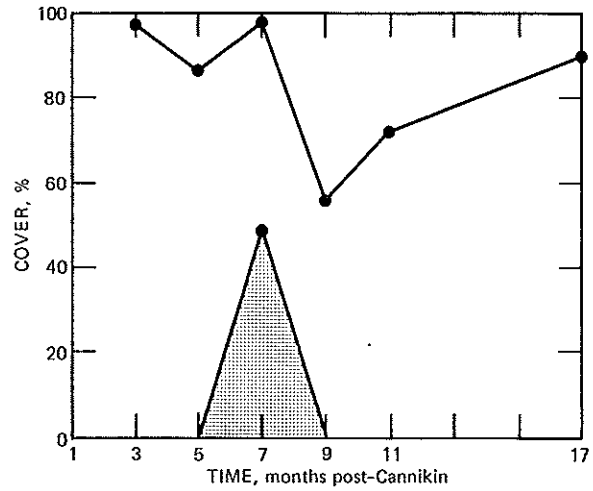

Fig. 25—Percent cover of *Laminaria longipes* versus time at IA-2 (dead cover of *L. longipes* indicated by shading), February 1972 to April 1973. Preshot elevation, −93.2 cm (−37 in.); postshot, 1.7 cm (1 in.); uplift, 94.9 cm (37 in.).

months after Cannikin, two species were present: (1) A large population of *Cladophora* sp. and (2) numerous plants of *Porphyra* sp. (*P. pseudolinearis*?). Two months after that, in April 1973, both species had decreased in cover whereas *Halosaccion glandiforme* had become dominant in two plots and *Rhodymenia palmata* in one. *Alaria crispa* had appeared in two of the plots; this was the first indication of the appearance of a kelp canopy.

The four plots established in the final habitat were on a low rock bench with a uniform seaward slope that was subtidal pre-Cannikin but became intertidal post-Cannikin. Observations after the uplifting indicated a threefold preshot zonation from landward to seaward dominated by *Laminaria longipes, Thalassiophyllum clathrus,* and *Alaria fistulosa–Laminaria groenlandica.* The first two dominants were represented by one plot each and the last one by two plots that reached to the outermost portion of the bench emersed at low tide. By April 1973 the *L. longipes* population had died in the plot originally dominated by it. During 1972 *Rhodymenia palmata* appeared and reached a maximum in October 1972 but still was abundant (64%) in April 1973. The appearance of *Fucus distichus* and *Alaria crispa* in April 1973 signaled the reestablishment of a kelp canopy in the plot. At the plot where *T. clathrus* was the dominant species pre-Cannikin, *Rhodymenia palmata* initially showed an increase but was soon covered by a burgeoning *Alaria crispa* population that first appeared in June 1972 and occupied 100% of the plot by April 1973. At the outermost plots *Laminaria longipes* settled and dominated one (75%) and *Alaria crispa* dominated the other (80%). *Rhodymenia palmata* was fairly abundant in these two plots in June and August 1972 before its populations were covered by the growing kelp plants.

The second area, IA-3 (Fig. 26), established to study effects of Cannikin, had only 13 plots survive after Cannikin since 2 of the original plots were buried by rockfall. Although the IA-3 area underwent an average uplift of only 50 cm (20 in.) as compared with 91 cm (36 in.) at IA-2, mortality was nearly as complete. As of April 1973, five plots had no live algae; eight had one or both of two *Porphyra* species; *Ulva lactuca* occurred on three plots; and *Rhodymenia palmata, Analipus filiformis,* and *Halosaccion glandiforme* each occurred on one plot in insignificant amounts. Only at one plot, where a small *Fucus distichus* population had settled and started to develop, was there an indication of permanent colonization. Except for this last plot, no midlittoral vegetation colonized the IA-3 plots after the Cannikin test. New

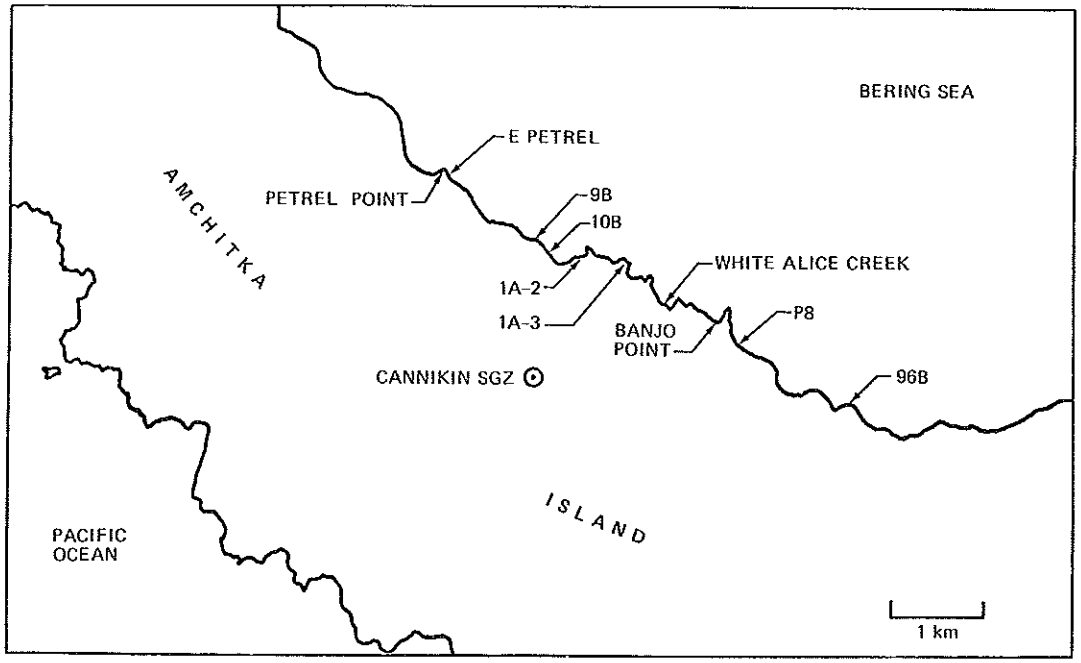

Fig. 26—Location of points discussed in the Bering Sea coast survey.

plots were not established at IA-3 to document colonization, but we did make general observations. By April 1973 there was heavy *Fucus distichus* colonization just below the original plots. *Alaria crispa* appeared to be newly abundant and dominant near low water levels [at the −0.5-m (−2-ft) tidal level]. There was little evidence of *Laminaria longipes* or *Hedophyllum sessile*.

So that the data taken at the IA-2 and IA-3 plots could be generalized, observations were made at low tide along the 15.4-km (10-mile) stretch of shore between Sea Otter Point and Crown Reefer Point (see Geological Survey map in the pocket at the back of this volume). Walks were made in August 1971, 2½ months before Cannikin, and in April 1972 and 1973, 5 and 17 months afterward (Table 1).

The observations made in April 1972 on algal die-off on this stretch of shore are summarized in Fig. 27. Coastal landslides were visible west of Petrel Point, but algal die-off did not become apparent until just east of Petrel Point. From there to point 9B, die-off was light and patchy. Between points 9B and 10B, die-off was more extensive and involved more species. From just west of point 10B to the mouth of White Alice Creek, die-off was extensive and comparable to that at IA-2 except that near where the creek flowed over the bench *Iridaea cornucopiae* appeared to be less affected. East of White Alice Creek to point P8, die-off was moderate and discontinuous. At Banjo Point only the *Alaria* zone showed die-off. Elsewhere portions of the populations of *I. cornucopiae, L. longipes,* and crustose coralline algae showed die-off. Eastward from point P8 to point 96B, only *I. cornucopiae* and *L. longipes* mortality was observed, and beyond point 96B no test-related die-off was seen at all.

Severe damage was observed along 1.9 km (1 mile) of shore, including the IA-2 and IA-3 areas. Moderate damage was seen on 1.5 km (1 mile) of shore and damage detectable along 2.7 km (2 miles) of shore. Altogether, 6.1 km (4 miles) of shore was affected.

In April 1973, except for a slight increase in mortality around Petrel Point, the distribution of mortality was similar to that in April 1972. Dead plants not yet removed by wave action made it difficult to detect colonization in the moderately affected areas. In the severely affected areas, colonization occurred as reported for IA-2.

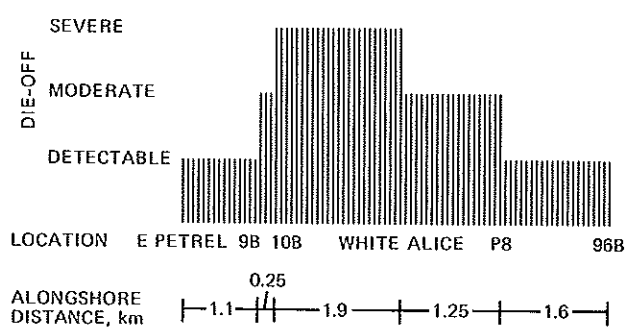

Fig. 27—Alongshore die-off of littoral algae due to Cannikin, April 1972.

Following the field studies of Lebednik, observations of the IA-2 and IA-3 areas were made in May and August 1974 by other FRI staff members and were reported by Kirkwood (1974; 1975). No quantitative data on cover values of the species were presented; however, significant changes in species composition appear to have occurred since August 1973 in 8 of the 11 plots discussed previously. It is estimated that the total area of intertidal bench uplifted into the supralittoral fringe by Cannikin was 5.8 ha (O'Clair, Chap. 18, this volume).*

The effects of uplifting from underground testing at Amchitka and those of uplifting from the Alaska earthquake of 1964 as reported by Johansen (1971) were similar. In both localities littoral populations did not tolerate the environmental conditions at higher elevations and extensive mortality resulted. A subsequent succession of species in the disturbed areas led eventually to a return to the original pattern of zonation, which was consistent with the new elevations and changes in exposure.

Uplifting at Amchitka will probably have a significant long-term effect because of the presence of flat rock benches in the midlittoral region. These benches were lifted above the midlittoral region at IA-2 and IA-3 following the Cannikin test. A new midlittoral vegetation in those localities will have far less area on which to develop. Because the supralittoral fringe populations depend on wave splash, which occurs only at the edge of the benches, only a small portion of the bench area will be colonized by these species.

Mortality may occur over a period of months in uplifted populations, depending on the habitat and amount of uplifting. The early stages of colonization appear to be strongly influenced by seasonal spore production. A disturbed plot may remain nearly devoid of algae or with unchanged vegetation during the winter months but may exhibit rapid changes in species composition and abundance in the spring. The return to a normal community may require years, as exemplified by the marked changes in the *Fucus* populations at IA-1 3½ years after the Milrow test and the changes observed in Cannikin-disturbed areas nearly 3 years after that test.

SUMMARY

The climate, sea conditions, and topography of Amchitka Island are favorable for the development of an abundant and diverse marine algal flora. A review of phycological research in the North Pacific Ocean, in particular that of Russian workers, indicates a dearth of knowledge of the marine algal flora of the Aleutians.

A somewhat unusual topographic feature, extremely flat rock benches, occurs at about mean tide level around the southeastern third of the island. These benches provide an exceptionally large area for the development of littoral vegetation. The seaward edge of the bench, where waves are often breaking, is the most exposed portion, whereas the landward edge is usually quite protected. Cloud cover and humidity are very high throughout the year, and thus the littoral algae do not experience much desiccation. Air temperatures are generally about the same as seawater temperatures except that in the winter subfreezing conditions prevail for short periods. Heavy wave action is characteristic of Amchitka. Seawater temperatures range from 2 to 10°C at the shore, and the water is exceptionally clear. The extensive rocky areas, cool moist climate, and clear water conditions provide an ideal environment for marine algae.

The littoral marine vegetation was studied by means of two transects, one each on the Pacific Ocean and Bering Sea coasts. The littoral region can be classified into the supralittoral fringe and midlittoral areas. The supralittoral fringe is composed of three zones, from top to bottom: (1) *Prasiola*, (2) *Rhodochorton*, and (3) *Porphyra–Ulothrix*. The last zone is practically absent in the fall and winter and reaches its highest development in late spring and summer. The upper limit of the midlittoral area, usually taken as the upper limit of the barnacle zone, was assigned to the upper limit of the *Fucus* zone owing to the lack of a barnacle zone at Amchitka. The next lower zone is a *Hedophyllum* zone that usually occupies the greatest area because its occurrence coincides with the level of most of the rock benches. Six associations can be recognized within the *Hedophyllum* zone: (1) *Ulva*, (2) *Analipus*, (3) *Corallina*, (4) *Halosaccion*, (5) *Hedophyllum*, and (6) *Iridaea*. The greatest number of species and the most complex vegetation were observed in this zone. The third zone of the midlittoral area, the *Alaria* zone, occurs primarily near the outer edge of the benches. The sublittoral fringe consists of the *Laminaria longipes* zone, in which several sublittoral species have their upper limit. Tide pools are rare, but channels running across the benches and connected with the sea at low tide have a sublittoral flora. The bench topography influences littoral vegetation in that the distribu-

*Previously reported as 57.6 ha (Kirkwood, 1975).

tions of many species were correlated with horizontal distance perpendicular to the shore regardless of elevation. Seasonal photographic sampling indicated that most littoral species occur throughout the year. Most species appeared to release spores in late winter–early spring, and the appearance of sporelings follows this period. Growth of sporelings as well as of older plants reached a peak in late spring–early summer. The *Porphyra–Ulothrix* zone and the *Halosaccion* association were annual, occurring from early spring to late summer. The littoral zonation was nearly identical to that described at the Commander Islands and was similar to that described at the northern Kurile Islands. The zonation at Amchitka was also compared with that of southeastern Kamchatka, Sakhalin Island, Hokkaido, Japan, and the Strait of Juan de Fuca.

Total removal of organisms from rocky intertidal plots resulted in a colonization sequence of diatoms and filamentous algae, leafy green algae, and larger red and brown algae. In plots where only the kelp canopy had been removed, the sequence was similar but faster. Initial settlement occurred most quickly in exposed areas at low levels. Colonization was strongly influenced by the length of time between the clearing of plots and the next annual spore release of the species originally dominant in that plot. Three of the five species whose stands were denuded and two of the three whose canopies had been removed attained a coverage of at least 80% in their own zone by the end of the study. Those which did not attain this degree of coverage were *Laminaria longipes* and *Corallina vancouveriensis* in denuded areas and *Alaria crispa* in areas where the canopy had been removed. The low recovery of *L. longipes* was attributed to its low degree of sexual reproduction. The scarcity of *A. crispa* was attributed to the lack of bare substratum needed for settlement. The establishment and maintenance of algal zones and associations, at times in almost pure stands, are enhanced by the physical homogeneity of the intertidal bench, the relatively few species of dominant algae, and the lack of excessive physical and biological disturbances.

The sublittoral communities are extremely dense. *Alaria fistulosa*, which forms huge floating kelp beds, was observed down to about 20 m (66 ft). These kelp beds have a considerable damping effect on wave action. A dense covering of kelp occurs on the bottom from the intertidal area down to about 20 m (66 ft) and was formed by species in the genera *Laminaria, Thalassiophyllum, Cymathere, Alaria,* and *Agarum*. A third level of vegetation is made up of filamentous and foliose red algae, such as *Ptilota asplenioides, P. filicina, Hypophyllum ruprechtianum, Cirrulicarpus gmelini*, and *Constantinea rosa-marina*. The fourth level of vegetation, consisting of crustose forms and extending well below 30 m (100 ft), included the green alga *Codium ritteri* and the coralline genera *Clathromorphum, Lithothamnium,* and *Mesophyllum*. The richness and density of marine algae at Amchitka might be due to the removal of invertebrate herbivores by sea otters. A strong relationship between the Amchitka flora and the western Pacific, eastern Pacific, and Arctic floras was found by comparing species lists. The initial results of a long-term taxonomic study have resulted in the description of three new genera and eight new species from Amchitka.

The Milrow nuclear test caused a 12-cm (5-in.) uplifting of a portion of intertidal bench totaling about 4 ha (10 acres). Mortality ensued in the upper portions of all zones, especially the *Hedophyllum* zone, within 6 months after the test. Although new vegetation characteristic of the higher levels had begun to develop, significant changes were still observed in some plots 3½ years after the test. The Cannikin test caused a maximum uplift at the shore of about 1 m (3 ft), which occurred in one of two study areas. Total mortality of all algal species ensued in both study areas with uplifting of 0.5 to 1 m (1.5 to 3 ft) and along 1.9 km (1 mile) of coastline. Moderate mortality was observed along an additional 1.5 km (1 mile) of coastline, and some mortality was detected for a further 2.7 km (2 miles). A total of 6.1 km (4 miles) was affected. New plots were established in formerly sublittoral areas, and colonization was followed. Significant changes were occurring in these plots when last observed, nearly 3 years after the test. As was the case with the Milrow-disturbed areas, new vegetation was forming in consonance with the new elevations and exposure of the disturbed areas. In contrast to the Milrow disturbance, which will have no long-term effects, the Cannikin disturbance has resulted in a marked reduction of area at midlittoral levels by permanent lifting of the intertidal bench into the supralittoral fringe. Supralittoral fringe species, which require constant wave splash, will be able to colonize only the outer edges of the uplifted benches.

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REFERENCES

Adey, W. H., T. Masaki, and H. Akioka, 1976, The Distribution of Crustose Corallines in Eastern Hokkaido and the Biogeographic Relationships of the Flora, *Bull. Fac. Fish., Hokkaido Univ.*, 26: 303-313.

Armstrong, Robert H., 1971, Physical Climatology of Amchitka Island, Alaska, *BioScience*, 21(12): 607-609.

Biebl, R., 1972, Temperature Resistance of Marine Algae, in *Proceedings of the Seventh International Seaweed Symposium*, Aug. 8–12, 1971, pp. 23-28, University of Tokyo Press.

——, 1970, Vergleichende Untersuchungen zur Temperaturresistenz von Meeresalgen entlang der pazifischen Küste Nordamerikas, *Protoplasma*, 69: 61-83.

Blinova, E. I., 1968, Morskie vodorosli severo-vostochnoĭ chasti Okhotskogo morya [Marine Algae of the Northeast Part of the Sea of Okhotsk], *Novosti sistematiki nizshikh rasteniĭ, Akad. Nauk SSSR, Bot. Inst.*, 5: 33-38.

——, and I. S. Gusarova (Subbotina), 1970, Morskie vodorosli, novye dlya poberezh'ya vostochnoĭ Kamchatki [New Marine Algae from the Coast of Eastern Kamchatka], *Novosti sistematiki nizshikh rasteniĭ, Akad. Nauk SSSR, Bot. Inst.*, 7: 68-71.

——, and A. D. Zinova, 1967, Novyĭ vid Rhodymenia iz severo-vostochnoĭ chasti Okhotskogo morya [A New Species of *Rhodymenia* from the Eastern Part of the Sea of Okhotsk], *Novosti sistematiki nizshikh rasteniĭ, Akad. Nauk SSSR, Bot. Inst.*, 4: 107-109.

Bokenham, N. A. H., 1938, The Colonization of Denuded Rock Surfaces in the Intertidal Region of the Cape Peninsula, *Ann. Natal. Mus.*, 9: 47-81.

Burgner, R. L., and R. E. Nakatani, 1972, Amchitka Bioenvironmental Program, Research Program on Marine Ecology, Amchitka Island, Alaska, Annual Progress Report, July 1, 1970–June 30, 1971, with contributions by J. S. Isakson, L. G. Gilbertson, P. A. Lebednik, C. E. O'Clair, J. F. Palmisano, C. A. Simenstad, and G. J. Tutmark, of the Fisheries Research Institute, University of Washington, USAEC Report BMI-171-144, Battelle Memorial Institute.

——, J. S. Isakson, and P. A. Lebednik, 1970, Observations on the Effect of the Milrow Nuclear Test on Marine Organisms at Amchitka, *BioScience*, 21: 671-673.

——, et al., 1971, Amchitka Bioenvironmental Program, Research Program on Marine Ecology, Amchitka Island, Alaska, Annual Progress Report, July 1, 1969–June 30, 1970, USAEC Report BMI-171-137, Battelle Memorial Institute.

——, et al., 1969, Amchitka Bioenvironmental Program, Annual Progress Report, July 1, 1968–June 30, 1969, Research Program on Marine Ecology and Oceanography, Amchitka Island, Alaska, USAEC Report BMI-171-128, Battelle Memorial Institute.

——, et al., 1968, Amchitka Bioenvironmental Program. Annual Progress Report, July 1, 1967–June 30, 1968, Research Program on Marine Ecology and Oceanography, Amchitka, USAEC Report BMI-171-114, Battelle Memorial Institute.

Chapman, V. J., 1943, Zonation of Marine Algae on the Sea-Shore, *Trans. Linn. Soc. London*, 1941: 239-253.

Chihara, M., 1967, Some Marine Algae Collected at Cape Thompson of the Alaskan Arctic, *Bull. Natl. Sci. Mus., Tokyo*, 10(2): 183-200, plates 1-4.

Conway, E. C., T. F. Mumford, Jr., and R. F. Scagel, 1976, The Genus *Porphyra* in British Columbia and Washington, *Syesis*, 8: 185-244.

Dawson, E. Y., 1961, A Guide to the Literature and Distributions of Pacific Benthic Algae from Alaska to the Galapagos Islands, *Pac. Sci.*, 15: 370-461.

Dayton, P. K., 1975, Experimental Studies of Algal Canopy Interactions in a Sea-Otter Dominated Community at Amchitka Island, Alaska, *Fish. Bull.*, 73: 230-237.

——, 1971, Competition, Disturbance, and Community Organization: The Provision and Subsequent Utilization of Space in a Rocky Intertidal Community, *Ecol. Monogr.*, 41: 351-389.

DeCew, T. C., and J. West, in press, Culture Studies on Two Marine Red Algae, *Hildenbrandia occidentalis* Setchell and *H. prototypus* Nardo (Cryptonemiales, Hildenbrandiaceae), *Bull. Jap. Soc. Phycol.*

Doty, M. S., 1957, Rocky Intertidal Surfaces, in *Treatise on Marine Ecology and Paleoecology*, Vol. 1, Ecology, J. W. Hedgpeth (Ed.), pp. 535-585, Geological Society of America, New York, N. Y.

——, 1946, Critical Tide Factors that are Correlated with the Vertical Distribution of Marine Algae and Other Organisms Along the Pacific Coast, *Ecology*, 27: 315-328.

Druehl, L. D., 1970, The Pattern of Laminariales Distribution in the Northeast Pacific, *Phycologia*, 9: 237-248.

——, 1968, Taxonomy and Distribution of Northeast Pacific Species of *Laminaria*, *Can. J. Bot.*, 46: 539-547, plates I–VII.

Elenkin, A. A., and L. Ol', 1950a, Bibliografiya al'gologicheskikh trudov v predelakh SSSR s 1931 po 1935 g. vklyuchitel'no [Bibliography of Algological Studies in the USSR from 1931 to 1935 Inclusive], *Tr. Bot. Inst., Akad. Nauk SSSR*, Ser. 2: *Sporovye rasteniya*, No. 5: 95-115.

——, and L. Ol', 1950b, Dopolnitel'nye dannye po bibliografii algologicheskikh trudov v predelakh SSSR. Dopolnenie II. [Supplementary Data for the Bibliography of Algological Studies in the USSR. Supplement II], *Tr. Bot. Inst., Akad. Nauk SSSR*, Ser. 2: *Sporovye rasteniya*, No. 6: 5-22.

——, and L. Ol', 1935, Bibliografiya al'gologicheskikh trudov v predelakh SSSR s 1926 g. po 1930 g. vklyuchitel'no [Bibliography of Algological Studies in

the USSR from 1926 to 1930 Inclusive], *Tr. Bot. Inst., Akad. Nauk SSSR*, Ser. 2: *Sporovye rasteniya*, No. 2: 171-255.

——, and L. Ol', 1929, Bibliografiya al'gologicheskikh trudov v predelakh SSSR s 1900 po 1925 gg. vklyuchitel'no [Bibliography of Algological Studies in the USSR from 1900 to 1925 Inclusive], *Tr. Bot. Sada (Acta Horti Petrop.)*, 42(1): 1-139 (not seen by authors).

Gaĭdukov, N. M., 1901, Literaturnye istochniki k russkoĭ flore vodorosleĭ [Literary Sources for Russian Flora and Algae], *Tr. Bot. Sada (Scripta Bot. Horti Imp. Petrop.)*, 17: 1-126 (not seen by authors).

Gail, F. W., 1918, Some Experiments with *Fucus* to Determine the Factors Controlling Its Vertical Distribution, *Publ. Puget Sound Biol. Sta., Univ. Wash.*, 2: 139-151.

Gmelin, S. G., 1768, *Historia fucorum*, [10] + 239 + 6 pp., plates 1A, 1B, 2A, 2B, 3-33, Typographia Academiae Scientiarum, Petropoli.

Gollerbakh, M. M., A. A. Elenkin, L. K. Krasavina, and L. A. Ol', 1966, Bibliografiya sovetskoĭ literatury po vodoroslyam za 1936–1940 gg. (s dopelneniem za predydushchie gody). [Bibliography of Soviet Literature on Algae for the Years 1936–1940 (with a Supplement for the Last Year)], Akademiya Nauk SSSR, Botanical Institute (not seen by authors).

——, and L. K. Krasavina, 1971, Vodorosli. Svodnyĭ ukazatel' k otechestvennym bibliografiyam po vodoroslyam za 1737-1960 gg. [Algae. A Consolidated Guide to Native (Russian) Bibliographies on Algae for the Years 1737–1960], V. L. Komarov, Akademiya Nauk SSSR, Botanical Institute.

Guryanova, E. F., 1935, The Commander Islands and Their Marine Littoral Fauna and Flora, *Priroda*, 11: 64-72. [Translation by L. Sagen, *The Soviet Fishery Pertinalia*, No. 16 (Mar. 25, 1974), pp. 1-17, College of Fisheries, University of Washington, Seattle.]

Gusarova, I. S., 1972, Novye vodorosli dlya nekotorykh ostrovov bol'shoĭ Kuril'skoĭ gryady [New Algae from Some Islands of the Big Kurile Chain], *Novosti sistematiki nizshikh rasteniĭ, Akad. Nauk SSSR, Bot. Inst.*, 9: 32-34.

——, and Yu. E. Petrov, 1972, Novyi rod i vid laminarievykh vodorosleĭ c O. Simushir (Kuril'skie Ostrova) [A New Genus and Species of Laminarian Algae from Simushir Island (Kurile Islands)], *Novosti sistematiki nizshikh rasteniĭ, Akad. Nauk SSSR, Bot. Inst.*, 9: 39-44.

——, and Yu. E. Petrov, 1970, Novyi rod i vid laminarievykh vodorosleĭ s Kuril'skikh ostrovov [A New Genus and Species of Laminarian Algae from the Kurile Islands], *Novosti sistematiki nizshikh rasteniĭ, Akad. Nauk SSSR, Bot. Inst.*, 7: 87-90.

den Hartog, C., 1959, The Epilithic Algal Communities Occurring Along the Coast of the Netherlands, *Wentia*, I: 1-241.

Johansen, H., 1971, Effects of Elevation Changes on Benthic Algae in Prince William Sound, in *The Great Alaska Earthquake of 1964*, pp. 35-68, Biology, National Academy of Sciences, Washington, D.C.

Johnson, W. S., A. Gigon, S. L. Gulman, and H. A. Mooney, 1974, Comparative Photosynthetic Capacities of Intertidal Algae Under Exposed and Submerged Conditions, *Ecology*, 55: 450-453.

Kardakova-Prezhentsova, E. A., 1938, Vodoroslevaya rastitel'nost' Komandorskikh Ostrovov [The Algal Vegetation of the Komandorski Islands], *Iz. Tikhookean. Nauchno-Issled. Inst. Rybn. Khoz. Okeanogr.*, 14: 77-108.

Kireeva, M. S., 1965, Syr'evye resursy vodorosleĭ moreĭ sovetskogo soyuza [Natural Resources of Marine Algae of the Soviet Union], *Okeanologiya*, 5(1): 14.

Kirkwood, J. B. (Comp.), 1975, Bioenvironmental and Hydrologic Studies, Amchitka Island, Alaska. Fall 1974 Task Force Report, ERDA Report BMI-171-158, Battelle Memorial Institute.

—— (Comp.), 1974, Amchitka Bioenvironmental Program. Bioenvironmental Safety Studies, Amchitka Island, Alaska, Spring, 1974 Task Force Report, USAEC Report BMI-171-157, Battelle Memorial Institute.

Kitching, J. A., 1937, Studies in Sublittoral Ecology. II. Recolonization at the Upper Margin of the Sublittoral Region; with a Note on the Denudation of *Laminaria* Forest by Storms, *J. Ecol.*, 25: 482-495.

Kjellman, F. R., 1889, Om Beringhafvets algfloran, *Kgl. Svenska Vetenskapsakad. Handl.*, 23: 1-58.

Komarov, F., 1962, Botany, in *The Pacific Russian Scientific Investigations*, pp. 126-136 (English Edition; Original Published in 1926, not seen by author), Greenwood Press Inc., Westport, Conn.

Kongiser, R. A., 1933, Gidrobiologicheskie raboty v Beringovom more u severo-vostochnogo poberezh'ya Kamchatki [Hydrobiological Studies in the Bering Sea Near the Northeast Coast of Kamchatka], *Issled. Dal'nevost. Moreĭ SSSR*, 19: 115-124.

Krasavina, L. K., 1968, Bibliografiya sovetskoĭ literatury po vodoroslyam za 1941–1960 gg [Bibliography of Soviet Literature on Algae for the Years 1941-1960], *Akademiya Nauk SSSR, Botanical Institute* (not seen by authors).

Kusakin, O. G., 1961, Nekotorye zakonomernosti raspredeleniya fauny i flory v osuchnoĭ zone yuzhnykh Kuril'skykh ostrovov [Certain Regularities of the Distribution of the Fauna and Flora in the Intertidal Zone of the Southern Kurile Islands], *Issled. Dal'nevost. Moreĭ SSSR*, VII: 312-343.

Lebednik, P. A., in press, a, Postfertilization Development and Evolution in the Rhodophyta, *J. Phycol.*, 13(Suppl.): (abstract).

——, in press, b, Algal Communities of the Aleutian Islands, *J. Phycol.*, 13(Suppl.): (abstract).

——, in press, c, Postfertilization Development in *Clathromorphum*, *Melobesia* and *Mesophyllum*, with Comments on the Evolution of the Corallinaceae and the Cryptonemiales, *Phycologia*, 16:

——, 1977, The Corallinaceae of Northwestern North America. I. *Clathromorphum* Foslie emend. Adey, *Syesis*, 9: 59-112.

——, 1975, Biosystematic Studies of *Clathromorphum* and *Mesophyllum* with Comments on the Taxonomy of the Corallinaceae, *J. Phycol.*, 11(Suppl.): 17 (abstract).

——, 1974, The Genera *Clathromorphum* and *Mesophyllum* (Corallinaceae) from the Northeast North Pacific Ocean, Ph. D. Thesis, University of Washington. [*Diss. Abstr. Int.*, 36(Sect. B): 2596-B (1975).]

——, 1973, Ecological Effects of Intertidal Uplifting from Nuclear Testing, *Mar. Biol.*, 20: 197-207.

——, F. C. Weinmann, and R. E. Norris, 1971, Spatial and Seasonal Distributions of Marine Algal Communities at Amchitka Island, Alaska, *BioScience*, 21: 656-660.

Lewis, J. R., 1964, *The Ecology of Rocky Shores*, English Universities Press, London.

Markham, J. W., 1972, Distribution and Taxonomy of *Laminaria sinclairii* and *L. longipes* (Phaeophyceae, Laminariales), *Phycologia*, 11(2): 147-157.

McAlister, W. B., 1971, Oceanography in the Vicinity of Amchitka Island, Alaska, *BioScience*, 21: 646-651.

McRoy, C. P., 1968, A Eurasian Alga in Alaska, *Pac. Sci.*, 22(1): 138.

Mertens, Heinrich, 1829, Über verschiedene Fucus-Arten, *Linnaea*, 4: 43-58.

Mokievskiĭ, O. B., 1967, Izmeneniya litoral'noi bioty ot Beringova morya do zondskogo proliva [Variations of Littoral Biota from the Bering Sea to the Zond Straits], *Okeanologiya*, 2: 321-324.

Morris, R. H., 1971, Marine Terraces of the Western Aleutian Islands, Alaska, USAEC Report USGS-474-139, U. S. Geological Survey.

Nagai, M., 1941, Marine Algae of the Kurile Islands. II. *J. Fac. Agric. Hokkaido Univ.*, 46: 139-310, plates IV–VI.

——, 1940, Marine Algae of the Kurile Islands. I. *J. Fac. Agric. Hokkaido Univ.*, 46: 1-137, plates I–III.

Nakatani, R. E., and R. L. Burgner, 1974, Amchitka Bioenvironmental Program, Research Program on Marine Ecology, Amchitka Island, Alaska, Annual Progress Report, July 1972 Through September 1973, and Summary Report, 1967 Through 1973, with contributions by J. S. Isakson, P. A. Lebednik, C. E. O'Clair, J. F. Palmisano, and C. A. Simenstad, USAEC Report BMI-171-156, Battelle Memorial Institute.

——, J. S. Isakson, and R. L. Burgner, 1973, Amchitka Bioenvironmental Program, Research Program on Marine Ecology, Amchitka Island, Alaska, Annual Progress Report, July 1, 1971–June 30, 1972, USAEC Report BMI-171-150, Battelle Memorial Institute.

National Ocean Survey, 1971, *Tide Tables, West Coast of North and South America, 1972*, Superintendent of Documents, U. S. Government Printing Office, Washington, D. C.

Neal, Marie C., 1930, Hawaiian Marine Algae, *Bull. Bernice Pauahi Bishop Museum*, 67: 1-84.

Northcraft, R. D., 1948, Marine Algal Colonization on the Monterey Peninsula, California, *Amer. J. Bot.*, 35: 396-404.

Okamura, K., 1933, On the Algae from Alaska Collected by Y. Kobayashi, *Rec. Oceanogr. Works Jap.*, 5: 85-97.

——, 1928, Algae from Kamtschatka, *Rec. Oceanogr. Works Jap.*, 1: 52-55, plates xiii–xv.

Palmisano, J. F., 1975, Sea Otter Predation: Its Role in Rocky Intertidal Community Structure at Amchitka and Other Aleutian Islands, Ph. D. Thesis, University of Washington. [*Diss. Abstr. Int.*, 37(2): 595-B.]

Perestenko, L. P., 1967, O dvukh vidakh vodoresleĭ iz roda Rhodoglossum J. Ag., obitayushchikh v moryakh dal'nego vostoka [Concerning Two Species of Algae of the Genus *Rhodoglossum* J. Ag., Occurring in the Seas of the Extreme East], *Novosti sistematiki nizshikh rasteniĭ, Akad. Nauk SSSR, Bot. Inst.*, 4: 150-152.

Petrov, Yu. E., 1968, Rod Sargassum C. Ag. v dal'nevostochnykh moryakh SSSR [The Genus *Sargassum* C. Ag. in the Extreme Eastern Seas of the USSR], *Novosti sistematiki nizshikh rasteniĭ, Akad. Nauk SSSR, Bot. Inst.*, 5: 42-53.

——, 1966, Rod Cystoseira C. Ag. v dal'nevostochnykh moryakh SSSR [The genus *Cystoseira* C. Ag. in the Extreme Eastern Seas of the USSR], *Novosti sistematiki nizshikh rasteniĭ, Akad. Nauk SSSR, Bot. Inst.*, 3: 96-99.

——, and V. B. Vozzhinskaya, 1970, Novye vidy roda Laminaria iz Okhotskogo morya [New Species of the Genus *Laminaria* from the Sea of Okhotsk], *Novosti sistematiki nizshikh rasteniĭ, Akad. Nauk SSSR, Bot. Inst.*, 7: 81-87.

Polanshek, A. R., 1975, Hybridization Studies on Cultured *Petrocelis* Species from California and the Aleutians, *J. Phycol.*, 11(Suppl.): 17 (abstract).

——, and J. A. West, 1976, Culture and Hybridization Studies on *Petrocelis* (Rhodophyta) from Alaska and California, *J. Phycol.*, 11: 434-439.

Postels, A., and F. Ruprecht, 1840, Illustrationes Algarum in itinere circa Orbem. . . Executo in Oceano Pacifico Imprimis Septentrionali ad littora Rossica Asiatico–Americana Collectarum, St. Petersburg.

Powell, H. T., 1957, Studies in the Genus *Fucus* L. I. *Fucus distichus* L. emend. Powell, *J. Mar. Biol. Ass. UK*, 36: 407-432.

Powers, H. A., R. R. Coats, and W. H. Nelson, 1960, *Geology and Submarine Physiography of Amchitka Island, Alaska*, U. S. Geological Survey, Bulletin 1028-P, pp. 521-554.

Rees, T., 1940, Algal Colonization at Mumbles Head, *J. Ecol.*, 28: 403-437.

Rigg, G. B., and R. C. Miller, 1949, Intertidal Plant and Animal Zonation in the Vicinity of Neah Bay, Washington, *Proc. Calif. Acad. Sci.*, 26: 323-351.

Ruprecht, F. J., 1851, Tange des Ochotskischen Meeres, in A. T. von Middendorff, Reise in den aüssersten Norden und Osten Sibiriens während der Jahre 1843 und 1844, Vol. 1(2): 191-435, Botanik, plates 9–18, St. Petersburg.

Saunders, DeA., 1901, Papers from the Harriman Alaska Expedition, XXV. The Algae, *Proc. Wash. Acad. Sci.*, 3: 391-486.

Savich", V. P., 1914, Al'gologicheskiĭ ob"ezd" Avachinskoe guby v" Mae 1909 g [Algological Circuit of the Gulf of Avacha in May 1909], *Kanchatskaya Ekspeditsiya*, 2: 449-472, 593-594.

Scagel, R. F., 1966, Marine Algae of British Columbia and Northern Washington, Part I: Chlorophyceae (Green Algae), *Nat. Mus. Can. Bull.*, 207.

——, 1963, Distribution of Attached Marine Algae in Relation to Oceanographic Conditions in the Northeast Pacific, in *Marine Distributions*, M. J. Dunbar (Ed.), Royal Society of Canada, Special Publication 5, pp. 37-50, University of Toronto Press.

——, 1962, Coastal Studies of Marine Algae in British Columbia and the North Pacific, in *Proceedings of the National Coastal and Shallow Water Research Conference*, D. S. Gorsline (Ed.), pp 748-750, National Science Foundation–Office of Naval Research, Tallahassee, Fla.

——, 1957, An Annotated List of the Marine Algae of British Columbia and Northern Washington, *Nat. Mus. Can. Bull.*, 150.

Setchell, W., 1899, XXIV, Algae of the Pribilof Islands, in The Fur Seals and Fur-Seal Islands of the North Pacific Ocean, D. S. Jordan, Part III, pp. 589-596, Special Papers Relating to the Fur Seal and to the Natural History of the Pribilof Islands, Washington, D. C.

——, and N. L. Gardner, 1903, Algae of Northwestern America, *Publ. Botany, Univ. Calif., Berkeley*, 1: 165-418, plates 17–27.

Shchapova, T. F., 1948, Geograficheskoe rasprostranenie predstaviteleĭ poryadka Laminariales v severnoĭ chasti tikhogo okeana [Geographical Distribution of Representatives of the Family Laminariales in the North Pacific Ocean], *Tr. Inst. Okeanol., Akad. Nauk SSSR*, 2: 89-138.

——, 1946, On the Amphipacific Distribution of Certain Species of Phaeophyceae, *Compt. Rend. (Doklady) Acad. Sci. URSS, Nouv. Ser.*, 52(2): 171-173.

——, and V. B. Vozzinskaya, 1960, Vodorosli Litorali Zapadnogo Poberezh'ya Sakhalina [Algae of the Littoral of the West Coast of Sakhalin], *Tr. Inst. Okeanol., Akad. Nauk SSSR*, 34: 123-146.

——, O. B. Mokievskiĭ, and F. A. Pasternak, 1957, Flora i Fauna Litorali Zapadnogo Sakhalina (Predvaritel'noe soobshchenie) [Flora and Fauna of the Littoral of Western Sakhalin (Preliminary Report)], *Tr. Inst. Okeanol., Akad. Nauk SSSR*, 23: 102-111.

Shetler, S. G., 1967, *The Komarov Botanical Institute*, Smithsonian Institution Press, Washington, D. C.

Southward, A. J., 1956, The Population Balance Between Limpets and Seaweeds on Wave-Beaten Rocky Shores, *Rep. Mar. Biol. Sta., Port Erin*, 68: 20-29.

Spasskiĭ, N. N., 1961, Litoral' yugo-vostochnogo poberezh'ya Kamchatki [The Littoral Zone of the Southeast Shore of Kamchatka], *Issled. Dal'nevost. Moreĭ SSSR*, VII: 261-311.

Stephenson, T. A., and A. Stephenson, 1949, Universal Features of Zonation Between Tide Marks on Rocky Coasts, *J. Ecol.*, 37: 289-305.

Taniguti, M., 1962, *Phytosociological Study of Marine Algae in Japan*, I–III, Inoue and Company, Ltd., Tokyo.

Tanner, C., in preparation, A Study of the Northeast Pacific Species of *Ulva*, Ph. D. Thesis, University of British Columbia.

Tatewaki, M., and Y. Kobayashi, 1934, A Contribution to the Flora of the Aleutian Islands, *J. Fac. Agric. Hokkaido Univ.*, 36(1): 1-118.

Tokida, J., 1954, The Marine Algae of Southern Saghalien, *Mem. Fac. Fish. Hokkaido Univ.*, 2(1): 264 pp., 14 plates.

——, and H. Hirose, 1975, *Advance of Phycology in Japan*, W. Junk, The Hague.

Ushakov, P. V., 1951, Litoral' Okhotskogo morya [The Littoral Zone of the Sea of Okhotsk], *Dokl. Akad. Nauk SSSR, Novaya Ser.*, 76(1): 127-130.

Vinogradova, K. L., 1973a, O novykh vidakh Rhodomela Ag. i Polycerea J. Ag. iz Beringova morya [Concerning New Species of *Rhodomelae* Ag. and *Polycereae* from the Bering Sea], *Novosti sistematiki nizshikh rasteniĭ, Akad. Nauk SSSR, Bot. Inst.*, 10: 22-28.

——, 1973b, Vidovoi sostav vodoroslei na litorali i sublitorali severo-zapadnoi chasti Beringova morya [Composition of Species of Algae in the Littoral and Sublittoral Zones of the Northwestern Part of the Bering Sea], *Novosti sistematiki nizshikh rasteniĭ, Akad. Nauk SSSR, Bot. Inst.*, 10: 32-44.

Voronikhin", N. N., 1914, Morskiya vodorosli Kamchatki [The Marine Algae of Kamchatka], *Kamchatskiya Ekspeditsiya*, 2: 473-524, 592-593.

Vozzhinskaya, V. B., 1967, Novye vodorosli dlya severnykh poberezhiĭ Okhotskogo morya [New Algae from the Northern Shore of the Sea of Okhotsk], *Novosti sistematiki nizshikh rasteniĭ, Akad. Nauk SSSR, Bot. Inst.*, 4: 138-140.

——, 1965a, Morskie vodorosli zapadnogo poberzh'ya Kamchatki [Marine Algae of the West Coast of Kamchatka], *Novosti sistematiki nizshikh rasteniĭ, Akad. Nauk SSSR, Bot. Inst.*, 2: 73-78.

——, 1965b, Raspredelenie vodorosleĭ u beregov zapadnoĭ Kamchatki [Distribution of Algae Off the Coasts of Western Kamchatka], *Okeanologiya*, 5: 348-353.

——, 1964a, Novye vodorosli dlya Sakhalina, II [New Algae from Sakhalin, II] *Novosti sistematiki nizshikh rasteniĭ, Akad. Nauk SSSR, Bot. Inst.*, 1: 151-153.

——, 1964b, Makrofity morskikh poberezhiĭ Sakhalina [Marine Macrophytes of the Coast of Sakhalin], *Tr. Inst. Okeanol.*, 69: 330-441. (English Translation: Macrophytes of the Sakhalin Sea Coast, U. S. Naval Oceanographic Office, Translation 462.)

——, 1960a, Novye vodorosli dlya Sakhalina [New Algae from Sakhalin], Botanicheskie materialy, *Akad. Nauk SSSR, Bot. Inst.*, 13: 119-128.

——, 1960b, Nekotorye endofity Sakhalinskikh vodorosleĭ, I. [Some Endophytes of Algae from Sakhalin, I], Botanicheskie materialy, *Akad. Nauk SSSR, Bot. Inst.*, 13: 128-130.

——, and E. I. Blinova, 1970, Materialy raspredeleniyu i sostavu vodorosleĭ Kamchatki (Okhotskoe more) [Materials on the Distribution and Composition of Algae of Kamchatka (Sea of Okhotsk)], *Tr. Inst. Okeanol., Akad. Nauk SSSR*, 88: 298-307.

——, and N. M. Selitskaya (Vishnevskaya), 1970a, Vidovoĭ sostav, raspredelenie i zapasy fukoidov v Okhotskom more [The Composition, Distribution, and Quantities of Fucoid Algae in the Sea of Okhotsk], *Tr. Inst. Okeanol., Akad. Nauk SSSR*, 88: 281-287.

——, and N. M. Selitskaya (Vishnevskaya), 1970b, Morskaya ratitel'nost' pribrezh'ya O-va bol'shoi Shantar (Okhotskoe more) [Marine Vegetation of the Coast of Big Shantar Island (Sea of Okhotsk)], *Tr. Inst. Okeanol., Akad. Nauk SSSR*, 88: 288-297.

——, and N. M. Vishnevskaya (Selitskaya), 1968, Redkie i novye vidy vodorosleĭ dlya severnykh i zapadnykh poberezhiĭ Okhotskogo morya [Rare and New Species of Algae from the Northern and Western Shores of the Sea of Okhotsk], *Novosti sistematiki nizshikh rasteniĭ, Akad. Nauk SSSR, Bot. Inst.*, 5: 53-56.

Weinmann, F. C., 1969, Amchitka Bioenvironmental Program. Aspects of Benthic Marine Algal Ecology at Amchitka Island, Alaska, USAEC Report BMI-171-115, Battelle Memorial Institute.

——, 1968, Aspects of Benthic Marine Algal Ecology at Amchitka Island, Alaska, M. Sc. Thesis, University of Washington.

Widdowson, T., 1971a, A Taxonomic Revision of the Genus *Alaria* Greville, *Syesis*, 4: 11-50.

——, 1971b, A Statistical Analysis of Variation in the Brown Alga *Alaria*, *Syesis*, 4: 125-144.

——, 1965, A Taxonomic Study of the Genus *Hedophyllum* Setchell, *Can. J. Bot.*, 43: 1409-1420.

Widdowson, T. B., 1975, The Marine Algae of British Columbia and Northern Washington: Revised List and Keys. Part II. Rhodophyceae (Red Algae), *Syesis*, 7: 143-186.

——, 1973, The Marine Algae of British Columbia and Northern Washington: Revised List and Keys. Part I. Phaeophyceae (Brown Algae), *Syesis*, 6: 81-96.

Wilson, O. T., 1925, Some Experimental Observations of Marine Algal Succession, *Ecology*, 6: 303-311.

Wynne, M. J., 1975, Further Studies of the Delesseriaceae of Amchitka Island (Aleutian Islands), *J. Phycol.*, 11(Suppl.): 17 (abstract).

——, 1972, The Genus *Porphyra* at Amchitka Island, Aleutians, in *Proceedings of the Seventh International Seaweed Symposium*, Aug. 8–12, 1971, pp. 100-104, University of Tokyo Press.

——, 1971, Concerning the Phaeophycean Genera *Analipus* and *Heterochordaria*, *Phycologia*, 10: 169-175.

——, 1970a, Marine Algae of Amchitka Island (Aleutian Islands). I. Delesseriaceae, *Syesis*, 3: 94-144.

——, 1970b, Marine Algae of Amchitka Island (Aleutian Islands). II. Bonnemaisoniaceae, *Pac. Sci.*, 24: 433-438.

Zinova, A. D., 1970, Dopolnenie k stat'e o novom vide laminarii c O. Sakhalin [An Addition to the Comments on the New Species of *Laminaria* from Sakhalin Island], *Novosti sistematiki nizshikh rasteniĭ, Akad. Nauk SSSR, Bot. Inst.*, 6: 65-68.

——, 1965, Predstaviteli sem. Delesseriaceae (Rhodophyta) v severnoĭ chasti tikhogo okeana [The Family Delesseriaceae (Rhodophyta) in the North Pacific Ocean], *Novosti sistematiki nizshikh rasteniĭ, Akad. Nauk SSSR, Bot. Inst.*, 2: 78-97.

——, 1964, Novyĭ vid Laminaria u beregov Sakhalina [A New Species of *Laminaria* Near the Coasts of Sakhalin], *Novosti sistematiki nizshikh rasteniĭ, Akad. Nauk SSSR, Bot. Inst.*, 1: 125-126.

Zinova, E. S., 1954a, Morskie vodorosli yugo-vostochnoĭ Kamchatki [Marine Algae of Southeastern Kamchatka], *Tr. Bot. Inst., Akad. Nauk SSSR, Ser. 2: Sporovye Rasteniya*, 9: 365-400.

——, 1954b, Vodorosli Okhotskogo morya [Algae of the Sea of Okhotsk], *Tr. Bot. Inst., Akad. Nauk SSSR, Ser. 2: Sporovye Rasteniya*, 9: 259-310.

——, 1940, Morskie vodorosli Komandorskikh ostrovov [Marine Algae of the Komandorsk Islands], *Tr. Tikhookean. Kom.*, V: 166-243.

——, 1933, Vodorosli Kamchatki [Algae of Kamchatka], *Issled. Moreĭ SSSR*, 17: 7-42.

——, 1930, Vodorosli Okhotskogo morya s poberezhiĭ bol'shogo Shantarskogo ostrova [Algae of the Sea of Okhotsk Off the Shores of Big Shantar Island], *Tr. Leningrad. Obshch. Estest.*, 60(3): 81-125.

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Marine Invertebrates in Rocky Intertidal Communities

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Previous knowledge of Aleutian marine benthic invertebrates was based on few observations and collections, the history of which is summarized. In this study three belt transects (one sampled once and two sampled seven times) and two intertidal arrays (sampled twice each) of 0.25-m^2 quadrats were used for descriptive studies of intertidal communities at Amchitka Island. These communities are dominated by algae at all tidal levels. Three communities designated according to their dominant macrophytes are the Laminaria *community, the* Alaria–Hedophyllum *community, and the* Halosaccion–Fucus *community. Invertebrates in these communities are mostly inconspicuous. Despite the large proportion of North American species in the fauna of Amchitka, species that play key roles in structuring intertidal communities elsewhere on the west coast of North America are absent or in low abundance at Amchitka. Invertebrates in subtidal communities are discussed briefly. An annotated list of over 365 littoral and sublittoral invertebrate species is appended.*

Seven zoogeographical elements were recognized in the shallow-water marine fauna of Amchitka. The greatest proportion of species are North Pacific or North American in their distribution. Two oceanographic features (the Alaskan Stream and the Kamchatka Current) and one geologic feature (the Aleutian "stepping-stone" islands between Amchitka and the Asian and North American mainlands) increase the immigration rates of North American species over Asiatic species.

The effects of Cannikin were determined with the use of two intertidal arrays of fixed 0.25-m^2 quadrats (totaling 40 plots) examined twice preevent and ten times postevent (over 33 months) and an intertidal grid (control) sampled randomly once preevent and twice (over 9 months) postevent. The rate of die-off and emigration of intertidal species in maximally uplifted (as much as 1 m) areas depended on exposure to open ocean waves. Most preevent intertidal species were replaced by supralittoral fringe species.

The marine invertebrate fauna of the Aleutian Islands has received little attention beyond the initial taxonomic descriptions that have followed mainly the collecting activities of E. Wosnesenski and W. H. Dall. Except for the pioneering work of Gurjanova (1935; 1966) on Bering Island (Ostrov Beringa) and the brief description by Barabash-Nikiforov (1947) of the benthic fauna at Copper Island (Ostrov Mednyi) in the Commander Islands (Komandorskie Ostrova) (Fig. 1), little has been published on the ecology of Aleutian benthic marine invertebrates. Some ecological information can be gleaned from those systematic monographs which have included collections from the Aleutian Islands (see history of previous investigations below), but it is chiefly anecdotal and incomplete.

Here I describe some patterns of distribution and abundance of invertebrates in rocky intertidal communities at Amchitka Island, Alaska, and note some of the salient differences in community structure between these communities and other comparable North Pacific intertidal communities. Descriptive studies alone provide little insight into community organization, and they have largely been replaced by approaches of a comparative or experimental nature. I justify a descriptive approach here by pointing out the absence of a previous detailed study of Aleutian intertidal communities and by noting the peculiarities of the intertidal communities at Amchitka. Detailed descriptive studies are not necessary prerequisites for mechanistic studies, especially when the community can be observed directly. However, at Amchitka patterns of invertebrate distribution and abundance are not obvious; invertebrates are usually inconspicuous, and patterns in the distribution of populations are obscured by dominant macrophytes.

I also discuss the zoogeographical affinities of three major taxa of littoral and shallow sublittoral [to a depth of 60 m (200 ft)] invertebrates (Polychaeta, Crustacea, and Mollusca) at Amchitka and

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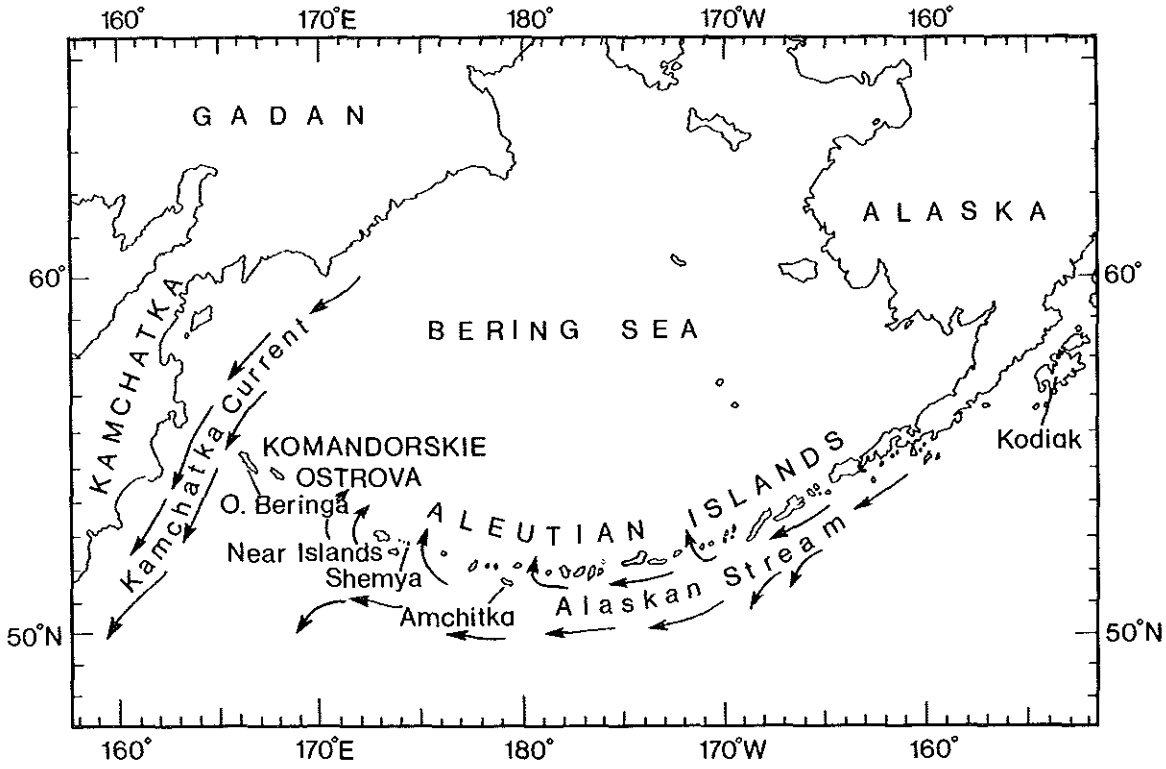

Fig. 1—Map of the northern North Pacific Ocean and Bering Sea showing the location of Amchitka Island, Alaska, the Alaskan Stream (information from Favorite, 1967), and the Kamchatka Current (information from Dodimead, Favorite, and Hirano, 1963).

describe the most destructive and long-lasting effects on some rocky intertidal communities due to uplift of the intertidal benches by the underground nuclear test, Cannikin.

PREVIOUS INVESTIGATIONS IN THE ALEUTIANS

Georg Wilhelm Steller's important contributions marked the beginning of zoological investigations in the North Pacific. We do not know whether Steller collected or described invertebrates from Bering Island, the only Aleutian island on which he set foot, because most of his collections from Bering Island and his manuscripts on invertebrates were lost (Stejneger, 1936). We do know that he collected and described invertebrates from Kamchatka, e.g., *Cryptochiton stelleri** and *Mya truncata*. Steller and those early naturalists who came after him (Merck, Sauer, Tilesius, Chamisso, Eschscholtz, and Mertens) into this region during the late eighteenth and early nineteenth centuries participated in expeditions whose primary mission was to discover and explore new lands. The opportunities for naturalists to make observations on the shores of this region were limited. When it was possible to go ashore, their attention was drawn to the more obvious flora and fauna, such as marine mammals, birds, and the more conspicuous terrestrial plants. The only publications on Aleutian invertebrates that emerged from these early expeditions were very brief descriptive accounts of the fauna of one or two islands (Sauer, 1802; Chamisso, 1821) and some taxonomic work (Chamisso and Eysenhardt, 1821; Eschscholtz, 1833).

The first real scientific documentation of Aleutian invertebrates came about the middle of the nineteenth century in the taxonomic works of Middendorff (1846; 1849a; 1849b; 1849c; 1851), Brandt (1849; 1850; 1851), and Grube (1855), which describe several species collected in the Aleutians primarily by E. Wosnesenski. Prior to Wosnesenski's excursions, which extended to Atka and Attu Islands, invertebrate collecting had been limited to the ends of the Aleutian chain, espe-

*Dall (1884) states that specimens of *Cryptochiton stelleri*, described by Steller under its Kamchatkan name "Keru," were collected by Steller on Bering Island. Dall cites as his reference Steller's *Beschreibung von dem Lande Kamschatka*; however, I could find no reference to Bering Island in Steller's description, and Middendorff (1846) lists only Peter and Paul (Petropavlovsk) Harbor in Kamchatka as the collection locality of *C. stelleri*.

cially around Unalaska in the east and the Commander Islands in the west.

The greatest contribution to our knowledge of Aleutian invertebrates has come from William H. Dall, whose assignments in the Aleutians under the U. S. Coast Survey from 1871 to 1874 enabled him to make collections on a number of islands, including Amchitka, from which invertebrates had not previously been collected. Dall subsequently described most of the species he had collected, especially the mollusks (see Boss, Rosewater, and Ruhoff, 1968). Collectively, these publications on the systematics and zoogeography of Aleutian mollusks constitute the definitive source of information on this the best known group of Aleutian invertebrates. In addition, Dall's collections have provided most of the Aleutian littoral material for a number of publications on other invertebrate groups: hydroids (Clark, 1876), barnacles (Pilsbry, 1916), isopods (Richardson, 1905), starfish (Fisher, 1911; 1928; 1930), and others.

After Dall, collecting activity was again mostly restricted to the eastern and western ends of the Aleutian chain. Investigations near the eastern end of the Aleutians have included the trawling and dredging activities of the U. S. Fish Commission steamer *Albatross* in the waters from Unimak to Umnak Islands in 1888, 1890, and 1893 and the Harriman Alaska Expedition in the vicinity of Unalaska in 1899. At the western end of the chain, the Commander Islands were visited by the *Vega* expedition under Nordenskiold in August 1879; by Stejneger under the auspices of the Smithsonian Institution and the U. S. Signal Service in 1882, 1883, and 1895; by the *Albatross* in 1892, 1895, 1896, and 1906; and by several Russian naturalists (see Gurjanova, 1935). However, some collections were made near Amchitka. They include those made by investigators on board the *Albatross* at Kiska Island in 1894 and near Semisopochnoi Island in 1906 and by V. Scheffer aboard the *Brown Bear* in 1937 at Amchitka. More recently, Newell (1950; 1951) and Yamada (1955) have published on collections from this area.

Despite all the collecting activity, very little has been published on the ecology of Aleutian benthic invertebrates. Dall (1884) and Annenkova (1934) have provided some information on the natural history of the littoral mollusks and polychaetes of Bering Island, but their publications were primarily taxonomic in nature. The studies on the distribution of algae and invertebrates at Bering and Mednyi Islands by Gurjanova (1935; 1966) and Barabash-Nikiforov (1947), respectively, represent the only published attempts to deal with the benthic communities of any Aleutian island.

PHYSICAL ENVIRONMENT

Tides

The most important phenomenon ultimately controlling the lives of most littoral invertebrates is the tidal cycle. The amplitude and frequency of tidal fluctuations determine the length of time a particular level on the shore is either submerged or exposed to atmospheric conditions, which, in turn, generally determines, directly or indirectly, whether a species can maintain a population at that level. For example, the upper limit of distribution of a particular species may be determined directly by the amount of time it is subject to the stress of desiccation; at the same time its lower limit may be set indirectly at that level below which it is excluded by marine predators or competitors more susceptible to the stresses of emersion. [There are exceptions to this generality, e.g., R. T. Paine (personal communication) finds that the mussel *Mytilus californianus* sets the upper limit of the alga *Alaria marginata.*]

Unlike the semidiurnal tides that predominate throughout the world, the tides in the vicinity of the Aleutian Islands are irregular diurnal (Plate 1 of Doty, 1957), being primarily diurnal but tending toward mixed during neap tides (for definition of terms, see U. S. Department of Commerce, 1949). Figure 2 shows representative tidal curves for March and June 1969 at Amchitka.

The tidal range at Amchitka is narrow compared with those at other locations where descriptive studies of littoral communities have been performed. For example, the diurnal range, the difference between mean higher high water (MHHW) and mean lower low water (MLLW), at South Bight, Amchitka, is 1.1 m, whereas it is 2.5 m at Three Saints Bay, Kodiak Island, Alaska, 2.4 m at Neah Bay, Wash., and 1.6 m (5.2 ft) at Monterey Bay, Calif. (U. S. Department of Commerce, 1969). The maximum tidal range at Amchitka is just over 2 m (2.1 m in 1969 at South Bight). (Computed from hourly tidal height measurements at Sweeper Cove, Adak, Alaska, 1969, which were corrected for Amchitka with the corrections published in the tide tables.)

Temperature and Salinity

McAlister (1971) has discussed several aspects of the offshore marine physical environment in the vicinity of Amchitka. Two aspects of the inshore marine environment, water temperature and salinity, were monitored during the course of our studies.

Water temperature was monitored in Constantine Harbor with 45-day recording thermographs

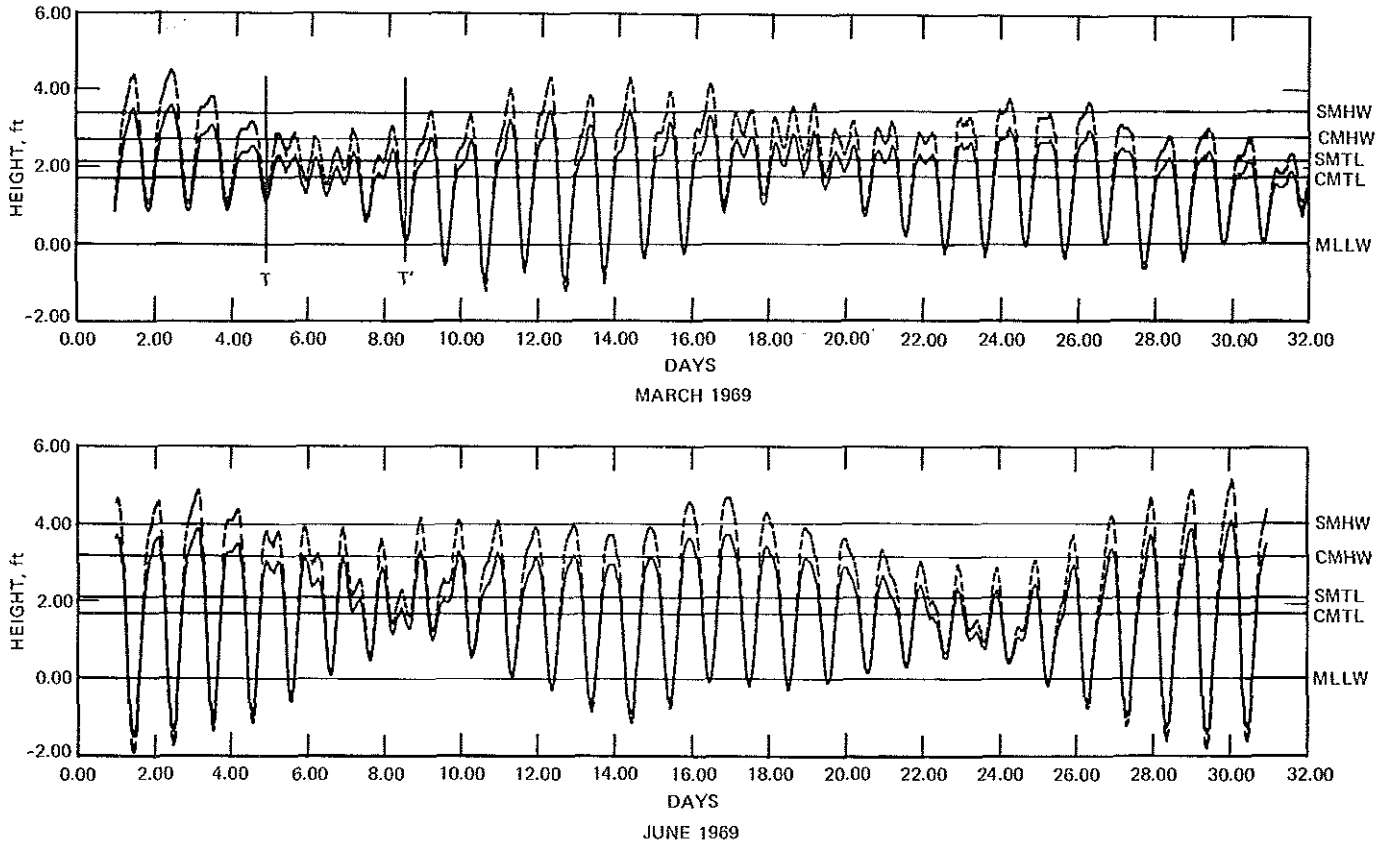

Fig. 2—Representative tidal curves for March and June 1969. The curves were constructed from hourly tidal height measurements at Sweeper Cove, Adak, Alaska, 1969, obtained from the National Ocean Survey. The hourly tidal heights were corrected for Amchitka with the use of the Constantine Harbor (c) and South Bight (s) corrections published in the tide tables. The corrections are mean values of range and tidal planes computed from automatic tide gauge records. The value for Constantine Harbor on the Bering Sea side of Amchitka is based on a 6-month record by automatic tide gauge, August 1946 through January 1947. The value for South Bight on the Pacific Ocean side is based on a 6-day record by automatic gauge from June 29 to July 5, 1945.

hung approximately 6 m (20 ft) below mean tide level beneath a dock. Figure 3 shows the mean, maximum, and minimum monthly temperature variability for Constantine Harbor based on thermograph data (32 tapes) collected intermittently from 1968 to 1973.

The curve inset in Fig. 3 shows the same water temperature characteristics as the main figure but it is drawn from sea-surface isotherms shown for the vicinity of Amchitka in U. S. Naval Oceanographic Office Publication on Sea Surface Temperatures of the North Pacific Ocean (1969). The curve of mean water temperatures for Constantine Harbor differs very little from that based on Naval Oceanographic Office data except that mean summer temperatures were lower. The position of the thermograph 6 m (20 ft) below the surface may have influenced the readings. Variability in the extreme water temperatures at Constantine Harbor, for the most part, falls within the range for the U. S. Naval Oceanographic Office data. Surface temperatures of sea water over the intertidal rocky benches show a greater variability than those recorded in Constantine Harbor. Temperatures taken (178) of the water over the bench show a low of 1.1°C in January 1970 at Square Bay and a high of 12.1°C in June 1970 at Makarius Bay.

Samples of surface sea water for salinity analysis were taken in citrate of magnesia bottles concurrently with surface temperature readings at our study sites. Samples were usually taken on an incoming tide at a water level between mean lower low water (MLLW) and mean tide level (MTL). The analysis was done on a laboratory salinometer at the Department of Oceanography, University of Washington. Salinities at the study sites remained, for the most part, between 32 ‰ and 34 ‰. Extremely low salinities were often recorded at Makarius Bay on days with onshore winds. The study site at Makarius Bay is less than 100 m from

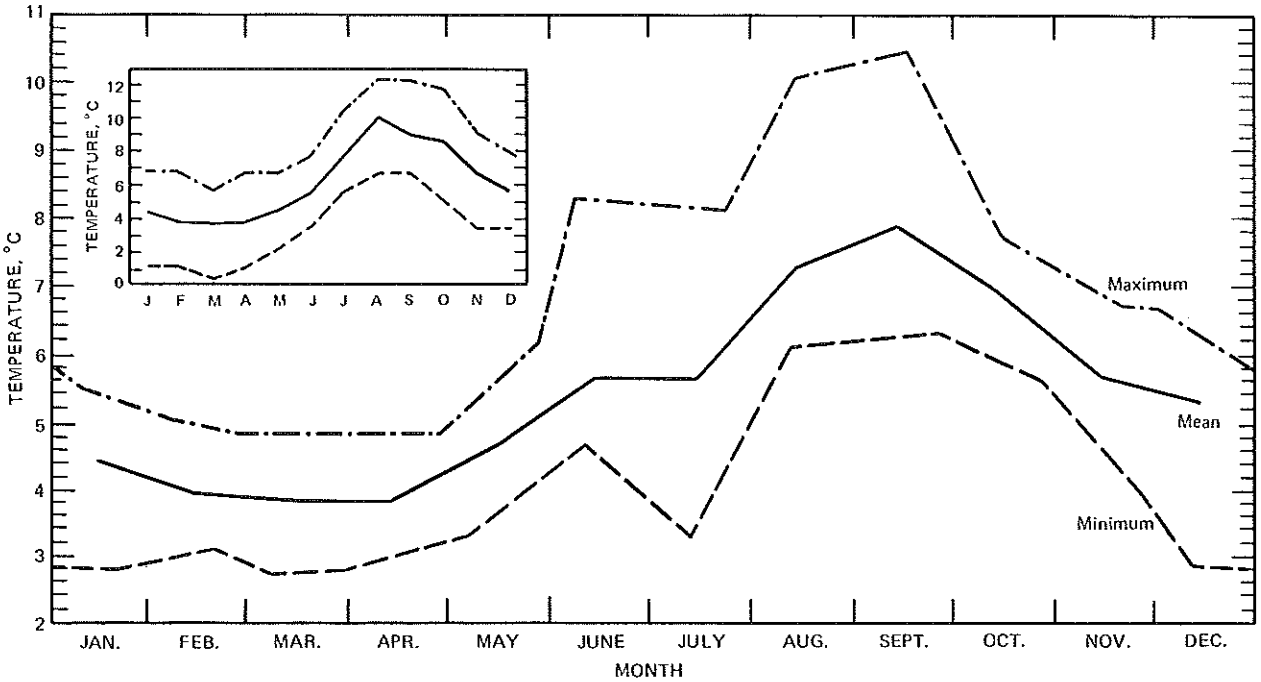

Fig. 3—Water temperatures at Constantine Harbor, Amchitka Island. Records are from 32 recording thermograph tapes taken intermittently from April 1968 through January 1972. Inflections in the curve of means reflect variability resulting from few tapes. Minimum and maximum values are plotted opposite the time of month at which they were recorded. Inset shows the same temperature characteristics based on sea–surface isotherms shown for the vicinity of Amchitka in U. S. Naval Oceanographic Office Special Publication 123.

the mouth of a short stream draining a 10-ha (25-acre) lake (Clevenger Lake). Dye releases at the mouth of the stream indicate that, when onshore winds prevail, much of the stream's effluent is swept south nearshore over the bench.

Climate

The stresses of the physical environment are most severe on marine organisms when they are exposed during low tides. Aspects of the atmospheric climate which are important to these organisms are air temperature, precipitation, insolation, relative humidity, and wind. The following discussion is based on the climatological data of Armstrong (1971; Chap. 4, this volume), who has summarized the surface weather observations of the U. S. Department of the Air Force (Army Air Corps before 1947) at Amchitka during the period February 1943 through June 1948.

As is characteristic of maritime environments, the mean daily and mean annual ranges in air temperature (3.9°C or less and 9.4°C, respectively) are relatively narrow at Amchitka. However, my records from thermographs placed intertidally show that the range in temperature (from submersion to emersion) to which intertidal organisms on Amchitka are exposed during a single tidal cycle may be as great as the annual range in mean air temperature at Amchitka. Glynn (1965) recorded temperatures in the *Endocladia–Balanus* association at Pacific Grove, Calif., for an 8-hr period in September 1961 and found that the range between the highest and lowest of his in situ measurements on exposed rock surface was greater than the range between the mean monthly maximum (September) and minimum (December) air temperature for the year at that locality (see also Hedgpeth and Gonor, 1969).

Severe osmotic stress occurs when emersed intertidal organisms are exposed to heavy rain. However, heavy rains are infrequent at Amchitka; the mean annual precipitation is only 83 cm, and the average number of days with greater than 1 cm precipitation is only 16. Light rain benefits intertidal organisms by reducing desiccation rates.

Other aspects of the maritime climate that promote low rates of desiccation in the intertidal area are a cloudy sky, high relative humidity, and onshore wind. The total frequency of broken and overcast skies at Amchitka is at least 70% every month of the year. Also, heavy cloud cover and fog are most frequent in the summer (90 to 95% and 30 to 52%, respectively) when low tides occur in daylight hours (Armstrong, Chap. 4, this volume).

There is no published summary of relative humidity at Amchitka, but at Shemya Island, 180 miles (290 km) west of Amchitka, the mean monthly relative humidity is 80% or more for all months (U. S. Department of Commerce, 1971).

Winds increase desiccation rates by increasing evaporation; however, onshore winds increase wave splash and sea spray and, if strong enough, may even prevent complete tidal ebbing. Winds from the southwest prevail during the summer; thus desiccation rates of intertidal organisms along the Pacific coast of Amchitka with its southerly aspect are ameliorated during daylight low tides.

Substrate

Powers, Coats, and Nelson (1960) and Gard (Chap. 2, this volume) describe the geology of Amchitka. The general map of the geology of Amchitka in Powers et al. (1960) indicates that the so-called Banjo Point formation, described as "bedded marine sandstone, conglomerate, tuffaceous shale and some lapilli tuff of basaltic composition," forms the substratum of all the study areas to be discussed in this chapter. However, in some areas, especially at Rifle Range Point, the substrate is highly indurated.

METHODS

Transects and Intertidal Arrays

Study Sites. Two intertidal belt transects previously established in March 1968 by F. C. Weinmann at Makarius Bay (T_1) and Square Bay (T_2) for studies of algal ecology were selected as initial benthic invertebrate study sites (Fig. 4). In July 1969 I established a third transect at Rifle Range Point (T_4) (T_4 is not the T-3 of Lebednik and Palmisano, Chap. 17, this volume), and in August 1970 P. A. Lebednik established intertidal arrays (IA-2 and IA-3) of 0.25-m^2 quadrats on the Bering Sea side of the island. These five study sites provided data on invertebrate distribution and abundance from sheltered and exposed areas on both coasts. On the Pacific Ocean side, T_1 is in a sheltered area and T_4 is an exposed site. On the Bering Sea side, T_2 is sheltered, IA-3 is slightly less sheltered, and IA-2 is exposed. The azimuths and profiles of the transects and the elevations of the plots in the arrays were fixed by standard surveying techniques. All measurements of elevations were subsequently related to mean lower low water (MLLW) for Amchitka by a professional surveying crew. The true azimuth and length of each transect are given in Table 1. In addition to sampling these five main study sites, I made observations of and collections from over 300 additional plots at these and 12 other intertidal sites (Fig. 4). Most of the time I spent at Amchitka (432 days) was from June to September, but I have made observations there in every month except November.

Sampling Procedures. Each of the three transects was divided along its length into sections on the basis of substrate or dominant algal cover. A minimum of two 0.25-m^2 plots judged to be typical of each section were selected for sampling. The algal canopy of each plot was photographed and then removed. As the fronds were removed, individuals of each species of invertebrate epifaunal on them were identified and counted. The plot was photographed again. This second photograph was used to determine the percent cover of algal understory and the relative abundance of such invertebrates as *Halichondria panicea,** an encrusting sponge. The number of individuals of each of the larger macroinvertebrate species was then recorded. This number was combined with the individual counts of species epifaunal on the fronds of the algal canopy. Invertebrates that were too small and too numerous to count over the whole plot were subsampled with a 5-cm(2-in.)-diameter circular ring. Everything within the ring was removed down to bare rock. The number of subsamples taken varied with the heterogeneity of the algal understory and substrate cover. It was sometimes necessary to extrapolate counts of large invertebrates from subareas of a plot when the plot was threatened with imminent tidal inundation or contained one or two species too numerous to count completely in the time available. Subsamples and representatives of unidentified species were removed to the laboratory where they were fixed in 10% neutral-buffered Formalin. The subsamples were sieved through a 1-mm sieve, sorted, and the animals identified.

Most invertebrates were initially identified from the literature. When possible, representative specimens were compared with museum specimens or sent to specialists for identification or verification (see the appendix).

Transects T_1 and T_2 were sampled in winter, early spring, late spring, summer, and early fall (Table 1). I did not sample the same quadrats on different dates (Figs. 7, 10, and 12 show the locations of quadrat centers sampled on dates other than August–October 1969 at Square Bay). Because of the difficulty of identifying and count-

*The appendix contains a partial list of invertebrates collected at Amchitka including the authority and date of the original description for each scientific name.

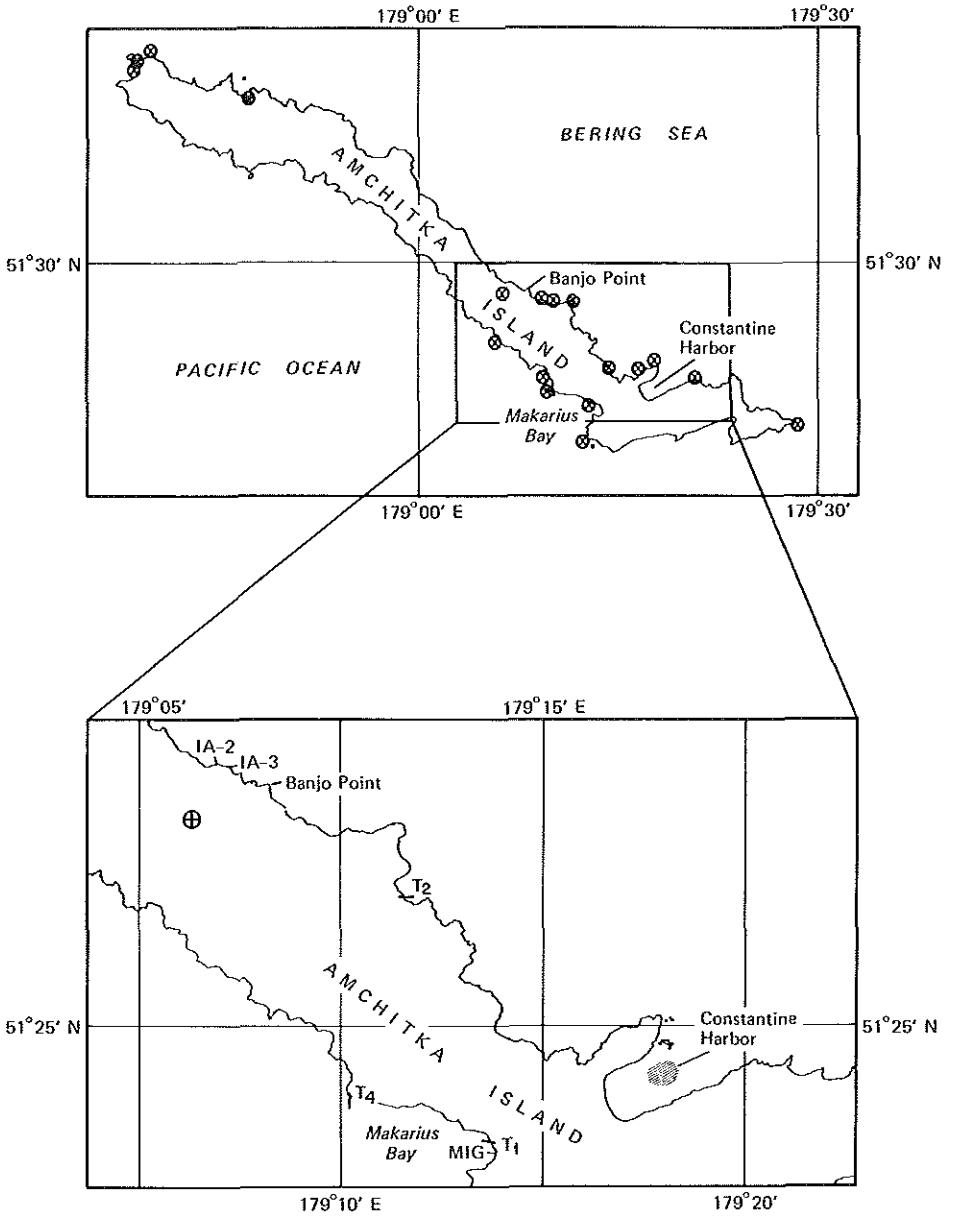

Fig. 4—Maps of Amchitka Island showing intertidal collecting areas (⊗, upper map) and major study sites, Cannikin surface zero (⊕) and area of *Chionoecetes bairdi* catches (shaded area, lower map).

ing small invertebrates in situ in the dark in early fall and winter, data from T_1 and T_2 are inadequate for determining seasonal variability in invertebrate abundance. Seasonal data were used only to refine the distributional limits of invertebrates. [If a species was recorded at a position along the transect other than one of those sampled in August–October 1969 (but within the same community) in a different season and there was no a priori reason for not expecting it at that position in August–October 1969, its distribution was extended accordingly.] I found it impossible to continue sampling more than one control when I began the study of the effects of Cannikin (see below); the transects were abandoned after March 1970.

In August 1970 two intertidal arrays (IA-2 and IA-3) of 0.25-m^2 quadrats were established by Lebednik (Lebednik and Palmisano, Chap. 17, this volume) on the Bering Sea coast of Amchitka (Fig. 4). Forty quadrats (25 at IA-2 and 15 at IA-3) were placed in patches of more or less uniform algal cover and distributed over the surface of the intertidal bench so that all major algal zones were represented. Each plot was marked in the center and at two corners with flags of polypropylene rope nailed to the bench surface with concrete nails. When data collection on the

Table 1—Azimuths, Lengths (or Size), and Sampling Dates of Three Transects and One Intertidal Grid and Sampling Dates for Two Arrays at Amchitka Island

Study site	Azimuth	Length, m	Sampling dates	Number of plots	
				T_1	T_2
Makarius Bay (T_1)	308°02′ True	61.0	Aug. 7–10, 1968*	12	14
			Jan. 1–2, 1969	3	5
			Mar. 24–26, 1969	7	11
			June 12–15, 1969	8	8
Square Bay (T_2)	098°58′ True	74.1	Aug. 25 to Oct. 17, 1969	16	15
			Jan. 3–12, 1970	7	7
			Mar. 12–16, 1970†		
Rifle Range Point (T_4)	179°35′ Mag.	78.4	July 30 to Aug. 24, 1969	13	
				IA-2	IA-3
IA-2 and IA-3			Aug. 15–18, 1970	25	6
			Sept. 6–12, 1971	22	15
			Dec. 2–7, 1971	13	6
			Feb. 21–25, 1972	13	7
			Apr. 15–26, 1972	22	13
			June 14–19, 1972	22	13
			Aug. 2–12, 1972	21	12
			Oct. 22–24, 1972	18	12
			Apr. 13–20, 1973	22	12
			Aug. 22 to Sept. 2, 1973	21	11
			May 22–27, 1974	20	12
			Aug. 27–28, 1974	22	12
		Size, m^2			
Makarius Bay intertidal grid	x 192°55′ True y 282°55′ True	3717.5 (61-m square)	Oct. 7–12, 1971	12	
			Feb. 20–24, 1972	11	
			Aug. 18–22, 1972	11	

*Both T_1 and T_2 were visited during each time span through March 1970.

†General observations and physical surveying were done during this period; no plots were sampled.

algae in each quadrat was completed (see Lebednik and Palmisano, Chap. 17, this volume), the number of individuals of the larger macrofaunal invertebrate species (those retained by a 2-mm sieve) were recorded, and the percent coverage of all colonial species within each plot was estimated by visually bisecting the plot into equal-sized rectangles and then subdividing these rectangles into even smaller equal-sized units until an estimate could be gained. It was impossible to obtain consistently accurate counts of individuals of the smaller macrofauna (the majority of whose adults would be retained by a 1-mm sieve) owing to the dense algal cover on most plots, especially in the *Halosaccion—Fucus* community. In August 1970 plots that contained almost exclusively these tiny abundant species were subsampled with an 8-cm-diameter, 1.4-cm-deep circular ring in a manner similar to that used to subsample the quadrats on the transects. However, because of the effect on subsequent observations of sampling without replacement on the same plots, subsampling was stopped after August 1970. Thereafter only semiquantitative data were collected on small abundant species. Counts of individuals per species were made twice (August 1970 and September 1971) prior to Cannikin. Postevent counts began 1 month after the test and continued on a bimonthly schedule for 10 months. Thereafter counts were made at 17, 22, 30, and 33 months postevent. Rockfalls due to Cannikin buried seven plots (five at IA-2 and two at IA-3). So that the loss of these plots could be compensated for, two stations were added at IA-2 in February 1972. Table 1 gives sampling dates and the number of plots sampled for each date for IA-2 and IA-3. An intertidal grid established at Makarius Bay for another study acted as the control.

Intertidal Grid

A stratified random sampling scheme with major algal zones as strata was adopted for sampling populations of invertebrates at Makarius Bay. A 200-ft(61-m)-square grid was laid out with standard surveying equipment to fix the azimuths of the axes. Each axis was then divided along its length into 10-ft (3.1-m) intervals, each of which was marked with a flag of polypropylene rope or surveyor's flagging nailed to the bench surface with a concrete nail and washer. These markers facilitated the procedure for mapping the major algal zones within the grids and helped in locating the positions of the plots to be sampled.

Mapping of Algal Zones. The procedure for mapping the major algal zones was as follows: A surveyor's tape was stretched out the width of the grid in a direction perpendicular to one of the grid axes from one of the marked points along the axis. The algal zone within which the tape intersected the axis was recorded. I then walked along the tape and recorded the sequence and widths of the major algal zones where they were intersected by the tape. The tape was stretched tight before each measurement was taken. This procedure was repeated for the remainder of the marked points along the same axis and all the points along the perpendicular axis. Forty runs were made on the grid. The runs were reproduced to scale on graph paper as lines whose segments represented segments of the surveyor's tape which passed over a particular algal zone. By connecting the points that marked the boundaries of the algal zones along the line segments, I obtained a map of the distribution of the major algal zones within the grid. When there was doubt about the position of the boundaries, as in areas of irregular topography where algal zones changed rapidly and irregularly, the map was compared directly with the algal distribution in the field.

The algal map was used to determine the allocation of sample size within strata (algal zones). After the map had been drawn up, the relative areas of each algal zone within the grid were determined with a compensating polar planimeter. The number of quadrats allotted to each stratum was proportional to the relative area of that stratum in the grid.

The coordinates of each plot were taken from a random-number table and plotted on the map of the grid. The numbers taken from the table represented distances (in meters) from the grid origin along the axes. Coordinates were taken in this manner until the sample size quota for all the algal zones was met. If the quota of one algal zone was filled before the others, coordinates that subsequently fell in that zone were ignored.

Quadrats were positioned in the field by measuring the distance of one coordinate along one axis (usually that axis parallel to the shore) and then stretching a surveyor's tape in a perpendicular direction to a length equal to the other coordinate. Perpendicularity was determined with a Brunton pocket transit. The length on the surveyor's tape corresponding to the second coordinate marked the center of the quadrat to be sampled.

Quadrats with a surface area of $1/16$ m^2 were used to sample the grid. As each quadrat was positioned, a photograph was taken to record the percent cover of the canopy-forming algae. The fronds of these algae falling within the quadrat were then removed and placed in a polyethylene bag, and the plot was rephotographed to record the percent cover of understory algae, holdfasts of canopy algae, and colonial invertebrates, such as encrusting sponges. The plot was then stripped to bare rock with paint scrapers, stone chisels, and modified spoons, the contents were placed in the polyethylene bag with the canopy algal fronds, and the bag was labeled. The plot was then marked at one corner with a concrete nail, washer, and surveyor's flagging for future reference. When all plots had been sampled in each season, their elevations were related (using standard surveying techniques) to points whose elevations were determined by a professional surveying crew. The samples were removed to the laboratory for processing. Time did not permit full processing of the samples at the field station; so most samples were fixed in 10% neutral-buffered Formalin and shipped to Seattle. Makarius Bay was sampled in the fall 1 month prior to Cannikin and in late winter and late summer following Cannikin (Table 1). No obvious changes (i.e., no uplifting) had occurred on the grid after Cannikin, and therefore it was not remapped.

Each sample was screened successively through standard screens with mesh openings of 4, 2, and 0.991 mm and the invertebrates were separated for species abundance counts. All invertebrates were counted and preserved in 70% isopropyl alcohol containing 2% glycerin. Invertebrates retained by the 0.991-mm screen were counted under a dissecting microscope. Invertebrates of the major taxonomic groups Mollusca, Echinodermata, and Crustacea, excluding Amphipoda, were identified to species, and the individuals of each of these species were counted. Invertebrates of minor phyla were identified to species when possible.

Sources of Bias and Error. The grid at Makarius Bay was established primarily to act as a control for another study. Because the sample surfaces ($1/16$ m^2 versus $1/4$ m^2) and the sampling schemes for Makarius Bay and IA-2 and IA-3, respectively, were different, the Makarius Bay grid was not a proper control for the plots at IA-2 and IA-3. However, limits on field time and resources precluded the maintenance of two controls. In view of the striking changes that occurred at IA-2 and IA-3 following Cannikin, the results would probably not have been different had an additional control been added at Makarius Bay using a sampling scheme and sample surface identical to that at IA-2 and IA-3. Both sample surfaces and associated data-collection procedures were used at Makarius Bay, and those used on the intertidal grid always turned up more species and individuals in a given plot despite the reduced sample surface and would be expected to be at least as sensitive to changes in species abundance patterns as that used at IA-2 and IA-3 even with the introduced spatial variability in abundances due to random sampling.

Other sources of error are as follows:

1. The abundances of certain highly motile forms, e.g., gammarids, capable of withdrawing deeply into the holdfast systems of algae when emersed or of escaping unnoticed from quadrats during sampling were probably often underestimated as compared with the less active species with the use of both of the sampling schemes described above.

2. The abundances of the smaller forms of both the large (retained by a 2-mm or larger mesh screen) and small (retained only by a 1-mm screen) size classes were probably underestimated as compared with the larger forms, depending on the sampling procedure.

3. Small species about the same size may be under- or overrepresented because different growth forms have different probabilities of retention by the sieves.

4. Since invertebrates were assigned to communities on the basis of their distributions as determined by sampling of emersed populations, we do not have a completely accurate picture of the composition of these communities or of the spatial relationships between species when the communities are immersed and fully functioning. Nevertheless, although the spatial relationships of the motile invertebrates may change slightly with the tide, extensive vertical migrations are precluded by the essentially horizontal nature of the intertidal benches. Moreover, the dense cover of macroscopic algae probably reduces the stresses associated with emersion and thus reduces the necessity for organisms to move to lower levels with the receding tide. The spatial relationships among sessile organisms, such as barnacles, of course, do not change with the tide.

5. Because of the dense algal cover on the IA-2 and IA-3 plots prior to Cannikin, it was often difficult to get complete counts of even the larger macrofauna. As the algal cover died and sloughed off, blew away, or was washed away in storm waves after Cannikin, invertebrates became much easier to see, and species counts could be made easily. Therefore the probability of underestimating the preshot abundances of species in the IA-2 and IA-3 plots was much greater than that for the postshot counts.

Three sources of error may have affected my zoogeographic analyses. The first results from the tendency of early taxonomists to describe more species than are valid. Thus some species of mollusks described by Dall from the Aleutians may prove to be synonymous with previously described forms as have, for example, some of the tellinids he described (Coan, 1971). This type of error would bias my zoogeographic analysis by erroneously inflating the number of endemic species.

A second and opposite source of error results from the tendency of students newly initiated to a fauna to force their specimens into existing keys, thereby missing new species and wrongly assigning specimens to more widely distributed species. I have made every effort to have my identifications verified by specialists (see the appendix), therefore the above sources of error are probably negligible.

Another source of error results from an incomplete knowledge of the distributions of some species. Because of the relative inaccessibility of the Russian and Japanese literature, my determination of the relative contributions of Asiatic and North American faunas to the benthic invertebrate fauna of Amchitka may be biased. The recent papers of Spassky (1961) and Golikov and Kussakin (1962), which include extensive lists of invertebrates occurring on the shores of Kamchatka and the Kurile Islands, help reduce the magnitude of this source of error.

RESULTS AND DISCUSSION

Intertidal Communities

Assemblages of marine intertidal species have been treated traditionally as "random aggregations of species sharing similar physical tolerances" (Dayton, 1971). This viewpoint particularly characterizes the literature on intertidal zonation (see

reviews by Lewis, 1964; Ricketts, Calvin, and Hedgpeth, 1968; Stephenson and Stephenson, 1972), yet recent studies have demonstrated conclusively that these aggregations of species are indeed organized systems of species, i.e., communities, whose structure is based on dynamic interactions, including competition and predation (Connell, 1961a; 1961b; 1970; Paine, 1966; 1974; Dayton, 1971; 1975).

The definition of community used here is an operational one: "a group of species which are often found living together" (Fager, 1963). Communities are designated following the dominance—constancy school (Stephenson, 1973) with algae as characterizing species. Under this school identification of communities is subjective, and boundaries between communities are frequently artificial; subdominants (in this case invertebrates) often do not conform to the distributional patterns of dominants (Stephenson, 1973). This system of community classification is used here for the following three reasons:

1. Marine intertidal communities can be observed directly, although observation usually takes place when species are emersed and less active and fewer interactions are occurring. Still, not all species interactions in the intertidal area cease at low tide, and the spatial relationships between most species probably do not change drastically whether the community is immersed or emersed. Since these communities can be observed directly, numerical classification (Stephenson, 1973) is unnecessary.

2. The dominance—constancy school is particularly applicable to Amchitka because, depending on tidal level, exposure, and shore topography, one or another dominant algal species essentially forms a pure stand (see Lebednik and Palmisano, Chap. 17, this volume).

3. Our knowledge of the interactions structuring marine invertebrate communities at Amchitka is meager; species known to play important roles in structuring rocky intertidal communities elsewhere in the North Pacific (Paine, 1966; 1974; Connell, 1970; Dayton, 1971) are either absent or in low abundance. We simply do not know enough about the species interactions at Amchitka to base our designation of invertebrate communities on them.

The following rocky intertidal communities were identified: (1) the *Laminaria* community, (2) the *Alaria—Hedophyllum* community, and (3) the *Halosaccion—Fucus* community. All these communities are within the region of the midlittoral and sublittoral fringe zones of Stephenson and Stephenson's (1949) universal scheme. The supralittoral fringe was not sampled quantitatively at any of the five main study sites, although species characteristic of it are listed in the appendix.

Drift-kelp windrows are also a conspicuous feature on the shore at Amchitka. These are made up chiefly of reducer and decomposer organisms, including the amphipod (*Orchestia* sp.), coelopid flies, and nematodes (Chew, 1969). Judging from the great biomass of dead and dying algae periodically washed ashore and the high rate at which it is broken down, these windrows probably contribute a great deal to the productivity of the neritic and nearshore benthic environment in the form of dissolved organic matter, detritus, and food organisms. My observations and those of others indicate that these drift-kelp windrows provide an important food resource for the Norway rat (*Rattus norvegicus*) and probably also seasonally important to several species of birds, e.g., Winter Wrens (*Troglodytes troglodytes*), Rock Sandpipers (*Calidris ptilocnemis*), and Ruddy Turnstones (*Arenaria interpres*).

Where do invertebrates fit in this scheme of communities? Species that characterize a particular community should show high fidelity for that community (i.e., occur there more frequently than in other communities) and show a high constancy, or frequency, in that community (i.e., occur in a large proportion of the samples from that community) (Fager, 1963). Invertebrates were "assigned" to that community to which they were most faithful. Fidelity (f) was measured as the proportion of quadrats containing the species that was in a particular community. A species was considered to be faithful to a particular community if one-half or more of the quadrats containing the species were in that community. Constancy (c) was measured as the proportion of quadrats from a particular community that contained the species.

Species in each community were ranked on fidelity and constancy (1, lowest rank for both categories). Large species were ranked separately from small species. An average of the ranks ($\bar{R}$) of these two statistics for each species was then calculated after the ranks were corrected, if necessary, for inequality in the highest ranks; so fidelity and constancy have equal weight in the rank ($\bar{R}$) of each species. Species were then listed in order of decreasing $\bar{R}$. Species with equal $\bar{R}$ were listed in order of decreasing abundance. Species with the highest ranks ($\bar{R}$) (five large species and five small species) were then selected as characteristic of each community.

Laminaria Community. The *Laminaria* community has its greatest development at the seaward edges of the intertidal benches; it is also found in channels that cut the benches, but its upper limit is

lowered as one progresses shoreward, where it may be completely replaced by the *Alaria–Hedophyllum* community. The *Laminaria* community is dominated by *Laminaria longipes* at all degrees of exposure. It ranges from –3 or –5 m (Lebednik and Palmisano, Chap. 17, this volume) to as high as +0.61 m in exposed situations.

Of the 142 species of invertebrates (excluding those not identified to species) found at the five main study sites, 110 were found in the *Laminaria* community. The average number of species per 0.25 m^2 among the large species was also greater in the *Laminaria* community (13 species) than in the next richest community (*Alaria–Hedophyllum*, 11 species). Considering data from transects T_2 and T_4 only and including small species, the difference between these two communities is more pronounced (42 vs. 32 species per sample). The number of species that were faithful (f greater than 0.5) to the *Laminaria* community (73 species) far exceeded that for the other two communities (19 species and 17 species for the *Alaria–Hedophyllum* and *Halosaccion–Fucus* communities, respectively).

Within the *Laminaria* community species counts were greatest among the Polychaeta (30 species) and the Gammaridea and Gastropoda (19 species each). Figures 5 and 6 show the distributions and relative abundances of species in the *Laminaria* community for two transects representative of an exposed location [Rifle Range Point (T_4)] (Fig. 7) and a sheltered one [Square Bay (T_2)] (Fig. 8).

The ten most characteristic invertebrates of the *Laminaria* community are listed in Table 2 along with several statistics suggestive of their role in community structure (see Fager, 1963). Species are listed in order of decreasing mean rank ($\bar{R}$) for each size class (large-size class on top). They include a sponge, four polychaetes, two echinoderms, two gastropods, and an amphipod.

Other species among the large-size class with large rank ($\bar{R}$) included *Ophiopholis aculeata* (10.5), *Henricia leviuscula* (10.5), *Aleutiaster schefferi* (10), *Natica clausa* (9.5), and *Halichondria panicea* (8). The first four species showed high fidelity for the *Laminaria* community (f = 1.0, 1.0, 0.72, and 0.86, respectively), but they were rare. The sponge *Halichondria panicea* showed a high constancy (c = 10/15) for the *Laminaria* community, but it also occurred frequently in the *Alaria–Hedophyllum* community; therefore f was small (0.53).

Three of the large-size-class species in Table 2 (*Strongylocentrotus polyacanthus, Notoacmea scutum,* and *Leptasterias aleutica*) had comparable abundances and did not differ greatly in average rank ($\bar{r}$, see Table 2 for a definition of this statistic) or dominance. *Mitrella amiantis* by contrast was clearly more abundant and had a higher average rank and greater dominance than the other three species. However, because *M. amiantis* is much smaller than an average individual of the above species, it is clearly not dominant in biomass. Statistics based on abundance were not calculated for the sponge *Scypha compressa* because abundance was measured as percent cover, not numbers of individuals.

The assignment of characteristic species status to the five species of the small-size class is tentative because the number of plots sampled for the small species in the *Laminaria* community (3) is extremely small. Three species, *Demonax* sp., *Autolytus beringianus,* and *Cercops compactus,* were found in only one sample, but that sample occurred in the *Laminaria* community, making their fidelity 1.0; so their rank ($\bar{R}$) was consequently high. Several other species, including *Balcis randolphi, Syllis (Typosyllis)* sp., and *Dexiospira* sp., occurred frequently in the *Laminaria* community at Makarius Bay and IA-2, but data from these two localities are not complete for all species and were not included in the calculations for the small species. If these data are considered, *Balcis,* especially, shows both high constancy in (0.73) and high fidelity for (0.80) the *Laminaria* community.

The sea urchin *Strongylocentrotus polyacanthus* has potentially the most important role in structuring the *Laminaria* community of all the invertebrates found there. Descriptive–comparative studies (Estes and Palmisano, 1974; Chap. 22, this volume) of islands with low (Amchitka and Adak) and high (Shemya and Attu) urchin biomass indicate that this species can have a profound effect on populations of lower intertidal and shallow subtidal algae and probably other invertebrates as well. These authors argue that overexploitation of urchins by sea otters (*Enhydra lutris*) reduces considerably the impact of the sea urchin at Amchitka. They contend that, in the presence of otter predation, urchin individual size and population biomass are reduced, permitting benthic algae and associated invertebrates to flourish.

Other species that may be important to the structure of the *Laminaria* community are the starfish *Leptasterias alaskensis* and *L. aleutica* (see taxonomic note in the appendix). Preliminary feeding observations on these species in the field indicate that they are generalist predators that feed mostly on gastropods and peracaridan crustaceans (personal observations; Palmisano, 1975). These two species were not distinguished during these

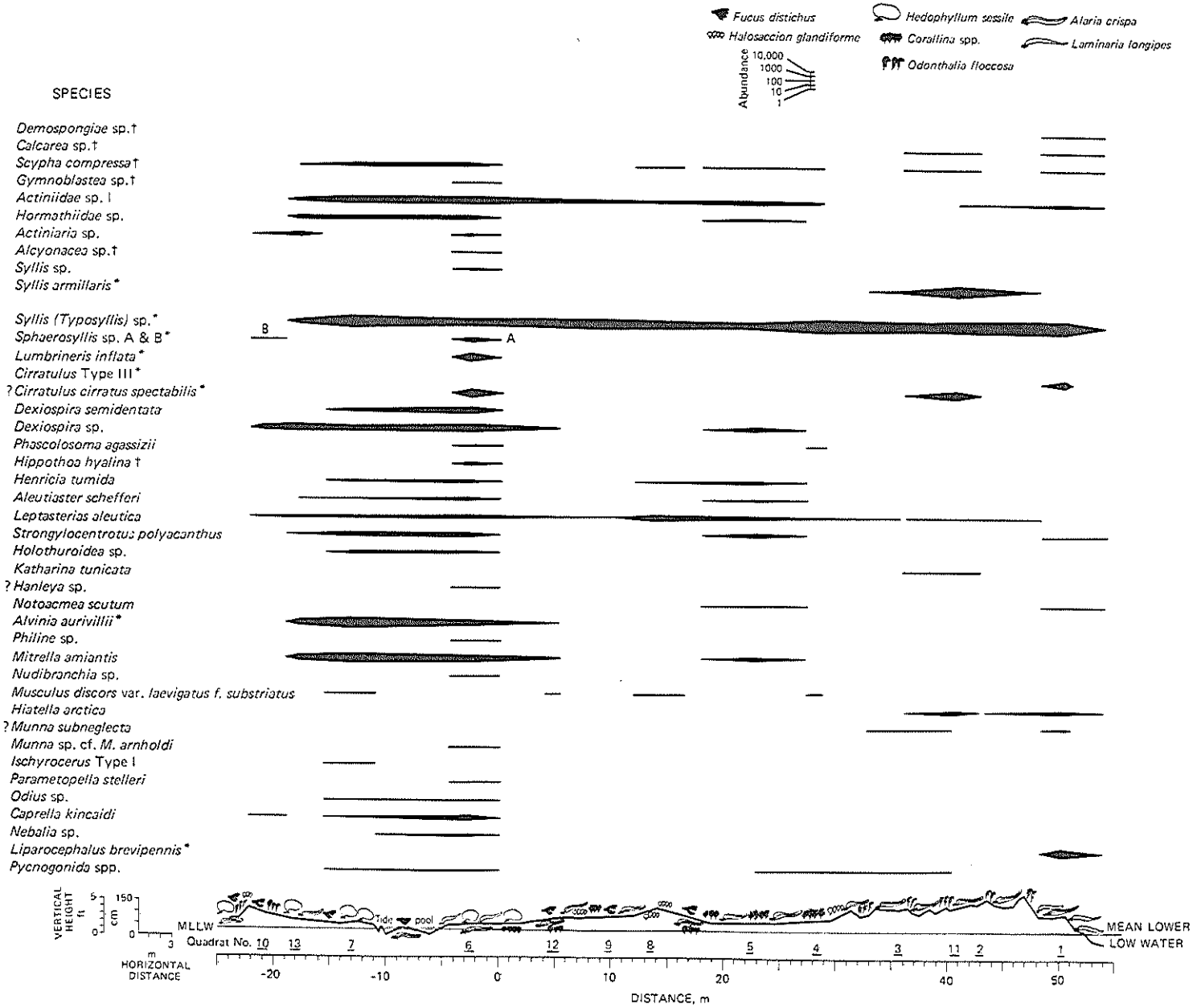

Fig. 5—Distributions and abundances of species that were most abundant in the *Laminaria* community at Rifle Range Point (T_4), Amchitka Island, in August 1969. Abundances are numbers of individuals per 0.25 m^2 except as noted. *, Estimates based on two or more subsamples of 19.6 cm^2. †, Scale is in units of percent cover.

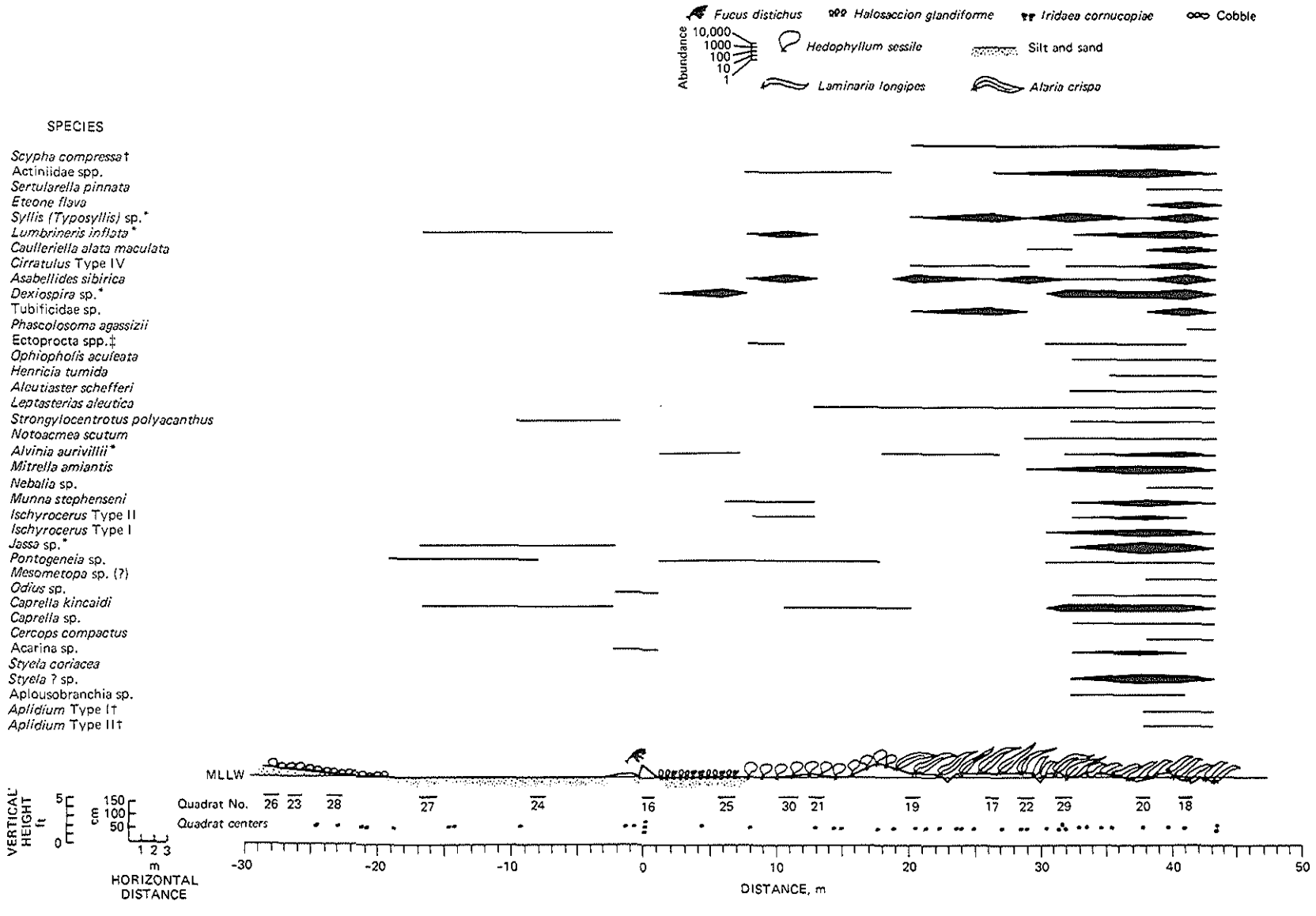

Fig. 6—Distributions and abundances of species that were most abundant in the *Laminaria* community at Square Bay (T_2), Amchitka Island, in August and September 1969. Abundances are numbers of individuals per 0.25 m^2 except as noted. Centers of quadrats sampled on dates other than August and September 1969 are shown below the quadrat numbers of August and September 1969. *, Estimates based on two or more subsamples of 19.6 cm^2. †, Scale is in units of percent cover. ‡, Presence data only.

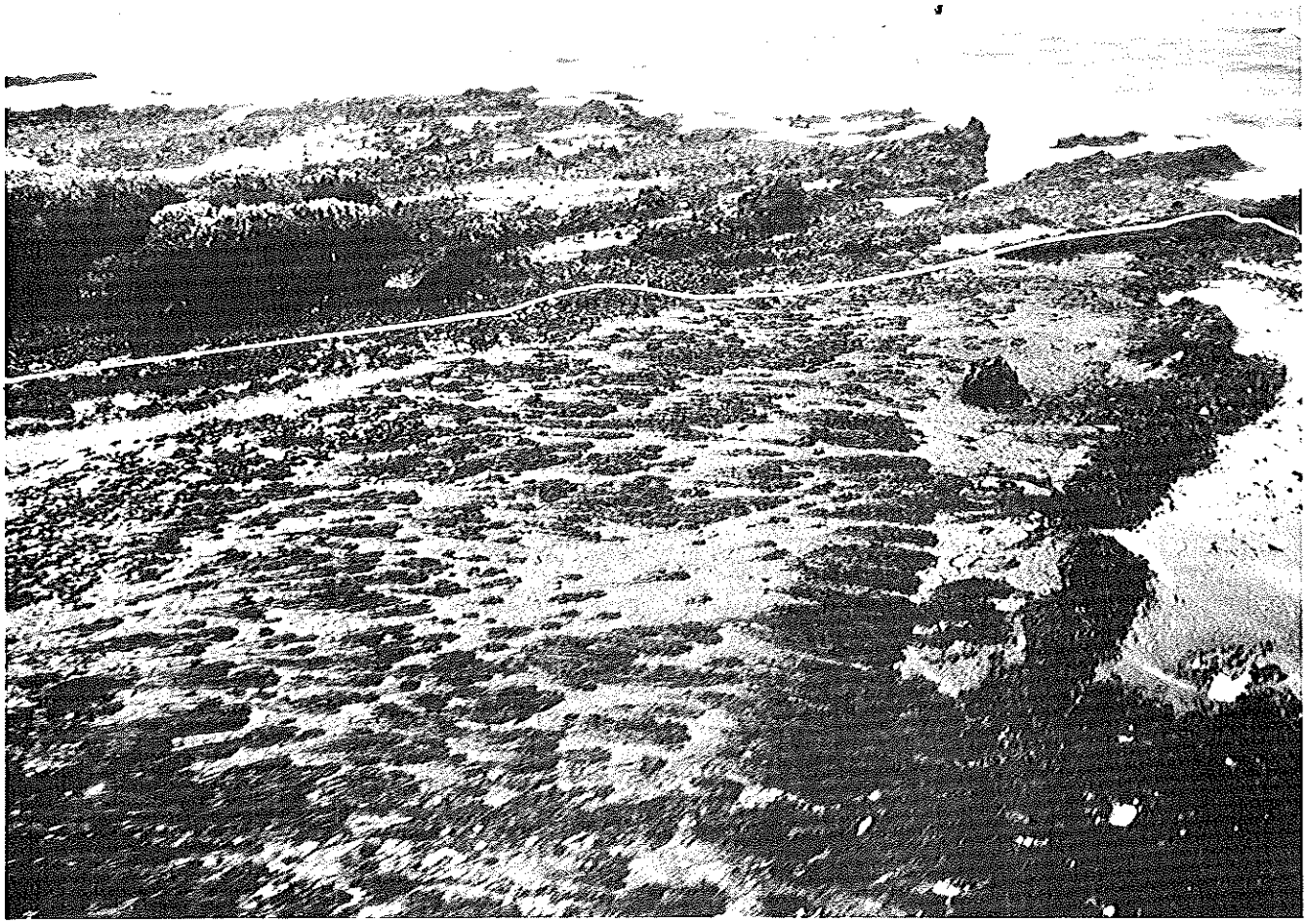

Fig. 7—Rifle Range Point transect (T_4). (Photograph taken by C. A. Simenstad in May 1974.)

feeding observations, so we do not know how their diets differ. Our observations are scanty, but neither species appears to feed on barnacles as does the closely related *L. hexactis* (Mauzey, Birkeland, and Dayton, 1968; Menge, 1972). Presumably this is because of the low abundance of *Balanus glandula* and *B. cariosus* at Amchitka.

A fourth species that may be an important occupier of space is *Halichondria panicea,* because of its encrusting growth form, potentially large size (mean and range of percent cover were 12.6%, 1 to 55% for all those 0.25-m^2 quadrats in which it was found), and relative commonness in the lower intertidal area (c, 33/60). Interactions involving *Halichondria* include possible predation on it by the starfish *Henricia tumida* and parasitism by the snail *Cerithiopsis stejnegeri. Henricia* has been seen pressed against *H. panicea*; when the starfish was removed, the sponge tissue beneath it was found to be discolored. Mauzey et al. (1968) discuss the possibility that another North Pacific congener, *H. leviuscula,* may also prey on encrusting sponges.

Cerithiopsis stejnegeri was rare at the five main study sites, but, because of its small size, it can be easily overlooked in the field. Since it was rare it did not show high affinity with *Halichondria.* However, *C. stejnegeri* was found only in quadrats containing *H. panicea*; when seen in the field, the snail was almost invariably on or under the sponge. Another North Pacific snail, *C. stephensae,* has been observed in association with *H. panicea* (Bakus, 1966). In the British Isles *C. tubercularis* is known to eat *Halichondria* and other sponges (Fretter, 1951).

Alaria–Hedophyllum Community. The *Alaria–Hedophyllum* community ranged in vertical distribution from −53.4 to +9.1 cm (−21 to +3.6 in.) in extreme shelter (transect T_1) to 0 to +160.1 cm (0 to 63 in.) in extreme exposure (transect T_4). *Hedophyllum sessile* usually dominates this community in sheltered situations, but, as exposure increases, *Alaria crispa* becomes dominant (Lebednik and Palmisano, Chap. 17, this volume). In exposed localities *Hedophyllum* is

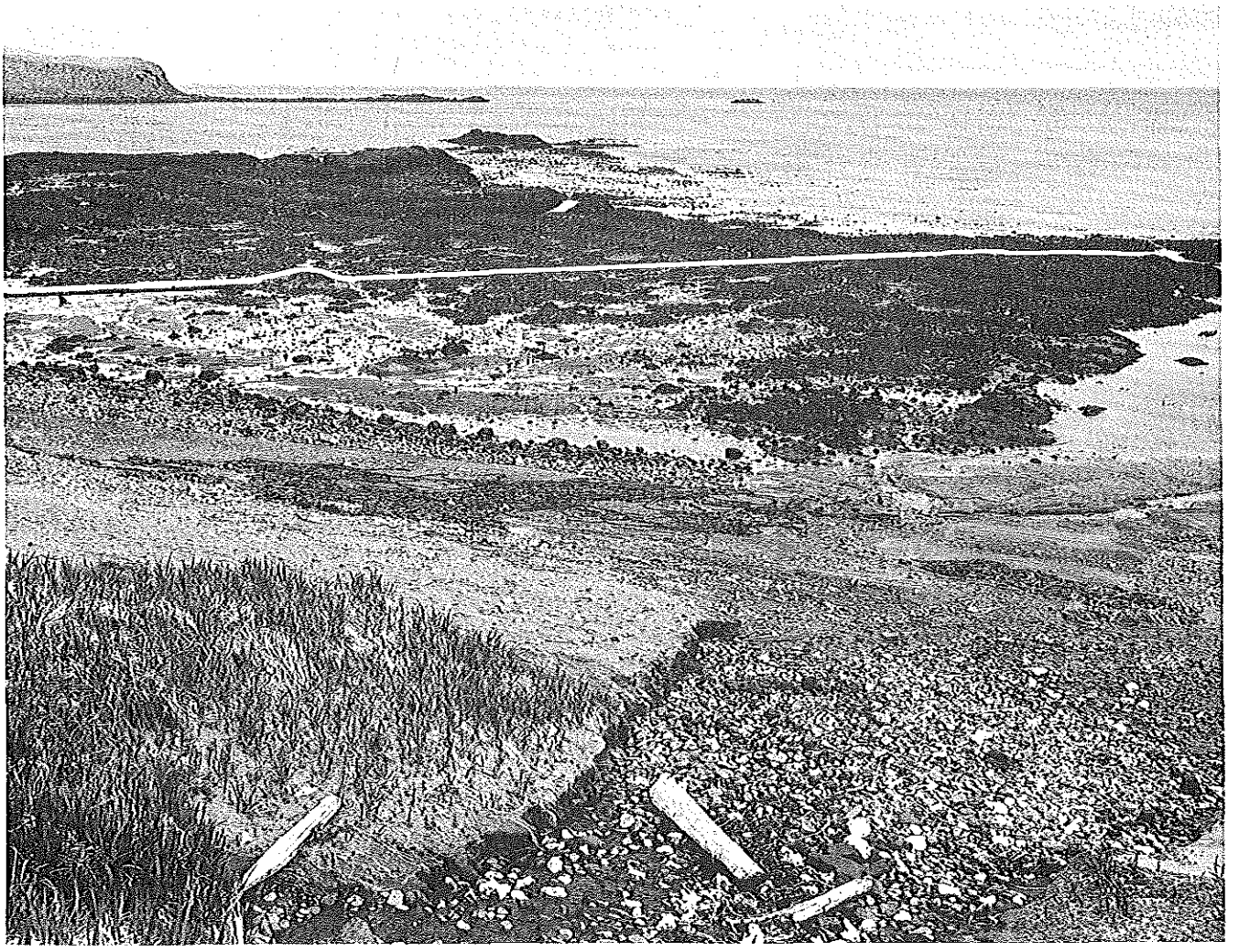

Fig. 8—Square Bay transect (T_2). (Photograph taken by Charles E. O'Clair on May 26, 1974.)

usually absent except well back from the seaward edge of the benches in depressions, tide pools, and drainage channels (Fig. 9). *Alaria* can be found in patches at Makarius Bay, the most sheltered locality studied (see Lebednik and Palmisano, Chap. 17, this volume).

Despite the fact that the species of algae dominating this community changed with the degree of exposure, invertebrate species composition was similar regardless of which species of algae dominated. Only two species of invertebrate present in more than one quadrat were restricted to the *Hedophyllum*-dominated quadrats, and none were restricted to *Alaria*-dominated quadrats. If differences in the relative abundances of species of invertebrates between *Hedophyllum*-dominated quadrats and *Alaria*-dominated quadrats are considered, there does appear to be an increase in the abundances of certain suspension-feeding species, such as mussels, *Mytilus edulis*, and barnacles, *Balanus cariosus*, with increasing exposure and therefore with increasing dominance of *Alaria*. However, these differences did not justify the establishment of two separate communities, one dominated by *Hedophyllum* and one dominated by *Alaria*.

The total species count in the *Alaria–Hedophyllum* community was great (114 species), but few species (19) were faithful to it. As in the *Laminaria* community, species counts were greatest among the Polychaeta (35 species), followed by Gastropoda (23 species) and Gammaridea (18 species). The distributions and relative abundances of species in the *Alaria–Hedophyllum* community are shown in Figs. 9 and 10 for representative localities, T_4 and T_2, respectively.

Table 3 shows the ten most characteristic invertebrates of the *Alaria–Hedophyllum* community and their statistics. This table contains all the

Table 2—Statistics for the Five Most Characteristic Species of Invertebrates of Two Size Classes from the *Laminaria* Community*

Species	Taxon†	Fidelity (f.)‡	Constancy (c.)§	$\bar{R}$¶	Abundance**	Average rank ($\bar{r}$)††	Dominance‡‡	Dispersion§§	Vitality
					Larger Species Counted in 0.25-m^2 Quadrats				
Strongylocentrotus polyacanthus¶¶	E	0.84	10/15	16	2, 1-10 (1, 1-10)	1.4	1/15	$\hat{K}_1$ = 0.6 Aggregated	Sizes up to 30-mm test diameter present.
Mitrella amiantis	G	0.73	13/15	15	12, 1-124 (16, 1-49)	4.8	7/15	$\hat{K}_1$ = 1.2 Aggregated	All stages present.
Notoacmea scutum	G	0.92	6/15	14	1, 1-2 (1, 1-2)	0.47	0/15	Random	Present year round.
Scypha compressa	P	0.78	9/15	13.5	2.5%, 1-5% (3.2%, 1-9%)				Present year round.
*Leptasterias aleutica****	A	0.62	13/15	12.5	3.2, 1-21 (2.5, 1-9)	2.73	2/15	$\hat{K}_1$ = 2.4 Slightly aggregated	Juvenile and adult stages present.
					Small Species Whose Abundances Were Estimated from 50-mm-Diameter Subsamples of Quadrats				
Lumbrineris inflata	Pc	0.89	2/3	7	69, 38-90 (80, 69-90)	8.3	1/3	$\hat{K}_1$ = 1.2 Aggregated	Adults present.
Caulleriella alata maculata	Pc	0.80	2/3	6	38, 1-167 (38, 23-54)	7.0	1/3	$\hat{K}_1$ = 0.9 Aggregated	Adults present.
Demonax sp.	Pc	1.0	1/3	6	6	1.33	0/3	$\hat{K}_1$ = 0.4 Aggregated	Adults present.
Autolytus beringianus	Pc	1.0	1/3	6	2	0.67	0/3	$\hat{K}_1$ = 0.68 Aggregated	Adults present.
Cercops compactus	C	1.0	1/3	6	1	0.33	0/3	Random	Adults present.

*Format modified after Table 2 of Fager and McGowan (1963).

†A, Asteroidea; E, Echinoidea; C, Caprellidea; G, Gastropoda; P, Porifera; Pc, Polychaeta.

‡Proportion of quadrats containing the species that was in this community corrected for differences in sample size between communities.

§Proportion of quadrats from this community that contained the species.

¶Average of ranks of fidelity and constancy for each species.

**Median and range of numbers of individuals per 0.25 m^2 in all quadrats in which the species was found and (in parentheses) these same statistics for quadrats from this community in which the species was found. Abundance of *S. compressa* is the mean and range of percent cover per quadrat; other statistics based on abundance are not included for *Scypha*.

††Ranks for each species were averaged over 15 (large species) and 3 (small species) quadrats. The average ranks of the most abundant large and small species in the *Laminaria* quadrats were 6.53 and 12.66, respectively (1, least abundant).

‡‡Proportion of quadrats from this community in which the species was among those making up 50% of the individuals. Summation in each quadrat began with the most abundant species.

§§$\hat{K}_1$, the first approximation of the exponent K of the negative binomial distribution. Overdispersion increases as K goes to 0. Dispersion was judged random if the quotient of the sample variance divided by the sample mean was not significantly different from one; the relation $\chi^2 = ns^2/\bar{X}$ was used for tests of significance.

¶¶See taxonomic note under *S. polyacanthus* in appendix.

***See taxonomic note under *L. aleutica* in appendix.

large species that are faithful to this community and slightly more than one-third of the small species owing to the small number of faithful species.

Species that we might predict to have important roles (as successful competitors for space) in structuring the *Alaria—Hedophyllum* community are *Mytilus edulis* and *Balanus cariosus*, although this proved not to be true at Amchitka. *Mytilus edulis* is a widely distributed species in north temperate and subarctic regions and forms conspicuous belts in the midlittoral zone (Stephenson and Stephenson, 1972), frequently to the exclusion of other species, such as barnacles and limpets (Lewis, 1964, p. 95). Whether *M. edulis* competitively excludes these species has yet to be demonstrated. *Mytilus californianus* has been shown to displace other upper intertidal species when it is released from predation by experimental removal of its primary predator, the starfish, *Pisaster ochraceus* (Paine, 1966; 1974). For at least one species, *Anthopleura elegantissima*, Paine has observed competitive exclusion by *Mytilus californianus* (see Dayton, 1971).

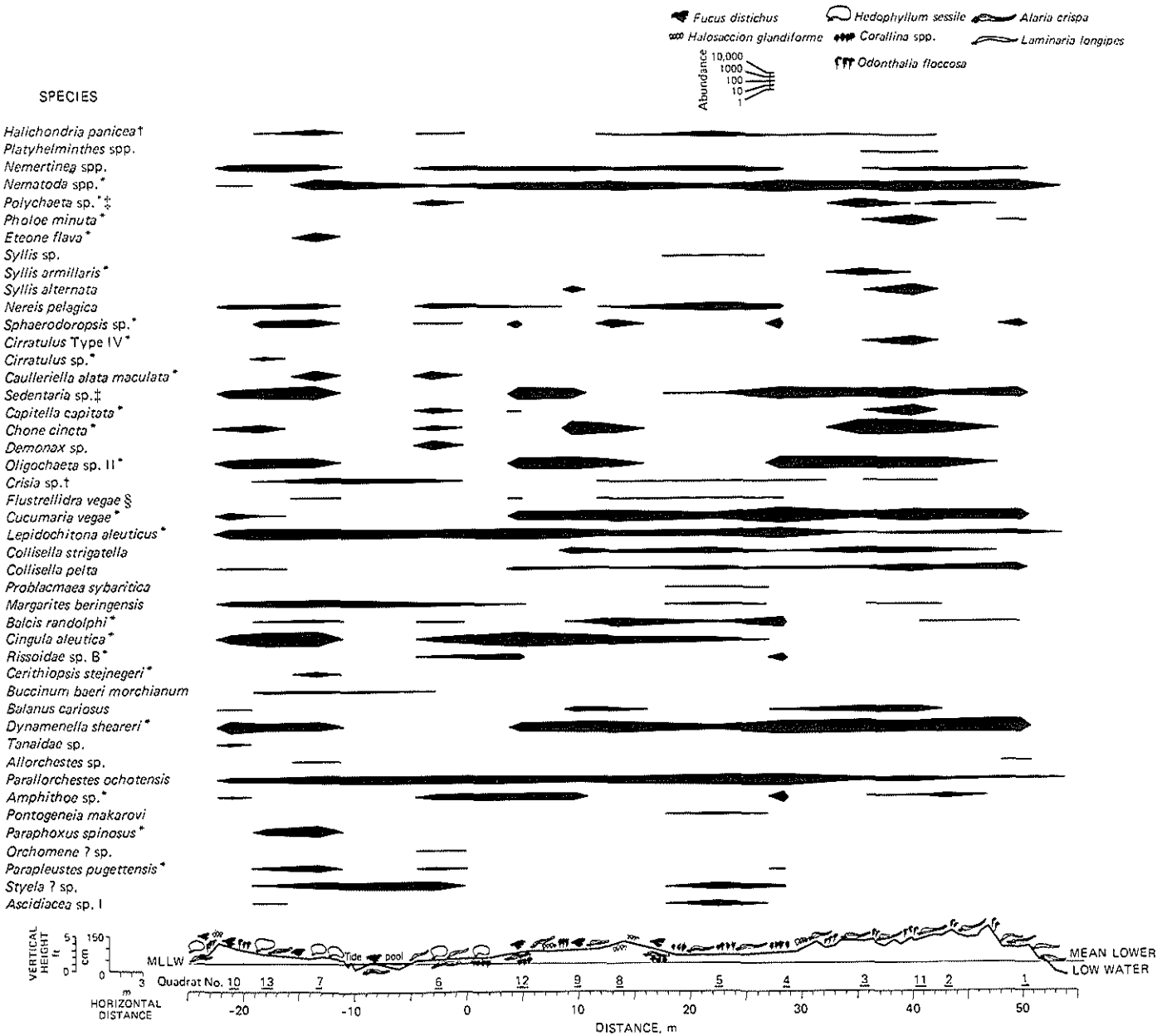

Fig. 9—Distributions and abundances of species that were most abundant in the *Alaria–Hedophyllum* community at Rifle Range Point (T_4), Amchitka Island, in August 1969. Abundances are numbers of individuals per 0.25 m^2 except as noted. *, Estimates based on two or more subsamples of 19.6 cm^2. †, Scale is in units of percent cover. ‡, Specimens incomplete and unidentifiable. §, Presence data only.

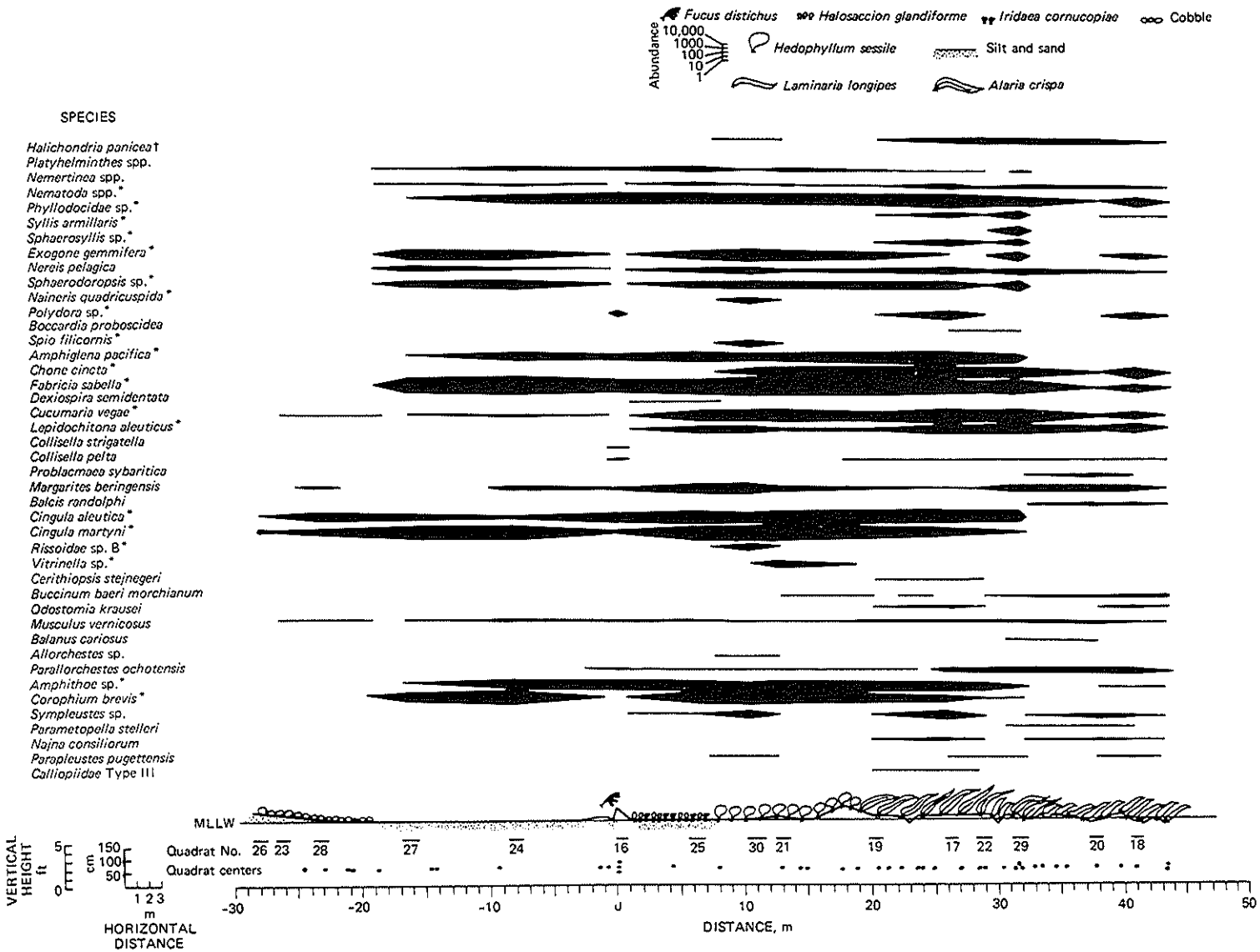

Fig. 10—Distributions and abundances of species that were most abundant in the *Alaria–Hedophyllum* community at Square Bay (T_2), Amchitka Island, in August and September 1969. Abundances are numbers of individuals per 0.25 m^2 except as noted. Centers of quadrats sampled on dates other than August and September 1969 are shown below the quadrat numbers of August and September 1969. *, Estimates based on two or more subsamples of 19.6 cm^2. †, Scale is in units of percent cover.

Table 3—Statistics for the Five Most Characteristic Species of Invertebrates of Two Size Classes from the *Alaria–Hedophyllum* Community*

Species	Taxon†	Fidelity (f.)‡	Constancy (c.)§	R̄¶	Abundance**	Average rank ($\bar{r}$)††	Dominance‡‡	Dispersion§§	Vitality
					Larger Species Counted in 0.25-m^2 Quadrats				
Mytilus edulis	B	0.7	6/44	3.5	4, 1-40 (5, 1-40)	0.50	1/44	$\hat{K}_1$ = 0.66 Strongly aggregated	Present year round.
Balanus cariosus	Ci	0.67	10/44	3.5	4, 1-24 (4, 1-24)	0.65	1/44	$\hat{K}_1$ = 0.1 Strongly aggregated	Present year round. All benthic stages present.
Katharina tunicata	Am	1.0	2/44	2.5	1 (1)	0.04	0/44	Random	Juveniles and adults present.
Macoma calcarea	B	0.66	3/44	2.0	2, 1-3 (1, 1-2)	0.07	0/44	$\hat{K}_1$ = 0.2 Strongly aggregated	Juveniles present.
Anisogammarus confervicolus	Ga	0.57	3/44	1.5	11, 1-26 (3, 1-4)	0.18	0/44	$\hat{K}_1$ = 0.08 Strongly aggregated	Juveniles and adults present.
					Small Species Whose Abundances Were Estimated from 50-mm-Diameter Subsamples of Quadrats				
Corophium brevis	Ga	0.62	5/12	3.5	412, 1-3937 (190, 1-2201)	2.92	0/12	$\hat{K}_1$ = 0.16 Strongly aggregated	All stages present.
Cerithiopsis stejnegeri	G	1.0	2/12	3.5	6, 1-11 (6, 1-11)	0.33	0/12	$\hat{K}_1$ = 0.1 Strongly aggregated	Juveniles and adults present.
Lumbricillus sp.	O	0.57	12/12	3	328, 11-2661 (372, 100-1698)	9.67	1/12	$\hat{K}_1$ = 1.3 Aggregated	Juveniles and adults present.
Vitrinella sp.	G	1.0	1/12	3	64 (64)	0.25	0/12	$\hat{K}_1$ = 0.08 Strongly aggregated	Adults present.
Sphaerosyllis sp.B	Pc	0.66	2/12	3	54, 1-64 (59, 54-64)	1.08	0/12	$\hat{K}_1$ = 0.2 Strongly aggregated	Immature stages present.

*Format modified after Table 2 of Fager and McGowan (1963).

†Am, Amphineura; B, Bivalvia; Ci, Cirripedia; G, Gastropoda; Ga, Gammaridea; O, Oligochaeta; Pc, Polychaeta.

‡Proportion of quadrats containing the species that was in this community corrected for differences in sample size between communities.

§Proportion of quadrats from this community that contained the species.

¶Average of ranks of fidelity and constancy for each species.

**Median and range of numbers of individuals per 0.25 m^2 in all quadrats in which the species was found and (in parentheses) these same statistics for quadrats from this community in which the species was found.

††Ranks for each species were averaged over 44 (large species) and 12 (small species) quadrats. The average ranks of the most abundant large and small species in the *Alaria–Hedophyllum* quadrats were 7.02 and 13.67, respectively (1, least abundant).

‡‡Proportion of quadrats from this community in which the species was among those making up 50% of the individuals. Summation in each quadrat began with the most abundant species.

§§$\hat{K}_1$, the first approximation of the exponent K of the negative binomial distribution. Overdispersion increases as K goes to 0. Dispersion was judged random if the quotient of the sample variance divided by the sample mean was not significantly different from one; the relation $\chi^2 = ns^2/\bar{X}$ was used for tests of significance.

At Amchitka small to large (from about 15 mm to about 40 mm* in shell length) *M. edulis* showed a high fidelity for the *Alaria–Hedophyllum* community but occurred there relatively infrequently and in low abundance. Its low numerical dominance is not suggestive of a successful monopolizer of space. However, very small individuals of *Mytilus* were found to be quite numerous (see discussion of *Halosaccion–Fucus* community).

Dayton (1971) has shown that, in the absence of predation by the snails, *Thais* spp., and the starfish, *Pisaster ochraceus*, and of disturbance by limpets, *Collisella* spp., *Balanus cariosus* competitively excludes other species of barnacles and

*Shell length was measured from beak to posterior edge of shell.

dominates space in the lower middle intertidal area. Indeed, *B. cariosus* may escape the effects of limpets and *Thais* and eventually occupy 100% of the space if the probability of being removed by drift logs is low.

Pisaster is absent from Amchitka, and only the sea otter is close to the starfish's ecological equivalent. Kenyon (1969) reports on the examination of stomachs from 475 otters killed at Amchitka in 1962 and 1963. *Balanus cariosus* was not reported from any of them. However, Barabash-Nikiforov (1947) found that *B. cariosus* remains were occasionally present in sea otter feces, and sea otters have been seen feeding on *B. cariosus* in the Aleutians (J. F. Palmisano, personal communication). The population statistics for *B. cariosus* indicate that it is uncommon, low in abundance, and rarely numerically dominant at Amchitka (Table 3). Yet at Shemya Island, approximately 180 miles (300 km) to the west, *B. cariosus* is more frequent (60% of *Alaria–Hedophyllum* plots) and more abundant (median abundance, 17; range 1 to 77) per $1/16$ m^2 and forms a conspicuous belt in the lower middle intertidal area. Considering the data of Kenyon (1969) and Barabash-Nikiforov (1947) on the diet of sea otters, it is unlikely that *B. cariosus* populations are directly limited by sea otter predation on Amchitka. However, the difference in densities of *B. cariosus* on Amchitka and Shemya suggests that *B. cariosus* populations on Amchitka may be affected indirectly by otter predation (Palmisano and Estes, Chap. 22, this volume).

Halosaccion–Fucus Community. The *Halosaccion–Fucus* community ranges in vertical distribution from −21 to +76 cm (−8.3 to +30 in.) in sheltered localities and about +30 cm to at least +174 cm (+69 in.) in exposed localities. *Fucus distichus* dominates this community on igneous boulders and rock fragments in channels or on erosion-resistant knobs projecting above the bench (Lebednik and Palmisano, Chap. 17, this volume), whereas *Halosaccion glandiforme* usually dominates the benchflat. However, mixed stands of *Halosaccion, Fucus,* and a third alga, *Iridaea cornucopiae,* are common on the shoreward and upper levels of the benches.

The *Halosaccion–Fucus* community had the lowest species count (91 species) of all three communities. The average species count per 0.25 m^2 was also low (large species, 8; including small species, 11). Seventeen species (8 large and 9 small) were faithful to the *Halosaccion–Fucus* community. Within the *Halosaccion–Fucus* community, species counts were greatest among the Polychaeta (24 species), followed by the Gastropoda (20 species) and the Gammaridea (15 species). The distributions and relative abundances of species in the *Halosaccion–Fucus* community are shown in Figs. 11 and 12 for Rifle Range Point and Square Bay, respectively.

Table 4 shows ten characteristic invertebrates of the *Halosaccion–Fucus* community and their statistics. All the large species are herbivorous gastropods. Two other species, *Balanus glandula* and *Collisella strigatella,* had the same rank ($\bar{R}$) as *Littorina aleutica,* but their median abundances were less.

Balanus glandula ranges from the Aleutian Islands to Ensenada, Baja Calif., and is normally one of the most abundant animals in the upper intertidal area (Ricketts et al., 1968), forming along with other barnacles a distinct zone (Stephenson and Stephenson, 1972). Yet, at the five main study sites on Amchitka, the median [I use the median here; it is a better statistic of location than is the mean when species have clumped distributions (e.g., Fager, 1963)] number of individuals of *B. glandula* per 0.25 m^2 in quadrats in which it was found was very low (3), much lower than the median number of individuals (235 per 400 cm^2 = 1470 per 0.25 m^2) reported by Glynn (1965, Table XXIV) for Monterey Bay, Calif. Glynn, however, selected his quadrat sites where *Endocladia muricata* and *B. glandula* dominated, and therefore the median number of individuals of *B. glandula* would be expected to be high. Nybakken (1969) reports an abundance of 16.18 (mean number of individuals in 0.25-m^2 plots containing the species) for *B. glandula* at Three Saints Bay, Kodiak Island, Alaska, which is lower than that for Amchitka (143 per 0.25 m^2) (Nybakken did not report the median number of *B. glandula* per 0.25 m^2 in his study areas), but the relatively high mean recorded at Amchitka is due to an individual count of 1760 in one quadrat. If that count is excluded, the mean drops to 8.5. Moreover, the low abundance recorded for *B. glandula* by Nybakken may be a result of competitive exclusion by the competitive dominant *B. cariosus.* Nybakken reports that *B. cariosus* dominated the barnacle zone at the site where *B. glandula* abundance was estimated. Nowhere on Amchitka does *B. glandula* have densities as high as those recorded in Puget Sound, Wash. (Shelford et al., 1935), the outer coast of Washington (Dayton, 1971), and Monterey Bay, Calif. (Glynn, 1965); yet at Shemya Island my counts have been as high as 2532 per 0.062 m^2.

Most of the area of the intertidal rock bench at Amchitka is below the optimal tidal height for *B. glandula.* My sampling was restricted to these

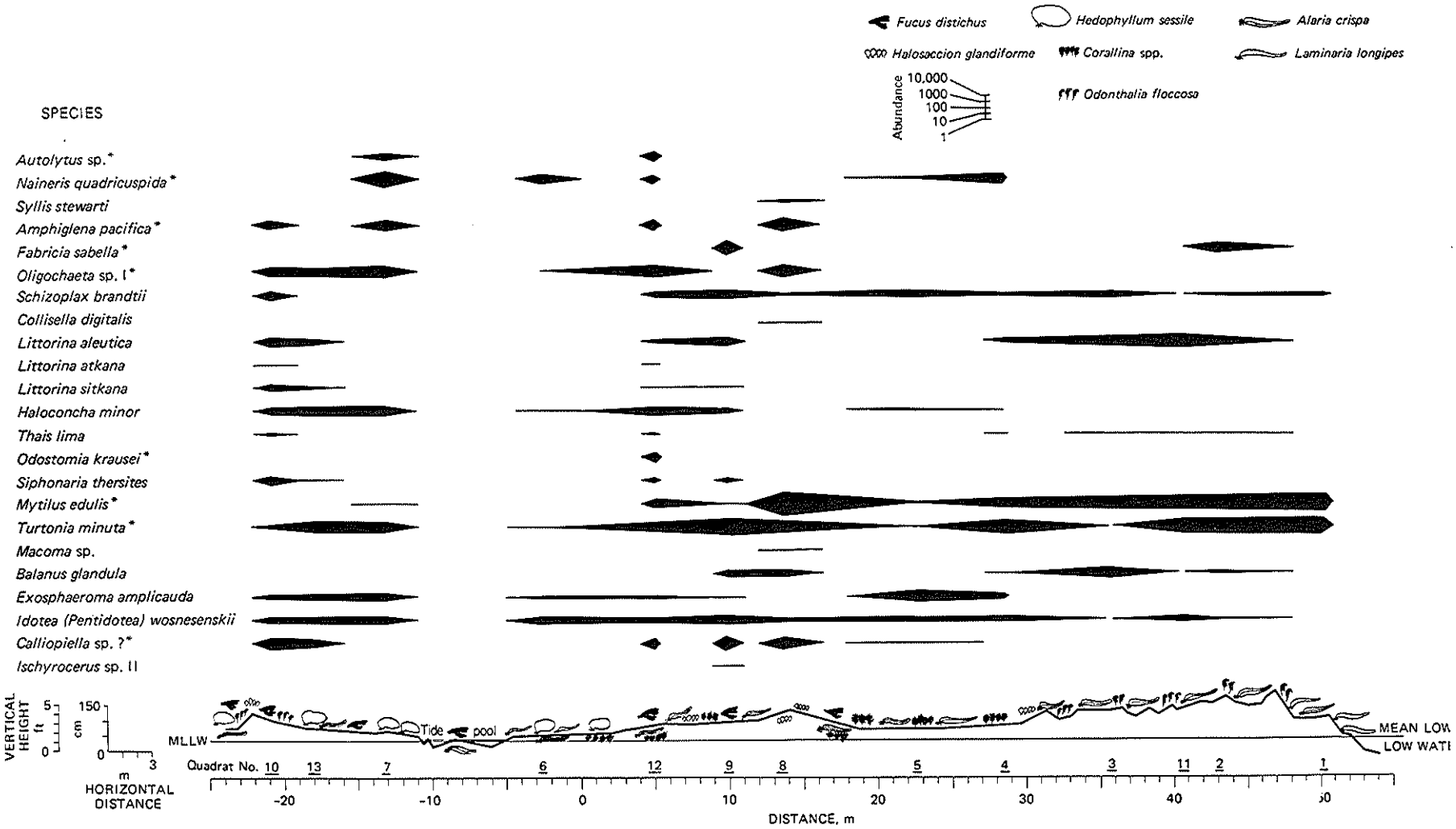

Fig. 11—Distributions and abundances of species that were most abundant in the *Halosaccion–Fucus* community at Rifle Range Point (T_4), Amchitka Island, in August 1969. Abundances are numbers of individuals per 0.25 m^2 except as noted. *, Estimates based on two or more subsamples of 19.6 cm^2.

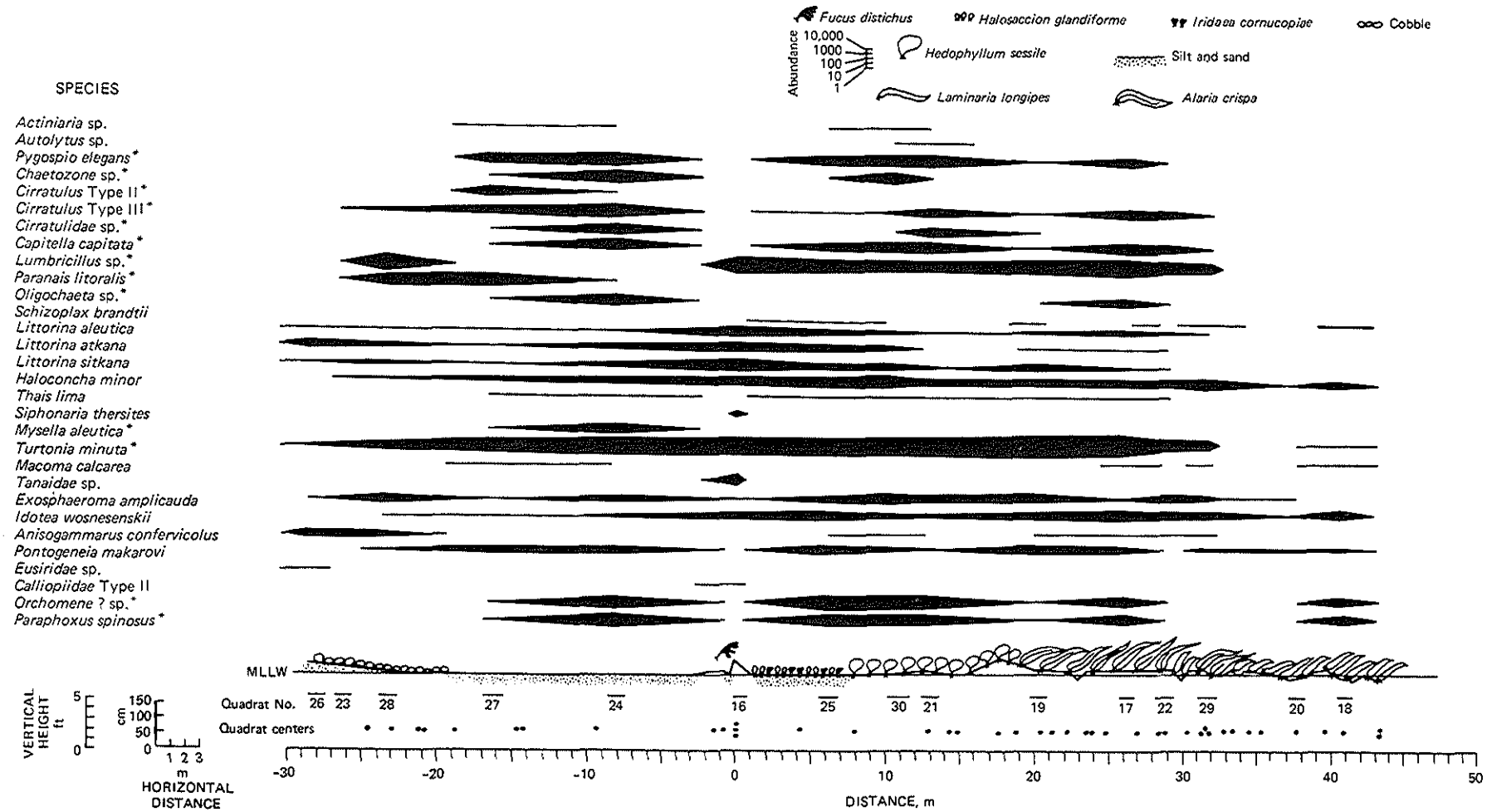

Fig. 12—Distributions and abundances of species that were most abundant in the *Halosaccion–Fucus* community at Square Bay (T_2), Amchitka Island, in August and September 1969. Abundances are numbers of individuals per 0.25 m^2 except as noted. Centers of quadrats sampled on dates other than August and September 1969 are shown below the quadrat numbers of August and September 1969. *, Estimates based on two or more subsamples of 19.6 cm^2.

Table 4—Statistics for the Five Most Characteristic Species of Invertebrates of Two Size Classes from the *Halosaccion–Fucus* Community*

Species	Taxon†	Fidelity (f.)‡	Constancy (c.)§	$\bar{R}$¶	Abundance**	Average rank ($\bar{r}$)††	Dominance‡‡	Dispersion§§	Vitality
					Larger Species Counted in 0.25-m^2 Quadrats				
Littorina atkana	G	0.67	41/53	6.5	6, 1-844 (6, 1-844)	2.79	11/53	$\hat{K}_1$ = 0.1 Strongly aggregated	Present year round.
Siphonaria thersites	G	0.7	23/53	6	2, 1-32 (4, 1-32)	1.45	3/53	$\hat{K}_1$ = 0.3 Strongly aggregated	All stages present.
Littorina sitkana	G	0.58	49/53	5.5	8, 1-214 (10, 1-214)	3.94	15/53	$\hat{K}_1$ = 0.4 Aggregated	Present year round.
Collisella digitalis	G	1	3/53	5.5	1	0.06	0/53	Random	Present year round.
Littorina aleutica	G	0.54	37/54	4	4, 1-129 (8, 1-129)	2.91	12/53		Present year round.
					Small Species Whose Abundances Were Estimated from 50-mm-Diameter Subsamples of Quadrats				
Cingula martyni	G	0.57	7/11	3.8	234, 2-3810 (14, 2-3810)	3.27	1/11	$\hat{K}_1$ = 0.3 Strongly aggregated	All benthic stages present.
Paranais littoralis	O	1	2/11	3.5	190, 127-254 (190, 127-254)	0.91	0/11	$\hat{K}_1$ = 0.2 Strongly aggregated	Adults present.
Calliopiella(?) sp.	Ga	0.8	4/11	3.4	85, 24-345 (89, 51-345)	2.91	1/11	$\hat{K}_1$ = 0.2 Strongly aggregated	Adults and young present.
Mysella aleutica	B	1	1/11	3	127	0.27	0/11	$\hat{K}_1$ = 0.1 Strongly aggregated	Adults present.
Cirratulus Type II	Pc	1	0/11	3	64	0.36	0/11	$\hat{K}_1$ = 0.1 Strongly aggregated	

*Format modified after Table 2 of Fager and McGowan (1963).

†B, Bivalvia; G, Gastropoda; Ga, Gammaridea; O, Oligochaeta; Pc, Polychaeta.

‡Proportion of quadrats containing the species that was in this community corrected for differences in sample size between communities.

§Proportion of quadrats from this community that contained the species.

¶Average of ranks of fidelity and constancy for each species.

**Median and range of numbers of individuals per 0.25 m^2 in all quadrats in which the species was found and (in parentheses) these same statistics for quadrats from this community in which the species was found.

††Ranks for each species were averaged over 53 (large species) and 11 (small species) quadrats. The average ranks of the most abundant large and small species in the *Halosaccion–Fucus* quadrats were 6.02 and 8.91, respectively (1, least abundant).

‡‡Proportion of quadrats from this community in which the species was among those making up 50% of the individuals. Summation in each quadrat began with the most abundant species.

§§$\hat{K}_1$, the first approximation of the exponent K of the negative binomial distribution. Overdispersion increases as K goes to 0. Dispersion was judged random if the quotient of the sample variance divided by the sample mean was not significantly different from one; the relation $\chi^2 = ns^2/\bar{X}$ was used for tests of significance.

benches. Sea stacks and vertical rock cliffs represent a smaller area of the intertidal region and were not sampled quantitatively. Therefore my sampling may have underestimated the species abundance, but this is unlikely. *Balanus glandula* is rare on the cobble and boulder beaches, which extend shoreward of and above the benches. Even when nearly optimal conditions for *B. glandula* are sought out on the island, such as on vertical surfaces in exposed localities, a distinct barnacle zone is rarely found, and even then individuals are scattered and do not form dense sheets as elsewhere in the

eastern North Pacific. There seems little doubt that lower *B. glandula* abundances are a real phenomenon at Amchitka.

Why are *B. glandula* abundances low at Amchitka? One might expect that, since the Aleutians are near the northern limit of *B. glandula*, populations at Amchitka may frequently suffer winter kill or poor reproductive success in spring owing to low temperatures. However, if we compare the long-term data on water temperature in the vicinity of Amchitka (inset, Fig. 3) with that for Kodiak Island, Alaska (Nybakken, 1969, Fig. 5), where *B. glandula* maintains populations, we see that the minimum water temperature recorded in the vicinity of Amchitka is higher than the mean water temperature in the coldest month of the year at Woman's Bay, Kodiak Island. Similarly, comparing air temperatures between the two islands, we find that the average monthly temperatures recorded at the Kodiak Naval Station in winter and early spring from 1942 through 1956 are about the same (29 to 36°F) (Rieger and Wunderlich, 1960) as those recorded at Amchitka from 1943 through 1948 (31 to 36°F) (Armstrong, 1971; Chap. 4, this volume), but the record lows at Kodiak (–5° to 10°F) are much lower than those at Amchitka (4° to 20°F). Further, large populations of *B. glandula* are present on islands to the east and west of Amchitka (Adak and Shemya). The apparent tolerance of *B. glandula* to a wide range of environmental conditions indicates that it is unlikely that such factors as low salinities or low oxygen content in the water are limiting *Balanus* populations at Amchitka.

Balanus cariosus populations are also in low abundance at Amchitka; so competitive exclusion of *B. glandula* by *B. cariosus* is ruled out. The results of previous studies of the effect of other species on *B. glandula* populations (Connell, 1970; Dayton, 1971) suggest that predation by *Thais lima* and/or disturbance by limpets of the genus *Collisella* and perhaps other herbivorous gastropods may be limiting *B. glandula* populations at Amchitka. Palmisano (1975) has found that 93.6% (N = 106) of the diet of *T. lima* on Amchitka consists of *Littorina* spp.; only 2.8% consists of barnacles (*B. glandula* and *B. cariosus*). I have made very few feeding observations of *T. lima* (N = 7), but on only one occasion did I see *Thais* feeding on a barnacle (a young *B. cariosus*). *Thais* may maintain its population size by preying on littorines and switch to barnacles when *B. glandula* recruitment makes it energetically worthwhile for *Thais* to do so. The threshold of barnacle density, above which the time required for *Thais* to search for its prey is significantly reduced and it becomes energetically feasible for *Thais* to begin preying on *B. glandula*, may not be very high since barnacles are probably easier to capture and handle than littorines.

Dayton (1971) concludes from his studies that limpet disturbance alone cannot completely limit barnacle populations but does reduce barnacle recruitment. In the presence of both limpets and *Thais*, recruitment and survival of *B. glandula* are virtually nil. At Amchitka two species of limpets, *Collisella digitalis* and *C. strigatella*, show high fidelity for the *Halosaccion–Fucus* community. *Collisella digitalis* was rare in the *Halosaccion–Fucus* community because it was near its lower limit of vertical distribution. *Collisella strigatella* occurred somewhat more frequently in the *Halosaccion–Fucus* community (c = 19/53) than in the *Alaria–Hedophyllum* community (c = 11/44), but it was relatively uncommon in both communities. A third species, *C. pelta*, also occurred in the *Halosaccion–Fucus* community, but it was more common and more abundant in the *Alaria–Hedophyllum* community. Dayton's exclusion experiments included the above three species as well as a fourth, *Notoacmea scutum*. At Amchitka *N. scutum* rarely occurred in the *Halosaccion–Fucus* community. Densities for these four species at Amchitka are, for the most part, much lower than those recorded by Dayton. Nevertheless, *C. digitalis*, *C. strigatella*, and *C. pelta* may play an important role in limiting barnacle recruitment at Amchitka.

Sublittoral Invertebrates

A variety of semiquantitative sampling methods were used to collect sublittoral invertebrates and to assess their populations. These methods have included 215 shrimp trap sets, 37 crab trap sets, 26 minnow trap sets, and 11 amphipod trap sets. In addition, I made a limited number of direct observations (23 scuba dives) of sublittoral invertebrate communities to a depth of 34 m (112 ft). Sampling of communities below 34 m (112 ft) to a depth of 183 m (600 ft) was accomplished by dredging with rock and pipe dredges (10 hauls). Sublittoral and neritic invertebrates were also collected incidentally during sampling for fish with midwater and otter trawls, bottom gill nets, trammel nets, and long lines by Fisheries Research Institute biologists. Bottom longlines were particularly effective in capturing *Ptilosarcus* sp. Planktonic organisms were collected with a plankton pump. The appendix lists those sublittoral and neritic invertebrates which have been identified.

Sampling of sublittoral invertebrates with traps was patchy. Traps were set in the depth range 1 to

61 m (3 to 200 ft) and almost exclusively in Constantine Harbor on the Bering Sea side of the island and in Makarius Bay on the Pacific Ocean side; most were set in Constantine Harbor. The traps were both species and size selective, presumably selecting species the foraging behavior of which includes scavenging and which are in the size range that can enter yet be retained by the traps. The species that was most numerous and most frequent in and on the shrimp and crab traps was *Strongylocentrotus polyacanthus.* Other species frequently collected included *Fusitriton oregonensis, Leptasterias* spp., and *Buccinum* spp.

Traps set near the middle of Constantine Harbor on a sandy substrate (Fig. 4) consistently caught *Chionoecetes bairdi.* A total of 78 crabs ranging in carapace width from 24 to 77 mm were recorded from this area. The size of these crabs indicated that they were young; nevertheless, 20% of the females were gravid. The presence of adults in Constantine Harbor is not precluded by these trap data, but the largest of these crabs was well below the size selectivity of the traps. Relatively shallow bays, such as Constantine Harbor, may therefore be important in the early life history of this species.

Direct observations of sublittoral communities were made at various localities, mostly along the coast of the southeastern third of the island. Most observations were made in rocky inshore habitat dominated by four species of *Laminaria, Alaria fistulosa, Agarum cribrosum,* or *Thalassiophyllum clathrus.* Beneath this algal canopy the encrusting coralline algae (*Clathromorphum* spp.) usually covered the bedrock (Lebednik and Palmisano, Chap. 17, this volume).

The most common conspicuous benthic invertebrate encountered in the sublittoral communities was the small (up to 31 mm) *Strongylocentrotus polyacanthus,* which can reach densities of over 160 individuals per 0.25 m^2 (Barr, 1971). Other species that were found to be locally abundant in cracks between *Clathromorphum* plants were the brittle star *Ophiopholis aculeata* and the echiurid *Bonelliopsis alaskana.*

Where topographic relief was great, as at the edge of the intertidal benches, especially where massive blocks had been loosened and removed from the intertidal platform by waves, species richness appeared to be greatest, particularly on vertical surfaces. Here much of the rock surface was encrusted with sponges and tunicates. The stalked tunicate *Styela clavata* and various species of Actiniaria, including *Metridium* sp., were often numerous. Common motile species included *Margarites* sp., *Diadora* sp., dorid nudibranchs, *Musculus vernicosus, Henricia* sp., and *Pteraster* sp. Occasionally the small crabs *Cancer oregonensis* and *Dermaturus mandtii* could be seen in pits and crevices in the rock surface. At the base of these blocks, shell and rock rubble usually accumulated, among which the tubes of *Chaetopterus variopedatus* could be seen.

All the dredge hauls were made on the Bering Sea side of the island. Of these, one-half were made in the outer sublittoral zone on the insular shelf and one-half were made in the upper bathyal zone. The appendix lists those species from the dredge hauls which have been identified along with the depths at which these species were caught.

Zoogeography

The Aleutian Island archipelago falls within the Aleutian province, a marine biogeographic subdivision of the Pacific boreal region. The Aleutian province extends from Dixon Entrance off British Columbia to Nunivak Island at about 60°N latitude (Briggs, 1974), but its western limit has never been precisely established. It has long been recognized that the Kamchatka current determines this limit (e.g., Ekman, 1953), but how far to the east does the influence of this current extend? As we shall see, the relatively high arctic boreal and low North American contributions to the fauna of the Commander Islands (Table 5) would indicate that these islands probably fall in the Asiatic High–Boreal province (Tzvetkova, 1975) and that the western limit of the Aleutian province falls somewhere to the east of them.

Zoogeographical Affinities

The following seven zoogeographical elements are present in the Amchitkan invertebrate fauna: (1) "Widely distributed" species, including those invertebrates whose distributions extend into the tropics and southern hemisphere as well as those which are cosmopolitan or bipolar; (2) the "arctic–boreal" element, including circumpolar forms; (3) the "amphiboreal" element, including those species present in the boreal fauna of the Atlantic and Pacific Oceans but whose ranges do not extend into the arctic; (4) "North Pacific" species whose ranges extend to both Asiatic and North American shores; (5) "Asiatic" and (6) "North American" species whose ranges extend only to shores of the western and eastern Pacific, respectively; and, finally (7) the "endemic" element consisting of those species restricted to the Aleutian (and Commander) Islands. This definition of "endemic" refers to a much more limited geographic area than previously considered (O'Clair and Chew, 1972),

Table 5—Number and Percent of Species of Intertidal and Shallow Sublittoral* Invertebrates of Three Major Taxonomic Groups at Amchitka Island and Two Groups in the Commander Islands Distributed According to Their Zoogeographical Affinities

	Zoogeographical elements†														
	Endemic		North American		Asiatic		North Pacific		Arctic–Boreal		Amphiboreal		Widely distributed		Total
	S‡	%	S‡	%	S‡	%	S‡	%	S‡	%	S‡	%	S‡	%	S‡
Amchitka Island															
Polychaeta	1	5.9	4	23.5	2	11.8	2	11.8	3	17.6	0	0	5	29.4	17
Mollusca	3	7.5	10	25.0	5	12.5	15	37.5	6	15.0	0	0	1	2.5	40
Crustacea	1	3.3	10	33.3	6	20.0	12	40.0	0	0	1	3.3	0	0	30
Commander Islands															
Polychaeta§	4	14.8	2	7.4	2	7.4	1	3.7	10	37.0	1	3.7	7	25.9	27
Mollusca¶	1	3.1	2	6.2	7	21.9	14	43.8	8	25.0	0	0	0	0	32

*Restricted to species that are not found below a depth of 60 m.
†See text for geographical areas included in zoogeographical elements.
‡S, number of species.
§Compiled from Annenkova (1934), who examined material from Bering Island only.
¶Compiled from Dall (1884), Barabash-Nikiforov (1947), Skarlato (1960), and Golikov and Kussakin (1962).

reducing the endemic element considerably. For the purposes of discussion of the relative contributions of major faunal source areas to Amchitka, the present definition is preferable because it restricts "endemic" to "insular" only.

Table 5 shows the zoogeographical affinities of three major taxonomic groups of Amchitkan invertebrates. These three taxa were selected for illustration because they were the most abundantly represented macrofauna. The distributions of all the identified intertidal and shallow subtidal (to a depth of 60 m) species of these three groups were used to construct Table 5. Only intertidal and shallow subtidal species are considered here for the purposes of the discussion of the relative contributions of Asia and North America to the fauna of Amchitka. Species that do not "view" the Aleutian Islands as islands, i.e., those with very broad depth distributions, are excluded from the discussion. The depth limit was arbitrarily set at 60 m because this depth is shallower than all the passes separating major island groups in the Aleutians as well as many of the passes separating islands within these groups. The distributions of species included in Table 5 are noted following the species name in the appendix. The following sources were used to compile lists of species from the Commander Islands to obtain the percentages used in Table 5: Annenkova (1934) (polychaetes) and Dall (1884), Barabash-Nikiforov (1947), Scarlato (1960), and Golikov and Kussakin (1962) (mollusks).

Except in the Polychaeta (Table 5), widely distributed species do not represent a large component of the invertebrate fauna of Amchitka or of Bering Island. This holds true among the species that have been identified whether or not species with broad depth distributions are included.

The amphiboreal element of the invertebrate fauna of Amchitka is either very small or nonexistent, depending on the taxonomic group (Table 5). Except for one crustacean, all species found on North Atlantic and North Pacific shores also range into the Arctic. These arctic–boreal species constitute from 0 (crustaceans) to 18% (polychaetes) of the shallow-water fauna of Amchitka. It is noteworthy that, for those groups for which we have comparable species lists from the Commander Islands, the arctic–boreal element on the Commander Islands is consistently greater (37% for polychaetes and 25% for mollusks) than that on Amchitka.

For the three taxonomic groups included in this discussion, between 12 and 40% (depending on the group) of the species restricted to the North Pacific are found on both Asiatic and North American shores. Of greater interest are the remaining North Pacific species, whose ranges extend either to Asiatic or North American shores but not to both.

Asian vs. North American Faunal Contributions

Amchitka lies midway between the tip of the Alaskan peninsula and the easternmost point on Kamchatka, yet, in all the major invertebrate groups considered here, the number of Asiatic species on the island is fewer than the number of North American species (Table 5). This trend of dominance of North American over Asian contributions is also found in marine fish on Amchitka

(Simenstad et al., Chap. 19, this volume; Wilimovsky, 1964), in terrestrial arthropods in the western Aleutians (Lindroth, 1963), and in the terrestrial flora of the islands in the vicinity of Amchitka: of the 33 species of vascular plants occurring in the Rat Island group (of which Amchitka is a member) whose ranges extend to continental Alaska or Kamchatka but not to both, 27 are found in Alaska but only 6 in Kamchatka (compiled from Hultén, 1960). (However, Hultén concluded that the flora of the Aleutians as a whole shows a closer affinity for Asia than for North America.) On the other hand, the Asiatic and North American contributions to the biota of Amchitka are about equal for marine algae (Lebednik and Palmisano, Chap. 17, this volume) and for birds (Emison, Williamson, and White, 1971; White, Williamson, and Emison, Chap. 11, this volume).

Why should an island equidistant between two major source areas have such a large representation of marine invertebrates from one source (North America) as compared with the other (Asia)? I have no information on extinction rates of marine invertebrates at Amchitka (although it seems a priori likely that, if a propagule lands on the island, the probability of it becoming extinct is independent of whether it is from Asia or North America). Further, I do not know whether Amchitka is at equilibrium with respect to its benthic marine invertebrates. Therefore I consider the question of disproportionate Asiatic and North American representation from the standpoint of differential rates of immigration alone.

Two important oceanographic features and one geologic feature affect the relative immigration rates of Asiatic and North American species: (1) the Alaskan Stream, (2) the Kamchatka Current, and (3) the Aleutian "stepping-stone" islands between Amchitka Island and the two continents. The Alaskan Stream is a westward-flowing current originating in the Gulf of Alaska (Fig. 1). It can affect the colonization of the Aleutians by providing directed dispersal westward along the Aleutian Chain for those species on the Alaskan Peninsula and in southeastern Alaska which are dispersed passively with surface-water currents. Included in this group of species are all those littoral and shallow sublittoral benthic invertebrates with benthic life stages dispersed by rafting as well as those with pelagic larvae. The Alaskan Stream extends as far west as longitude 170°E (Favorite, 1967; McAlister and Favorite, Chap. 16, this volume) and therefore probably exerts a negative effect on immigrants to Amchitka from Asia.

The Kamchatka Current is a southward-flowing stream of arctic water which passes between the coast of Kamchatka and the western Aleutian Islands (Fig. 1). As Dall (1884) and Ekman (1953, p. 156) have suggested, this current probably acts as a barrier to faunal exchange between northwestern America and northern Asia. [Briggs (1974) surmises that the "deep" between Kamchatka and the Aleutians is a barrier, but it is probably insignificant for most invertebrates, especially those with pelagic larvae.] I can envision two ways by which this current of arctic water reduces the colonization of the Aleutian Islands by Asiatic benthic invertebrates. First, the northern extent of the populations of some potential Asiatic emigrants would be forced southward, thereby increasing the distance over which propagules would have to disperse. If, for example, the northern limit of many potential Aleutian immigrants was forced southward from Kamchatka to the Kuril Islands, then Aleutian colonization from Asia would be reduced not only through an increase in the distance required for dispersal but also through a drastic reduction in the species pool because of the reduction in size of the nearest source area.

The second way by which the Kamchatka Current might reduce Aleutian colonization would be to sweep propagules emigrating from populations on Kamchatka and even on the Kuril Islands southward, which is normal to the direction that would facilitate immigration to the Aleutian Islands. We might expect this current to be particularly effective in reducing the Aleutian immigration of species that rely on pelagic larvae for dispersal. Many of these species spawn in the spring; Reid (1973) has reported extremely high rates of geostrophic transport of the Kamchatka Current in late winter and early spring.

The third important feature is the chain of Aleutian Islands which act as stepping stones between Amchitka and its two major faunal source areas, Asia and North America, and which increase the rate of immigration to Amchitka. Although these stepping stones occur both east and west of Amchitka, we would expect that the North American faunal source area would be favored over the Asiatic one because not only are there more major stepping stones to the east (13) than to the west (6) but also the total periphery of the islands between Amchitka and the Alaskan peninsula is roughly four times that of the islands between Amchitka and Kamchatka. Insular periphery has been used here instead of insular area because littoral and shallow sublittoral invertebrates are distributed around the periphery of the islands. Finally, the mean distance between major groups of islands lying east of Amchitka is approximately 50 miles (80 km), whereas it is 130 miles (210 km) between those to the west.

The net effect of these three features (the Alaskan Stream, the Kamchatka Current, and the other islands of the Aleutian Chain) is to reduce the immigration rate of colonizers to Amchitka from Asia to the extent that they are always outnumbered by North American species.

The endemic element is not represented by a large number of individuals in any of the three major taxonomic groups included in our discussion. Between one and four species, depending on the taxonomic group, are endemic to the Aleutian Islands.

A number of workers have noted a tendency toward a loss of dispersal power among endemic plants, insects, and birds on islands (for reviews, see MacArthur and Wilson, 1967; Carlquist, 1973). Although not yet well documented in marine invertebrates, we might expect this trend to hold for this group as well (Vermeij, 1972). Thus we might expect the endemic fauna of Amchitka to show a tendency toward direct larval development, a type that limits dispersal.

Throughout this discussion little has been said about the role of extinction in invertebrate colonization of Amchitka. In fact, we have little in the way of direct evidence relating to benthic invertebrate extinction on the island. But how do we account for the apparent failure of such species as *Pisaster ochraceus, Chthamalus dalli, Cancer magister, Telmessus cheiragonus, Cryptochiton stelleri, Thais lamellosa,* and *Mytilus californianus* (for other examples, see Palmisano and Estes, Chap. 22, this volume; Palmisano, 1975) to maintain populations on Amchitka when we consider the following? First, for marine benthic organisms oceanic islands like Amchitka can be thought of as mainland islands (MacArthur, 1972) in the sense that dispersal over water is much less hazardous for them than it is for such organisms as birds or insects. Second, all the species above have been recorded from mainland Alaska and on large islands near the Alaskan peninsula (Pilsbry, 1916; Oldroyd, 1924; 1927; Rathbun, 1930) and could presumably benefit from the Alaskan Stream and stepping-stone islands east of Amchitka to increase their immigration rates to Amchitka [*Cryptochiton stelleri, Chthamalus dalli,* and *Telmessus cheiragonus* have been reported from Kamchatka (Spassky, 1961)]. Finally, all the species above except *T. lamellosa* have planktotrophic larval development and consequently good dispersal power. These species would therefore be expected to have rather high Aleutian immigration rates. In fact, we have collected one individual each of *C. magister* and *M. californianus* on Amchitka, which indicates that immigration is occurring, but extensive sampling has not turned up other representatives of these species. The remains of *T. cheiragonus* and *C. stelleri* in the form of an empty carapace and several shell plates, respectively, have been found on Amchitka, but I have no evidence of extant populations of these species there. I have nothing to indicate that *C. dalli* or *T. lamellosa* ever colonized the island. Accepting the premise that there has been ample time for these species to colonize Amchitka and that undetected populations do not exist on the island,* the alternative explanation for populations of these species being absent from Amchitka is that they have recently become extinct there.

I have so little information on the extinction of marine invertebrates in the Aleutians that I can only speculate about its causes on Amchitka. Competition may play a role in preventing *C. dalli, M. californianus,* and *T. lamellosa* from successfully colonizing Amchitka. The lower limit of distribution of *Chthamalus stellatus* on North Atlantic shores has been shown to be determined by competition for space with other barnacles of the genus *Balanus* rather than by predation (Connell, 1961a). Dayton (1971) reports that *C. dalli* suffers in competition with *B. glandula* and *B. cariosus.* Yet *B. glandula* is not common on Amchitka, and it seems unlikely that *Balanus* alone could exclude *C. dalli* from the island. Similarly, Harger (1972) argues convincingly that in California the two mussels *Mytilus edulis* and *M. californianus* compete for space, although *M. californianus* is never completely excluded except perhaps in very sheltered areas. Whether *M. californianus* at the edge of its geographic range could be excluded by *M. edulis* from an island that contains no habitats as exposed as those on the outer coasts of California is a matter only for speculation.

The low abundance of *Balanus cariosus* and *B. glandula* on Amchitka may support but one species of predatory snail. Why this snail should be *Thais lima* and not *T. lamellosa* may have to do with the former's adaptations. *Thais lima* is very similar morphologically to *T. emarginata*; in fact, Kincaid (1964) considered the two species to be

*This latter assumption is almost certainly true for the intertidal species *M. californianus, T. lamellosa,* and *C. dalli.* We cannot be completely certain that it holds for the sublittoral species *C. magister, T. cheiragonus,* and *C. stelleri* because our sublittoral sampling was not as extensive as our littoral work (see the appendix). If populations of these species do exist on Amchitka, their population levels are probably so low that they run a high risk of extinction from random population fluctuations.

synonymous. *Thais lima* and *T. emarginata* are small compared to other members of the genus, and both possess a comparatively thin shell, a large opening, and a short spire. Connell (1970) suggests that these adaptations allow *T. emarginata* to persist at upper shore levels provided that its main food supply, *B. glandula,* is very dependable. At low shore levels the thin shell of *T. emarginata* makes it vulnerable to predation by crabs that live there, whereas *T. lamellosa,* which has a thicker shell, avoids this predation (Connell, 1970). On Amchitka, crabs inhabiting the intertidal zone are *Dermaturus mandtii, Hapalogaster grebnitzkii, Pagurus hirsutiusculus, Cancer oregonensis,* and *Pugettia gracilis.* All these species are small and in low abundance* and it is unlikely that any of them prey on *Thais. Thais lima* may therefore be free of crab predation at low shore levels on Amchitka. If, in addition, *T. lima,* because of its smaller size and thinner shell, can subsist on a lower rate of intake of food than *T. lamellosa,* as Connell (1970) has suggested for *T. emarginata* vs. *T. lamellosa,* then *T. lima* may be able to exclude *T. lamellosa* from lower shore levels. (However, there is no documented evidence of competitive exclusion among thaids.)

Another possible cause for extinction of marine invertebrates on Amchitka is predation, especially by sea otters (*Enhydra lutris*) (see Palmisano and Estes, Chap. 22, this volume). Size selective predation by otters on *M. californianus,* which grows larger and matures later than *M. edulis* (Harger, 1972), may contribute to the former species being excluded from Amchitka. However, *M. californianus* is also absent from Shemya Island where sea otter predation is negligible. Sea otter predation may also be responsible for the extinction or near extinction of *C. magister, T. cheiragonus,* and *C. stelleri* populations on Amchitka.

Effects of Cannikin

Immediate Effects. The underground nuclear test, Cannikin (Nov. 6, 1971), produced several effects traumatic to intertidal invertebrates. Immediate effects associated with the passage of the ground shock wave (Merritt, 1972) could have caused mortality in the following ways:

1. Some invertebrates dislodged or overturned by the shock wave would be unable to reattach (barnacles and ascidians) or right themselves (limpets) and would be subject to starvation, desiccation, and predation.

2. Animals were probably crushed by falling boulders and rubble overturned or propelled upward from the bench surface when the shock wave passed.

3. Immersed organisms were subjected to overpressures that may have been as high as 100 psi (Merritt, 1972) followed by underpressures and cavitation.

These immediate effects alone would not have had a profound influence on community structure.

A more important source of mortality to invertebrate populations on those parts of the intertidal benches near the bases of cliffs and sea stacks was burial by rockfalls and turf slides. Although the total volume of these falls and slides has been estimated by the U. S. Geological Survey to be 35,000 m^3 (Kirkwood, 1974), most of this material was deposited on the beach shoreward of the intertidal benches and affected intertidal organisms only in localized areas (Lebednik and Palmisano, Chap. 17, this volume, and personal observations). At the edges of the benches, bench spall resulted in large chunks of rock and accompanying organisms plunging from the edge of the bench into the sea (however, some of this material probably washed onto the bench surface). The fate of animals not killed in these rockfalls is unknown. Most of the evidence accumulated so far indicates that intertidal animals are excluded from the sublittoral area by predators and competitors (Connell, 1972). Intertidal invertebrates that survived the plunge into the sublittoral area probably will not be able to maintain populations there.

Long-Term Effects. All the disturbances discussed above, although by no means inconsequential to intertidal invertebrate communities, are relatively transitory in ecological time; i.e., though mortality may be high as a result of these disturbances, recolonization is rapid compared with the generation time of most of the species involved unless the habitat is made unsuitable for recolonization. The most disruptive and lasting disturbance to intertidal communities resulting from Cannikin was the permanent uplifting of the Bering Sea coast near the site of Cannikin. Detectable uplift in the range of 3.4 cm (1.3 in.) to 1.1 m (3.6 ft) was recorded along at least 7.8 km (4.8 miles) of coastline (Kirkwood and Fuller, 1972, Table A-5). Lebednik and Palmisano (Chap. 17, this volume) have detected mortality in algal populations along at least 6 km (4 miles) of coast (Fig. 13). I consider below changes in invertebrate populations attributable to uplifting.

*In May 1968 numerous individuals of *D. mandtii* were seen in the *Laminaria* community at Makarius Bay (J. S. Isakson, personal communication), but subsequent attempts to find crabs there have proved fruitless.

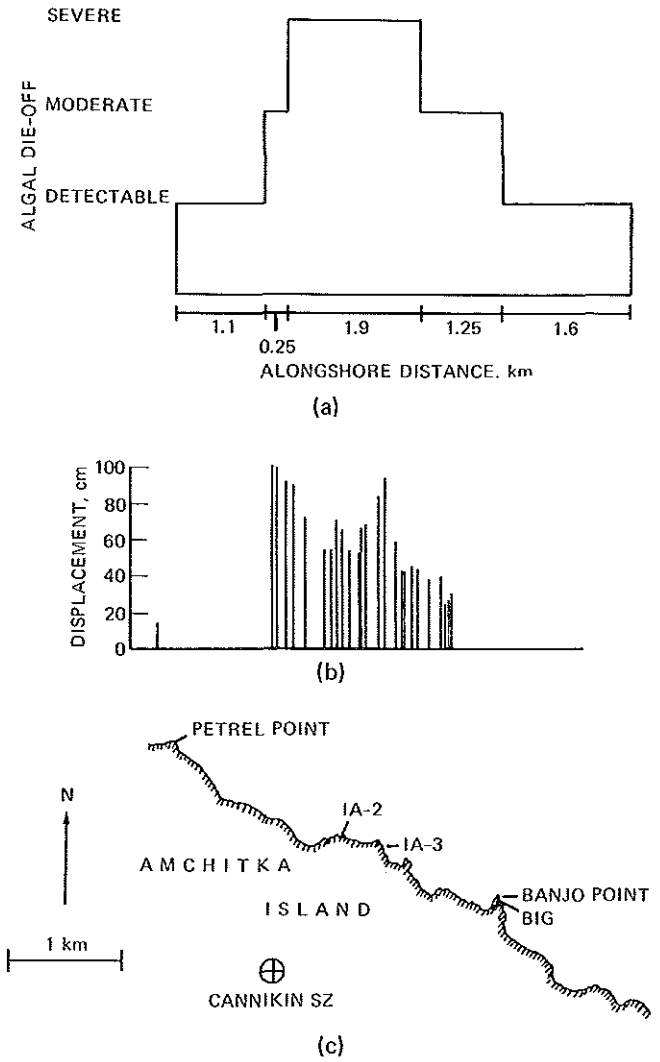

Fig. 13—(a) Distribution and relative magnitude of algal die-off due to Cannikin along the section of coastline shown on the map in part (c). Detectable, from one to a few species showing die-off. Moderate, a few species showing extensive die-off (more than about one-third of the total population). Severe, all abundant species showing extensive to complete die-off. (Data from Lebednik and Palmisano, Chap. 17.)

(b) Vertical displacement at several locations along the same section of coastline as part (a). (Data from Kirkwood and Fuller, 1972, Table A-5.)

(c) Map of a section of Bering Sea coastline adjacent to Cannikin surface zero (SZ). Points along the shore that are depicted in parts (a) and (b) are directly above the appropriate locations on map.

The 25 plots initially established at IA-2 were uplifted from 75 cm to 1.1 m (3.6 ft), depending on the plot, as a result of Cannikin (Table 6). Sixteen were uplifted above extreme high water of spring tides for the Bering Sea coast of Amchitka (146 cm in 1969); four were lifted above mean high water. Five plots were buried by rockfalls.

Figures 14 and 15 show the changes in mean species counts with time following Cannikin for three intertidal communities at IA-2 and IA-3, respectively, compared with Makarius Bay (control). The plots in the *Halosaccion—Fucus* community at IA-2 were divided into two groups. The first group contains plots nearer the seaward edge of the bench (outer plots). The second group contains plots nearer the shoreward edge of the bench away from the area of frequent wetting by wave splash and salt spray when emersed (inner plots). IA-3 and Makarius Bay are relatively sheltered, and all plots at these sites were subject to the same degree of exposure; therefore outer and inner plots were not distinguished. All species on the plots that could be distinguished are included in Figs. 14 and 15. Species of Platyhelminthes, Nemertea, Oligochaeta, Nematoda, and Ectoprocta were not distinguished. Polychaetes, except *Nereis pelagica, Dexiospira semidentata*?, and *Dexiospira* sp., and gammarids, except *Parallorchestes ochotensis* and *Orchestia* sp., were lumped into Polychaeta and Gammaridea, respectively. Actiniaria were divided into species that were and that were not members of the Family Actiniidae.

Species counts at IA-2 began declining in all communities immediately after Cannikin (Fig. 14). From the beginning the greatest source of mortality of invertebrates not crushed or buried by rock and soil was prolonged emersion due to uplift, especially for the sessile species, such as sponges, sedentary polychaetes, bivalves, and ascidians. Some motile species at the seaward edges of the benches which were not thrown into the water with the passage of the shock wave may have migrated to lower levels soon after uplift. Predation by gulls and oyster catchers may also have been an important source of mortality in the first few days following uplift. During this period large flocks of gulls (*Larus glaucescens*) and oyster catchers (*Haematopus bachmani*) were seen at IA-2 (C. Simenstad, personal communication). Also, a large number of overturned and empty limpet shells (*Collisella* spp.) were observed on the bench. How much of the activities of these birds can be attributed to predation and how much to scavenging of dead and dying animals is not known.

The fifteen plots established at IA-3 were uplifted from 47 to 56 cm, depending on the plot (Table 6). Only one plot was uplifted above extreme high water of spring tides. However, probably because IA-3 is more sheltered than IA-2, mean species counts there declined similarly to but less drastically than at IA-2 (Fig. 15). The sole exception to this trend was plot 1.

Plot 1 (Table 7) was established in the *Laminaria* community pre-Cannikin. It had been up-

Table 6—Physical Survey Data for 0.25-m^2 Plots at IA-2 and IA-3 Before and After Cannikin*

Plot	Elevation, cm Before	Elevation, cm After	Upward displacement, cm	Plot	Elevation, cm Before	Elevation, cm After	Upward displacement, cm
		IA-2				IA-2 (Continued)	
1	40.7	150.7	110.0	24	59.6	138.5	78.9
2	57.0	157.7	100.7	25	34.3	122.1	87.8
3	51.4	151.0	99.6	26	38.2†	133.1	94.9
4	41.8	139.6	97.8	27	58.3	153.2	94.9
5	139.1	234.0	94.9				
6	68.8	Buried					
7	15.4	Buried				IA-3	
8	12.6	Buried					
9	47.7	145.6	97.9	1	16.3	70.5	54.2
10	131.9	229.5	97.6	2	20.4	72.8	52.4
11	80.5	177.7	97.2	3	36.9	89.4	52.5
12	6.2	99.1	92.9	4	28.6	80.8	52.2
13	45.2	138.5	93.3	5	67.8	124.3	56.5
14	53.7	146.5	92.8	6	40.6	88.4	47.8
15	81.2	171.8	90.6	7	20.4	67.9	47.5
16	69.0	Buried		8	43.0	90.6	47.6
17	33.4	117.5	84.1	9	53.3	100.5	47.2
18	66.6	153.5	86.9	10	44.8	92.2	47.4
19	99.8	189.5	89.7	11	59.1	Buried	
20	66.0	156.4	90.4	12	93.8	Buried	
21	20.0	Buried		13	43.2	92.3	49.1
22	47.5	122.2	74.7	14	32.6	82.7	50.1
23	47.5	125.6	78.1	15	32.7	83.5	50.8

*Compiled by P. A. Lebednik from Holmes and Narver and Fisheries Research Institute survey data.

†Preevent elevations of plots 26 and 27 were back-calculated assuming that each plot was uplifted equally with the nearest original IA-2 plot.

lifted 54 cm to an elevation of 70 cm. Species counts on this plot at first declined after Cannikin but increased again by 3 months post-Cannikin. Part of this increase was an artifact in that species, such as Actiniaria spp., *Dexiospira* sp., *Phascolosoma agassizii,* and *Balcis randolphi* (Table 7), were probably present pre-Cannikin but were missed in the dense *Laminaria* holdfast cover. Also contributing to the increased species count on plot 1 at 3 months was the addition, to the remnant populations of species of the *Laminaria* community, of species common to higher levels in the intertidal area, such as *Littorina* spp., which had migrated into the plot when their former habitat was uplifted above the intertidal area (Table 7). By 7 months postevent, the character of the fauna on plot 1 had changed from *Laminaria* community to a fauna containing species with broader vertical ranges and species of higher intertidal levels. As we will see later, IA-3 plot 1 is the only plot at either IA-2 or IA-3 to show signs of recolonization by intertidal organisms after 33 months postevent.

The total number of species seen preevent in each community decreased steadily after Cannikin to relatively stable levels within 1 year (Fig. 16). Conversely, the total number of new species not previously recorded on plots in each of the three communities increased. The new species consisted chiefly of species from upper intertidal levels, especially the supralittoral fringe, and included Collembola, Diptera (*Saunderia marinus* and *Paraclunio alaskensis*), Acarina (*Neomolgus littoralis, Parasitus* sp., etc.), *Ligia pallasii,* and the gammarid *Orchestia* sp. The only intertidal species that persisted throughout the year on the uplifted plots were the gastropods *Littorina* spp.

The control at Makarius Bay showed a slight decrease in mean species count per plot in February 1972 (3 months postevent) and then a return nearly to October 1971 levels by August 1972 (9 months postevent) (Figs. 14 and 15). However, the decline was only 23 to 24% of the October 1971 levels, depending on the community. The decrease by February 1972 at IA-2 varied from 3

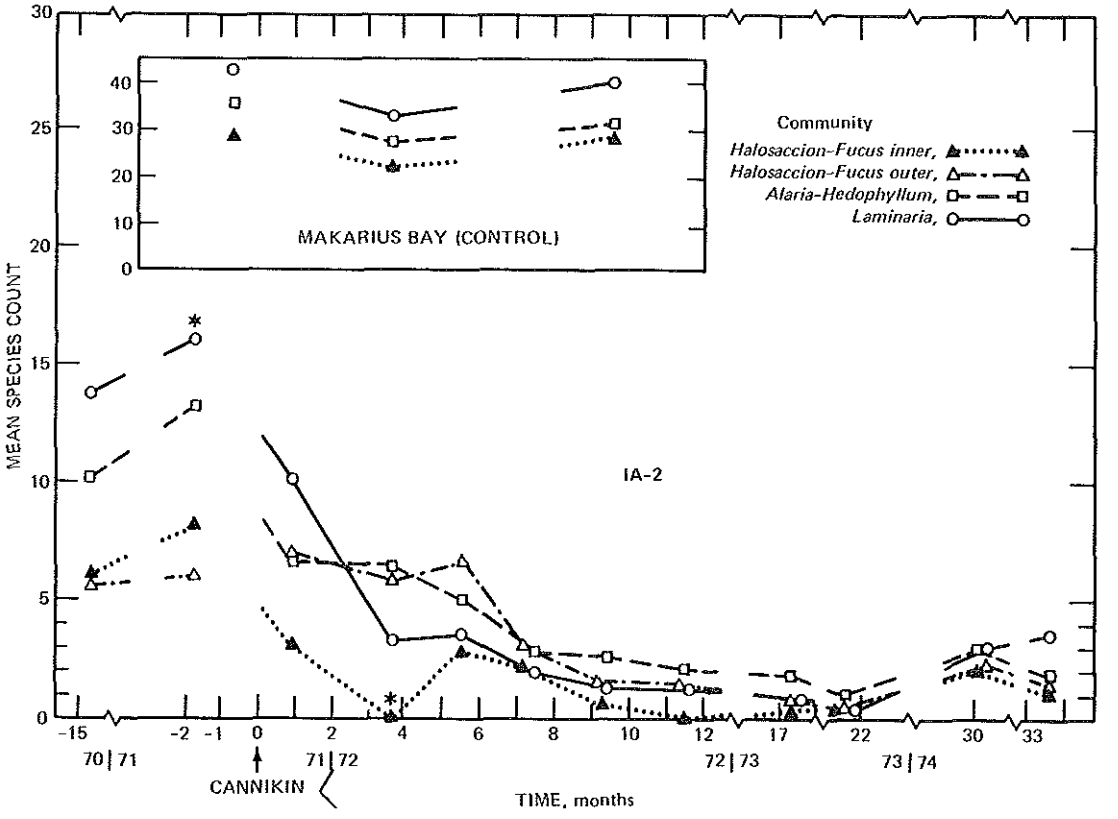

Fig. 14—Mean species counts for each algal zone before and after Cannikin at IA-2 and Makarius Bay (control). Asterisk indicates a sample size of 1. All macroscopic species at IA-2 with distinguishable individuals are included. Anemones, polychaetes, and gammarids, which could not be distinguished to species in the field, were lumped into their respective taxonomic groups. At Makarius Bay all identifiable species with distinguishable individuals retained by a 1-mm sieve are included.

to 100% of the September 1971 levels, depending on the community. The decrease at IA-3 was 53% and 58% in the *Halosaccion–Fucus* and *Alaria–Hedophyllum* communities, respectively. The only *Laminaria* community plot (IA-3 plot 1) showed an increased species count of 36%. I attribute the decrease in mean species count in February 1972 at Makarius Bay to seasonal changes in species composition. The Makarius Bay grid was not sampled at 17 and 30 and 33 months postevent because of inadequate field time and poor tides, respectively. The grid was sampled at 22 months, but the data are not included here. General observation of the grid at these sampling times did not reveal obvious departures from the normal pattern of seasonal change in the intertidal communities at Makarius Bay.

The mean number of individuals per plot in all communities at IA-2 and IA-3 generally decreased throughout the year following Cannikin (Figs. 17 and 18, respectively). However, the decline was erratic in some communities. At IA-2 the outer *Halosaccion–Fucus* and the *Alaria–Hedophyllum* communities showed increases in the mean number of individuals per plot, especially in April and June 1972. At IA-3 the *Laminaria* and *Alaria–Hedophyllum* plots showed increases in the mean number of individuals of comparable magnitude in August 1972. Both of these increases are accounted for by increases in the abundances of *Littorina* spp., especially *L. atkana*. Further, littorines too small to be assigned to species in the field also showed increases in April, June, and August 1972 (Figs. 19 and 20).

The drop in the mean number of individuals per plot in the *Halosaccion–Fucus* community at Makarius Bay is probably seasonal (Figs. 17 and 18). *Halosaccion glandiforme* dominates this community at Makarius Bay and shows seasonal die-off in late fall and winter which extends to late spring (Lebednik and Palmisano, Chap. 17, this volume, and personal observations). The drop in the number of individuals may be due to the loss of the moderating effect of the algae on the microclimate

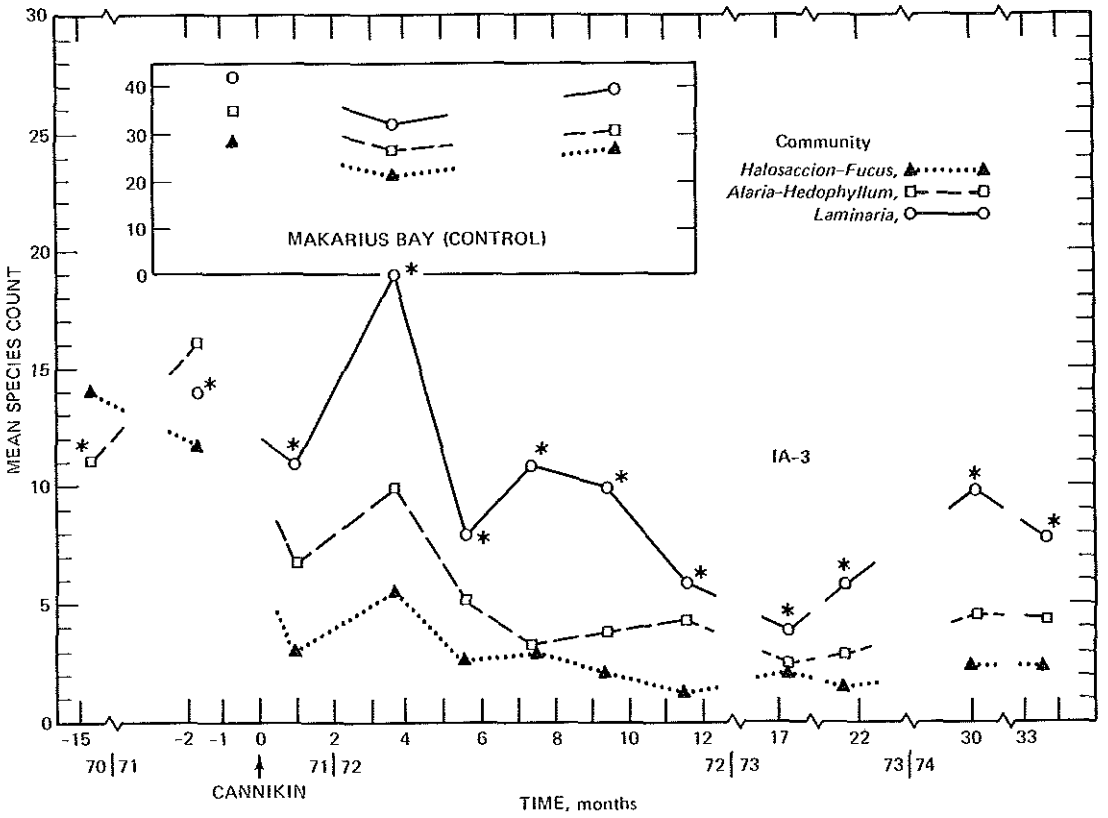

Fig. 15—Mean species counts for each algal zone before and after Cannikin at IA-3 and Makarius Bay (control). Asterisk indicates a sample size of 1. All macroscopic species at IA-3 with distinguishable individuals are included. Anemones, polychaetes, and gammarids, which could not be distinguished to species in the field, were lumped into their respective taxonomic groups. At Makarius Bay all identifiable species with distinguishable individuals retained by a 1-mm sieve are included.

of the invertebrates and perhaps to a reduction in the spatial heterogeneity in this community in winter.

After 1 year post-Cannikin, mean species counts per plot at IA-2 and IA-3 remained in the range 0 to 4 (Figs. 14 and 15, respectively). The total number of species formerly present in each community before Cannikin at both IA-2 and IA-3 never exceeded seven in those communities during the period of 12 to 33 months postevent (Fig. 16). Counts of individuals also remained low during this period, seldom exceeding a mean of 10 individuals per plot at IA-2 (Fig. 17). In May 1974 (30 months postevent), former *Halosaccion–Fucus* community plots at the seaward edges of the benches at IA-2 showed large numbers of tiny pink mites (Acarina sp.), but these mites were present in large numbers on only one plot (formerly in the *Alaria–Hedophyllum* community) in August 1974. These tiny abundant mites also accounted for most of the increase in the mean number of individuals in plots in the *Alaria–Hedophyllum* and *Halosaccion–Fucus* communities at IA-3 in May 1974. Large numbers of littorines, especially *L. atkana* (Fig. 20), on some plots kept the mean number of individuals relatively high in the former *Alaria–Hedophyllum* community at IA-3 in August 1974. Most of the invertebrates observed on the IA-2 and IA-3 plots after 1 year postevent were in moist depressions and crevices or beneath pieces of dead kelp which were tossed up on the benches during storms and which had become hung up on the nails marking the plots. Other species, such as the flies *Saunderia marinus* and mites *Neomolgus littoralis*, moved through the plots very rapidly.

IA-3 plot 1 was the only plot at either IA-2 or IA-3 that showed some signs of recovery by the end of the study. Species counts there reached a minimum sometime between 12 and 22 months postevent but then began showing some signs of recovery. By 17 months postevent a few young *Fucus distichus* plants were seen on the plot (Lebednik and Palmisano, Chap. 17, this volume), and by 33 months the percent cover of *F. distichus*

Table 7—Species Abundances per 0.25 m^2 on IA-3 Plot 1 Before and After Cannikin

Species	Taxon*	Months before Cannikin†	Months after Cannikin									
		2	1	3	5	7	9	11	17	22	30	33
Scypha compressa†	P	+‡	1									
Halichondria panicea†	P	25	12	25								
Actiniidae spp.	C	+	1	2								
Dexiospira semidentata	Pc			2(32)§								
Lepidochitona aleuticus	Am	49	1	8	2(5)	1						
Haloconcha minor	G	4	1	1								
Cingula spp.¶	G	+	2	22	16	15	142	22				7
Mitrella amiantis	G	16		1				1				
Buccinum baeri morchianum	G	3										
Margarites beringensis	G	18	8	3								
Idotea wosnessenskii	I	15	8				26				1	27
Parallorchestes ochotensis	Ga	43	3									
Leptasterias aleutica	A	2										
Cucumaria vegae	H	5		2	(1)							
?*Styela coriacea*	As	8	20	38								
Actiniaria sp.	C			6			3	2				
Nemertea spp.											1	
Oligochaeta sp.							3			3		
Phascolosoma agassizii	S			1	1		1					
Schizoplax brandtii	Am						1					
Collisella pelta	G			(2)								
Notoacmea scutum	G			(1)								
Balcis randolphi	G			1								
Littorina aleutica	G				3	2	3		1	1		2
Littorina atkana	G			1	5	10	80	3	1	10	262	535
Littorina sitkana	G			2		13	103		3		17	50
Alvinia aurivillii	G			2	5	2	1					
Musculus vernicosus	B				1	1						
Mytilus edulis	B								1			
Turtonia minuta	B			5	7(+)	2	31	11	3	8	57	33
Macoma sp.	B					1						
Exosphaeroma amplicauda	I		1									4
Pontogeneia makarovi	Ga							2				17
Anisogammarus confervicolus	Ga											3
Gammaridea spp.				1							1	
Liparocephalus brevipennis	In										2	
Saunderia marinus	In										11A**	
Paraclunio alaskensis	In					1A				2A		
Diptera sp.	In									2A		
Insecta spp.										1L	6L	
Neomolgus littoralis	Ac					1						
Acarina spp.							2				62	

*A, asteroidea; Ac, acarina; Am, amphineura; As, ascidiacea; B, bivalvia; C, cnidaria; G, gastropoda; Ga, gammaridea; H, holothuroidea; I, isopoda; In, insecta; P, porifera; Pc, polychaeta; S, sipuncula.

†Abundance is percent cover.

‡Plus signs indicate relative abundance: +, present.

§Numbers in parentheses indicate number of dead individuals.

¶ *Cingula aleutica* and *C. martyni* not distinguished.

**Letters accompanying abundances refer to life stages: L, larva; A, adult.

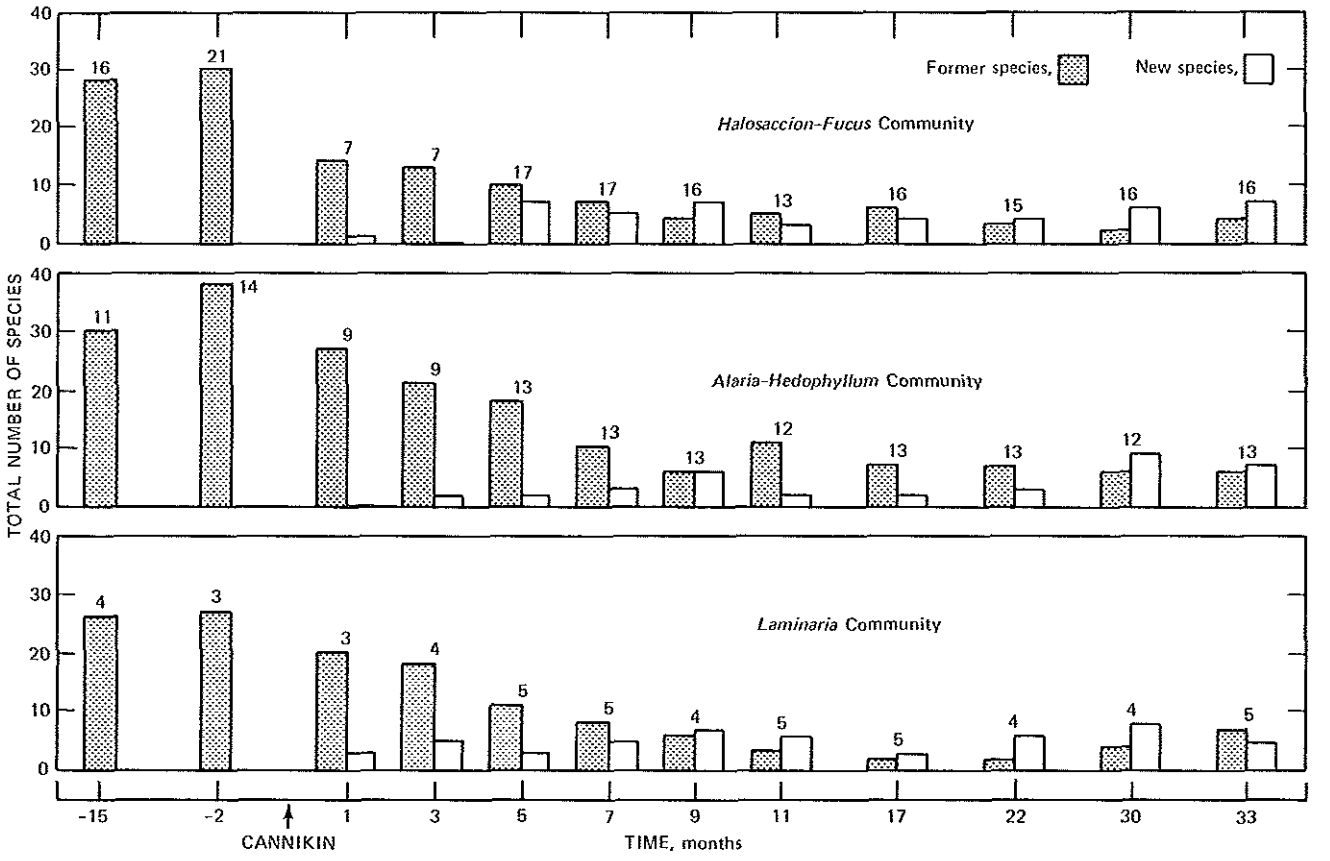

Fig. 16—Replacement following Cannikin of original species by species not previously recorded on plots in three communities at IA-2 and IA-3 combined. The numbers directly above the vertical bars indicate the number of plots sampled.

had increased to 40% (C. Simenstad, personal communication). Invertebrate populations increased in size with the increase in *Fucus* cover (Fig. 18 and Table 7), but the species count was well below the mean species count recorded for undisturbed *Halosaccion—Fucus* plots by 33 months postevent. Apparently plot 1 at 33 months postevent was near the upper limit of the *Halosaccion—Fucus* community (the highest intertidal community) for the degree of exposure at IA-3.

How much of the pre-Cannikin intertidal zone was uplifted into the supralittoral fringe? Thirty-three months after Cannikin was detonated, I made an estimate of this area in the field by superimposing plane geometric figures on the bench surface. The areas included within the figures were essentially bare rock containing scattered supralittoral invertebrates and no macrophytes. The estimate arrived at was 5.8 ha (14.3 acres). This estimate is conservative because:

1. The method treats the bench as a plane surface and ignores irregularities.

2. The estimate excludes areas of offshore islets that could not be reached.

3. The estimate does not include uplifted bench area east of Banjo Point or west of Sand Beach Cove. Although the length of coastline included in this estimate is only half that wherein algal damage was detectable (Lebednik and Palmisano, Chap. 17, this volume), the area of bench outside this length of coastline that was uplifted out of the intertidal zone is probably small by comparison.

Before Cannikin the intertidal zone was a nearly horizontal plane between Banjo Point and Sand Beach Cove. In this stretch of coastline, the new intertidal area is a steep slope at the outer edge of the uplifted bench and occupies a much smaller area than before. Finally, intertidal recolonization of the former bench surface may not be complete; there is some evidence that the uplifted bench is being eroded. By spring 1974 mechanical and chemical weathering appeared to have reduced the level of the uplifted bench by 1 to 2.5 cm,

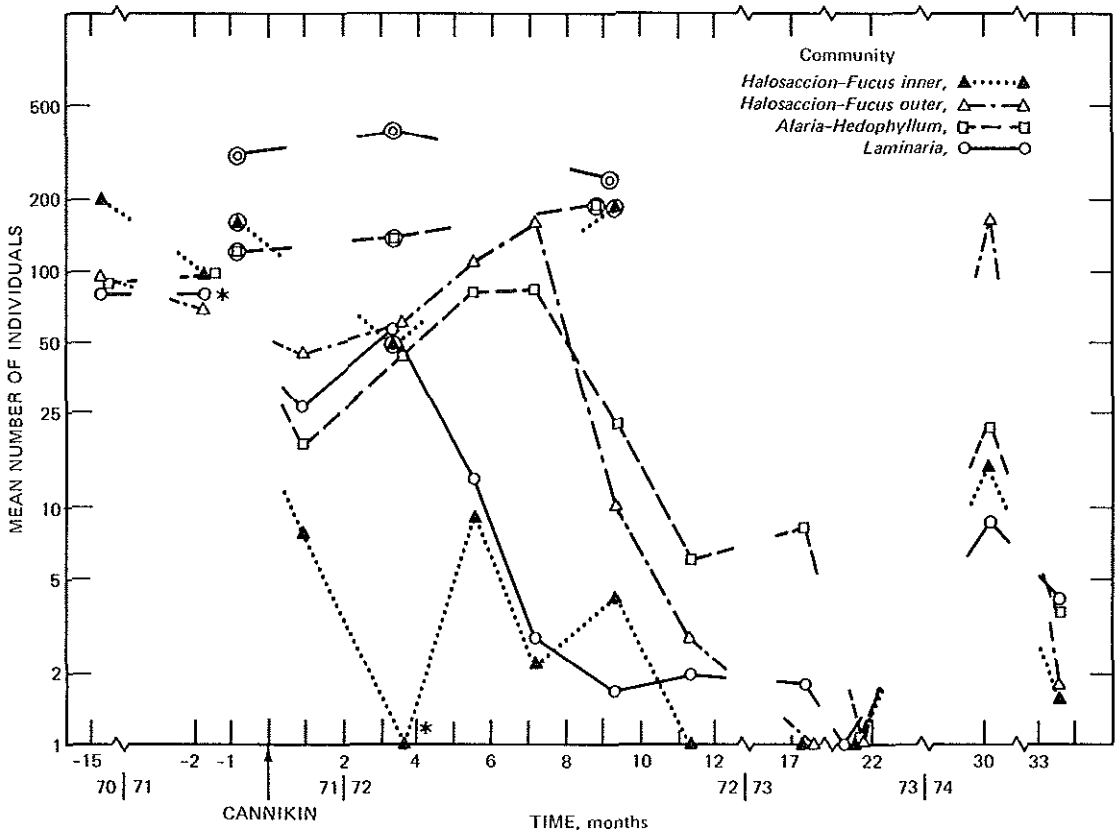

Fig. 17—Mean number of individuals in plots for each algal zone before and after Cannikin at IA-2 and for the control, Makarius Bay (circled symbols). Asterisk indicates a sample size of 1. Species not retained by a 2-mm sieve, such as oligochaetes, *Turtonia minuta*, and *Cingula* spp., gammarids, except *Parallorchestes ochotensis* and *Orchestia* spp., polychaetes, except *Nereis pelagica*, and the holothurian *Cucumaria vegae* are excluded. All gammarids and polychaetes at Makarius Bay are excluded.

depending on bedrock lithology (Kirkwood, 1974). However, the rate seems to be decreasing, and it is uncertain when this erosion will bring these uplifted areas back down to sea level. The fate of the upper surface of the rock bench lifted above the intertidal area is still in doubt.

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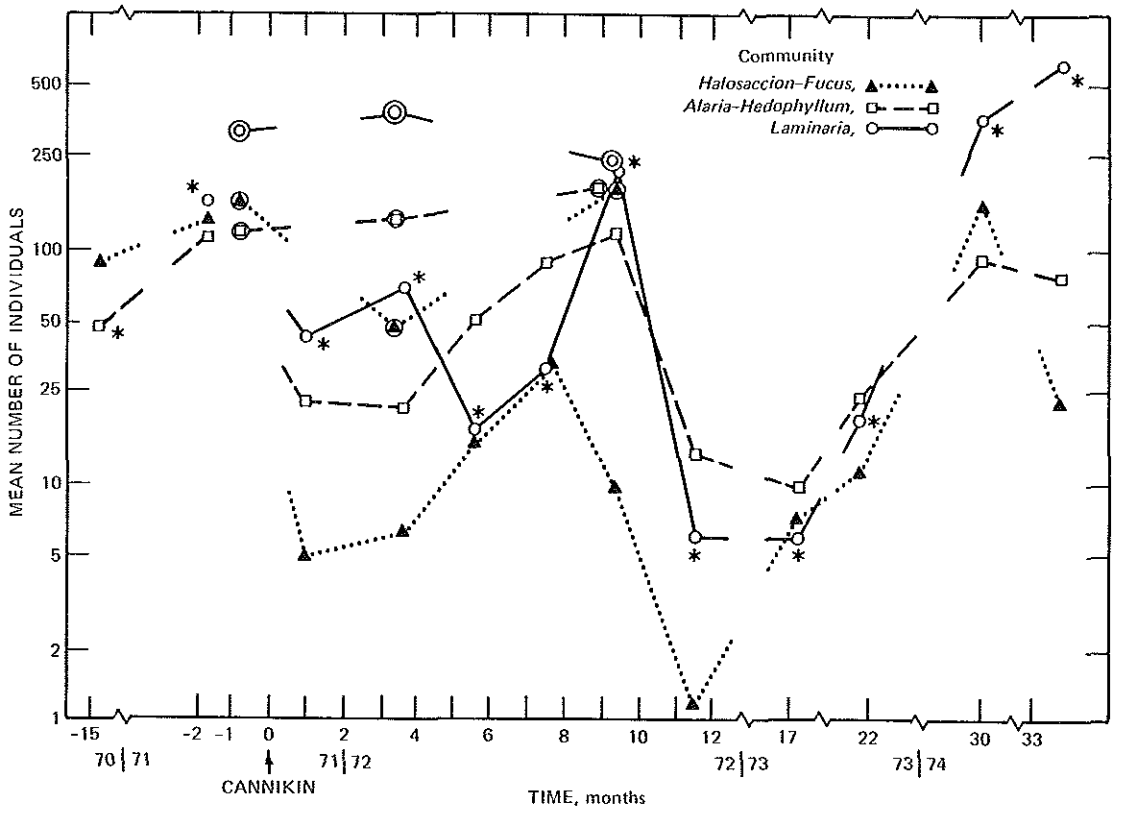

Fig. 18—Mean number of individuals in plots for each algal zone before and after Cannikin at IA-3 and for the control, Makarius Bay (circled symbols). Asterisk indicates a sample size of 1. Species not retained by a 2-mm sieve, such as oligochaetes, *Turtonia minuta*, and *Cingula* spp., gammarids, except *Parallorchestes ochotensis* and *Orchestia* spp., polychaetes, except *Nereis pelagica*, and the holothurian *Cucumaria vegae* are excluded. All gammarids and polychaetes at Makarius Bay are excluded.

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REFERENCES

Abbott, R. T., 1974, *American Seashells; the Marine Molluska of the Atlantic and Pacific Coasts of North America*, Van Nostrand Reinhold Co., New York.

Annenkova, N. P., 1934, Kurze Übersicht der Polychaeten der Litoralzone der Bering-Insel (Kommandor—Inseln), nebst Beschreibung neuer Arten, *Zool. Anz.*, 106: 322-331.

Armstrong, R. H., 1971, Physical Climatology of Amchitka Island, Alaska, *BioScience*, 21: 607-609.

Bakus, G. J., 1966, Marine Poecilosclerida Sponges of the San Juan Archipelago, Washington, *J. Zool.*, 149: 415-531.

Ball, I. R., 1974, Contributions to a Revision of the Marine Triclads of North America: The Monotypic Genera *Nexilis*, *Nesion*, and *Foviella* (Turbellaria: Tricladida), *Can. J. Zool.*, 53: 395-407.

Banse, K., and K. D. Hobson, 1974, *Benthic Errantiate Polychaetes of British Columbia and Washington*, Fisheries Research Board of Canada, Bulletin 185.

Barabash-Nikiforov, 1947, The Sea Otter, Council of Ministers of the RSFSR. Main Administration of Reserves. (Translated from Russian by Israel Program for Scientific Translations, Jerusalem, No. 621, 1962.)

Barnard, J. L., 1962, Benthic Marine Amphipoda of Southern California: Families Amphilochidae, Leucothoidae, Stenothoidae, Argissidae, Hyalidae, *Pac. Naturalist*, 3: 116-163.

——, 1960, The Amphipod Family Phoxocephalidae in the Eastern Pacific Ocean, with Analyses of Other Species and Notes for A Revision of the Family, Allan Hancock Pacific Expeditions, Vol. 18, pp. 175-375.

Barnes, R. D., 1974, *Invertebrate Zoology*, 3rd ed., W. B. Saunders Company, Philadelphia.

Barr, L., 1971, Studies of Populations of Sea Urchins, *Strongylocentrotus* sp., in Relation to Underground Nuclear Testing at Amchitka Island, Alaska, *BioScience*, 21: 614-617.

Barr, N., 1973, Extension of the Known Range of the Crab, *Cryptolithodes typicus* Brandt, to Amchitka Island, Alaska (Decapoda, Anomura, Lithodidae), *Crustaceana (Leiden)*, 25: 320.

Boss, K. J., J. Rosewater, and F. A. Ruhoff, 1968, *The Zoological Taxa of William Healey Dall*, U. S. National Museum, Bulletin 287.

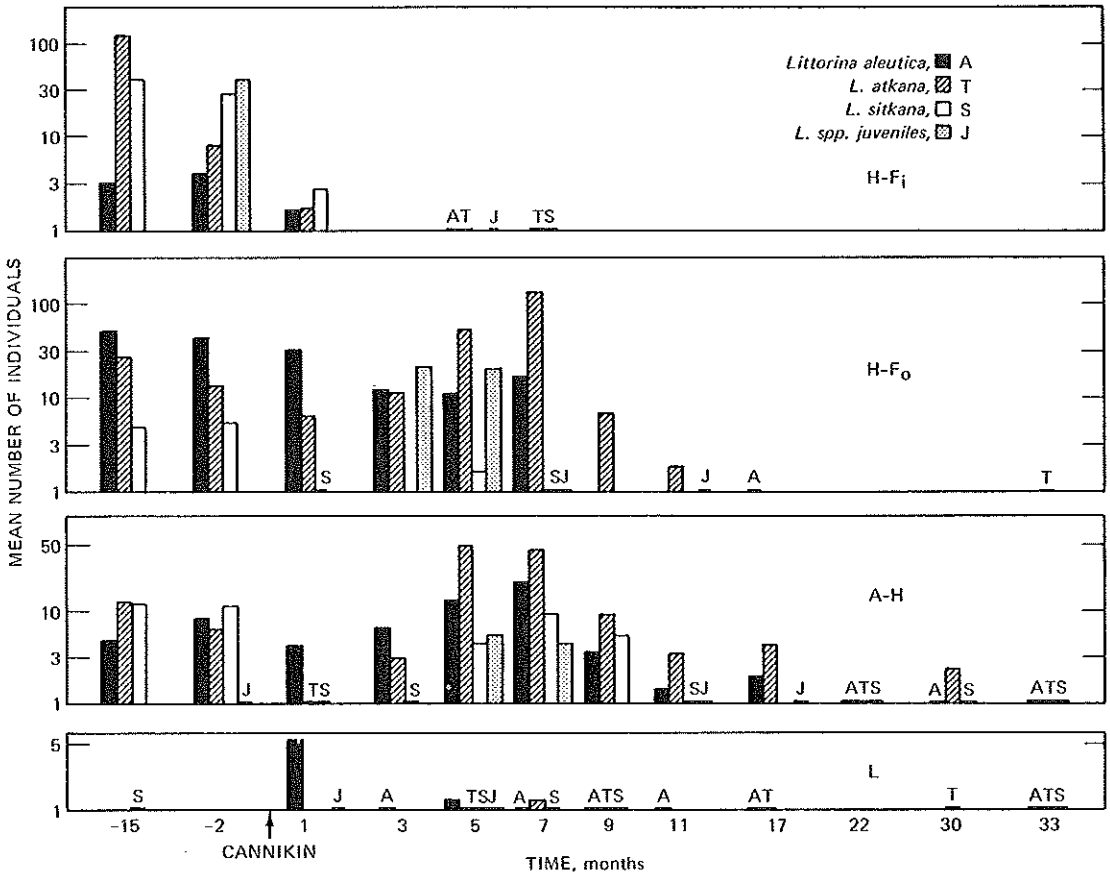

Fig. 19—Mean abundances of littorines on 0.25-m^2 plots in three communities before and after Cannikin at IA-2. H—F_i, *Halosaccion—Fucus* community inner plots; H—F_o, *Halosaccion—Fucus* community outer plots; A—H, *Alaria—Hedophyllum* community; L, *Laminaria* community.

Brandt, J. F., 1851, Krebse, in *Reise in den äussersten Norden und Osten Sibiriens,* A. Th. V. Middendorff, Vol. 2, pp. 77-148.

——, 1850, Vorläufige Bemerkungen über eine neue aus zwei noch unbeschriebenen Gattungen und Arten gebildete Unterabteilung (*Hapalogastrica*) der *Tribus Lithodina,* begleitet von einer Characteristik der eben genannten *Tribus* der Anomuren, *Bull. Cl. Phys.—Math. Acad. Imp. Sci., St. Petersbourg,* 8: 266-269.

——, 1849, Die Gattung Lithodes Latreille nebst vier neuen ihr verwandten von Wosnessenski entdeckten, als Typen einer besondern Unterabteilung (Tribus Lithodea) der Edwards'schen Anomuren, *Bull. Cl. Phys.—Math. Acad. Imp. Sci., St. Pétersbourg,* 7: 171-176.

Briggs, J. C., 1974, *Marine Zoogeography,* McGraw-Hill Book Company, New York.

Bulycheva, A. I., 1957, The Sea Fleas of the USSR and Adjoining Waters (Amphipoda—Talitroidea), *Acad. Sci. USSR Zool. Inst.,* 65: 7-185. (Translated from Russian by The Bureau for Translations of the Department of the Secretary of the State of Canada.)

Burgner, R. L., K. K. Chew, J. S. Isakson, and O. A. Mathisen, 1969, Amchitka Bioenvironmental Program. Annual Progress Report, July 1, 1968—June 30, 1969, Research Program on Marine Ecology and Oceanography, Amchitka Island, Alaska, USAEC Report BMI-171-128, pp. 45-46, Battelle Memorial Institute.

Burton, M., 1963, A Revision of the Classification of the Calcareous Sponges, British Museum of Natural History, London.

Carlquist, S., 1973, *Island Biology,* Columbia University Press, New York.

Chamisso, A. V., 1821, Remarks and Opinions of the Naturalist of the Expedition, in *A Voyage of Discovery into the South Sea and Beering's Straits,* Otto von Kotzebue, Bibliotheca Australiana, No. 18, Vol. 2, pp. 351-433, No. 19, Vol. 3, pp. 1-318, Da Capo Press, New York.

——, and G. G. Eysenhardt, 1821, De animalibus quidbusdam e classe vermium Linneana, in circumnavigatione terrae, auspicante Comite N. Romanzoff, duce Ottone de Kotzebue, annis 1815-1818, Fasc. 2, *Nova Acta Physico-Medica, Acad. Caesareae Leopoldino-Carolinae Bonn. Naturae Curiosorum,* 10: 343-374.

Clark, H. L., 1911, *North Pacific Ophiurans in the Collection of the U. S. National Museum,* U. S. National Museum, Bulletin 75.

Clark, S. F., 1876, Report on the Hydroids Collected on the Coast of Alaska and the Aleutian Islands by W. H. Dall, U. S. Coast Survey, and Party, from 1871 to 1874 Inclusive, *Proc. Acad. Natur. Sci., Philadelphia,* 3: 209-235.

Coan, E. V., 1971, The Northwest American Tellinidae, *Veliger,* 14(Suppl.): 1-63.

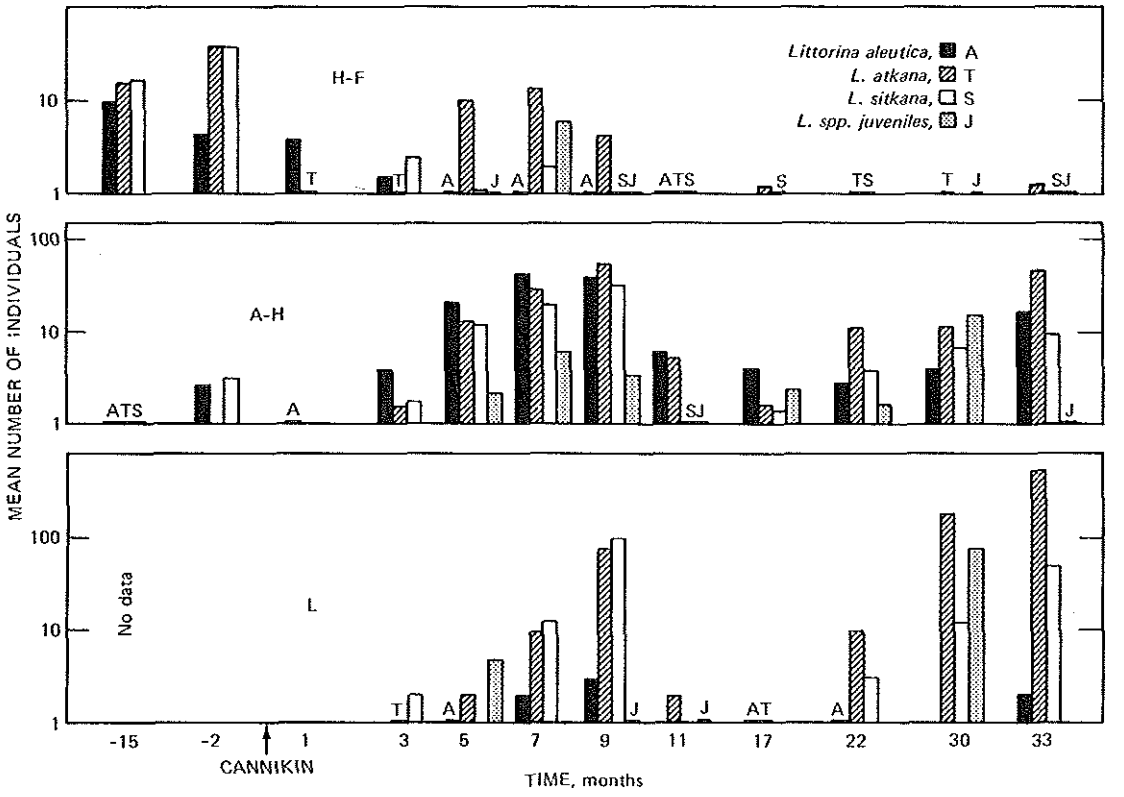

Fig. 20—Mean abundances of littorines on 0.25-m^2 plots in two communities [*Halosaccion–Fucus* (H–F) and *Alaria–Hedophyllum* (A–H)] and abundances on one plot in the *Laminaria* (L) community before and after Cannikin at IA-3. Data collected in the *Laminaria* community 15 months before Cannikin were lost at sea.

Connell, J. H., 1972, Community Interactions on Marine Rocky Intertidal Shores, *Ann. Rev. Ecol. Syst.*, 3: 169-192.

——, 1970, A Predator-Prey System in the Marine Intertidal Region, I. *Balanus glandula* and Several Predatory Species of *Thais*, *Ecol. Monogr.*, 40: 49-78.

——, 1961a, The Influence of Interspecific Competition and Other Factors on the Distribution of the Barnacle *Chthamalus stellatus*, *Ecology*, 42: 710-723.

——, 1961b, Effects of Competition, Predation by *Thais lapillus*, and Other Factors on Natural Populations of the Barnacle *Balanus balanoides*, *Ecol. Monogr.*, 31: 61-104.

Dall, W. H., 1884, Report on the Mollusca of the Commander Islands, Bering Sea; Collected by Leonhard Stejneger in 1882 and 1883, *Proc. U. S. Nat. Mus.*, 7: 340-349.

Dayton, P. K., 1975, Experimental Evaluation of Ecological Dominance in a Rocky Intertidal Algal Community, *Ecol. Monogr.*, 45: 137-159.

——, 1971, Competition, Disturbance, and Community Organization: the Provision and Subsequent Utilization of Space in a Rocky Intertidal Community, *Ecol. Monogr.*, 41: 351-389.

Dodimead, A. J., F. Favorite, and T. Hirano, 1963, Salmon of the North Pacific Ocean, Part II. Review of Oceanography of the Subarctic Pacific Region, International North Pacific Fisheries Commission, Bulletin 13.

Doty, M. S., 1957, Rocky Intertidal Surfaces, in *Treatise on Marine Ecology and Paleoecology*, Vol. 1, Ecology, J. W. Hedgpeth (Ed.), pp. 535-585, Geological Society of America, Memoir 67, New York, N. Y.

D'yakonov, A. M., 1954, Ophiuroids of the U.S.S.R. Seas, *Opred. Faune SSSR, Izdav. Zool. Inst. Akad. Nauk. SSSR*, 55. (Translated from Russian by Israel Program for Scientific Translations, Jerusalem, No. 1880, 1967.)

——, 1950, Sea Stars (Asteroids) of the USSR Seas, *Opred. Faune SSSR, Izdav. Zool. Inst. Akad. Nauk. SSSR*, 34. (Translated from Russian by Israel Program for Scientific Translations, Jerusalem, No. 1922, 1968.)

Ekman, S., 1953, *Zoogeography of the Sea*, Sidgwick & Jackson, Ltd., London.

Emison, W. B., F. S. L. Williamson, and C. M. White, 1971, Geographical Affinities and Migrations of the Avifauna on Amchitka Island, Alaska, *BioScience*, 21: 627-631.

Eschscholtz, J. F., 1829-1833, *Zoologischer Atlas*, G. Reiner, Berlin.

Estes, J. A., and J. F. Palmisano, 1974, Sea Otters: Their Role in Structuring Nearshore Communities, *Science*, 185: 1058-1060.

Fager, E. W., 1963, Communities of Organisms, in *The Sea, Ideas and Observations on Progress in the Study of the Seas*, Vol. 2, The Composition of Sea-Water Comparative and Descriptive Oceanography, M. N. Hill (Ed.), pp. 415-437, Interscience Publishers, Inc., now John Wiley & Sons, Inc., New York.

——, and J. A. McGowan, 1963, Zooplankton Species Groups in the North Pacific, *Science*, 140: 453-460.

Favorite, F., 1967, *The Alaskan Stream*, International North Pacific Fisheries Commission, Bulletin 21, pp. 1-20.

Fisher, W. K., 1938, Hydrocorals of the North Pacific Ocean, *Proc. U. S. Nat. Mus.*, 84: 493-554.

——, 1930, *Asteroidea of the North Pacific and Adjacent Waters*, Part 3, Forcipulata (concluded), U. S. National Museum, Bulletin 76, pp. 1-356.

——, 1928, *Asteroidea of the North Pacific and Adjacent Waters*, Part 2, Forcipulata (part), U. S. National Museum, Bulletin 76, pp. 1-245.

——, 1911, *Asteroidea of the North Pacific and Adjacent Waters*, Part 1, Phanerozonia and Spinulosa, U. S. National Museum, Bulletin 76, pp. 1-419.

Fraser, C. M., 1937, *Hydroids of the Pacific Coast of Canada and the United States*, University of Toronto Press, Toronto.

Fretter, V., 1951, Observations on the Life History and Functional Morphology of *Cerithiopsis tubercularis* (Montagu) and *Triphora perversa* (L.), *J. Mar. Biol. Ass. U. K.*, 29: 567-586.

Garth, J. S., 1958, Brachyura of the Pacific Coast of America, Oxyrhyncha, Allan Hancock Pacific Expeditions, Vol. 21.

Glynn, P. W., 1965, Community Composition, Structure, and Interrelationships in the Marine Intertidal *Endocladia muricata–Balanus glandula* Association in Monterey Bay, California, *Beaufortia*, 12: 1-198.

Golikov, A. N., and O. G. Kussakin, 1972, Sur la Biologie de la Reproduction des Patelles de la Famille Tecturidae (Gastropoda: Docoglossa) et sur la Position Systematique de ses Subdivisions, *Malacologia*, 11: 287-294.

——, and O. G. Kussakin, 1962, Fauna and Ecology of Gastropod Prosobranchian Mollusks (Gastropoda, Prosobranchia) of the Littoral of Kurile Islands, *Issled. Dal'nevost. Morei SSSR*, 8: 248-346. (In Russian.)

Grube, A. E., 1855, Beschreibungen neuer oder wenig bekannter Anneliden, *Arch. Naturgesch.*, 21: 81-136.

Gurjanova, E. F., 1966, Comparative Research of Biology of the Littoral in the Far Eastern Seas, *Proc. Pac. Sci. Congr., 9th*, 19: 75-86.

——, 1951, Bokoplavy morei SSSR i Sopredel'nykh vod (Amphipoda, Gammaridea), *Opred. Faune SSSR, Izdav. Zool. Inst. Akad. Nauk. SSSR*, 41: 1-1029.

——, 1935, Komandorskie Ostrova i ikh Morskaya Pribezhnaya Fauna i Flora (The Commander Islands: Their Littoral Fauna and Flora), *Priroda*, 11: 64-72. (Translated from Russian by Leda V. Sagen.)

Gustus, R. M., 1972, A Species of the Genus *Eunice* (Polychaeta) from the Pacific Northwest Coast, *Northwest Sci.*, 46: 257-269.

Harger, J. R., 1972, Variation and Relative "Niche" Size in the Sea Mussel *Mytilus edulis* in Association with *Mytilus californianus*, *Veliger*, 14: 275-283.

Hartman, O., 1969, Atlas of the Sedentariate Polychaetous Annelids from California, Allan Hancock Foundation, Los Angeles, Calif.

——, 1959, Catalogue of the Polychaetous Annelids of the World, Parts I and II, Allan Hancock Foundation, Occasional Paper No. 23.

Hedgpeth, J. W., and J. J. Gonor, 1969, Aspects of the Potential Effect of Thermal Alteration on Marine and Estuarine Benthos, in *Biological Aspects of Thermal Pollution*, Proceedings of the National Symposium on Thermal Pollution, pp. 80-118, Vanderbilt University Press.

Hobson, K. O., and K. Banse, Benthic Sedentariate Polychaetes of British Columbia and Washington, in preparation.

Hultén, E., 1960, *Flora of the Aleutian Islands*, 2nd ed., J. Cramer, Weinheim.

Kenyon, K. W., 1969, *The Sea Otter in the Eastern Pacific Ocean*, U. S. Department of the Interior, Bureau of Sport Fisheries and Wildlife, North American Fauna, No. 68.

Kincaid, T., 1964, Notes on *Thais* (*Nucella*) *lima* (Gmelin), a Marine Gastropod Inhabiting Areas in the North Pacific Ocean, The Calliostoma Company, Seattle, Wash.

Kirkwood, J. B., 1974, Amchitka Bioenvironmental Program. Bioenvironmental Safety Studies, Amchitka Island, Alaska, Spring, 1974 Task Force Report, USAEC Report BMI-171-157, Battelle Memorial Institute.

——, and R. G. Fuller (Comps.), 1972, Bioenvironmental Safety Studies, Amchitka Island, Alaska, Cannikin D+2 Months Report, USAEC Report BMI-171-147, Battelle Memorial Institute.

Laubitz, D. R., 1970, Studies on the Caprellidae (Crustacea, Amphipoda) of the American North Pacific, *Publications in Biological Oceanography, National Museum of Natural Sciences, Ottawa*, No. 1.

Lewis, J. R., 1964, *The Ecology of Rocky Shores*, English Universities Press Ltd., London.

Lindroth, C. H., 1963, The Aleutian Islands as a Route for Dispersal Across the North Pacific, in *Pacific Basin Biogeography, Tenth Pacific Science Congress*, Honolulu, J. L. Gressitt (Ed.), pp. 121-131, Bishop Museum Press.

MacArthur, R. H., 1972, *Geographical Ecology*, Harper & Row Publishers, Inc., New York.

——, and E. O. Wilson, 1967, *The Theory of Island Biogeography*, Princeton University Press, Princeton, N. J.

MacGinitie, N., 1959, Marine Mollusca of Point Barrow, Alaska, *Proc. U. S. Nat. Mus.*, 109: 59-208.

Makarov, V. V., 1938, Crustacea: Anomura, *Opred. Faune SSSR, Izdav. Zool. Inst. Akad. Nauk. SSSR*, N. S., 16. (Translated from Russian by Israel Program for Scientific Translations, Jerusalem, No. 225, 1962.)

Mauzey, K. P., C. Birkeland, and P. K. Dayton, 1968, Feeding Behavior of Asteroids and Escape Responses of Their Prey in the Puget Sound Region, *Ecology*, 49: 603-619.

McAlister, B. W., 1971, Oceanography in the Vicinity of Amchitka Island, Alaska, *BioScience*, 21: 646-651.

McLaughlin, P. A., 1974, The Hermit Crabs (Crustacea Decapoda, Paguridae) of Northwestern North America, *Zool. Verh. (Leiden)*, No. 130.

McLean, J. H., 1969, Marine Shells of Southern California, Los Angeles County Museum of Natural History, Science Series 24, Zoology, No. 11.

——, 1966, West American Prosobranch Gastropoda: Superfamilies Patellacea, Pleurotomariacea and Fissurellacea, Ph. D. Thesis, Stanford University.

Menge, B. A., 1972, Foraging Strategy of a Starfish in Relation to Actual Prey Availability and Environmental Predictability, *Ecol. Monogr.*, 42: 25-50.

Menzies, R. J., 1952, Some Marine Asellote Isopods from Northern California, with Descriptions of Nine New Species, *Proc. U. S. Nat. Mus.*, 102: 117-159.

Merritt, M. L., 1972, Cannikin Ground Motion and Water Pressures, in Amchitka Bioenvironmental Program, Bio-

environmental Safety Studies, Amchitka Island, Alaska, Cannikin D+2 Months Report, USAEC Report BMI-171-147, Battelle Memorial Institute.

Middendorff, A. Th., 1851, Mollusken, in *Reise in den äussersten Norden und Osten Sibiriens,* A. Th. v. Middendorff, Vol. 2, No. 1, pp. 163-508.

——, 1849a, Beiträge zu einer Malacozoologia Rossica. I. Beschreibung und Anatomie ganz neuer, oder für Russland neuer Chitonen, *Mém. Acad. Imp. Sci., St. Pétersbourg, Ser. 6, Sci. Nat.,* 6: 67-215.

——, 1849b, Beiträge zu einer Malacozoologia Rossica. II. Aufzählung und Beschreibung der zur Meeresfauna Russlands gehörigen Einschaler, *Mém. Acad. Imp. Sci., St. Pétersbourg, Ser. 6, Sci. Nat.,* 6: 329-516.

——, 1849c, Beiträge zu einer Malacozoologia Rossica. III. Aufzählung und Beschreibung der zur Meeresfauna Russlands gehörigen Zweischaler, *Mém. Acad. Imp. Sci., St. Pétersbourg, Ser. 6, Sci. Nat.,* 6: 517-596.

——, 1846, Vorläufige Anzeige bisher unbekannter Mollusken, als Vorarbeit zu einer Malacozoologia Rossica, veröffentlicht durch, *Bull. Cl. Phys.—Math., Acad. Imp. Sci., St. Pétersbourg,* 6: 113-122.

Mortensen, T., 1943, *A Monograph of the Echinoidea, Camarodonta II, Echinidae, Strongylocentrotidae, Parasaleniidae, Echinometridae,* Vol. 3, Part 3, C. A. Reitzels, Forlag, Copenhagen.

Newell, I. M., 1951, New Species of *Agaue* and *Thalassarachna* from the Aleutians, *Amer. Mus. Novit.,* 1489: 1-19.

——, 1950, New Species of *Copidognathus* from the Aleutians, *Amer. Mus. Novit.,* 1476: 1-19.

Nybakken, J. W., 1969, Pre-Earthquake Intertidal Ecology of Three Saints Bay, Kodiak Island, Alaska, *Biol. Pap. Univ. Alaska,* 9: 1-123.

O'Clair, C. E., and K. K. Chew, 1971, Transect Studies of Littoral Macrofauna, Amchitka Island, Alaska, *BioScience,* 21: 661-664.

Oldroyd, I. S., 1924 and 1927, Marine Shells of the West Coast of North America, Stanford University Publication, University Series, Geological Science, Vols. I and II, Parts 1, 2, and 3.

Paine, R. T., 1974, Intertidal Community Structure, Experimental Studies on the Relationship Between a Dominant Competitor and Its Principal Predator, *Oecologia,* 15: 93-120.

——, 1966, Food Web Complexity and Species Diversity, *Amer. Natur.,* 100: 65-75.

Palmisano, J. F., 1975, Sea Otter Predation: Its Role in Rocky Intertidal Community Structure at Amchitka and Other Aleutian Islands, Ph. D. Thesis, University of Washington.

Pilsbry, H. A., 1916, *The Sessile Barnacles (Cirripedia) Contained in the Collections of the U. S. National Museum, Including a Monograph of the American Species,* U. S. National Museum, Bulletin 93.

Powers, H. A., R. R. Coats, and W. H. Nelson, 1960, *Geology and Submarine Physiography of Amchitka Island, Alaska,* U. S. Geological Survey, Bulletin 1028-P, pp. 521-554.

Rathbun, M. J., 1930, *The Cancroid Crabs of America of the Families Euryalidae, Portunidae, Atelecyclidae, Cancridae and Xanthidae,* U. S. National Museum, Bulletin 152, pp. 1-609.

Reid, J. L., 1973, *Northwest Pacific Ocean Waters in Winter,* Johns Hopkins Oceanographic Studies No. 5, Johns Hopkins University Press, Baltimore, Md.

Richards, B. R., and C. I. Belmore, 1976, Occurrence of the Woodborer, *Limnoria lignorum* (Rathke) at Amchitka Island, Alaska, *J. Fish. Res. Board Can.,* 33: 1642-1644.

Richardson, H., 1905, *Monograph on the Isopods of North America,* U. S. National Museum, Bulletin 54, pp. 1-727.

Ricketts, E. F., J. Calvin, and J. W. Hedgpeth, 1968, *Between Pacific Tides,* 4th ed., Stanford University Press, Stanford, Calif.

Rieger, S., and R. E. Wunderlich, 1960, Soil Survey and Vegetation of Northeastern Kodiak Island Area, Alaska, U. S. Department of the Interior, Bureau of Land Management, Soil Conservation Service, Soil Survey Series 1956, No. 17.

Sauer, M., 1802, *An Account of a Geographical and Astronomical Expedition to the Northern Parts of Russia, for Ascertaining the Degrees of Latitude and Longitude of the Mouth of the River Kovima; of the Whole Coast of the Tshutski, to East Cape; and of the Islands in the Eastern Ocean, Stretching to the American Coast, by Commodore Joseph Billings, in the Years 1785 to 1794,* A. Strahan, London.

Scarlato, O. A., 1960, The Bivalved Molluscs of the Far East Seas of USSR (Order Dysodonta), *Opred. Faune SSSR, Izdav. Zool. Inst. Akad. Nauk. SSSR,* 71: 1-150. (In Russian.)

Schultz, G. A., 1969, *How to Know the Marine Isopod Crustaceans,* William C. Brown Co., Publishers, Dubuque, Iowa.

Shelford, V. E., A. O. Weese, L. A. Rice, D. I. Rasmussen, and A. MacLean, 1935, Some Marine Biotic Communities of the Pacific Coast of North America. Part I. General Survey of the Communities—Their Extent and Dynamics, *Ecol. Monogr.,* 5: 249-332.

Soot-Ryen, T., 1955, A Report on the Family Mytilidae (Pelecypoda), Allan Hancock Pacific Expeditions, Vol. 20, pp. 1-174.

Spassky, N. N., 1961, The Intertidal Zone of the South-East Shore of Kamchatka, *Issled. Dal'nevost. Morei SSSR,* 7: 261-311. (In Russian.)

Stejneger, L., 1936, *Georg Wilhelm Steller, The Pioneer of Alaskan Natural History,* Harvard University Press, Cambridge, Mass.

Stephen, A. C., and S. J. Edmonds, 1972, The Phyla Sipuncula and Echiura, British Museum of Natural History.

Stephenson, T. A., and A. Stephenson, 1972, *Life Between Tidemarks on Rocky Shores,* W. H. Freeman & Co., San Francisco, Calif.

——, and A. Stephenson, 1949, Universal Features of Zonation Between Tidemarks on Rocky Coasts, *J. Ecol.,* 37: 289-305.

Stephenson, W., 1973, The Validity of the Community Concept in Marine Biology, *Proc. R. Soc. (Queensland),* 84: 73-86.

Tzvetkova, N. L., 1975, Geographical Distribution of Species of the Genus *Anisogammarus* Derzhavin (Amphipoda, Gammaridae), *Crustaceana (Leiden),* 28: 191-199.

Ushakov, P. V., 1955, Polychaeta of the Far Eastern Seas of the U.S.S.R., *Opred. Faune SSSR, Izdav. Zool. Inst. Akad. Nauk. SSSR,* No. 56. (Translated from Russian by Israel Program for Scientific Translations, Jerusalem, No. 1259, 1965.)

U. S. Department of Commerce, 1971, National Oceanic and Atmospheric Administration, *Local Climatological Data, Annual Summary with Comparative Data,*

Shemya, Alaska, Superintendent of Documents, U. S. Government Printing Office, Washington, D. C.

——, Environmental Sciences Services Administration, 1969, *Tide Tables, West Coast North and South America,* Superintendent of Documents, U. S. Government Printing Office, Washington, D. C.

——, Coast and Geodetic Survey, 1949, *Tide and Current Glossary,* Special Publication No. 228, Superintendent of Documents, U. S. Government Printing Office, Washington, D. C.

U. S. Naval Oceanographic Office, 1969, Monthly Charts of Mean, Minimum and Maximum Sea Surface Temperature of the North Pacific Ocean, Special Publication No. SP-123.

Van Name, W. G., 1945, The North and South American Ascidians, *Bull. Amer. Mus. Nat. Hist.,* 84.

Vermeij, G. J., 1972, Endemism and Environment: Some Shore Molluscs of the Tropical Atlantic, *Amer. Natur.,* 106: 89-101.

Wilimovsky, N. J., 1964, Inshore Fish Fauna of the Aleutian Archipelago, in *Proceedings of the Fourteenth Alaska Science Conference,* pp. 172-190.

Yamada, M., 1955, Some Hydroids from Agattu, in the Aleutian Islands, *Annot. Zool. Jap.,* 28: 121-125.

APPENDIX: ANNOTATED SPECIES LIST OF THE INVERTEBRATES AT AMCHITKA ISLAND, ALASKA

The following species list is a partial list of the species of invertebrates collected by Fisheries Research Institute personnel in the vicinity of Amchitka Island, Alaska. A number of specialists have contributed their expertise to the preparation of this list. These specialists are listed below and are acknowledged preceding the taxonomic groups or species they identified.

Dr. Donald P. Abbott, Hopkins Marine Station of Stanford University, Pacific Grove, Calif. *Styela clavata.*

Ms. Suzanne Allyson, Research Branch, Biosystematics Research Institute, Agriculture Canada, Ottawa, Ontario, Canada. Lepidoptera.

Dr. Gerald J. Bakus, University of Southern California, Los Angeles, Calif. *Halichondria panicea.*

Dr. Karl Banse, Department of Oceanography, University of Washington, Seattle, Wash. *Syllis.*

Mr. Louis Barr, National Marine Fisheries Service, Biological Laboratory, Auke Bay, Alaska. *Rhinolithodes wosnessenskii.*

Dr. Edward C. Becker, Research Branch, Biosystematics Research Institute, Agriculture Canada, Ottawa, Ontario, Canada. Coleoptera.

Dr. Edward L. Bousfield, National Museum of Natural Sciences, Ottawa, Ontario, Canada. Gammaridea.

Dr. J. Milton Campbell, Research Branch, Biosystematics Research Institute, Agriculture Canada, Ottawa, Ontario, Canada. Coleoptera.

Dr. David G. Cook, Department of the Environment, Fisheries and Marine Service, Ottawa, Ontario, Canada. Oligochaeta.

Mr. Matthew Dick, 1902 State St., Alamosa, Colo. Bryozoa.

Dr. Maureen E. Downey, Department of Invertebrate Zoology, National Museum of Natural History, Washington, D. C. Asteroidea.

Dr. Arthur R. Fontaine, Department of Biology, University of Victoria, Victoria, British Columbia, Canada. *Bonelliopsis.*

Ms. Madeline Green, College of Fisheries, University of Washington, Seattle, Wash. *Japetella heathi.*

Dr. Olga Hartman, deceased, formerly at the Allan Hancock Foundation, University of Southern California, Los Angeles, Calif. *Cirratulus.*

Dr. Melville H. Hatch, Burke Memorial Museum, University of Washington, Seattle, Wash. *Liparocephalus.*

Dr. Charlotte Holmquist, Sekt. Evertebratzool, Naturhistoriska Riksmuseet, Stockholm, Sweden. *Paracanthomysis kurilensis.*

Dr. Paul L. Illg, Department of Zoology, University of Washington, Seattle, Wash. *Blakeanus.*

Dr. Margit Jensen, Zoological Museum, University of Copenhagen, Copenhagen, Denmark. *Strongylocentrotus.*

Dr. A. Myra Keen, Department of Geology, Stanford University, Stanford, Calif. Mollusca.

Dr. Allan J. Kohn, Department of Zoology, University of Washington, Seattle, Wash. *Phascolosoma.*

Dr. Eugene N. Kozloff, Department of Zoology, University of Washington, Seattle, Wash. *Tetrastemma.*

Ms. Diana R. Laubitz, National Museum of Natural Sciences, Ottawa, Ontario, Canada. *Cercops.*

Dr. Ulf Lie, Biological Station Espegrend, Blomsterdalen, Norway. Gammaridea.

Dr. Evert E. Lindquist, Research Branch, Biosystematics Research Institute, Agriculture Canada, Ottawa, Ontario, Canada. Acarina.

Dr. James H. McLean, Los Angeles County Museum of Natural History, Los Angeles, Calif. Mollusca.

Dr. Carl F. Nyblade, Department of Zoology, University of Washington, Seattle, Wash. Paguridae.

Dr. Rita M. O'Clair, Friday Harbor Laboratories, Friday Harbor, Washington. Polychaeta.

Mr. Gordon W. O'Connell, Department of Biology, University of Victoria, Victoria, British Columbia, Canada. Pycnogonida.

Dr. Donald R. Oliver, Research Branch, Biosystematics Research Institute, Agriculture Canada, Ottawa, Ontario, Canada. Diptera.

Dr. Bruce Ott, Institute of Marine Sciences, McGill University, Montreal, Quebec, Canada. Porifera.

Dr. David L. Pawson, Department of Invertebrate Zoology, National Museum of Natural History, Washington, D. C. Echinodermata.

Dr. Stephen Prudhoe, Department of Zoology, British Museum (Natural History), London, England. Turbellaria.

Ms. Famida Rafi, National Museum of Natural Sciences, Ottawa, Ontario, Canada. *Idotea.*

Dr. Gordon A. Robilliard, Woodward-Envicon, Inc., San Diego, Calif. Nudibranchia.

Dr. Mary E. Roussel, Research Branch, Biosystematics Research Institute, Agriculture Canada, Ottawa, Ontario, Canada. Diptera.

Mr. Kenneth Sebens, Department of Zoology, University of Washington, Seattle, Wash. Actiniaria.

Mr. Ronald Shimek, Department of Zoology, University of Washington, Seattle, Wash. *Suavodrillia.*

Mr. Peter N. Slattery, Moss Landing Marine Laboratories, Moss Landing, Calif. Gammaridea.

Dr. Herbert J. Teskey, Research Branch, Biosystematics Research Institute, Agriculture Canada, Ottawa, Ontario, Canada. Diptera.

Mr. Gregory J. Tutmark, 2200 Northeast 75th Street, Seattle, Wash. Cephalopoda and Crustacea.

Dr. Charles W. Thayer, Department of Geology, University of Pennsylvania, Philadelphia, Pa. Brachiopoda.

Unless otherwise noted, I identified the rest of the species included in the list from the literature, and references are included following the names, authors, and dates of these species. Additional annotations include the vertical distribution of the species in the vicinity of Amchitka, and, for those species covered in Table 5, the geographical distribution. (Species in those groups covered whose ranges extend to a depth greater than 60 m were not included in Table 5.) Information on intertidal invertebrates occurring at the five main study sites includes the population statistics fidelity (f.), constancy (c.), and abundance (a.). Classification generally follows Barnes (1974). Specimens have been deposited in the invertebrate collections of the National Museum of Natural Sciences, Ottawa, and the College of Fisheries, University of Washington. Abbreviations used in this species list are listed below.

a (abundance), median and range of numbers of individuals per 0.25 m^2 in quadrats in which the species was found.

c (constancy), proportion of quadrats from the community to which the species was assigned that contained the species.

f (fidelity), proportion of all quadrats containing the species that was in the community to which the species was assigned. A species was assigned to that community where the value of *f.* was greatest.

NMNS, National Museum of Natural Sciences, Ottawa, Canada.

USNM, National Museum of Natural History, Washington, D. C.

Phylum Porifera (Unless otherwise noted, all Porifera identified by B. Ott and deposited in the NMNS.)

Class Calcarea

Scypha compactum (Lambe, 1894). Sublittoral, 6 m.

Scypha compressa (Fabricius, 1780). Compared with NMNS specimens of *Grantia monstruosa* (Breitfuss, 1898) [= *S. compressa* (see Burton, 1963)] from Bering Island. Verified by B. Ott. See Table 2 for population statistics.

Leucandra taylori Lambe, 1900. *Alaria–Hedophyllum* community to 91 m.

Leuconia pyriformis (Lambe, 1894). *Alaria–Hedophyllum* community to 6 m.

Leuconia heathi (Urban, 1905). *Laminaria* community to 183 m.

Leuconia sp. A. Sublittoral, 6 to 24 m.

Rhabdodermella nuttingi Urban, 1905. Sublittoral, 91 m.

Class Hyalospongea

Rhabdocalyptus dawsoni (Lambe, 1893). Sublittoral, 183 m.

Hyalospongea sp. Sublittoral, 183 m.

Class Demospongiae

Haliclona permollis (Bowerbank, 1866). Sublittoral, 6 m.

Haliclona sp. Sublittoral, 91 m.

Gellius sp. Sublittoral, 183 m.

Sigmadocia edaphus de Laubenfels, 1930. Sublittoral, 55 m.
Isodictya quatsinoensis (Lambe, 1893). Sublittoral, 6 to 24 m.
Mycale hispida (Lambe, 1894). Sublittoral, 6 to 24 m.
M. lingua (Bowerbank, 1866). Sublittoral, 18 to 24 m.
M. loveni (Fristedt, 1887). Sublittoral, 91 m.
M. helios (Fristedt, 1887). Sublittoral, 91 m.
Mycale sp. Sublittoral, 91 m.
Anthoarcuata graceae Bakus, 1966. Sublittoral, 6 to 24 m.
Microciona primitiva Koltun, 1955. Sublittoral, 91 to 183 m.
Iotrochota magna Lambe, 1895. Specimen collected by R. Martin. Sublittoral, 15 to 23 m.
Lissodendoryx amaknakensis (Lambe, 1895). Sublittoral, 6 m.
L. firma (Lambe, 1895). *Laminaria* community to 91 m.
Stelodoryx alaskensis (Lambe, 1895). Sublittoral, 6 to 55 m.
Wigginsia wigginsi de Laubenfels, 1953. Sublittoral, 183 m.
Myxilla lacunosa Lambe, 1893. Sublittoral, 6 m.
Halichondria panicea (Pallas, 1766). Identification by G. J. Bakus of specimens collected by J. F. Palmisano.
Laminaria community; f, 0.53; c, 0.66; a, 12.6%, 1 to 55%.
H. lambei Brønsted, 1933. Sublittoral, 6 to 183 m.
Suberites domuncula domuncula (Olivi, 1792). Sublittoral, 12 to 128 m.
S. d. ficus (Olivi, 1792). Sublittoral, 55 to 183 m.
S. montiniger Carter, 1880. Sublittoral, 55 to 183 m.
Polymastia pachymastia de Laubenfels, 1932. Sublittoral, 6 to 274 m.
P. pacifica Lambe, 1894. Sublittoral, 91 to 183 m.
Latruculia tricincta Hentchel, 1929. Sublittoral, 183 m.
Tetilla villosa (Lambe, 1894). Sublittoral, 6 to 183 m.
T. spinosa (Lambe, 1894). Sublittoral, 6 to 183 m.
Corticium sp. Sublittoral, 34 m.
Geodinella robusta Lendenfeld, 1910. Sublittoral, 274 m.
Asbestopluma lycopodium (Levinsen, 1886). Sublittoral, 91 m.
Axinella sp. A. Sublittoral, 183 m.
Syringella amphispicula de Laubenfels, 1961. Sublittoral, 183 m.

Phylum Coelenterata
Class Hydrozoa (Fraser, 1937).
Order Hydroida
Syncoryne sp. *Laminaria* community; f, 1.0; c, 0.06; a, 1.
Sertularella pinnata Clark, 1876. *Laminaria* community; f, 1.0; c, 0.06; a, 1.
Order Stylasterina
?*Allopora campyleca* (Fisher, 1938). Sublittoral, 183 m.
Class Anthozoa
Order Pennatulacea
Ptilosarcus sp. Subtidal, 30 to 35 m. One very young specimen collected in *Laminaria* community at IA-2.
Order Actiniaria (All anemones were identified by K. Sebens except *Metridium* sp.)
Family Actiniidae
Cnidopus ritteri (Torrey, 1902). *Laminaria* community.
Epiactis sp. *Laminaria* community. Several specimens bearing young.
Tealia sp. *Laminaria* community.
Unidentified sp. B. *Laminaria* community; the most common anemone in the lower midlittoral zone and infralittoral fringe.
Unidentified sp. C. *Laminaria* community.
Unidentified sp. D. *Laminaria* community.
Family Hormathiidae
Unidentified sp. A. *Laminaria* community.
Family Metridiidae
Metridium sp. Subtidal.

Phylum Platyhelminthes
Class Turbellaria (All Turbellaria identified by S. Prudhoe.)
Order Alloeocoela
Plagiostomidae sp. *Halosaccion—Fucus* community: f, 0.66; c, 0.18; a, 1, 1-2.
Order Tricladida
Nexilis epichitonius Holleman and Hand, 1962. *Alaria—Hedophyllum* community: f, 0.6; c, 0.25, a, 9, 2-133. Not previously recorded northwest of Vancouver Island, British Columbia (Ball, 1974).
Nesion arcticum Hyman, 1956. Upper communities; f, 1.0; c, 0.09; a, 2.

Order Polycladida

Notoplana atomata (O. F. Müller, 1776). *Alaria–Hedophyllum* community; f, 1.0; c, 0.08; a, 1.

?*Leptoplana vesiculata* Hyman, 1939. Juvenile. *Laminaria* community; f, 1.0; c, 0.33; a, 1.

Phylum Nemertea

Class Enopla

Tetrastemma sp. Identification to genus by E.N. Kozloff of specimens collected by J. F. Palmisano.

Phylum Nematoda

Unidentified species. In the intertidal area, nematodes were most numerous among the holdfasts of *Laminaria longipes* and *Alaria crispa*, reaching densities as high as 261 per 0.062 m^2.

Phylum Annelida

Class Polychaeta

Harmothoe imbricata (Linnaeus, 1767). Collected and identified by K. Kimura.

Lepidonotus helotypus (Grube, 1877). Identified by R. M. O'Clair. Sublittoral, 183 m.

Pholoe minuta (Fabricius, 1780). Verified by R. M. O'Clair. *Laminaria* community; f. 0.8, c. 0.33, a. 50, 22-123.

Dysponetus pygmaeus Levinsen, 1879; Ushakov, 1955. *Laminaria* community; f. 0.8, c. 0.33, a. 50, 11-88. Arctic–boreal.

Euphrosine borealis Oersted, 1843. Identified by R. M. O'Clair. Sublittoral, 34 m.

Eteone flava (Fabricius, 1780). Identified by R. M. O'Clair. *Laminaria* community; f. 0.8, c. 0.33, a. 40, 23-56.

Eulalia (Eulalia) viridis (Linnaeus, 1767). *Laminaria* community. Widely distributed.

Eulalia (Eumida) longicornuta Moore, 1906. (Banse and Hobson, 1974). *Alaria–Hedophyllum* community. North American.

Notophyllum sp. Identified to genus by R. M. O'Clair. Sublittoral, 64 m.

Phyllodocidae sp. *Laminaria* community; f. 0.57, c. 0.33, a. 1.

Autolytus prismaticus (Fabricius, 1780). Identified by R. M. O'Clair. *Halosaccion–Fucus* community.

Autolytus beringianus Annenkova, 1934; Ushakov, 1955. *Laminaria* community; f. 1.0, c. 0.33, a. 2. Asiatic.

Autolytus sp. *Alaria–Hedophyllum* community; f. 0.66, c. 0.17, a. 6, 1-11.

Exogone gemmifera Pagenstecher, 1862. Identified by R. M. O'Clair. Lower communities; f. 0.36; c. 0.33, a. 127, 46-889.

Sphaerosyllis sp. A. cf. *S. pirifera* Claparède, 1868. *Laminaria* community; f. 0.8, c. 0.33, a. 5, 1-9.

Sphaerosyllis sp. B. *Alaria–Hedophyllum* community; f. 0.66, c. 0.17, a. 54, 1-64.

?*Syllis (Typosyllis) alternata* Moore, 1908; Banse and Hobson, 1974. Upper communities; f. 0.5, c. 0.09, a. 202, 24-380.

Syllis (Typosyllis) armillaris (O. F. Müller, 1776). Identified by R. M. O'Clair. Lower Communities; f. 0.5, c. 0.4, a. 30, 5-318. Widely distributed.

Syllis (Typosyllis) stewarti Berkeley, 1942. Verified by R. M. O'Clair. *Halosaccion–Fucus* community; f. 1.0, c. 0.09, a. 2.

Syllis (Typosyllis) sp. Verified to subgenus by K. Banse. *Laminaria* community; f. 0.52, c. 1.0, a. 90, 9-668.

Trypanosyllis gemmipara Johnson, 1901. Identified by R. M. O'Clair. Sublittoral, 34 m. The specimen examined is 315 mm long and 5 mm wide with 596 setigers. To my knowledge it is the largest recorded specimen of this species. Deposited in NMNS.

Nereis pelagica Linnaeus, 1758. Identified by R. M. O'Clair. *Laminaria* community; f. 0.42, c. 0.47, a. 4, 1-62, and sublittoral to 183 m.

Nereis vexillosa Grube, 1851. Identified by R. M. O'Clair. Collected by K. Kimura. Intertidal. Arctic–boreal.

Nephtys sp. Identification to genus by R. M. O'Clair. Sublittoral, 183 m.

Sphaerodoropsis sp., near *S. minuta* (Webster and Benedict, 1887). Lower communities; f. 0.35, c. 0.67, a. 62, 2-381.

Eunice kobiensis McIntosh, 1885. Identified by R. M. O'Clair. Sublittoral, 6 to 270 m (see Gustus, 1972).

Lumbrineris inflata Moore, 1911. Identified by R. M. O'Clair. *Laminaria* community. See Table 2 for population statistics. Widely distributed.

Naineris quadricuspida (Fabricius, 1780). Identified by R. M. O'Clair. *Laminaria* community; f. 0.44, c. 0.33, a. 37, 25-454. Arctic–boreal.

Polydora sp. (see Hobson and Banse, in preparation). *Laminaria* community; f. 0.66, c. 0.33, a. 38, 23-117.

Boccardia proboscidea Hartman, 1940. Identified by R. M. O'Clair. *Alaria–Hedophyllum* community; f. 1.0, c. 0.08, a. 1. North American.

Pygospio elegans Claparède, 1863. Identified by R. M. O'Clair. *Alaria–Hedophyllum* community; f. 0.6, c. 0.25, a. 212, 54-508. Widely distributed.

Spio filicornis (O. F. Müller, 1776). Identified by R. M. O'Clair. Upper communities; f. 0.5, c. 0.09, a. 20, 1-38. Widely distributed.

Chaetopterus variopedatus (Renier, 1804). Identified by R. M. O'Clair. Sublittoral; 2 to 183 m.

Caulleriella alata maculata (Annenkova, 1934). Verified by R. M. O'Clair. See Table 2 for population statistics.

Chaetozone sp., near *C. berkeleyorum* Banse and Hobson, 1968. Upper communities; f. 0.5, c. 0.09, a. 212, 169-254.

?*Cirratulus cirratus spectabilis* (Kinberg, 1866) (Hartman, 1969). *Laminaria* community; f. 1.0, c. 0.06, a. 20. North American.

Cirratulus Type I. Determination by O. Hartman. Near *C. c. spectabilis*. Acicular uncini present from the first notopodia and neuropodia; body short with about 40 setigers (O. Hartman, personal communication). *Alaria–Hedophyllum* community.

Cirratulus Type II. Determination by O. Hartman. Near *C. c. spectabilis*. Acicular uncini present from first notopodia and neuropodia; body long with 50 setigers (O. Hartman, personal communication). *Halosaccion–Fucus* community. See Table 4 for population statistics.

Cirratulus Type III. Determination by O. Hartman. Acicular uncini present from first neuropodia and from twelfth notopodia; body as in *C.* Type I (O. Hartman, personal communication). *Alaria–Hedophyllum* community; f. 0.38, c. 0.42, a. 54, 1-762.

Cirratulus Type IV. Acicular uncini present from first notopodia and from sixth to eighth neuropodia; tentacular cirri similar to *C. c. spectabilis*. Included with *C.* Type III in Figs. 6 and 12. *Laminaria* community; f. 0.5, c. 0.33, a. 1, 1-23.

Cirratulus sp. *Alaria–Hedophyllum* community; f. 1.0, c. 0.08, a. 4.

Cirratulidae sp. Upper communities; f. 0.5, c. 0.09, a. 96, 64-127.

Brada granulata Malmgren, 1867. Identified by R. M. O'Clair. Sublittoral; 183 m.

Flabelligera infundibularis Johnson, 1901. Identified by R. M. O'Clair. *Laminaria* community. North American.

Scalibregma inflatum Rathke, 1843. Identified by R. M. O'Clair. *Laminaria* community.

Capitella capitata (Fabricius, 1780). Identified by R. M. O'Clair. *Alaria–Hedophyllum* community; f. 0.38, c. 0.42, a. 127, 1-444.

Abarenicola claparedii oceanica Healy and Wells, 1959. Verified by R. M. O'Clair. Intertidal in moat (see Fig. 3 in Lebednik and Palmisano, Chap. 17, this volume). North Pacific.

Praxillella praetermissa (Malmgren, 1866). Identified by R. M. O'Clair. Sublittoral, 34 m.

Idanthyrsus armatus Kinberg, 1867. Identified by R. M. O'Clair. Sublittoral, 55 m.

Asabellides sibirica (Wirén, 1883) [= *Pseudosabellides littoralis* Berkeley and Berkeley, 1943] (see Hartman, 1959, p. 492). *Laminaria* community; f. 0.57, c. 0.33, a. 38, 38-276.

Amphiglena pacifica Annenkova, 1934. Identified by R. M. O'Clair. Upper communities; f. 0.5, c. 0.56, a. 127, 27-1562. Endemic. The type locality of *A. pacifica* is Bering Island, not Bering Strait as listed in Hartman (1959).

Chone cincta Zachs, 1933. Identified by R. M. O'Clair. *Alaria–Hedophyllum* community; f. 0.46, c. 0.83, a. 190, 4-1544. Asiatic.

C. infundibuliformis Krφyer, 1856. Identified by R. M. O'Clair. Sublittoral, 34 m.

Demonax? sp. *Laminaria* community. See Table 2 for population statistics.

Fabricia sabella (Ehrenberg, 1836). Identified by R. M. O'Clair. *Alaria–Hedophyllum* community; f. 0.41, c. 0.58, a. 3594, 23-29,274.

Myxicola infundibulum (Renier, 1804). Identified by R. M. O'Clair. Sublittoral, 34 m.

Potamilla reniformis (Leuckart, 1849). Identified by R. M. O'Clair. Sublittoral, 34 m.

Sabella crassicornis Sars, 1851. Identified by R. M. O'Clair. Sublittoral, 34 m.

Dexiospira semidentata (Bush, 1904). Identified by R. M. O'Clair. *Laminaria* community; f. 0.66, c. 0.33, a. 1, 1-24. North Pacific.

Dexiospira sp. *Laminaria* community; f. 0.62, c. 0.67, a. 32, 11-6632.

Class Oligochaeta (All Oligochaeta identified by D. G. Cook.)

Paranais littoralis (Müller, 1784). *Halosaccion–Fucus* community. See Table 4 for population statistics.

Tubificidae sp. Immature specimens. *Laminaria* community; f. 0.57, c. 0.67, a. 38, 1-124.

Lumbricillus sp. *Alaria–Hedophyllum* community. See Table 3 for population statistics.

Phylum Mollusca (Oldroyd, 1924–1927).

Class Gastropoda [The nomenclature of species of the superfamilies Patellacea and Fissurellacea generally follows McLean (1966; 1969)].

Problacmaea sybaritica (Dall, 1871) [= *Acmaea (Tectura) sybaritica* Dall, 1871]. Identified by A. M. Keen. Golikov and Kussakin (1972) include this species in the genus *Problacmaea* because it is ovoviviparous. Two specimens collected in August 1968 had been brooding young (520 individuals in one adult) dorsally beneath the wall of the visceral mass. *Laminaria* community; f. 0.6, c. 0.06, a. 1, 1-3. Asiatic.

Collisella pelta (Rathke, 1833). *Alaria–Hedophyllum* community; f. 0.4, c. 0.43, a. 2, 1-31. North Pacific.

Collisella digitalis (Rathke, 1833). *Halosaccion–Fucus* community. See Table 4 for population statistics. North American.

Collisella strigatella (Carpenter, 1864). Verified by J. H. McLean. *Halosaccion–Fucus* community; f. 0.59, c. 0.36, a. 4, 1-36. North American.

Notoacmea scutum (Rathke, 1833). *Laminaria* community. See Table 2 for population statistics. North Pacific.

Rhodopetala rosea (Dall, 1872) (= *Nacella rosea* Dall, 1872). Verified by J. H. McLean. This species was usually found on the holdfasts and fronds of *Laminaria yezoensis*. One specimen collected in May 1974 was brooding young (404 individuals) in its nuchal cavity. Other adults in the vicinity of this specimen at the time of collection were surrounded by many tiny, apparently newly released, limpets. Asiatic.

Diadora sp. Sublittoral, 6 m.

Puncturella (Puncturella) noachina (Linnaeus, 1771). [= *P. longifissa* Dall, 1914.] Verified by J. H. McLean. *Laminaria* community. Arctic–boreal.

Margarites beringensis (Smith, 1899). [= *M. helicinus excavatus* Dall, 1919. J. H. McLean (personal communication).] *Laminaria* community; f. 0.46, c. 0.6, a. 4, 1-468. Arctic–boreal.

M. vorticifera (Dall, 1873). Identified by J. H. McLean. *Laminaria* community.

Moelleria quadrae Dall, 1897. Verified by J. H. McLean. *Laminaria* community. North American.

Balcis randolphi (Vanatta, 1899). Verified by A. M. Keen. *Laminaria* community; f. 0.53, c. 0.67, a. 2, 1-188. North Pacific.

Littorina aleutica Dall, 1872. Verified by A. M. Keen. *Halosaccion–Fucus* community. See Table 4 for population statistics. Endemic.

L. atkana Dall, 1886. Verified by A. M. Keen. *Halosaccion–Fucus* community. See Table 4 for population statistics. North American.

L. sitkana Philippi, 1845. Verified by A. M. Keen. *Halosaccion–Fucus* com-

munity. See Table 4 for population statistics. North Pacific.

Haloconcha minor Dall, 1919. Identified by A. M. Keen. *Halosaccion–Fucus* community; f. 0.38, c. 0.7, a. 9, 1-368. North Pacific.

Alvinia castanella (Dall, 1886). Verified by J. H. McLean. *Laminaria* community. Endemic.

A. aurivillii (Dall, 1886). Verified by A. M. Keen. *Laminaria* community; f. 0.57, c. 0.67, a. 1, 1-306. Asiatic.

Cingula aleutica Dall, 1886. Compared with USNM specimens. *Halosaccion–Fucus* community; f. 0.46, c. 0.82, a. 602, 2-2032. North Pacific.

Cingula martyni Dall, 1886. Identified by A. M. Keen. *Halosaccion–Fucus* community; f. 0.57, c. 0.64, a. 234, 2-3810. Arctic–boreal.

Rissoidae sp. A. Verified to family by J. H. McLean. Lower intertidal communities.

Rissoidae sp. B. Verified to family by J. H. McLean. *Laminaria* community; f. 0.62, c. 0.67, a. 4, 2-62.

Vitrinella sp. Verified to genus by J. H. McLean. *Alaria–Hedophyllum* community. See Table 3 for population statistics.

Cerithiopsis sp. cf. *C. stephensae* Bartsch, 1909. Determination by A. M. Keen. *Alaria–Hedophyllum* community. North American.

Cerithiopsis stejnegeri Dall, 1884. Compared with USNM specimens. *Alaria–Hedophyllum* community. See Table 3 for population statistics. Asiatic.

Natica clausa Broderip and Sowerby, 1829. *Laminaria* community; f. 0.86, c. 0.13, a. 1, 1-2.

Polinices sp. Indeterminate juveniles. Identified to genus by A. M. Keen. Upper communities.

Velutina conica Dall, 1886. Compared with USNM specimens. *Laminaria* community. North Pacific.

Fusitriton oregonensis (Redfield, 1848). Sublittoral, 6 to 30 m.

Trophonopsis (= *Boreotrophon*) sp. Sublittoral, 18 to 38 m.

Thais lima (Martyn, 1784). *Alaria–Hedophyllum* community; f. 0.48, c. 0.52, a. 4, 1-16. North Pacific.

Buccinum baeri morchianum Fischer, 1858. Identified by A. M. Keen. *Laminaria* community; f. 0.56, c. 0.47, a. 3, 1-8. North Pacific.

Mitrella amiantis(Dall, 1919). Identified by A. M. Keen. *Laminaria* community. See Table 2 for population statistics. Endemic.

?*Arctomelon stearnsii* Dall, 1872. Sublittoral, 183 m. Collected by J. S. Isakson.

Antiplanes sp. Sublittoral, 91 m.

Suavodrillia kennicottii (Dall, 1871). Identified by R. Shimek. Shell containing hermit crab. Collected by J. S. Isakson and P. N. Slattery. Sublittoral.

Odostomia krausei Clessin, 1900. Identified by A. M. Keen. *Laminaria* community; f. 0.5, c. 0.33, a. 2, 1-49. North Pacific.

Diaphana brunnea Dall, 1919. Identified by J. H. McLean. One specimen collected in an area uplifted from the sublittoral by Cannikin. North American.

Philine sp. Verified to genus by J. H. McLean, *Laminaria* community; f. 1.0, c. 0.33, a. 1.

Diaulula sandiegensis (Cooper, 1862). Identified by G. Robilliard from photographs taken by Auke Bay, Alaska, Fisheries Laboratory personnel (L. Barr, personal communication). Sublittoral. North Pacific.

Triopha carpenteri (Stearns, 1873). Identified by G. Robilliard from photographs taken by Auke Bay, Alaska, Fisheries Laboratory personnel (L. Barr, personal communication). Sublittoral. North Pacific.

?Polyceratidae sp. Juvenile. *Laminaria* community.

Tritonia sp. Sublittoral, 91 m.

Aeolidia? sp. *Laminaria* community.

Siphonaria thersites Carpenter, 1864. Verified by A. M. Keen. *Halosaccion–Fucus* community. See Table 4 for population statistics. North American.

Onchidella borealis Dall, 1871. Compared with USNM specimens. *Alaria–Hedophyllum* community. North American.

Class Amphineura

Cryptochiton stelleri (Middendorff, 1846). Shell plates found by L. Sowl.

Lepidochitona aleuticus Dall, 1878. Compared with USNM specimens.

Lower communities; f. 0.41, c. 1.0, a. 45, 1-296. Asiatic.

Katharina tunicata (Wood, 1815). *Alaria–Hedophyllum* community. See Table 3 for population statistics. North Pacific.

Amicula sp. Subtidal, 37 m.

Mopalia sp. Sublittoral, 3 m.

Placiphorella sp. Subtidal, 5 to 24 m.

Schizoplax brandtii (Middendorff, 1846). *Alaria–Hedophyllum* community; f. 0.45, c. 0.36, a. 3, 1-42. North Pacific.

Hanleya ? sp. *Laminaria* community.

Class Bivalvia

Modiolus modiolus (Linnaeus, 1758) (Soot-Ryen, 1955). Sublittoral.

Musculus discors var. *laevigatus* (Gray, 1824). Identified by A. M. Keen. *Laminaria* community.

?*M. d.* var. *laevigatus* f. *substriatus* (Gray, 1824) (MacGinitie, 1959). *Laminaria* community; f. 0.61, c. 0.2, a. 1, 1-4.

Musculus vernicosus (Middendorff, 1849). Verified by A. M. Keen. *Laminaria* community; f. 0.46, c. 0.2, a. 2, 1-9. Also sublittoral to 12 m. Arctic–boreal.

Mytilus edulis Linnaeus, 1758 (Soot-Ryen, 1955). Large individuals, *Alaria–Hedophyllum* community. See Table 3 for population statistics. Small individuals, *Alaria–Hedophyllum* community; f. 0.47, c. 0.36, a. 62, 1-6200.

M. californianus Conrad, 1837 (Soot-Ryen, 1955). A single specimen found on Amchitka collected by J. F. Palmisano. North American.

Pododesmus macroschisma (Deshayes, 1839). Sublittoral, 12 m. North Pacific.

Kellia suborbicularis (Montagu, 1803). Compared with NMNS specimens. *Laminaria* community. Widely distributed.

Mysella aleutica (Dall, 1899). Identified by A. M. Keen. *Halosaccion–Fucus* community. See Table 4 for population statistics.

Turtonia minuta (Fabricius, 1780). Identified by A. M. Keen. *Laminaria* community; f. 0.35, c. 1.0, a. 252, 1-28,130. Arctic–boreal. Though widely distributed in the intertidal area at Amchitka, this little clam is most abundant in the upper communities. It appears to be ecologically similar to *Lasaea cistula* Keen (see Glynn, 1965). *Turtonia minuta* is similar in size and morphology to *L. cistula*. Both species are nestlers, although *T. minuta* appears to prefer areas of high siltation. Both species brood their young.

Serripes groenlandicus (Bruguière, 1789). Sublittoral. Shell only.

Spisula polynyma (Stimpson, 1860). Sublittoral. Arctic–boreal.

?*Siliqua media* Sowerby, 1839 [= *S. alta*? (Broderip and Sowerby, 1829) (Abbott, 1974)]. Shell only. Sublittoral.

Macoma calcarea (Gmelin, 1791). Identified by A. M. Keen. *Alaria–Hedophyllum* community. See Table 3 for population statistics.

M. obliqua (Sowerby, 1817) (Coan, 1971). Intertidal. North American.

Hiatella arctica (Linnaeus, 1767). *Laminaria* community; f. 0.75, c. 0.06, a. 4, 1-7. Also sublittoral to 210 m.

Class Cephalopoda [All cephalopods (except *Japetella*) collected and identified by G. J. Tutmark.]

Gonatus magister Berry, 1913. Pelagic.

G. fabricii (Lichtenstein, 1818). Pelagic.

Gonatopsis borealis Sasaki, 1923. Pelagic.

Galiteuthis armata Joubin, 1898. Pelagic.

Chiroteuthis veranyi (Férussac, 1835). Pelagic.

Architeuthis princeps Verrill, 1875. Pelagic.

Octopus ? sp. Intertidal to 30 m.

Japetella heathi (Berry, 1911). Identified by M. Green.

Phylum Arthropoda

Class Arachnida

Order Acarina

Family Bdellidae

Neomolgus littoralis (Linnaeus, 1758). Identified by E. E. Lindquist. Supralittoral zone.

Family Parasitidae

Parasitus sp. Identified to genus by E. E. Lindquist. Supralittoral zone.

Class Pycnogonida (All Pycnogonida identified by G. W. O'Connell.)

Pseudopallene circularis (Goodsir, 1842). Subtidal, 24 to 30 m.
Phoxichilidium femoratum (Rathke, 1799). Subtidal, 6 to 183 m.
Achelia latifrons (Cole, 1904). *Laminaria* community.
A. pribilofensis (Cole, 1904). Lower intertidal communities.
A. alaskensis (Cole, 1904). *Laminaria* community.
A. sp. 1. *Laminaria* community.
A. sp. 2. Subtidal, 24 m.
A. sp. 4. Subtidal, 12 m.
Colossendeis orientalis Losina-Losinsky, 1958. Subtidal, 274 m.
Rhopalorhynchus chitinosum (Hilton, 1943). Subtidal, 183 m.
Pycnogonum crassirostre Sars, 1888. *Laminaria* community to 24 m.
Pycnogonum cf. *P. ungellatum* Loman, 1911. Subtidal, 183 m.

Class Crustacea
Subclass Copepoda
Order Harpacticoida
Unidentified species. Nearly all individuals passed through the 1-mm sieve.
Order Notodelphyoida
Blakeanus corniger Wilson, 1921. Identified by P. L. Illg. In the branchial basket of Styelidae sp. Lower communities.
Subclass Cirripedia
Balanus cariosus (Pallas, 1788) (Pilsbry, 1916). *Alaria–Hedophyllum* community. See Table 3 for population statistics. North Pacific.
B. glandula Darwin, 1854; Pilsbry, 1916. *Halosaccion–Fucus* community; f. 0.64, c. 0.17, a. 3, 1-1760. North American.
Lepas anatifera (Linnaeus, 1758). On debris washed ashore.
Subclass Malacostraca
Order Nebaliacea
Nebalia sp. *Laminaria* community.
Order Mysidacea
Gnathophausia gigas Willemoes-Suhm, 1875. Identified by G. J. Tutmark. Pelagic.
Paracanthomysis kurilensis Ii, 1936. Identification by C. Holmquist of specimens collected by P. N. Slattery. Neritic.
Order Tanaidacea
Tanais alascensis Richardson, 1899. Identified by G. J. Tutmark. Sublittoral. Endemic.
Anatanais ? sp. Lower communities.
Tanaidae sp. *Alaria–Hedophyllum* community; f. 1.0, c. 0.08, a. 1.
Order Isopoda (Richardson, 1905) (Schultz, 1969).
Limnoria lignorum Rathke, 1799. See Richards and Belmore (1976) for collection data.
Exosphaeroma amplicauda (Stimpson, 1857). *Alaria–Hedophyllum* community; f. 0.39, c. 0.82, a. 4, 1-96. North American.
Gnorimosphaeroma oregonensis (Dana, 1855). *Halosaccion–Fucus* community; f. 0.83, c. 0.09, a. 1, 1-5. North Pacific.
Dynamenella sheareri (Hatch, 1947). *Alaria–Hedophyllum* community; f. 0.43, c. 0.5, a. 310, 32-1026. North American.
?*Arcturus longispinus* (Benedict, 1898). Sublittoral, 183 m.
Idotea (Idotea) ochotensis Brandt, 1851. Verified by F. Rafi. *Laminaria* community. North Pacific.
Idotea (Pentidotea) wosnesenskii (Brandt, 1851). Verified by F. Rafi. *Alaria–Hedophyllum* community; f. 0.36, c. 0.84, a. 6, 1-74, North American.
Ianiropsis kincaidi derjugini Gurjanova, 1933 (Menzies, 1952). *Laminaria* community. North Pacific. Females collected in October 1971 were carrying eggs and young.
Ligia pallasii Brandt, 1833. Supralittoral fringe. North American.
Munna (*Neomunna*) *stephenseni* Gurjanova, 1933. *Laminaria* community; f. 0.8, c. 0.33, a. 2, 1-2. North Pacific.
?*Munna subneglecta* Gurjanova, 1936. *Laminaria* community; f. 0.8, c. 0.33, a. 44, 1-88. Asiatic.
Munna sp. c.f. *M. (Neomunna)arnholdi* Gurjanova, 1933. *Laminaria* community; f. 1.0, c. 0.33, a. 1.
Order Amphipoda
Odius sp. *Laminaria* community; f. 0.8, c. 0.67, a. 1.
Amphithoe sp. *Alaria–Hedophyllum* community; f. 0.38, c. 0.75, a. 42, 1-500.

Calliopiella sp.A. Collected by P. N. Slattery. An undescribed species (Slattery, unpublished manuscript).

Calliopiella sp.B. Collected by P. N. Slattery. An undescribed species (Slattery, unpublished manuscript).

Calliopiella sp.C. Collected by P. N. Slattery. An undescribed species (Slattery, unpublished manuscript).

Calliopiella ? sp. *Halosaccion—Fucus* community. See Table 4 for population statistics.

Calliopiidae Type I. *Halosaccion—Fucus* community.

Calliopiidae Type II. *Halosaccion—Fucus* community; f. 1.0, c. 0.09, a. 1.

Calliopiidae Type III. *Alaria—Hedophyllum* community; f. 1.0, c. 0.08, a. 1.

Corophium brevis Shoemaker, 1949. Identified by U. Lie. *Alaria—Hedophyllum* community. See Table 3 for population statistics. North American.

Pontogeneia andrijaschevi Gurjanova, 1951. Tentative identification by E. L. Bousfield of specimens collected by P. N. Slattery (Slattery, unpublished manuscript). Asiatic.

P. ivanovi Gurjanova, 1951. Tentative identification by E. L. Bousfield of specimens collected by P. N. Slattery (Slattery, unpublished manuscript). Asiatic.

?*P. intermedia* Gurjanova, 1938 (Gurjanova, 1951). In pool on uplifted rock bench, probably stranded in a storm. North Pacific.

P. makarovi Gurjanova, 1951. Identification by E. L. Bousfield of specimens collected by P. N. Slattery. *Laminaria* community; f. 0.47, c. 0.27, a. 4, 1-69. Asiatic.

P. rostrata Gurjanova, 1938. Identified by P. N. Slattery and confirmed by W. S. Gray. North Pacific.

Pontogeneia sp. Confirmed to genus by P. N. Slattery. *Laminaria* community; f. 0.65, c. 0.2, a. 2, 1-8.

Eusiridae sp. *Halosaccion—Fucus* community; f. 1.0, c. 0.02, a. 1.

Anisogammarus confervicolus (Stimpson, 1857). Identified by U. Lie. *Alaria—Hedophyllum* community. See Table 3 for population statistics. North American.

Allorchestes sp. Near *A. carinata* Iwasa, 1939. Mature males unavailable for study. *Laminaria* community; f. 0.6, c. 0.06, a. 1, 1-2.

Parallorchestes ochotensis (Brandt, 1851) (Barnard, 1962). *Laminaria* community; f. 0.49, c. 0.67, a. 8, 1-137. North Pacific.

Ischyrocerus Type I. Verified to genus by U. Lie. Lower communities; f. 0.5, c. 0.2, a. 2, 1-10.

Ischyrocerus Type II. *Laminaria* community; f. 0.66, c. 0.33, a. 2, 1-3.

Jassa sp. Verified to genus by U. Lie. *Laminaria* community; f. 0.66, c. 0.33, a. 16, 1-32.

Orchomene ? sp. *Laminaria* community; f. 0.5, c. 0.67, a. 100, 1-318.

Paraphoxus spinosus Holmes, 1903 (Barnard, 1960). *Alaria—Hedophyllum* community; f. 0.46, c. 0.42, a. 106, 13-381. Amphiboreal.

Parapleustes pugettensis (Dana, 1853). Identified by U. Lie. *Laminaria* community; f. 0.57, c. 0.67, a. 2, 1-4. North American.

Pleustes sp. *Laminaria* community.

Sympleustes sp. Verified to genus by U. Lie. *Laminaria* community; f. 0.66, c. 0.33, a. 2, 1-85.

Mesometopa ? sp. Verified to family by E. L. Bousfield. *Laminaria* community; f. 1.0, c. 0.33, a. 1.

Parametopella stelleri Gurjanova, 1948. Tentatively identified by E. L. Bousfield. *Laminaria* community; f. 0.8, c. 0.33, a. 1. Asiatic.

?*Najna consiliorum* Derzhavin, 1937 (Bulycheva, 1957) (Barnard, 1962). Verified to genus by U. Lie. *Laminaria* community; f. 0.88, c. 0.33, a. 2, 1-3. North Pacific.

Orchestia sp. Supralittoral fringe.

Caprella kincaidi Cole, 1910. *Laminaria* community; f. 0.66, c. 0.67, a. 1, 1-19. Asiatic.

C. laeviuscula Mayer, 1903 (Laubitz, 1970). *Laminaria* community. North Pacific.

Cercops compactus Laubitz, 1970. Verified by D. Laubitz. *Laminaria* community. See Table 2 for population statistics. North American.

Caprella sp. *Laminaria* community; f. 1.0, c. 0.33, a. 2, 1-2.

Order Euphausiacea (All euphausids identified by G. J. Tutmark.)

Thysanoessa longipes Brandt, 1851. Pelagic.

T. inermis (Krφyer, 1846). Pelagic.

Euphausia pacifica Hansen, 1911. Pelagic.

Tessarobrachion oculatum Hansen, 1911. Pelagic.

Order Decapoda

Sergestes similis Hansen, 1903. Identified by G. J. Tutmark. Pelagic.

Hymenodora frontalis Rathbun, 1902. Identified by G. J. Tutmark. Pelagic.

Notostomus japonicus Bate, 1888. Identified by G. J. Tutmark. Pelagic.

Pandalus montagui tridens Rathbun, 1902. Sublittoral, 55 to 183 m.

Lebbeus groenlandica (Fabricius, 1775). Sublittoral, 55 to 183 m.

Lebbeus grandimanus (Brashnikov, 1907). Identified by G. J. Tutmark. Sublittoral, 5 m.

Eualus fabricii (Krφyer, 1841). Identified by G. J. Tutmark. Sublittoral, 1 m.

Spirontocaris arcuata Rathbun, 1902. Identified by G. J. Tutmark. Sublittoral.

Nectocrangon crassa Rathbun, 1899. Sublittoral, 55 m. North Pacific. Nomenclature of pagurids follows McLaughlin (1974).

Elassochirus gilli (Benedict, 1892). Identified by G. J. Tutmark. Verified by C. Nyblade. Sublittoral.

E. tenuimanus (Dana, 1851). Identified by G. J. Tutmark. Verified by C. Nyblade. Sublittoral, 55 m.

E. cavimanus (Miers, 1879). Identified by G. J. Tutmark. Verified by C. Nyblade. Sublittoral, 55 m.

Pagurus beringanus (Benedict, 1892). Identified by C. Nyblade. Sublittoral.

P. capillatus (Benedict, 1892). Identified by G. J. Tutmark. Verified by C. Nyblade. Sublittoral.

P. dalli (Benedict, 1892). Identified by G. J. Tutmark. Verified by C. Nyblade. Sublittoral, 183 m.

P. hirsutiusculus hirsutiusculus (Dana, 1851). Identified by C. Nyblade. Intertidal.

P. kennerlyi (Stimpson, 1864). Identified by G. J. Tutmark. Verified by C. Nyblade. Sublittoral, 26 m.

P. setosus (Benedict, 1892). Identified by G. J. Tutmark. Sublittoral.

P. stevensae Hart, 1971. Identified by C. Nyblade. Sublittoral.

P. trigonocheirus (Stimpson, 1858). Identified by C. Nyblade. Sublittoral, 55 m.

Cryptolithodes typicus Brandt, 1849. See Barr (1973). North American.

Dermaturus mandtii Brandt, 1850 (Makarov, 1938). Intertidal to 5 m.

Hapalogaster grebnitzkii Schalfeew, 1892 (Makarov, 1938). Sublittoral, 5 m.

Lithodes aequispina Benedict, 1894 (Makarov, 1938). Sublittoral, 91 to 302 m.

Oedignathus inermis (Stimpson, 1860). Identified by G. J. Tutmark. Sublittoral. North Pacific.

Paralithodes camtschatica (Tilesius, 1815) (Makarov, 1938). Sublittoral, 18 to 192 m.

Placetron wosnessenskii Schalfeew, 1892 (Makarov, 1938). Sublittoral, 21 to 192 m.

Rhinolithodes wosnessenskii Brandt, 1849. Collected and identified by L. Barr. Sublittoral.

Chionoecetes bairdi Rathbun, 1893 (Garth, 1958). Sublittoral, 24 to 192 m.

Oregonia gracilis Dana, 1851 (Garth, 1958). Sublittoral, 29 to 192 m.

Pugettia gracilis Dana, 1851 (Garth, 1958). Uplifted sublittoral fringe.

Erimacrus isenbeckii (Brandt, 1848). Sublittoral, 20 to 214 m.

Telmessus cheiragonus (Tilesius, 1815). Only remains of carapace found.

Cancer magister Dana, 1852. One specimen collected in gill net at a depth of 1 m.

C. oregonensis (Dana, 1852). Infralittoral fringe to –5 m.

Class Insecta

Order Coleoptera

Liparocephalus brevipennis Mäklin, 1853. Verified to genus by M. Hatch and to species by J. M. Campbell and E. C. Becker. *Laminaria* community; f. 0.65, c. 0.33, a. 46, 4-88.

Order Diptera

Family Chironomidae

Saunderia marinus (Saunders, 1928). Adults identified by D. R. Oliver;

larvae identified by M. E. Roussel. On rocky substrate uplifted into the supralittoral fringe zone by Cannikin.

Paraclunio alaskensis (Coquillett, 1900). Adults identified by D. R. Oliver; larvae identified by M. E. Roussel. Adults in supralittoral zone; larvae in upper intertidal communities and supralittoral fringe zone.

Telmatogeton sp. (pupa). Identified to genus by M. E. Roussel. *Halosaccion—Fucus* community.

Suborder? Sciomyzoidea (Unidentified species near Family Anthomyiidae, larva. Determination by H. J. Teskey. *Halosaccion—Fucus* community.)

Order Lepidoptera

Family Geometridae

?*Dysstroma* sp. (larva). Tentative identification to genus by S. Allyson. Supralittoral zone.

Phylum Sipuncula

Phascolosoma agassizii Keferstein, 1867. Identification by A. J. Kohn of specimens collected by C. A. Simenstad. *Laminaria* community; f. 0.75, c. 0.06, a. 2, 1-2.

Phylum Echiura

Bonelliopsis alaskana Fisher, 1946 (Stephen and Edmonds, 1972). Verified to genus by A. R. Fontaine. *Laminaria* community to −14 m.

Phylum Bryozoa (All bryozoans identified by M. Dick.)

Order Ctenostomata

Flustrellidra vegae (Silen, 1947). *Laminaria* community; f. 1.0, c. 0.06.

Order Cheilostomata

Cauloramphus sp. Sublittoral, 55 m.

Callopora sp.A. May be a geographical form of *C. horrida* (M. Dick, personal communication). Sublittoral, 55 m.

Callopora sp.B. Sublittoral, 55 m.

Bidenkapia spitsbergensis var. *alaskensis* Osburn, 1953. Sublittoral, 55 m.

Tegella sp. Sublittoral, 55 m.

Tricellaria erecta (Robertson, 1900). *Laminaria* community.

Dendrobeania murrayana (Johnson, 1847). *Laminaria* community.

D. m. var. *fruiticosa* (Packard, 1863). Sublittoral, 55 m.

Dendrobeania sp. Sublittoral, 55 m.

Beania sp.A cf. *B. columbiana* O'Donoghue, 1923. Sublittoral, 55 m.

Beania sp.B. Sublittoral, 55 m.

Reginella sp. Sublittoral, 55 m.

Cribrilinidae sp. Sublittoral, 55 m.

Hippothoa hyalina (Linnaeus, 1758). *Laminaria* community; f. 0.73, c. 0.4.

Rhamphostomella bilaminata (Hincks, 1877). Sublittoral, 55 m.

Myriozoum sp. May be a geographical form of *M. subgracile* d'Orbigny, 1852. (M. Dick, personal communication). Sublittoral, 55 m.

Order Cyclostomata

Fasciculipora pacifica Osburn, 1953. Sublittoral, 55 m.

Plagioecia patina (Lamarck, 1816). Sublittoral, 55 m.

Crisia sp. cf. *C. eburnea* (Linnaeus, 1758). *Laminaria* community; f. 0.69, c. 0.33.

Lichenopora sp. Sublittoral, 55 m.

Phylum Brachiopoda (All Brachiopoda identified by C. W. Thayer.)

Hemithyris psittacea (Gmelin, 1790). Subtidal, 9 to 183 m.

Laqueus vancouveriensis (Davidson, 1877). *Laminaria* community.

Phylum Echinodermata

Class Asteroidea [Asteroid nomenclature generally follows Fisher (1911; 1928; 1930)].

Order Phanerozonia

Hippasteria? sp. Sublittoral, 128 m.

Order Spinulosa

Crossaster papposus (Linnaeus, 1767) (Fisher, 1911). Sublittoral, 18 to 55 m.

Peribolaster biserialis (Fisher, 1905). Identified by M. E. Downey, Subtidal, 24 m.

Diplopteraster multipes (Sars, 1865) (Fisher, 1911). Sublittoral, 192 m.

Pteraster sp. Sublittoral, 6 to 12 m.

Aleutiaster schefferi (Clark, 1939). Identified by M. E. Downey. *Laminaria* community; f. 0.72, c. 0.4, a. 1, 1-9. Specimens deposited in the USNM and the British Museum (Natural History).

Henricia tumida Verrill, 1909 (D'yakonov, 1950). *Laminaria* community; f. 0.64, c. 0.27, a. 1, 1-4.

H. leviuscula (Stimpson, 1857) (Fisher, 1911). *Laminaria* community; f. 1.0, c. 0.06, a. 1.

Order Forcipulata

Leptasterias alaskensis (Verrill, 1909) (Fisher, 1930). *Laminaria* community; f. 0.75, c. 0.06, a. 2, 1-2.

L. aleutica (Fisher, 1930). *Laminaria* community. See Table 2 for population statistics. I could not distinguish small *L. alaskensis* from *L. aleutica* without examining the pedicellariae. These two species were not distinguished in field observations; however, *Leptasterias* in random samples from the intertidal area were mostly *L. aleutica*.

Class Ophiuroidea

Gorgonocephalus caryi (Lyman, 1860) (Clark, 1911). Sublittoral, 128 m.

?*Amphipholis squamata* (Delle Chiaje, 1828) (Clark, 1911; D'yakonov, 1954.) Sublittoral, 34 m.

Amphipholis sp. Sublittoral, 18 m.

Amphiura sp. Sublittoral, 12 to 18 m.

Ophiopholis aculeata (Linnaeus, 1767) (Clark, 1911) (D'yakonov, 1954). *Laminaria* community; f. 1.0, c. 0.06, a. 2. Also sublittoral to 274 m.

Ophiura maculata (Ludwig, 1886) (Clark, 1911) (D'yakonov, 1954). Infralittoral fringe to 37 m.

O. sarsii (Lütken, 1854) (Clark, 1911). Sublittoral, 91 m.

Ophiura sp. Sublittoral, 18 m.

?*Ophiacantha enneactis* Clark, 1911. Some specimens have characters nearer *O. nutrix* Baranova, 1954. The number of arms is variable. Several specimens were brooding young, which to my knowledge is the first record of brooding in this species. Sublittoral, 183 m.

Class Echinoidea

Strongylocentrotus polyacanthus Agassiz and Clark, 1907. Specimens examined were identified primarily on the basis of the size of the endtooth of globiferous pedicellariae and the shape of the valves of the ophicephalus pedicellariae (see Mortensen, 1943). Specimens collected subtidally at Amchitka by NMFS biologists from Auke Bay, Alaska, have been tentatively identified as *S. polyacanthus* by D. L. Pawson (L. Barr, personal communication). M. Jensen verified several intertidal specimens. *Laminaria* community. See Table 2 for population statistics. Also sublittoral to 35 m.

Dendraster ? sp. Sublittoral.

Class Holothuroidea

Cucumaria vegae (Théel, 1886). Verified by D. L. Pawson. *Alaria–Hedophyllum* community; f. 0.41, c. 0.92, a. 212, 1-4128.

Psolus sp. Sublittoral, 183 m.

Phylum Chordata

Class Ascidiacea

Styela clavata (Pallas, 1774). Identified by D. P. Abbott. *Laminaria* community; f. 1.0, c. 0.13, a. 2, 1-2. Also sublittoral to 12 m.

?*S. coriacea* (Alder and Hancock, 1848) (Van Name, 1945). *Laminaria* community; f. 0.88, c. 0.33, a. 8, 6-82.

Styela ? sp. (Van Name, 1945). *Laminaria* community; f. 0.57, c. 0.27, a. 23, 1-218.

Aplidium Type I (Van Name, 1945). *Laminaria* community; f. 0.82, c. 0.2, a. 1, 1-7 colonies.

Aplidium Type II. Near *A. translucidum* Ritter, 1901 (Van Name, 1945). *Laminaria* community; f. 1.0, c. 0.06, a. 1 colony.

Suborder Aplousobranchia

Unidentified species (Van Name, 1945). *Laminaria* community; f. 0.67, c. 0.13, a. 1, 1-4 colonies.

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19

Marine Fish Communities*

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Intensive multiple-gear sampling of the fish fauna occupying the marine waters adjacent to Amchitka Island showed 92 fish species distributed over seven basic communities according to their characteristic habitats—littoral, inshore/rock–algae, inshore/sand–gravel, offshore demersal/rock–sponge, offshore demersal/sand–gravel, epipelagic, and mesopelagic. Recurrent group analysis disclosed 13 statistically distinct species associations within five of these communities as well as several distinct predator–prey relationships. North American species predominated in the composition of the fish fauna, which reflects the principal dispersal role of the Alaska Stream current, which flows westward about Amchitka. Benthipelagic amphipods and mysids are the predominant prey organisms, and both serve a major role in the transfer of algae-based detritus to the inshore fish communities; euphausiids contribute similarly to offshore fish communities. The Pacific sand lance appears to be a significant importer of offshore-derived zooplankton biomass into the inshore fish communities. Among the three underground nuclear tests at Amchitka, Cannikin produced the most significant impact by kills of several fish species and changes in habitat through uplifting of some littoral rock benches. Although the recovery of the affected fish communities appeared to be complete within a year, the habitat and prey resources formerly provided by the bench that is now uplifted will remain unavailable for many years.

The Aleutian archipelago occupies a distinctive zoogeographic position as a shallow-water bridge joining temperate Asia and North America. As a result the assemblages of marine fishes inhabiting the waters adjacent to Amchitka Island are distinct within ichthyofauna of the North Pacific and within that of the Aleutian Islands of Alaska. Although deepwater species common to the Aleutians are distributed throughout the North Pacific basin, the Aleutian fish fauna of nearshore and intertidal waters is characterized predominantly by North American forms. This predominance appears to be due to the Alaska Stream, the nearshore westward-flowing surface current that originates in the Gulf of Alaska and eventually loses its distinctness as it is diverted north and east through the major passes in the western portion of the chain (Fig. 1, Chap. 16). The Alaska Stream, rather than the eastward-flowing subarctic Kuroshio (Japanese) current much farther to the south, is primary in dispersing the pelagic eggs, larvae, and juveniles of indigenous species. Wilimovsky (1964) called this mechanism of westward dispersal a "filter bridge" in that it not only limits eastward expansion of Asiatic species but also limits the westward expansion of North Pacific species. This filter bridge is further accentuated by Amchitka Pass [500 to 1000 m (275 to 550 fathoms) deep], which separates Amchitka Island from the Aleutian Islands to the east and which is a major point of exchange between the North Pacific Ocean and Bering Sea water masses (McAlister, 1971; McAlister and Favorite, Chap. 16, this volume).

The composition of Amchitka's fish fauna also reflects the island's distinctive littoral and nearshore topography. The extensive wide littoral benches and the broad sublittoral shelf on the North Pacific Ocean side of the island provide suitable habitat for large populations of littoral and inner sublittoral fishes.

HISTORICAL REVIEW

The first investigations of Aleutian fish fauna were made in 1741 by Georg Wilhelm Steller, a naturalist on the second Bering expedition. Steller, who accompanied Vitus Bering on the vessel *St. Peter*, discovered, named, and meticulously described a multitude of plants and animals, including 17 species of anadromous or marine fishes (Stejneger, 1936). Exploration and exploitation of

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the Aleutians by the Russian promyshlenniki, or fur hunters, followed soon thereafter. The original visit to Amchitka was probably either by the *Ieremiia* (Jeremiah) in 1753–1755 or by the *Petr i Pavel* (Sts. Peter and Paul) in 1756–1758. Both vessels were owned by Serebrennikov and captained by Bashmakov (Makarova, 1975). Although the promyshlenniki usually did not bother to collect "faunal specimens" other than sea mammal pelts, many Russian scientific expeditions carried naturalists who collected and described much of the newly encountered flora and fauna. Sarychef of the 1790–1792 Billings expedition, Tilesius and Langsdorff of the 1803–1806 Krusenstern expedition, Chamisso and Eschscholtz of the 1815–1818 Kotzbue expedition, Von Kitlitz, Postels, and Mertens of the 1826–1829 Lütke expedition, and Vosnesensky, on an expedition sponsored by the Leningrad Museum, all contributed significantly to the natural history of the Aleutians and Bering Sea. Ichthyofaunal specimens collected by Steller and succeeding Russian naturalists were formally described in the scientific literature by Tilesius, Pallas, Cuvier, Shmidt, and others (Jordan and Gilbert, 1899), the most comprehensive work being that of Pallas [*Zoographia Rosso-Asiatica* (1811–1842)] and Shmidt [*Pisces Marium Orientalium* (1904)].

Scientific investigations of Alaska and adjacent waters were instituted by the U. S. government soon after the purchase of Alaska from Russia in 1867 (see Fuller, Chap. 7, this volume, for a more complete discussion of scientific investigations in the western Aleutians after 1867). William H. Dall was in the first U. S. Coast and Geodetic Survey hydrographic and geographic reconnaissance of the Aleutians from 1871 to 1874, during which time he collected faunal specimens for deposit in the U. S. National Museum (Jochelson, 1925); he was the first American naturalist to study Amchitka's marine fishes (Dall, 1874 and 1877). From 1880 through the mid-1890s, the U. S. Coast Survey schooner *Yukon,* the U. S. Treasury revenue steamers *Corwin* and *Mohican,* and the U. S. Fish Commission steamer *Albatross* cruised the North Pacific Ocean and Bering Sea waters making hydrographic and meteorologic observations, patrolling for illicit fur seal hunters, and conducting biological collections. A. B. Alexander, Tarleton H. Bean, William H. Dall, Henry W. Elliott, Barton W. Evermann, Charles H. Gilbert, N. B. Miller, Charles H. Townsend, and L. M. Turner were among the notable collectors, naturalists, and ichthyologists accompanying these surveys; they also collected for the U. S. National Museum. Included in the records from this period were two Amchitka Island collections, one by L. M. Turner in 1881 (Turner, 1886) and another by personnel from the steamer *Albatross,* June 6–7, 1906 (U. S. Bureau of Fisheries, 1907). Collection records, taxonomic descriptions, and synopses of findings (including Aleutian records and specimens from these early surveys deposited in the U. S. National Museum) were published by Bean (1882a; 1882b), Jordan and Gilbert (1883; 1899), Nelson (1887), Gilbert (1895), Tanner (1892–1896), Jordan and Starks (1904), and Evermann and Goldsborough (1907).

U. S. Fish and Wildlife Service expeditions to the Aleutians from 1936 to 1938 assessed birds and mammals and also studied marine fishes and invertebrates (Scheffer, 1959). These investigations documented 48 species of fishes indigenous to the archipelago and included descriptions by Schultz (1939) of a new genus and two new species.

The most comprehensive description of Aleutian ichthyofauna existing at the start of our work was that by Wilimovsky (1964); he described the distribution of 135 littoral fishes throughout the length of the Aleutian chain. Earlier, Wilimovsky (1954) had listed 222 marine fishes from "all waters south of the Bering Strait and north of the Alaska Peninsula, including the Aleutian chain, Pribilof Islands, St. Matthew Island, and St. Lawrence Island," and had produced a provisional key to 241 species occurring within that range or more generally in the North Pacific Ocean (Wilimovsky, 1958). A survey of Amchitka's wildlife was also conducted by Fish and Wildlife Service biologists during the summer of 1962, in which they recorded 12 anadromous and marine species and several unidentified blennies, sculpins, liparids, and flounders (McCann, 1963).

Seventeen marine and anadromous fish species were observed in 1965 during the bioenvironmental safety program associated with the Long Shot nuclear test on Amchitka (Seymour and Nakatani, 1967).

Contemporary descriptive syntheses of North Pacific ichthyofauna, including some of the species encountered in these studies (Quast and Hall, 1972; Hart, 1973), have been used in the discussion in this chapter of the zoogeographical distribution of marine fishes that occur around Amchitka Island.

RECENT INVESTIGATIONS

The Fisheries Research Institute (FRI) of the University of Washington studied and evaluated the impact of two underground nuclear explosions

(Milrow on Oct. 2, 1969, and Cannikin on Nov. 6, 1971) on the marine fishes off Amchitka Island. The FRI fish investigations were conducted from the summer of 1967 to the fall of 1973 for the U. S. Atomic Energy Commission (AEC) by subcontract with the Columbus Laboratories of Battelle Memorial Institute (BCL). Reports of investigations were submitted annually to BCL and are summarized in Nakatani and Burgner (1974). Although previous information on marine fishes off Amchitka Island was largely limited to compilation of species check lists, FRI fish sampling also determined the distribution, relative abundance, and life-history aspects of fish species found in the vicinity of the test sites. The sampling was concentrated in summer and fall to coincide with the planned fall detonation times and because the frequent inclement weather limited sampling during winter and spring.

This chapter summarizes the basic information gathered on marine fishes off Amchitka Island and the extent to which their populations were affected by the underground tests. Figure 1 shows the location of coastal features of Amchitka.

MATERIALS AND METHODS

Fishing Vessels

In 1967 and 1969 the M. V. *Paragon,* a 27-m (90-ft) trawler, was used in the deeper offshore waters [depths greater than 38 m (125 ft)], and a variety of small outboard boats were used in the nearshore waters. From 1970 to 1972 the M. V. *Commander,* a 26-m (85-ft) purse seiner with multiple-gear capabilities, was used principally during fall months. Larger inboard—outboard boats were available during the latter period, which permitted nearshore sampling at greater distances from boat-launching sites.

The offshore sampling from the research vessels included bottom and midwater trawling, purse seining, salmon gill-netting and long-lining, bottom dredging, and the fishing of crab traps. Nearshore sampling included the use of bottom and surface experimental gill nets and trammel nets, bottom and surface longlines, shrimp, crab, minnow, and amphipod traps, plankton nets, rotenone, and miscellaneous hook-and-line and hand collections.

Gear Types

Bottom Trawl. The bottom trawl, the primary offshore sampling gear, was a 400-mesh two-seam eastern bottom (otter) trawl with a 22-m (71-ft) headrope and a 29-m (95-ft) footrope constructed with a 10-cm (4-in.)* mesh cod end of 96-thread nylon. Chafing mats protected the bottom and cod end, and rollers of various sizes were used on the footrope, depending on suspected bottom roughness. The net was fished with Formosan-type otter boards that weighed 430 kg (950 lb) in 1967 and 340 kg (750 lb) in 1969 and later years.

Midwater Trawl. The midwater trawl was a 27-m(90-ft)-long modified herring trawl with a 6-m(20-ft)-square opening which was fished with 227-kg (500-lb) otter boards at approximately 4 knots. Webbing ranged from 7.5-cm (3-in.) wings to 1.25-cm (0.5-in.) cod end. A standard 3-m (10-ft) Isaacs-Kidd midwater net was also used to capture smaller fishes missed by the larger midwater trawl.

Purse Seine. The purse seine was approximately 730 m (2400 ft) long and 37 m (120 ft) deep and was hung with 5-cm(2-in.)-mesh, 15-18 thread, knotless nylon web except for the center bunt, which was of 2.5-cm (1-in.) mesh. The net was generally held open toward the current to the northwest for 1.5 to 2 hr. The purse seine was fished only briefly in 1970.

Salmon Gill Nets. The surface salmon gill nets were composed of six to ten 91-m(300-ft)-long by 5.5-m(18-ft)-deep shackles of multifilament nylon that ranged in mesh size from 6.4 to 11.4 cm (2.5 to 4.5 in.).

Bottom Gill Nets. Monofilament gill nets were 2.7 m (9 ft) deep with six 12-m (40-ft, hung measure) panels of 2.5-, 3.8-, 5.0-, 6.4-, 7.6-, and 10-cm (1-, 1.5-, 2-, 2.5-, 3-, and 4-in.) web and with a low-buoyancy float line, which allowed the net to sink to the bottom.

Surface Gill Nets. Monofilament surface gill nets were identical to the sinking gill net except that they contained more floats.

Trammel Nets. The trammel nets used were made of green-dyed nylon outer walls of 50-cm (20-in.) web and inner walls of 10-cm (4-in.) web and were 91 m (300 ft) long and 1.8 m (6 ft) deep. They were weighted to sink but were buoyed sufficiently to hold them vertically above the bottom.

Salmon Longlines. Japanese surface salmon longlines were used to catch salmon offshore during the 1967 through 1969 sampling period. This gear generally consisted of 10 skates, each with a 22.6-kg test vinylon main line that was

*All mesh sizes are stretched measure.

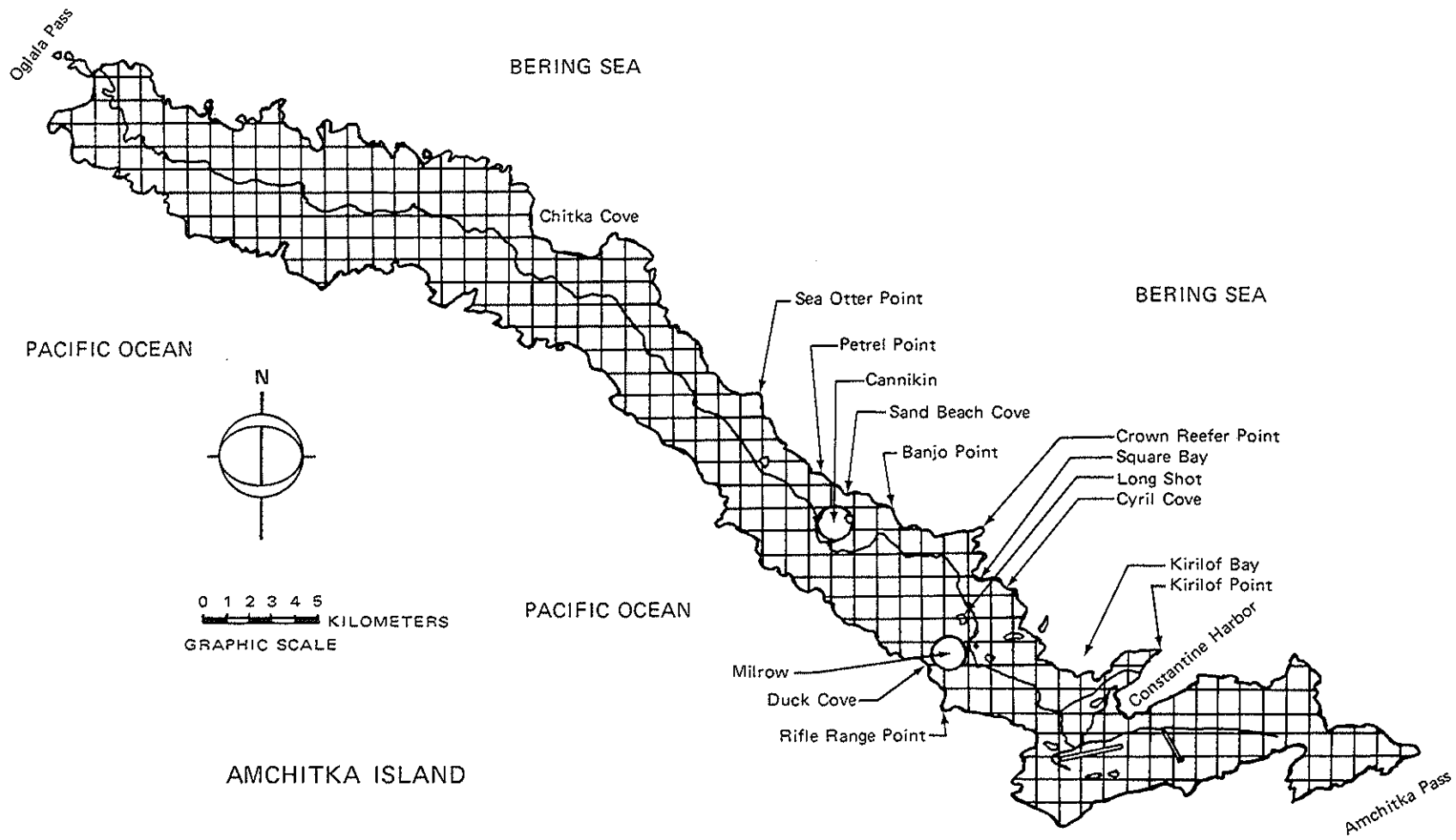


Fig. 1—Location of coastal features of Amchitka Island, Alaska.

approximately 138 m (450 ft) long with 49 evenly spaced [2.3 m (7.5 ft)] size-8 hooks on 1-m(3-ft)-long 10-kg (22-lb) test monofilament leaders. Ten evenly spaced wooden floats buoyed each skate. The bait used was 7- to 10-cm(3- to 4-in.)-long dried salted anchovy (*Engraulis japonica*). The total length of the longline set was approximately 1.4 km (0.75 nautical mile).

Surface Longlines. Surface longlines fished nearshore were made from standard 49-hook Japanese salmon longline gear with floats spaced five hooks apart. Octopus was most often used as bait.

Bottom Longlines. Longlines consisting of the standard 49-hook Japanese salmon longline without floats or a heavy-duty 8- to 10-hook anchored halibut longline were fished on the bottom in nearshore waters. Squid or octopus was usually used as bait.

Anchor Dredge. An anchor dredge with an 89- by 38-cm (35- by 15-in.) opening from the inclined plate into the 10-cm (4-in.) nylon 96-mesh collecting bag was cast from the offshore vessel and retrieved after digging into the bottom or briefly towed along the bottom surface. Several fish were caught with the benthos brought up with this dredge.

Shrimp Traps. Experimental shrimp traps [45 by 45 by 75 cm (18 by 18 by 30 in.)] were used in water 3 to 60 m (10 to 200 ft) deep. Fishes caught nearshore were used as bait. Several species of fish, which were probably attracted to the amphipods that were feeding on the bait, were captured in the traps.

Crab Traps. Commercial king crab pots [1.8 m (or 6 ft) in diameter] were used in 1967 but in later years were replaced by 86-cm(34-in.)-diameter Taylor crab traps. Nearshore fishes were used as bait. Fishes and various invertebrates as well as crab were captured in these pots.

Minnow Traps. Commercially built polypropylene traps, 43 cm (17 in.) long by 23 cm (9 in.) in diameter with 2.5-cm (1-in.) openings in each end, were baited with nearshore fish and usually anchored in littoral pools.

Amphipod Traps. Prior to the initiation of plankton pump sampling, amphipod traps made from 3.7-liter (1-gal) wide-mouth nalgene bottles with an inverted cone opening were used to collect scavenging crustaceans. Bait included octopus and nearshore fishes. A few small fishes were captured along with the invertebrates.

Plankton Nets. Plankton nets were used to collect fish eggs and larvae in nearshore areas. The nets were of standard 0.5-m (2-ft) No. 3 mesh (0.324-mm aperture) with a flowmeter attached. Both vertical and horizontal tows were made.

Rotenone. This poison was applied in 500-g warmwater-paste batches to isolated tide pools where suitable concentrations could be maintained and confined; larger tide pools required two batches. Tide pools selected ranged from less than 2.8 m^3 (100 ft^3) to over 5.7 m^3 (200 ft^3) in volume, differed in algal cover and substrate, and yielded a wide diversity of species.

Miscellaneous: Hook-and-Line and Hand Collections. These sampling methods were productive but were considered incidental and more selective than other sampling procedures. Hand collections included fishes captured during scuba surveys with a "slurp gun" or by hand during invertebrate and algae collections in the littoral zone.

Sampling Schedules and Areas

Sampling schedules varied with the type of gear used. Offshore bottom trawling and purse seining were usually done during the day and midwater trawling at night. An echo sounder was used during bottom trawling to detect the presence of fishes, to select the fishing depth and suitable bottom types for nearshore set net fishing, and to locate fishes during midwater trawling and purse seining. Surface salmon gill nets were fished at night, and surface salmon longlines were usually fished for a 1- to 3-hr period before daybreak.

Night sampling in small boats was not considered safe. Therefore most nearshore sampling took place during the day when weather allowed. Nets and longlines were commonly fished overnight except during winter and spring sampling when the unpredictable weather conditions limited sets to 2 to 5 hr during daylight. Thus fishing time per set varied from 2 to 24 hr, depending on safety considerations, the gear type, and season. Owing to the destructive predation of captured fishes by amphipods, bottom-set nets could not be fished for more than a couple of hours when stomachs or other critical samples were to be retained.

Constraints on the sampling program included the selectivity of the fishing gear; inability to sample at all seasons, particularly offshore where an expensive chartered vessel was necessary; and selection of sampling sites near underground nuclear test sites, which concentrated nearly all marine fish sampling effort around the southeast part of Amchitka Island. These limits should be considered in the following discussion of Amchitka's marine fishes and in the interpretation of results.

Sample Processing. All catches were counted (or total weight estimated for large trawl hauls) and recorded by species along with such information as date, depth, location, time of set, and time of recovery. Tow and wind directions were also recorded for all trawl catches.

During the first few years of the program, all fishes captured in nearshore waters were retained for life-history, meristic, and food-web studies. In later years some species were retained for continuing food-web studies whereas the rest were counted and released alive.

All the fishes returned to the field laboratory at Amchitka were measured for total length to the nearest millimeter and weighed to the nearest gram. Some species of particular interest were preserved whole in 10% buffered Formalin or frozen and returned to the Seattle laboratory as museum specimens or for further examination. However, most fishes were processed in the Amchitka laboratory for such information as sex, gonad weight, age (otolith or scale), and stomach sample. All fishes and accompanying information were identified by code numbers and sampling set numbers. Data were transferred to computer cards for ease of analysis. Several thousand fishes were processed each year.

Three basic taxonomic keys to fishes of the North Pacific—Andriyashev (1954), Clemens and Wilby (1961), and Wilimovsky (1958)—were used to identify the fishes collected at Amchitka. Further verifications were made from more specific taxonomic keys in the ichthyological literature.

Food-Web Studies. The description of the Amchitka marine food web resulted from the quantitative analysis of the stomach contents from almost 2000 fish specimens obtained during the Amchitka collections. The wet weight, number, and taxa of prey organisms and rank evaluations of stomach fullness and digestion were determined for each stomach sample (Burgner et al., 1969; Simenstad, 1971a). The raw data were analyzed specifically for the percentage of total weight of stomach contents by food organism with frequency of occurrence and numerical abundance providing supporting indexes of feeding habits. The ensemble of stomach sample data was analyzed with digital-computer programs designed specifically to address the Amchitka data set.

Tagging Studies. Prompted by the great abundance of rock greenling (*Hexagrammos lagocephalus*) in nearshore waters, in 1968 through 1971 we undertook to study their growth and movements by tagging. Rock greenling captured in the sampling nets were measured, weighed, sexed, tagged with green "spaghetti" tags measuring 3.8 cm (1.5 in.) long, and then released in the general area of capture. Posters requesting the return of tagged rock greenling from sport fishermen at Amchitka Island were displayed.

RESULTS AND DISCUSSION

Fish Occurrence

Table 1 lists the 92 identifiable species documented from Amchitka's nearshore and adjacent offshore marine waters. In addition, three species of cottids were identified from ichthyoplankton but do not necessarily represent established populations at Amchitka.

Contemporary accounts of North Pacific fish fauna [Quast and Hall (1972) and Hart (1973)] were used to group the species caught at Amchitka according to their geographical distributions (Table 2). According to these sources, nine of the species were known to range throughout the temperate and torrid zones of the North Pacific—mostly epipelagic, mesopelagic, and bathypelagic fishes ranging from near the surface to 3000 m (1650 fm) and deeper. Of the Amchitka species, 32 have been recorded as occurring throughout the temperate* and subarctic waters of the North Pacific basin (amphi-Pacific) and 21 are confined to the subarctic water masses of the North Pacific Ocean and Bering Sea. Twenty-four species have previously been reported in the eastern portion of the temperate and subarctic North Pacific only; of these, *Raja trachura, Coryphaenoides filifera,* and *Radulinus asprellus* had not been reported in the Aleutians before the FRI Amchitka studies, and *Chirolophis nugator, Sebastes babcocki,* and *Glyptocephalus zachirus* had not been recorded west of Unalaska Island in the easternmost region of the archipelago. Three species are considered to occur universally in arctic and subarctic northern hemisphere waters, one in north temperate waters. The longnose lancetfish (*Alepisaurus ferox*) is known throughout the tropic to subarctic regions of both the Atlantic and Pacific Oceans and the Mediterranean Sea. The toothed cod (*Arctogadus borisovi*), previously known from the arctic seas of North America only, was also captured during our bottom trawling at Amchitka, a significant southern extension of its documented range.

Three additional cottid species, *Furcina ishikawae, Ocynectes maschaus,* and *Scorpaenichthys marmoratus* (the cabezon), were iden-

*Temperate waters are here defined as extending to 45°N latitude.

Table 1—Marine Fishes Collected at Amchitka, 1967 Through 1972*

Scientific name	Common name
Class Cyclostomi	
Order Petromyzontiformes	
Family Petromyzonidae	Lampreys
Entosphenus tridentatus (Gairdner *in* Richardson, 1836)	Pacific lamprey
Class Chrondrichthyes	
Order Squaliformes	
Family Lamnidae	Mackerel sharks
Lamna ditropis (Hubbs and Follett, 1947)	Salmon shark
Order Rajiformes	
Family Rajidae	Skates
Raja binoculata (Girard, 1854)	Big skate
Raja parmifera (Bean, 1881)	Alaska skate
Raja trachura (Gilbert, 1891)	Roughtail skate
Class Osteichthyes	
Order Salmoniformes	
Family Salmonidae	Salmon and trout
Oncorhynchus gorbuscha (Walbaum, 1792)	Pink salmon
Oncorhynchus keta (Walbaum, 1792)	Chum salmon
Oncorhynchus kisutch (Walbaum, 1792)	Coho salmon
Oncorhynchus nerka (Walbaum, 1792)	Sockeye salmon
Oncorhynchus tshawytscha (Walbaum, 1792)	Chinook salmon
Salvelinus malma (Walbaum, 1792)	Dolly Varden
Family Bathylagidae	Deepsea smelts
Bathylagus milleri† (Jordan and Gilbert, 1898)	Stout blacksmelt
Bathylagus stilbius (Gilbert, 1890)	California smoothtongue
Family Gonostomatidae	Lightfishes
Cyclothone microdon† (Gunther, 1878)	Veiled anglemouth
Family Chauliodontidae	Viperfishes
Chauliodus macouni (Bean, 1890)	Pacific viperfish
Order Myctophiformes	
Family Alepisauridae	Lancetfishes
Alepisaurus ferox (Lowe, 1833)	Longnose lancetfish
Family Myctophidae	Lanternfishes
Diaphus theta (Eigenmann and Eigenmann, 1890)	California headlightfish
Electrona arctica‡ (Lutken, 1892)	Bigeye lanternfish
Lampanyctus regalis (Gilbert, 1892)	Pinpoint lampfish
Stenobrachius leucopsarus (Eigenmann and Eigenmann, 1890)	Northern lampfish
Tarletonbeania crenularis (Jordan and Gilbert, 1880)	Blue lanternfish
Order Gadiformes	
Family Gadidae	Codfishes
Arctogadus borisovi (Drjagin, 1932)	Toothed cod
Gadus macrocephalus (Tilesius, 1810)	Pacific cod
Theragra chalcogramma (Pallas, 1811)	Walleye pollock
Family Macrouridae	Grenadiers
Coryphaenoides acrolepis† (Bean, 1883)	Roughscale rattail
Coryphaenoides filifera† (Gilbert, 1895)	Filamented rattail
Order Gasterosteiformes	
Family Gasterosteidae	Sticklebacks
Gasterosteus aculeatus (Linnaeus, 1758)	Threespine stickleback
Order Perciformes	
Family Trichodontidae	Sandfishes
Trichodon trichodon (Tilesius, 1811)	Pacific sandfish
Family Bathymasteridae	Ronquils
Bathymaster caeruleofasciatus (Gilbert and Burke, 1912)	Alaskan ronquil
Bathymaster signatus (Cope, 1873)	Searcher
Ronquilus jordani (Gilbert, 1888)	Northern ronquil
Family Stichaeidae	Pricklebacks
Alectrias alectrolophus (Pallas, 1811)	Stone cockscomb
Anoplarchus purpurescens (Gill, 1861)	High cockscomb
Chirolophis nugator (Jordan and Williams, 1895)	Mosshead warbonnet
Gymnoclinus cristulatus (Gilbert and Burke, 1912)	Trident prickleback

(Table continues on page 458.)

Table 1 (Continued)

Scientific name	Common name
Phytichthys chirus (Jordan and Gilbert, 1880)	Ribbon prickleback
Poroclinus rothrocki (Bean, 1890)	Whitebarred prickleback
Family Pholidae	Gunnels
Pholis dolichogaster (Pallas, 1811)	Stippled gunnel
Pholis laeta (Cope, 1873)	Crescent gunnel
Family Ptilichthyidae	Quillfishes
Ptilichthys goodei (Bean, 1881)	Quillfish
Family Zaproridae	Prowfishes
Zaprora silenus (Jordan, 1896)	Prowfish
Family Ammodytidae	Sand lances
Ammodytes hexapterus (Pallas, 1811)	Pacific sand lance
Family Scorpaenidae	Scorpionfishes
Sebastes aleutianus (Jordan and Evermann, 1898)	Rougheye rockfish
Sebastes alutus (Gilbert, 1890)	Pacific ocean perch
Sebastes babcocki (Thompson, 1915)	Redbanded rockfish
Sebastes ciliatus (Tilesius, 1810)	Dusky rockfish
Sebastes polyspinis (Taranetz and Moiseev, 1933)	Northern rockfish
Sebastes proriger (Jordan and Gilbert, 1880)	Redstripe rockfish
Sebastolobus alascanus (Bean, 1890)	Shortspine thornyhead
Family Anoplopomatidae	Sablefishes
Anoplopoma fimbria (Pallas, 1811)	Sablefish
Family Hexagrammidae	Greenling
Hexagrammos decagrammus (Pallas, 1810)	Kelp greenling
Hexagrammos lagocephalus (Pallas, 1810)	Rock greenling
Pleurogrammus monopterygius (Pallas, 1810)	Atka mackerel
Family Cottidae	Sculpins
Blepsias cirrhosus (Pallas, 1811)	Silverspotted sculpin
Clinocottus acuticeps (Gilbert, 1895)	Sharpnose sculpin
Clinocottus embryum (Jordan and Starks, 1895)	Calico sculpin
Enophrys diceraus (Pallas, 1787)	Antlered sculpin
Gymnocanthus galeatus (Bean, 1881)	Armorhead sculpin
Gymnocanthus pistilliger§ (Pallas, 1811)	Threaded sculpin
Hemilepidotus hemilepidotus (Tilesius, 1810)	Red Irish lord
Hemilepidotus jordani (Bean, 1881)	Yellow Irish lord
Hemitripterus bolini (Myers, 1934)	Bigmouth sculpin
Icelus canaliculatus§ (Gilbert, 1895)	
Malacocottus kincaidi (Gilbert and Thompson, 1905)	Blackfin sculpin
Myoxocephalus polyacanthocephalus (Pallas, 1811)	Great sculpin
Nautichthys pribilovius (Jordan and Gilbert, 1899)	Eyeshade sculpin
Radulinus asprellus (Gilbert, 1890)	Slim sculpin
Triglops forficata (Gilbert, 1895?)	Scissortail sculpin
Triglops metopias§ (Gilbert and Burke, 1912)	
Triglops pingeli (Reinhardt, 1832)	Ribbed sculpin
Triglops scepticus (Gilbert, 1895)	Spectacled sculpin
Family Agonidae	Poachers
Agonus acipenserinus (Tilesius, 1811)	Sturgeon poacher
Aspidophoroides bartoni (Gilbert, 1895)	Aleutian alligatorfish
Hypsagonus quadricornis (Cuvier, 1829)	Fourhorn poacher
Pallasina barbata (Steindachner, 1876)	Tubenose poacher
Sarritor leptorhynchus (Gilbert, 1895)	Longnose poacher
Family Cyclopteridae	Lumpfishes and snailfishes
Aptocyclus ventricosus (Pallas, 1770)	Smooth lumpsucker
Careproctus gilberti† (Burke, 1912)	Smalldisk snailfish
Careproctus phasma§ (Gilbert, 1895)	
Crystallichthys cyclospilus (Gilbert and Burke, 1912)	Blotched snailfish
Eumicrotremus orbis (Gunther, 1861)	Pacific spiny lumpsucker
Lethotremus muticus§ (Gilbert, 1893)	
Liparis callyodon (Pallas, 1811)	Spotted snailfish
Liparis megacephalus§ (Burke, 1912)	
Nectoliparis pelagicus (Gilbert and Burke, 1912)	Tadpole snailfish
Polypera greeni (Jordan and Starks, 1895)	Lobefin snailfish

Table 1 (Continued)

Scientific name	Common name
Order Pleuronectiformes	
Family Pleuronectidae	Righteye flounders
Atheresthes stomias (Jordan and Gilbert, 1880)	Arrowtooth flounder
Glyptocephalus zachirus (Lockington, 1879)	Rex sole
Hippoglossoides elassodon (Jordan and Gilbert, 1880)	Flathead sole
Hippoglossus stenolepis (Schmidt, 1904)	Pacific halibut
Lepidopsetta bilineata (Ayres, 1855)	Rock sole
Reinhardtius hippoglossoides (Walbaum, 1792)	Greenland halibut
Ichthyoplankton specimens; not captured as adults:	
Order Perciformes	
Family Cottidae	
Furcina ishikawae (Jordan and Starks, 1904)¶	
Ocynectes maschaus (Jordan and Starks, 1904)¶	
Scorpaenichthys marmoratus (Ayers, 1854)	

*Nomenclature and species arrangement from the American Fisheries Society (1970) and Greenwood et al. (1966) except
†Hart (1973).
‡Renamed from *P. thompsoni* (Chapman, 1944), Hart (1973).
§Quast and Hall (1972).
¶Jordan and Starks (1904).

tified* from Amchitka ichthyoplankton. *Furcina ishikawae* and *Ocynectes maschaus* represent species hitherto believed to be restricted to the western North Pacific basin and unreported in North America, including the Aleutians. *Scorpaenichthys marmoratus* is a temperate eastern North Pacific species not previously reported west of the Gulf of Alaska. Although the identification of the larvae of the two Japanese species is reasonably positive, the larval cabezon could be confused with some species of the genus *Myoxocephalus*. In view of the lack of adult forms in the collections, the existence of viable reproducing populations of these particular cottids in the Amchitka vicinity is doubtful. In a true ecological sense, then, they are not confirmed as components of the Amchitka fish fauna.

We note that, although 24 species of fishes at Amchitka are represented as being near the western limit of their Alaskan distribution (including six westward extensions of known range), none of the species collected as adults at Amchitka are exclusively Asiatic species near the eastern limit of their distribution. The distinctive position of Amchitka Island amidst the North Pacific current systems, pointed out by Wilimovsky (1964) and discussed earlier herein, appears to be an important factor influencing the composition of Amchitka's fish fauna. The occurrence of two exclusively Asiatic cottids in our ichthyoplankton samples indicates, however, limited immigration from faunal sources to the west. Why these species have not become established remains a matter for speculation. Possibilities include competition from already established species, environmental conditions preventing maturation of larvae or juveniles, and predation.

The distribution of Amchitka's marine fishes according to the depth from which we collected them is shown in Fig. 2. Complete depth ranges are indicated by thin lines, depths of relatively high abundance by the heavy portion of these lines, and the location of infrequent captures by circles. Sampling methods produce biases in these patterns; so they must be considered as only approximate. (Fishes may occur at depths unsampled, fishes may change to other depths at other seasons, and some gears sample incompletely or sample during ascent from or descent to the desired depth.)

Amchitka Fish Communities

Following Whittaker (1970), we define a biotic community as a natural assemblage of populations that live together in a distinguishable habitat and interact with each other, "forming together a distinctive living system with its own composition, structure, environmental relations, development, and function." In earlier reports we discussed Amchitka fish communities subjectively on the basis of the species distribution according to four

*Taxonomic determination of ichthyoplankton specimens was made by W. E. Barraclough, Fisheries Research Board of Canada, Nanaimo Biological Station, Nanaimo, B.C., Canada.

Table 2—Zoogeographic Distributions of Marine Fishes Collected at Amchitka Island, Alaska, 1967 Through 1973 *

Distribution	Species
Temperate and subarctic North Pacific Ocean; Japan to western North America (amphi-Pacific) (32 species)	*Oncorhynchus gorbuscha*
	O. keta
	O. kisutch
	O. nerka
	O. tshawytscha
	Salvelinus malma
	Chauliodus macouni
	Gadus macrocephalus
	Theragra chalcogramma
	Trichodon trichodon
	Bathymaster signatus
	Ptilichthys goodei
	Zaprora silenus
	Sebastes alutus
	Sebastolobus alascanus
	Anoplopoma fimbria
	Hexagrammos lagocephalus
	Pleurogrammus monopterygius
	Blepsias cirrhosus
	Malacocottus kincaidi
	Myoxocephalus polyacanthocephalus
	Hypsagonus quadricornis
	Pallasina barbata
	Aptocyclus ventricosus
	Careproctus gilberti
	Eumicrotremus orbis
	Nectoliparis pelagicus
	Atheresthes stomias
	Hippoglossoides elassodon
	Hippoglossus stenolepis
	Lamna ditropis
	Lepidopsetta bilineata
Subarctic North Pacific Ocean and Bering Sea (21 species)	*Entosphenus tridentatus*
	Raja parmifera
	Bathymaster caeruleofasciatus
	Alectrias alectrolophus
	Pholis dolichogaster
	Sebastes polyspinis
	Enophrys diceraus
	Gymnocanthus galeatus
	G. pistilliger
	Hemilepidotus hemilepidotus
	H. jordani
	Hemitripterus bolini
	Icelus canaliculatus
	Nautichthys pribilovius
	Triglops forficata
	T. scepticus
	Agonus acipenserinus
	Aspidophoroides bartoni
	Sarritor leptorhynchus
	Careproctus phasma
	Crystallichthys cyclospilus
Eastern portion of the temperate and subarctic North Pacific, including the Aleutian Islands (24 species)	*Raja trachura*†
	Coryphaenoides filifera‡
	Chirolophis nugator§
	Ronquilus jordani
	Raja binoculata
	Anoplarchus purpurescens
	Gymnoclinus cristulatus
	Phytichthys chirus
	Poroclinus rothrocki
	Pholis laeta
	Sebastes aleutianus
	S. babcocki§
	S. ciliatus
	S. proriger
	Hexagrammos decagrammus
	Clinocottus acuticeps
	C. embryum
	Radulinus asprellus‡
	Triglops metopias
	Lethotremus muticus
	Liparis callyodon
	L. megacephalus
	Polypera greeni
	Glyptocephalus zachirus§
Torrid and temperate North Pacific (9 species)	*Bathylagus milleri*
	B. stilbius
	Cyclothone microdon
	Diaphus theta
	Electrona arctica
	Lampanyctus regalis
	Stenobrachius leucopsarus
	Tarletonbeani crenularis
	Coryphaenoides acrolepis
Universal in the North Pacific Basin, Bering Sea, and Arctic Ocean	*Ammodytes hexapterus*
	Triglops pingeli
	Reinhardtius hippoglossoides
Universal in the north temperate oceans	*Gasterosteus aculeatus*
Arctic seas of North America	*Arctogadus borisovi*§
Tropical to subarctic regions of the Atlantic and Pacific Oceans	*Alepisaurus ferox*

*This list does not include three unrecorded ichthyoplankton species as discussed in the text.
†Extension of known range: previously unrecorded west of the Gulf of Alaska.
‡Extension of known range: previously unrecorded west of Unalaska Island.
§Extension of known range: newly recorded in the subarctic North Pacific Ocean.

distinct habitats (Isakson, Simenstad, and Burgner, 1971). Quantitative association analyses of the Amchitka collection data with the use of recurrent group analysis (Fager, 1957) has identified 13 distinct groups and associated species with an affinity index of at least 0.40 (Fig. 3). These groupings define the structure of four offshore communities and one inshore community, a littoral assemblage. Many species, especially those captured in the inner sublittoral and neritic waters around Amchitka, did not fall into significant assemblages when an affinity index of 0.40 was used as a test of significance. When these results are incorporated with a detailed examination of species distributions, the existence of seven identifiable fish communities, identified here by their characteristic habitats, is suggested: Epipelagic, mesopelagic, offshore demersal/rock–sponge, offshore demersal/sand–gravel, inshore/sand–gravel,* inshore/rock–algae,* and littoral (Fig. 4 and Table 3), with some variations in species associations detectable within several of these. The community descriptions that follow are basically assembled with the use of these qualitative characterizations; more subtle relationships, such as heterogeneity within a habitat, mechanisms of species associations, and microhabitats, cannot be identified from the limited scope of our data.

Epipelagic Community. Fishes comprising the epipelagic community occur in the oceanic waters off Amchitka between the surface and 200 m. This community was sampled by salmon longline, surface-gill-net, and purse-seine fishing in the upper 10 m of these waters; the midwater trawl sampled the deeper portion of the habitat.

This community was characterized by a relatively low diversity of fishes, only 11 species having been found in it. The fishes are highly mobile, often representing migratory species, such as five of the six species of Pacific salmon (*Oncorhynchus* spp.). Only one two-species group, which was composed of *Oncorhynchus keta,* the chum salmon, and *O. nerka,* the sockeye salmon, was defined for this habitat by the recurrent group analysis. The majority of the salmonids found in the epipelagic community were chum and sockeye salmon. Other FRI studies have indicated that most of the chum salmon in the Amchitka area are of Asian origin and that the majority of the sockeye salmon are from Bristol Bay, Alaska, watersheds (Hartt, 1966; Nakatani and Burgner, 1974). The sockeye caught at Amchitka were preponderantly 3-year-old fish (having spent 2 years in freshwater and 1 year in the ocean) with a scattering of 4 year olds (2 years in freshwater and 2 years in the ocean). Both sockeye and chum are immature fishes moving in a general westerly drift exploiting the feeding grounds of the Bering Sea and the North Pacific Ocean immediately south of the west-central Aleutians. The only hexagrammid truly pelagic as an adult, the Atka mackerel, was also an abundant member of the epipelagic community. The Atka mackerel traveled in dense schools, especially when entering the inshore waters of the islands during June and July for spawning. The rock greenling, the adult dominant of the inshore/rock–algae community, was also found in epipelagic schools of 1- to 3-year-old juveniles. Pacific sand lance were frequently observed in extensive rapidly swimming schools near the surface at night.

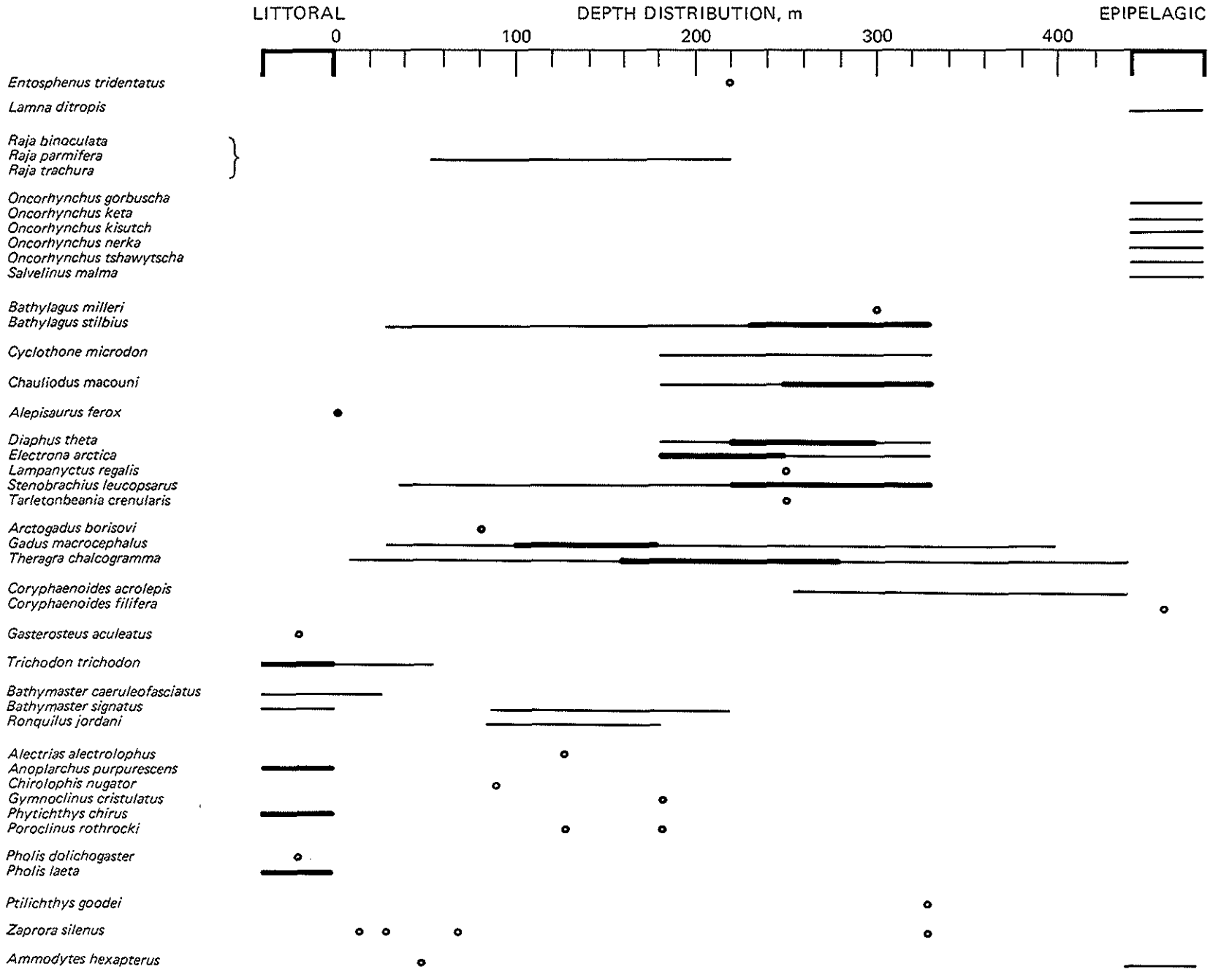
Mesopelagic Community. A distinct community of fishes apparently exists between 200 and 1000 m in the oceanic mesopelagic zone. We sampled only the upper region of this zone (200 to 300 m; 324 m maximum depth) and only during nighttime midwater trawling, concentrating in the productive upwelling waters of the Bering Sea off the eastern end of the island. Only slightly more diverse (18 species versus 11) than the epipelagic community, the mesopelagic community is dominated by lanternfish (family Myctophidae), deepsea smelt (family Bathylagidae), lightfish (family Gonostomatidae), and viperfish (family Chauliodontidae). All are typically zooplankton-feeding fishes and with their predators, grenadiers (family Macrouridae) and longnose lancetfish (family Alepisauridae), apparently perform extensive nightly vertical migrations for feeding in the upper mesopelagic layers.

We optimized our midwater trawl catches in sampling this community by using echo-sounding equipment to find the depth of the deep-water plankton and the associated fishes (deep-scattering layer). In the rich upwelling area, maximum catches exceeded 300 fish per hour compared to 10 fish per hour in other areas sampled. Peak abundance and species diversity in the samples occurred between 2400 and 0400 (BDT). In the most productive trawl sets, northern lampfish, California headlightfish, bigeye lanternfish, and Pacific viperfish were the most abundant fishes.

Catches of fishes corresponded closely with catches of euphausiids, mysids, and carid shrimp, common prey organisms of these fishes.

The recurrent group analysis suggested a microstructure to this community and definite associations between some midwater fishes and associated

*No significant recurrent groups were found in these communities at the affinity index selected as a test of significance.


LITTORAL
DEPTH DISTRIBUTION, m
EPIPELAGIC
0
100
200
300
400
Entosphenus tridentatus
Lamna ditropis
Raja binoculata
Raja parmifera
Raja trachura
Oncorhynchus gorbuscha
Oncorhynchus keta
Oncorhynchus kisutch
Oncorhynchus nerka
Oncorhynchus tshawytscha
Salvelinus malma
Bathylagus milleri
Bathylagus stilbius
Cyclothone microdon
Chauliodus macouni
Alepisaurus ferox
Diaphus theta
Electrona arctica
Lampanyctus regalis
Stenobrachius leucopsarus
Tarletonbeania crenularis
Arctogadus borisovi
Gadus macrocephalus
Theragra chalcogramma
Coryphaenoides acrolepis
Coryphaenoides filifera
Gasterosteus aculeatus
Trichodon trichodon
Bathymaster caeruleofasciatus
Bathymaster signatus
Ronquilus jordani
Alectrias alectrolophus
Anoplarchus purpurescens
Chirolophis nugator
Gymnoclinus cristulatus
Phytichthys chirus
Poroclinus rothrocki
Pholis dolichogaster
Pholis laeta
Ptilichthys goodei
Zaprora silenus
Ammodytes hexapterus

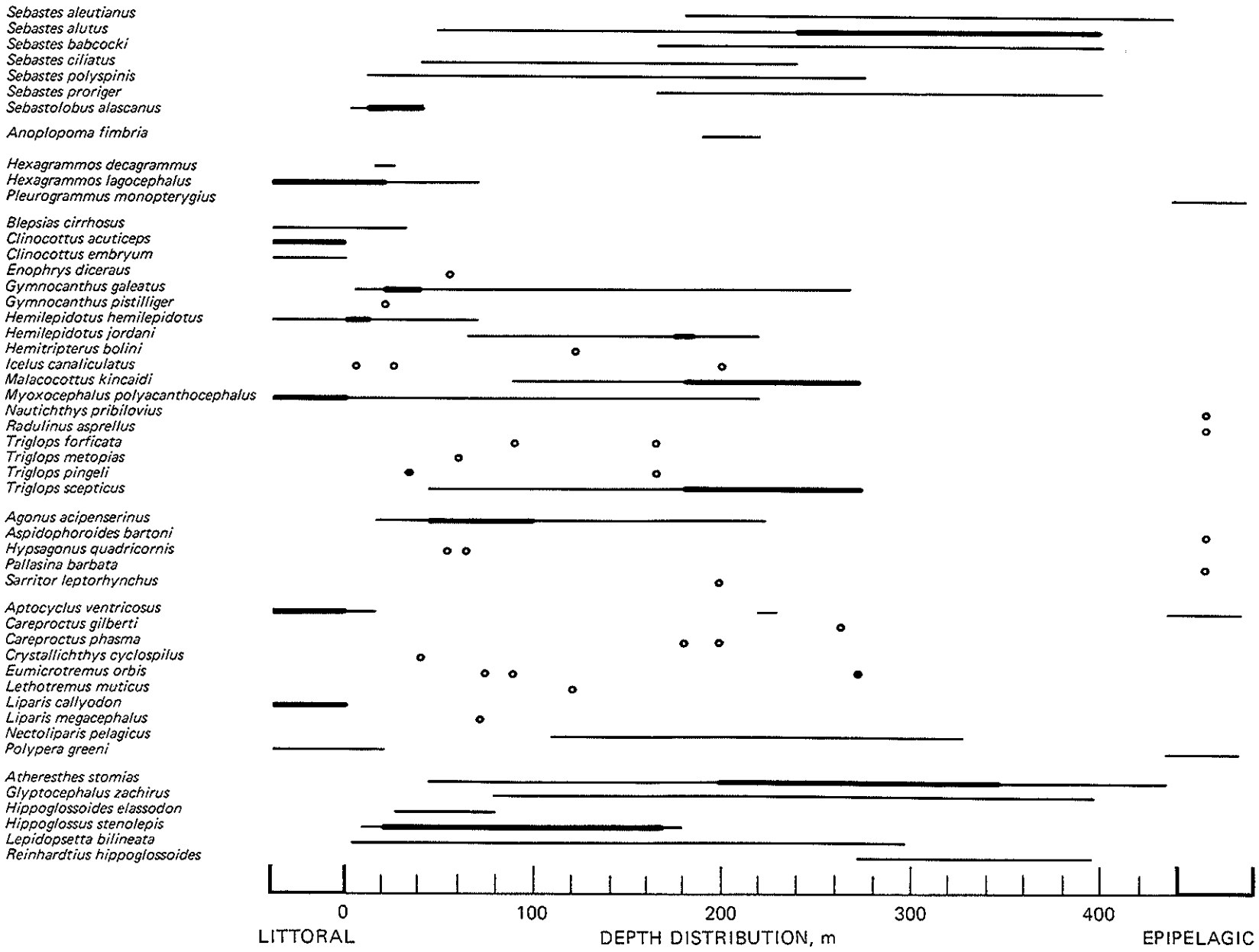


Fig. 2—Depth distribution of marine fishes collected at Amchitka Island, Alaska, 1967 to 1973. Thin lines show complete depth ranges, thick lines show high abundances, and circles show occasional captures only.

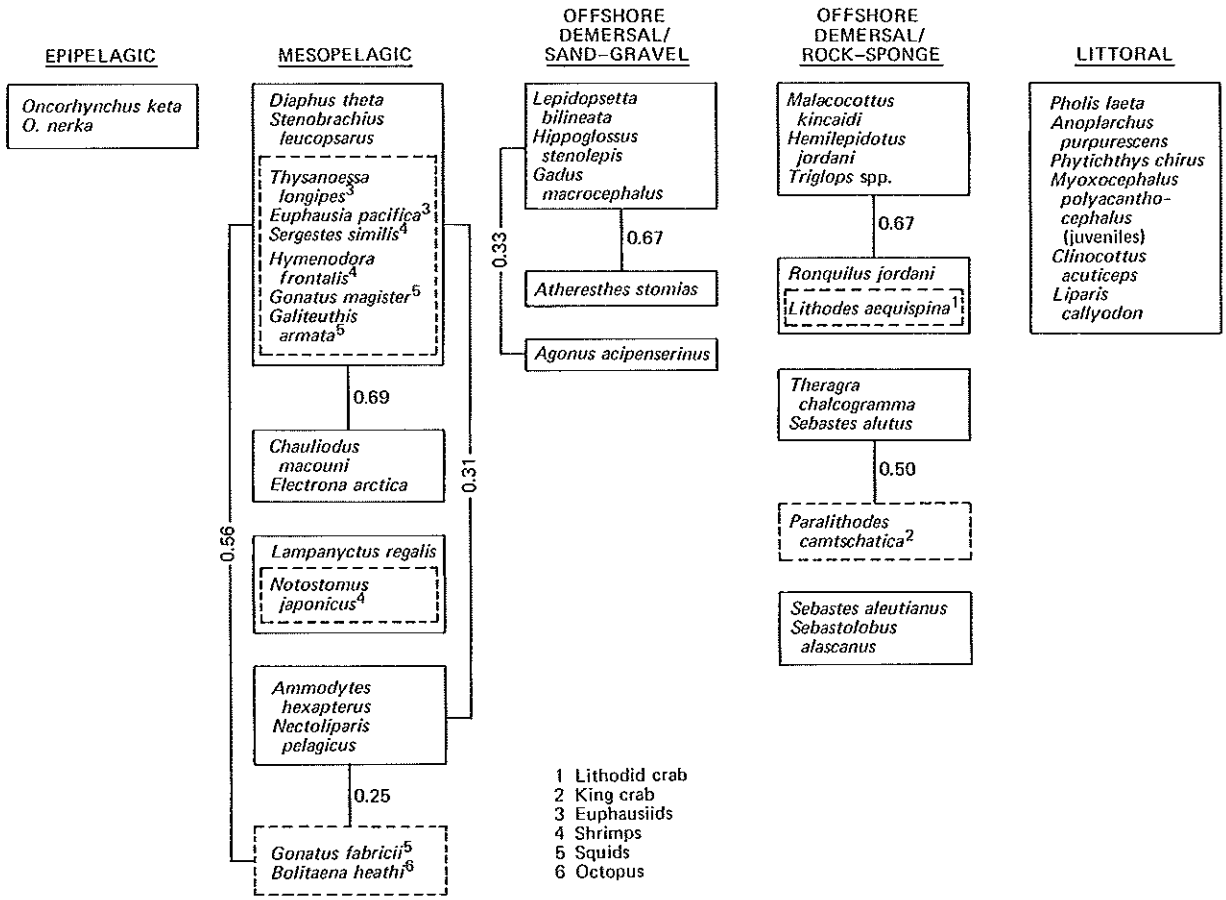


Fig. 3—Species associations of marine fishes and some associated invertebrates (dashed lines), Amchitka Island, 1967 to 1973, according to Fager's (1957) recurrent group analysis (affinity index, 0.40; sample size, 468).

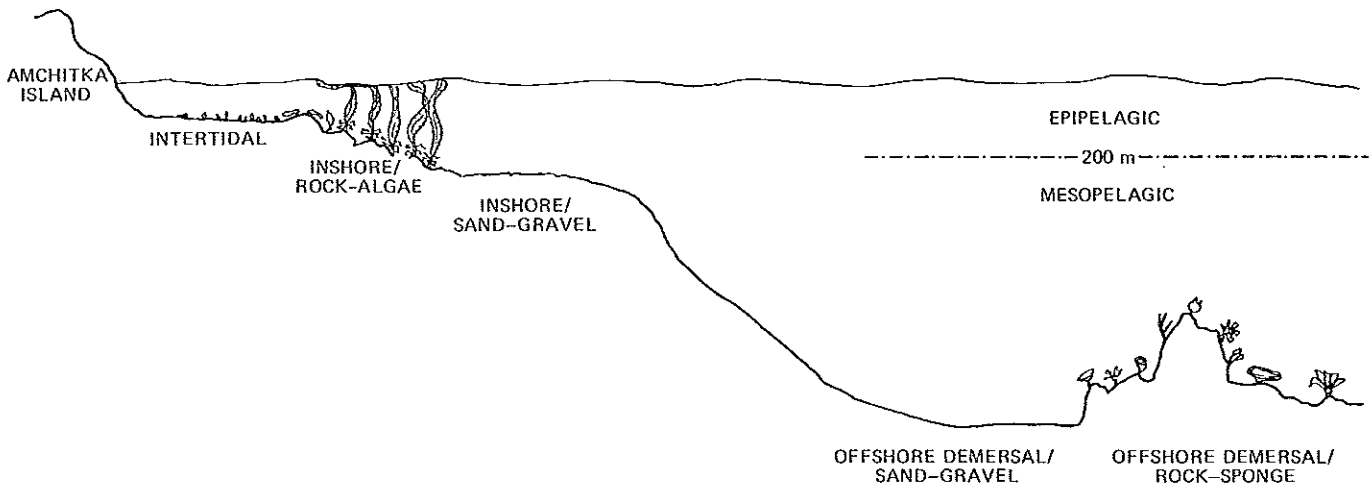


Fig. 4—Diagrammatic sketch showing marine habitats associated with Amchitka fish communities. (The 200-m depth division in the pelagic zone does not apply to the demersal habitats or communities.)

Table 3—Relative Distribution of Amchitka Marine Fishes According to Seven Identifiable Communities Identified by Their Characteristic Habitats

	Epipelagic	Mesopelagic	Offshore demersal/ rock—sponge	Offshore demersal/ sand—gravel	Inshore/ sand—gravel	Inshore/ rock—algae	Intertidal
Lamna ditropis	*						
Oncorhynchus gorbuscha	†				†		
O. keta	‡						
O. kisutch	†				†		§
O. nerka	‡						
O. tshawytscha	†						
Alepisaurus ferox	†	†					
Ammodytes hexapterus	¶			†	‡		
Pleurogrammus monopterygius	‡				‡		
Entosphenus tridentatus		*					
Bathylagus milleri							
B. stilbius		¶					
Cyclothone microdon		‡					
Chauliodus macouni		¶					
Diaphus theta		¶					
Electrona arctica		¶					
Lampanyctus regalis		‡					
Stenobrachius leucopsarus		¶					
Tarletonbeani crenularis		*					
Arctogadus borisovi				*			
Coryphaenoides acrolepis		‡					
C. filifera		*					
Ptilichthys goodei		*					
Zaprora silenus		*					
Nectoliparis pelagicus		¶					
Eumicrotremus orbis		‡	†				
Raja binoculata				*			
R. parmifera			*				
R. trachura			‡				
Gadus macrocephalus			¶	†	‡	†	
Theragra chalcogramma		†	¶		‡		
Ronquilus jordani			‡				
Alectrias alectrolophus			*				
Gymnoclinus cristulatus			*				
Poroclinus rothrocki			*				
Sebastes aleutianus			*				
S. alutus			¶				
S. babcocki			*				
S. polyspinis			‡				
S. proriger			‡				
Sebastolobus alascanus			*				
Anoplopoma fimbria			*				
Enophrys diceraus			*				
Hemilepidotus jordani			‡	†			
Hemitripterus bolini			*	*			
Icelus canaliculatus			*	*			
Malacocottus kincaidi			¶				
Myoxocephalus polyacanthocephalus			†			†	§
Triglops forficata			†		†		
T. metopias			‡				

(Table continues on page 466.)

Table 3—(Continued)

	Epipelagic	Mesopelagic	Offshore demersal/ rock—sponge	Offshore demersal/ sand—gravel	Inshore/ sand—gravel	Inshore/ rock—algae	Intertidal
T. scepticus			‡	†			
Careproctus gilberti			*				
C. phasma			*				
Lethotremus muticus			*				
Liparis megacephalus			*				
Gymnocanthus galeatus				‡	¶		
Hypsagonus quadricornis				*			
Sarritor leptorhynchus				*			
Atheresthes stomias			‡	‡			
Glyptocephalus zachirus				*			
Hippoglossoides elassodon				*	*		
Hippoglossus stenolepis			†	¶	¶		
Lepidopsetta bilineata			†	¶	‡		
Reinhardtius hippoglossoides				*			
Salvelinus malma					¶		§
Trichodon trichodon					‡		
Gymnocanthus pistilliger					*		
Radulinus asprellus					*		
Pallasina barbata					*		
Bathymaster caeruleofasciatus						‡	
B. signatus				‡		†	
Chirolophis nugator						*	
Sebastes ciliatus						‡	
Hexagrammos decagrammus						*	
H. lagocephalus	§	†			†	¶	‡
Blepsias cirrhosus						‡	
Hemilepidotus hemilepidotus			†		†	¶	
Nautichthys pribilovius						*	
Triglops pingeli						*	
Agonus acipenserinus				‡	‡	¶	
Aspidophoroides bartoni							
Aptocyclus ventricosus	†					†	§
Crystallichthys cyclospilus						*	
Polypera greeni						†	‡
Gasterosteus aculeatus							†
Anoplarchus purpurescens						†	¶
Phytichthys chirus						†	‡
Pholis dolichogaster							*
P. laeta						†	¶
Clinocottus acuticeps						†	¶
C. embryum						†	‡
Liparis callyodon						†	¶

*Uncommon in Amchitka waters.
†Infrequently encountered; seasonal or suspected (but undocumented) occurrence.
‡Frequently encountered.
§Abundant in juvenile life states.
¶Abundant; representative of this community.

invertebrates, many of which appear to be their major prey organisms. Several groups exist in the lower (150 to 330 m) strata of our sampling depth regime. The California headlightfish and the northern lampfish and their principal prey species, *Thysanoessa longipes, T. inermis, Euphausia pacifica* (euphausiids), *Sergestes similis, Hymenodora frontalis* (shrimps), and *Gonatus magister* and *Galiteuthis armata* (squids), occur with another fish group that is composed of the Pacific viperfish and the bigeye lanternfish and another invertebrate group of *Gonatus fabricii* (squid) and *Bolitaena heathi* (octopus). A fish–shrimp group of the pinpoint lampfish and *Notostomus japonicus*, an oplophorid shrimp, is defined for the deeper (220 to 330 m) strata, and an intermediate-depth (110 to 146 m) group of Pacific sand lance and tadpole snailfish is also designated.

Demersal fishes, such as the walleye pollock, appeared to enter the mesopelagic community when the planktonic scattering layers composed of euphausiids, shrimps, mysids, and squids migrated within their feeding range. Some of the species noted as being uncommon in the mesopelagic community may actually have been members of the epipelagic community which were captured during the movement of the midwater trawl through epipelagic waters. The occurrence of the Pacific lamprey, smooth lumpsucker, and rock greenling in this community may well be explained in this way. The Pacific lamprey, however, has been noted at depths of 300 to 400 m by Abakumov (1964) and may range through both communities.

Offshore Demersal/Rock–Sponge Community. What we originally described as one entity, the offshore/bottom community (Isakson et al., 1971), has since been redefined as two communities on the basis of expanded data from catches over two physically different deepwater bottom habitats. The habitat of the offshore demersal/rock–sponge community includes those areas adjacent to Amchitka which are rocky and rough bottomed, often with precipitous cliffs and pinnacles, and which form much of the bottom area between 55 and 180 m (180 and 590 ft) in depth on the southeastern side of Amchitka. The bottom material retrieved incidentally with the fishes during trawling included an abundance of sponge (family Axinellidae), coral (family Stylasteridae ?), and tunicates. Observations made while scuba diving over the extensive shoals indicate that the bottom (at least to 30 m deep) is also extensively blanketed by coralline algae (*Clathromorphum* spp.) (P. A. Lebednik, University of Washington, personal communication). The catches were distinctly biased because only the least-rugged terrain was fishable by trawl nets. Echo-sounding tracings of the sidewalls of submarine canyons and pinnacles showed large aggregations of fishes that could not be sampled with our nets. Their behavior indicated that these fishes were rockfish (family Scorpaenidae, probably Pacific ocean perch) or walleye pollock. The most abundant schooling fishes of the offshore demersal/rock–sponge community were Pacific ocean perch, redstripe rockfish, Pacific cod, and walleye pollock. The most abundant bottom fishes were yellow Irish lord, blackfin sculpin, ribbed sculpin, spectacled sculpin, northern ronquil, roughtail skate, and arrowtooth flounder.

Bottom trawl catches from this community ranged between 200 and 1000 fish per hour, the higher catch rate occurring when schools of Pacific ocean perch, Pacific cod, or walleye pollock were encountered. Catch composition typically ranged from 40 to 900 Pacific ocean perch, 30 to 55 walleye pollock, 20 to 45 Pacific cod, 20 to 30 sculpins (family Cottidae), 6 to 12 arrowtooth flounders, 6 to 7 rock sole, 2 to 6 Pacific halibut, and 0 to 1 poacher (family Agonidae) per trawling hour. Lithodid crabs, predominantly *Lithodes aequispina,* were taken in many trawls, their catch averaging 4 to 9 crabs per hour with maximum catches of 40 to 50 crabs per hour.

Three groups of fishes were designated by the recurrent group analysis as existing within this community, primarily as found on the Pacific Ocean side of Amchitka. A cottid group, which includes the blackfin sculpin, the yellow Irish lord, and several *Triglops* species and associated with the northern ronquil and the lithodid crab *(Lithodes aequispina),* occurs dominantly in the 150- to 200-m depth region. The Pacific ocean perch and walleye pollock occur in association with the king crab *(Paralithodes camtschatica)* in deeper water (from 250 to 400 m) and a distinct rockfish group, which includes the rougheye rockfish and shortspine thornyhead, was found in the 220-m depth region.

The offshore community is vulnerable to disturbance, as indicated by replacement of rockfish by walleye pollock after fishing by foreign vessels in fall 1972 and spring 1973 (Nakatani and Burgner, 1974). If we assume that the Pacific ocean perch populations were cropped to low population levels by the fishing fleets [and had not just moved out of the area (Chikuni, 1975)], it appears that populations of walleye pollock, apparently a successful competitor, had succeeded the rockfish. After an extensive period for recruitment to build up its population again, the longer lived

Pacific ocean perch may eventually supplant the walleye pollock.

Offshore Demersal/Sand–Gravel Community. The offshore demersal/sand–gravel community is the assemblage of fishes common to the offshore low-relief expanses of silt, sand, and rock cobbles found between approximately 55- and 95-m depths in the Bering Sea north of the Milrow and Cannikin test sites on Amchitka (Fig. 1). There appears to be very little encrusting benthic growth, such as sponges, corals, and hydroids, although sea pens (family Virgulariidae) occur on the outer (deeper) margins of this habitat. Cobbles brought up in the trawling operation were often entirely covered by the coralline alga *Mesophyllum* sp., which suggests that the habitat's cobble substrate is relatively loose and perhaps not stable (P. A. Lebednik, University of Washington, personal communication). The diversity of the fish fauna comprising this community is lower than that in the other offshore bottom habitat. Catch composition in the offshore demersal/sand–gravel community ranged to a maximum of 320 rock sole, 94 Pacific halibut, 50 armorhead sculpins, 5 searchers, and 10 sturgeon poachers per hour of trawling effort. The stomach contents of top carnivores, such as the Pacific halibut (see following food-web section), from this community indicated that pelagic schools of Pacific sand lance also were common members of this demersal community. Unlike fishes of the other offshore demersal fish community, two fishes, Pacific halibut and rock sole, in this community are relatively mobile, their concentrations shifting about locally, probably for feeding. They also change depth seasonally; this movement is perhaps associated with spawning activity. In the Bering Sea northeast of Amchitka, Pacific halibut maintain denser schools during the winter, dispersing and migrating into the shallower waters in late spring (Novikov, 1964), and rock sole concentrations disperse during a late summer–fall feeding migration (Shubnikov and Lisovenko, 1964).

The recurrent group analysis indicated that a basic group of three species, the rock sole, Pacific halibut, and Pacific cod, existed in distinct association with two other species, the arrowtooth flounder and sturgeon poacher. The Pacific cod association with the Pacific halibut and rock sole, however, was more pronounced on the Pacific Ocean side of Amchitka than in samples from the Bering Sea habitat.

Inshore/Sand–Gravel Community. Like its offshore counterpart, the habitat occupied by the inshore/sand–gravel community consists of a sand–gravel substrate that possesses little stabilized benthic growth. This type of habitat is prevalent in embayments, such as Constantine Harbor, South Bight, Cyril Cove, and Makarius Bay (Fig. 1), and occasionally occurs as narrow areas along the exposed coastline between kelp beds or reef promontories along the bottom of submarine canyons. In areas where rock pinnacles with associated abundant algal growth stand in the middle of a sand–gravel expanse, fishes of the two inshore subtidal communities often intermingle, especially at night. This may indicate the direct relationship between spatial heterogeneity of this habitat and the diversity of its resident fish community.

Pacific cod, walleye pollock, and Pacific halibut appear to be seasonal transients of the inshore/sand–gravel community; however, limited winter sampling precluded the determination of whether these are actual migratory movements. Cod and pollock are abundant from spring until mid-October. Pacific halibut occur commonly throughout the year except during January, February, and March when they apparently move offshore for spawning. Juvenile Pacific halibut and Pacific sand lance were observed regularly in nearshore waters year round. No significant recurrent groups were defined within this habitat.

Inshore/Rock–Algae Community. The inshore/rock–algae community is characterized by a diverse abundant assemblage of fishes intimately associated with the extensive algal growth dominating the rocky nearshore coast. Approximately 60 to 70% of Amchitka's shoreline is composed of exposed rock outcrops, cliffs, or flat-rock benches extending underwater as subtidal rock terraces out to depths of as much as 100 m (Gard, Chap. 2, this volume). Abundant submarine algal growth, such as encrusting corallines, species of fragile Rhodophyta, and various kelps cover these terraces; most conspicuous are the dense kelp beds of *Alaria fistulosa*, which sometimes extend to the 20-m depth contour (Lebednik and Palmisano, Chap. 17, this volume). *Alaria* contributes to the bottom habitat by its massive holdfasts and sporophylls and by its long fronds, which form a protective forest canopy reaching to the surface where the large floating blades form a microhabitat in themselves (Fig. 5). The kelp forest habitat may contribute the multilayered quality of a terrestrial forest that has been shown to influence bird species diversity through the vertical partitioning of niches (MacArthur and MacArthur, 1961; Cody, 1968; Orians, 1969). In addition to the luxuriant macrophytic growth, sessile benthic animals—sponges, bryozoans, anthozoans, and ascidians—

Fig. 5—*Alaria fistulosa* kelp bed (underwater photograph). Note school of pelagic fish.

encrust any firm rock substrate, which creates a bottom habitat of incredible diversity in form, texture, and color.

Associated with the algae for food and protection are abundant crustaceans, echinoderms, and molluscs. The benthipelagic* crustaceans [principally mysids (*Acanthomysis* sp.) and amphipods] were often found in extremely dense underwater swarms (Fig. 6).

These and other abundant invertebrate populations comprise a diverse array of food organisms available to the fishes frequenting the habitat (see later food-web discussion). The spatial heterogeneity of the entire habitat and the diversity of its algal growth and associated food resources are jointly responsible for an abundant diverse fish assemblage.

Representative species in the inshore/rock–algae community include the rock greenling, red Irish lord, northern ronquil, silverspotted sculpin, great sculpin, and dusky rockfish. Pacific cod were also captured in the inshore/rock–algae community habitat of the island's exposed coast, which they were assumed to have entered from the adjacent inshore/ or offshore/sand–gravel community. No recurrent groups were found in the inshore/rock–algae habitat samples with the use of the affinity index of 0.40.

This assemblage for the most part consists of sedentary bottom fishes; however, a few, notably the dusky rockfish, silverspotted sculpin, and some of the less abundant liparid species, occupy the pelagic kelp bed canopy and near-surface microhabitats. Although the latter fishes move freely about the *Alaria* blades and surface canopy either singly (silverspotted sculpin and liparids) or in schools (dusky rockfish), the bottom-associated fishes appeared restricted to a particular site. Scuba observations indicate that during daylight these fishes seldom move beyond the protection of the dense bottom algal cover, but at night they are seen among the benthipelagic swarms of mysids and amphipods.

The trammel net was the most productive sampling gear used in the inshore/rock–algae habitat. Sets of short duration, which avoided net saturation, yielded up to 36 fish of mixed species per hour, which averaged 75 to 80% rock greenling with the remainder red Irish lord, sturgeon poacher, Pacific cod, northern ronquils, and great sculpins. Dusky rockfish move in schools and were not consistently encountered; but, when they were encountered, they made up a significant proportion of the catch. Silverspotted sculpins and liparids were captured with surface plankton net tows through the *Alaria* fronds and were observed during scuba dives. During the winter, when the *Alaria* lose many of their surface fronds from wave

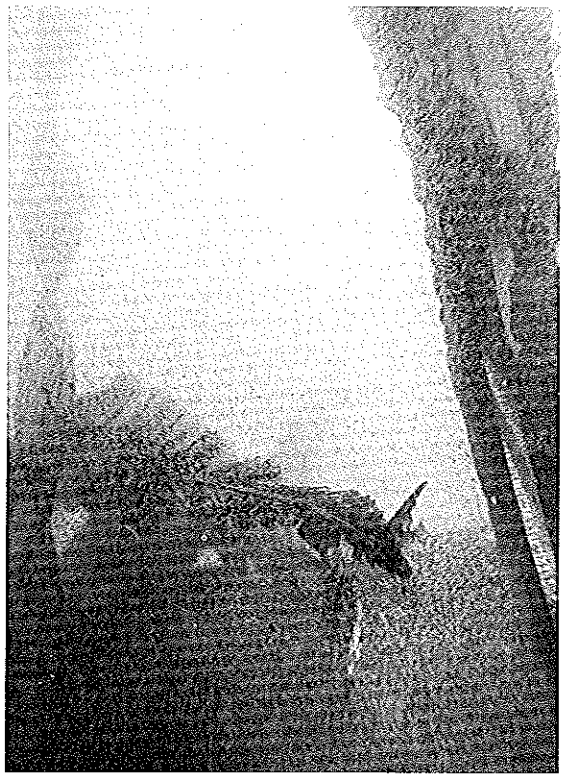


Fig. 6—Mysid, *Acanthomysis* sp., swarms in *Alaria* kelp bed (underwater photograph).

*Associated with bottom but rising pelagically off it.

action, the kelp forest is greatly thinned, and the pelagic fishes descend into the sublittoral fringe zone and its lush *Laminaria* growth. Other species, such as the dusky rockfish, also move from their summer habitat into deeper water during the winter, perhaps to avoid wave action or to follow their food resources.

The bottom-associated fishes are cryptically colored to resemble the reds and browns of the bottom habitat's flora and fauna. Even the distinctive silverspotted sculpin, which swims freely amidst the kelp fronds, is difficult to tell from a shred of algae when observed within its habitat. The male rock greenling, unlike the female, is marked with bright red bars that possibly are associated with reproductive or other social behavior. Although not so well camouflaged, it nevertheless blends well with the red algae of the understory. The rock greenling, red Irish lord, and sturgeon poacher are further concealed by their remaining motionless on the bottom supported by their broad pectoral fins. The suction disk on the ventral surface of liparids enables these small fishes to adhere to kelp fronds in the constant wave motion of the exposed kelp beds.

The rock greenling is by far the most abundant and widely distributed number of this community. This observation stimulated a detailed study of its life history, especially its feeding ecology (Simenstad, 1971a). Scuba observations indicate that adult rock greenling are territorial all months of the year and especially so during the spawning and incubating periods of late spring and early summer. The eggs are laid in purple masses that adhere to algae (usually *Laminaria* sp.) in the sublittoral fringe zone and are guarded by both the male and female. Even during incubating and nonspawning periods, individuals appear to maintain their established homesites, to which they return and rest after brief feeding forays.

Out of about 910 rock greenling in tagging studies, none of those recaptured moved along the shoreline more than 75 m (Burgner et al., 1971a). Simenstad (1971a) suggests that at high tide, especially at night, rock greenling leave their territories to forage on the invertebrate community of the littoral bench. The results from tagging imply that such departures for feeding are merely temporary excursions.

After the juvenile rock greenling hatch in the summer, they form pelagic schools and apparently move into offshore oceanic waters and into the epipelagic community. Although juvenile rock greenling were seldom captured in Amchitka's inshore waters, the purse seine catches of FRI's research vessels 65 to 95 km (40 to 60 miles) off Kagalaska Island, 290 km (180 miles) east of Amchitka, often included significant numbers of juvenile rock greenling. After 2 to 3 years, they apparently migrate back into the inshore areas and become solitary (Gorbunova, 1962; Simenstad, 1971a). This unquantified observation suggests random recruitment from the rock greenling stocks of the whole Aleutian archipelago. Rock greenling food habits and feeding ecology are discussed in more detail in the following section on food webs.

Littoral Community. The littoral fish community is that assemblage of fishes characteristic of the surge channels and tide pools of the rocky littoral bench that typifies much of Amchitka's shore (Fig. 7). Although this assemblage can logically be considered a shallow-water extension of the inshore/rock–algae community, it can be distinguished from that community by the presence of distinctive species. This habitat also provides a nursery ground for juvenile fishes.

This community was most often sampled at low tide; so the entries of Table 3 do not completely represent the community at high tide when species undetected in our sampling could have been present. Littoral-occurring fishes were collected with the use of rotenone in the tide pools (see method discussed by Wilimovsky, 1964), by hook-and-line fishing at high tide, and by setting gill nets on the littoral bench through a tidal cycle. As noted by Wilimovsky (1964) and generally confirmed in our sampling, the fishes of the littoral community responded to the rotenone sequentially according to their oxygen demands. We found that, after rotenone had been applied to a tide pool, fish succumbed in the following order: (1) silverspotted and great sculpins (the smaller specimens responded later), (2) sharpnose sculpins, (3) spotted

Fig. 7—Littoral bench at Rifle Range Point, Amchitka Island, Alaska. Note tide pools connected to sea by surge channels. Visible bench here averages 150 m in width.

snailfish and lobefin snailfish, (4) smooth lumpsuckers, (5) ribbon pricklebacks and high cockscombs, and (6) northern ronquils. The response behavior also varied between species, as with the liparids, which habitually swam to the tide-pool surface, in contrast to the rock greenling, which swam excitedly among the algae at the bottom of the pool and eventually died there. Such varied behavior and response rate may have biased the collection; however, an effort was made to obtain and record every fish in a treated tide pool.

The recurrent group analysis indicated a single group of littoral fishes, which included the crescent gunnel, high cockscomb, ribbon prickleback, juvenile great sculpin, sharpnose sculpin, and spotted snailfish. During high-tide periods when the littoral bench is flooded, adult rock greenling and anadromous Dolly Varden also cruise over the bench, feeding on the mysids, amphipods, and other macroinvertebrates exposed or brought in with the flooding tide.

Species richness was greatest during the summer season, at which time the common-resident littoral fishes were the high cockscomb, crescent gunnel, sharpnose and silverspotted sculpins, and spotted snailfish. In the few large tide pools or surge channels, adult rock greenling were also found in abundance, especially during the June to August spawning period when they laid their eggs among the *Laminaria* in the sublittoral fringe zone. In the spring juvenile great sculpins began appearing in profusion in the littoral area and remained until fall before migrating off the bench. These small juveniles constituted up to 55 to 85% of all fish found in the midsummer tide-pool population. Similarly, juvenile smooth lumpsuckers, Dolly Varden, coho salmon, and rock greenling were also abundant periodically during the summer according to the size of the tide pool, extent of algal cover, proximity to freshwater streams, substrate type, and distance from the seaward margin of the bench. Fish densities in the tide pools averaged 98 fish (range, 20 to 250) per 3- to 6-m^3 tide pool. Some of this variability in these catches undoubtedly was due to varying temperature, which is known to greatly influence the effectiveness of the rotenone. Reduction of the littoral algal cover and of available prey resources as well as the reduced effectiveness of rotenone in colder waters were factors contributing to the low numbers and diversity of fishes encountered during the winter months.

Amchitka Marine Food Web

Some knowledge of the food-web structure in the marine ecosystem was deemed necessary to serve the primary objective of our investigations, i.e., prediction of the potential consequences of a nuclear test or tests on Amchitka. Test-induced changes in the organizational structure of the marine food web, direct or secondary, could conceivably result from loss of habitat or from loss or change in numbers of important prey or predator species. Also, the food web is a potential route for transfer of radionuclides through the ecosystem and ultimately to man in the event of a release of radioactivity to the environment. Food-web studies were therefore undertaken to identify prey organisms of Amchitka marine fishes that (1) are most universally exploited throughout the food web, (2) have a major role in energy transfer or conversion, and (3) import significant amounts of energy into the food web from the high seas around the island.

Results of preliminary food-web analyses were presented in Burgner et al. (1969; 1971a), Burgner and Nakatani (1972), Nakatani et al. (1973), Nakatani and Burgner (1974), and schematically in Isakson et al. (1971), wherein the trophic interactions among fish communities and other exploiters (marine mammals, littoral-feeding birds, and man) were shown. In a practical sense, a relatively simple schematic cannot adequately display such complex relationships. However, it is possible to diagram the major trophic pathways and significant prey resources available to the upper-level components of the ecosystem. These aspects of the marine fish communities of Amchitka are shown in Figs. 8a and 8b. Although these figures are constructed from actual data, each link in the web represents an average derived from all samples, often collected over several seasons, including daytime and nighttime collections, and a range of predator sizes. This schematic model, a simplified condensed representation of the upper level of a very complex trophic structure, indicates the dominant members of the Amchitka fish communities relative to their more significant connections to other fishes and to the prey components of the system.

Although we detected some seasonal and year-to-year variations in the food habits of a few species, the limited extent of winter sampling and the small number of years of sampling preclude the incorporation of such variations into our model. Where appropriate, we have connected prey organisms to several predators. Although these predators may use common prey resources, this does not necessarily imply competition among these fishes for the same populations of prey or movement into adjacent communities for their exploitation. For many prey taxa (amphipods, shrimp, cephalopods, molluscs, and copepods), these general categories

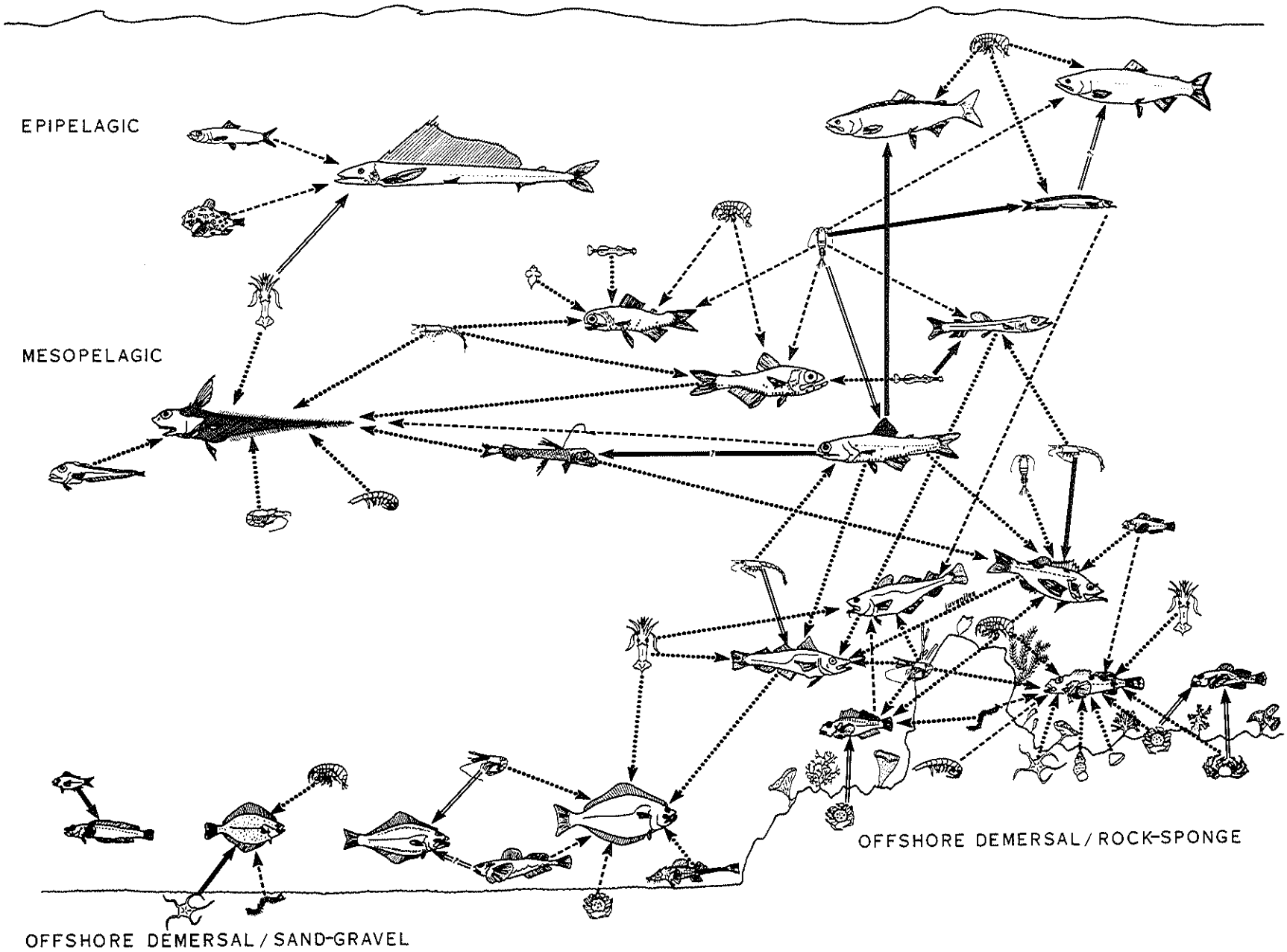


Fig. 8a—Offshore epipelagic, mesopelagic, demersal/sand–gravel, and demersal/rock–sponge fish communities illustrating semiquantitative food-web relationships.

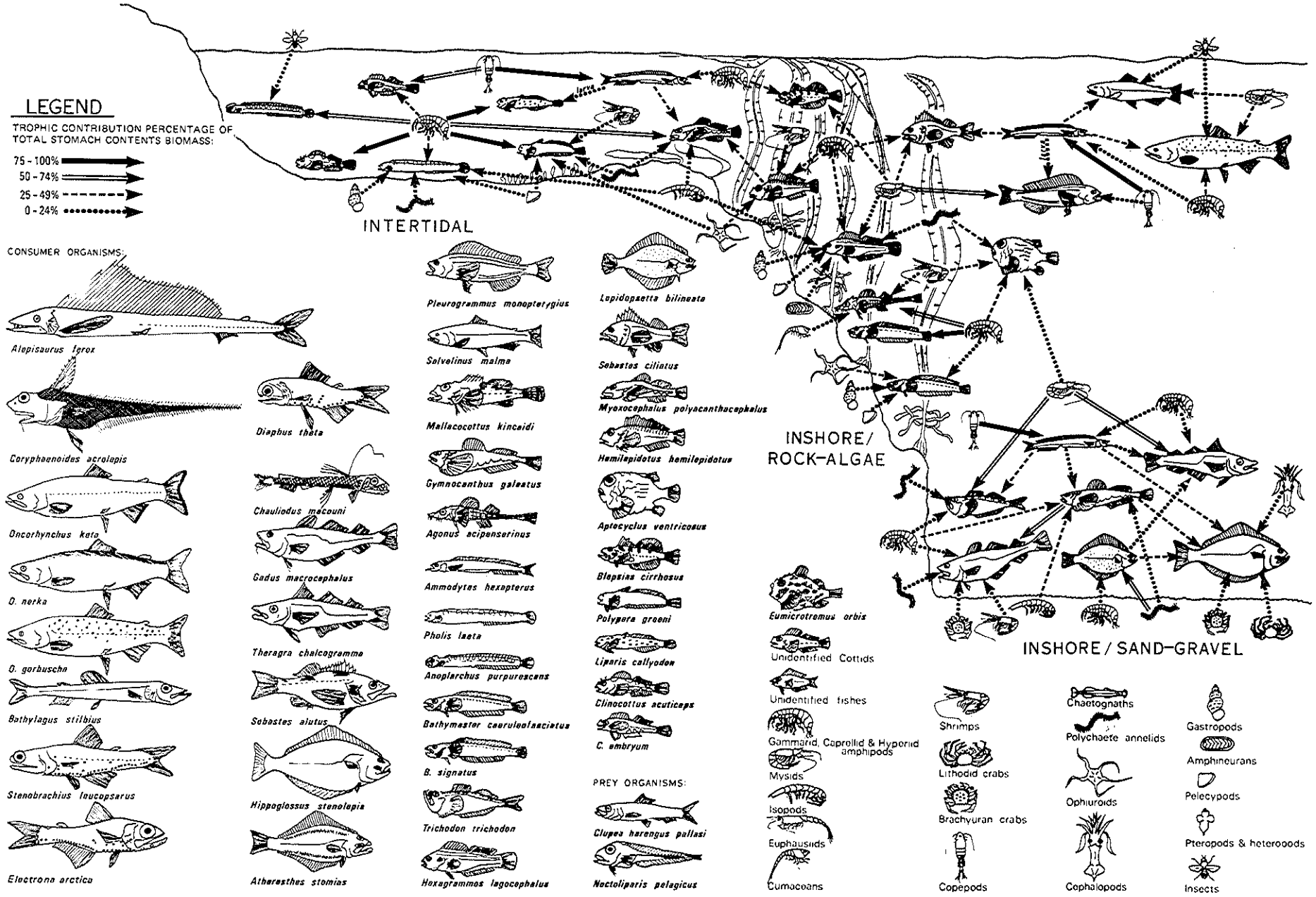


Fig. 8b—Inshore intertidal, rock–algae, and sand–gravel fish communities illustrating semi-quantitative food-web relationships.

include many diverse species representing different populations, niches, microhabitats, and/or behavior; it was impossible to determine, much less to indicate, where or how a fish captured any specific prey since we know little of each prey organism's distribution and behavior.

Frequency of occurrence of prey items (Table 4) provides an index of a fish's actual exploitation of the prey complementary to the biomass–percentage of total stomach contents indicated in Figs. 8a and 8b. The two kinds of information together show the trophic relationships among the components of Amchitka's marine fish communities.

Marine fishes in the littoral region rely on the diverse invertebrate communities associated with the extensive algal growth of that habitat. Especially in this habitat, the amphipod populations provide the major source of trophic energy to the littoral fishes and high-tide immigrants from adjacent communities. These amphipod populations reach high densities in the littoral area during the summer when the windrows of detached kelp and other algae piled on the beaches during the winter storm period contribute a tremendous source of detritus used by these crustaceans. The usually sedentary territorial character of many of the littoral fishes would restrict them to the food resources within their microhabitat or those which drift into it. With this restriction it is possible that they preferentially exploit the abundant "renewable" prey resources, the shifting amphipod, harpacticoid copepod, and drift insect populations, which pass through their territory. Most of the fishes that feed as specialists on these dense but patchy swarms of organisms make very limited use of the epibenthic invertebrates of this habitat. Thus the sedentary invertebrates are not heavily exploited except by the high cockscomb, lobefin snailfish, and that mobile forager from the adjacent inshore/rock–algae community, the rock greenling.

The diet and feeding ecology of the rock greenling, the most abundant fish of Amchitka's inshore marine environment, were the focus of an intensive study (Simenstad, 1971a). As an opportunistic feeder the rock greenling exploits the diverse community of macroinvertebrates found in abundance in the inshore/rock–algae and intertidal habitats. The fact that its stomach contains organisms from both littoral and inner sublittoral habitats suggests that the greenling move over the littoral bench during high tide for feeding. Although the adult rock greenling is not typically a free-swimming schooling species, schools of this fish (often only males) were observed foraging over the bench, often rising to the surface and making "rippling–popping" sounds (Simenstad, 1971a). They were swimming across the bench picking up benthic macroinvertebrates—gastropod and bivalve molluscs, amphipods, isopods, and polychaete annelids—when they were encountered.

Instead of confining their feeding to periodic intensive activity during the submersion of the intertidal bench, the greenling appear to forage to some degree continuously throughout the day and night. Although the greenling tend to feed slightly more during the day, at night they can safely leave the algal protection at the bottom and forage in the swarms of benthipelagic amphipods and mysids of the *Alaria* forest. Simenstad (1971a) suggested that, apparently because of the metabolic or survival cost of the uncertainty of encounter with the patchy swarms of crustaceans, the rock greenling maintain a generalistic feeding behavior until they encounter dense concentrations of amphipods or mysids. Then the fish feed on these crustacean swarms exclusively until satiation or until the crustaceans are too sparse to make it worth the effort. Simenstad considered predation pressures by the sea otter and other carnivores (Table 4) and maintenance of reproductive territories important factors in maintaining this feeding behavior. This pattern of feeding was often shown by rock greenling stomach contents, where homogeneous concentrations of mysids or amphipods were found preceded by or followed by a heterogeneous accumulation of ingested gastropods, isopods, and annelids. Similar feeding strategies have been discussed by Schoener (1969;1971), Rapport (1971), and Pulliam (1974) in their discussion of optimality theories in diet strategies.

Although none of the other dominant fishes of the inshore/rock–algae community are such generalistic feeders as the rock greenling, most also rely on the abundant benthic macroinvertebrates or benthipelagic crustaceans common to that habitat. Of these, the great sculpin and Alaskan ronquil seem to be the most opportunistic, the former being the only fish that is at all piscivorous; red Irish lords, sturgeon poachers, and searchers tend to be more specialistic in their feeding preferences. The only fishes with a narrow range of choice in their diet are the pelagic fishes of the community, the dusky rockfish and silverspotted sculpin, which exploit solely the benthipelagic mysid and amphipod populations within the *Alaria* forest.

The smooth lumpsucker seems to exploit food resources throughout the water column from the shrimp and polychaete annelids associated with the bottom to the benthipelagic amphipod and mysid swarms beneath the *Alaria* canopy. This fish may once have been a dominant component of this

nearshore community, but apparently it was severely reduced in abundance by sea otter predation since it is an extremely sluggish species and not efficient at escaping a predator like the sea otter (*Enhydra lutris*). Fish collections made in the 1950s produced abundant catches of the smooth lumpsucker (Kenyon, 1969, and personal communication); our recent intensive sampling with similar methods seldom produced more than two of these fishes a year, one-twentieth of a day's catch of 20 years ago. That the lumpsucker still persists in the Amchitka nearshore environment, despite the intense sea otter foraging pressure, is a result of its reproductive strategy of producing hundreds of thousands of pelagic eggs per fish. Eggs comprised 41% of the total weight of a female captured in late April 1972! As a result juvenile smooth lumpsuckers are found in tremendous numbers in the littoral zone every spring. Guryanova (1935) also noted the abundance of this fish in the Commander Islands during the spring and summer.

In the inshore/sand–gravel community is a two-compartment food web, one oriented to the neritic fishes, the salmonids, Atka mackerel, and Pacific sand lance, and the other oriented to the bottom-associated fishes, the gadids, pleuronectids, armorhead sculpin, and Pacific sandfish. The prey organisms in the neritic compartment are planktonic crustaceans, hyperid amphipods (mostly *Parathemisto abyssorum*), mysids and copepods (*Calanus cristatus, Pseudocalanus elongatus*), and adult and larval Pacific sand lance. *Oikopleura* sp. (a larvacean) are heavily preyed on during infrequent periods of high abundance in the plankton. In addition, Dolly Varden and pink salmon in inshore waters occasionally take drift insects that have been blown out from the adjacent land mass.

Bottom-associated fishes are almost all macrophagous. Prime examples of these are the Pacific halibut and Pacific cod. All but the rock sole are to some extent piscivorous in their diet. Partitioning of food resources among fishes of similar habitats is evident when the gadids and pleuronectid members of this community are compared. The Pacific cod is dependent on armorhead sculpins and mobile benthic crustaceans, shrimp, and the horse crab (*Erimacrus isenbeckii*), whereas the walleye pollock concentrates on mysids, with Pacific sand lance and rock sole providing incidental contributions to the diet. The rock sole is a benthophage that preys on polychaete annelids and benthic amphipods. The Pacific halibut is a higher order consumer that feeds principally on rock sole and Pacific sand lance and secondarily on squid, octopus, and the horse crab and two lithodid crabs, *Lithodes aequaspina* and king crab *Paralithodes camtschatica*. Armorhead sculpins rely predominantly on benthic amphipods and isopods and secondarily on polychaete annelids. These sculpins are somewhat opportunistic, as indicated by the dominance of *Oikopleura* in their diet during an abnormally high occurrence of these larvaceans in the inshore waters in August 1969.

The diets of the demersal fishes in the offshore portions of the sand–gravel habitat show some interesting differences from their inshore diets in those species common to both (Table 5). Offshore-caught rock sole consumed more ophiuroids than polychaete annelids and amphipods but there are fewer ophiuroids in nearshore areas. Skalkin (1963) and Shubnikov and Lisovenko (1964) indicated that rock sole in the southeastern Bering Sea depend on polychaetes and molluscs as their major food items, with crustaceans, Pacific sand lance, and echinoderms of secondary importance. This may reflect, in effect, differences in the benthic macrofauna associated with this habitat in the two regions. Offshore Pacific halibut prey on walleye pollock, armorhead and other unidentified sculpins, and sturgeon poachers rather than on Pacific sand lance and rock sole, even though the latter occur abundantly in this habitat. This apparent selectivity also occurred in this species' predation on decapod crustaceans, primarily horse crabs and shrimp, although king crabs appear to occur in equal abundance. The reason that rock sole and king crab were not preyed on is not apparent. The diet composition of offshore halibut was similar to that found by Gordeeva (1954) and Novikov (1964) in the western, northwestern, and central Bering Sea, where fishes (pollock, smelts, eelpouts, Pacific herring, and Pacific sand lance) and crustaceans [spider crabs (*Chionoecetes ?*), fiddler crabs, hermit crabs, and shrimp] are the primary prey and molluscs (octopuses) are secondary. A trend of changing diet composition by size, as noted by Novikov (1964), was also indicated at Amchitka—increasing dependence on fishes and molluscs and decreasing emphasis on crustaceans with increasing fish size (30 to 60 cm to 790 cm). If one considers the Pacific sand lance to be the western Aleutian ecological equivalent of smelt and herring, the diets of halibut throughout the Bering Sea are very similar. Even with a small sample size, the indications are that nearshore the halibut much prefers to eat amphipods (primarily bottom species) whereas offshore it is more piscivorous. The arrowtooth flounder, not found nearshore, appears to divide its diet between shrimp and an unidentified cottid, possibly the armorhead sculpin; again this is an inference from a small sample.

Table 4—Frequency of Occurrence of Prey Items in Stomach Contents of Amchitka Island Marine Fishes, Organized by Fish Community

Fish community	Fish species	No. in sample, stomachs with contents	Empty stomachs, %	Prey items: *Polychaete annelids*	Euphausiids	Isopods	Cumaceans	*Ophiuroids*	Sipunculids	Holothurians	Leptostracans	*Oikopleura* (appendicularian)	Insects	Insect larvae	Crab larvae	Hermit crabs	Stalked tunicates	Pycnogonids	Asteroids	Sea stars	Sand dollars	Fish/gastropod eggs	Nudibranchs	Chaetognaths	All miscellaneous, including detritus and unidentified	Gastropods (snails)	Squid and octopi	Bivalves	Chitons	Pteropods and heteropods	All molluscs, including unidentified	Shrimps	Brachyuran crabs
Epipelagic	*Oncorhynchus keta*	9	67																												20	20		
	O. nerka	5	7																						20									
	Alepisaurus ferox	2	0																						50		100					100		
Mesopelagic	*Bathylagus stilbius*	13	24		2																			62	62									
	Chauliodus macouni	2	7																															
	Diaphus theta	51	2		5																			14	25					5		5		
	Electrona arctica	60	35		9																			15	15									
	Stenobrachius leucopsarus	81	81		17																			5	25					1		1	2	
	Coryphaenoides acrolepis	4	20		25	25																			50		25					25		
Offshore demersal/rock–sponge	*Gadus macrocephalus*	4	0																								25					25	75	25
	Theragra chalcogramma	22	0		59																				59		5					14	9	
	Sebastes alutus	159	61		81																			23	100									
	Hemilepidotus hemilepidotus	6	0	33	17																				50								17	83
	Mallacocottus kincaidi	18	0	56		28		11		11								6							83	11	17	11				33	11	11
	Myoxocephalus polyacanthocephalus	4	0																															50
Offshore demersal/sand–gravel	*Bathymaster signatus*	1	0																						100									
	Atheresthes stomias	4	33																														25	
	Hippoglossus stenolepis	57	8	4	2	4		2				2			7										32		4	2		4	4	10	28
	Lepidopsetta bilineata	19	5	53				100																	100	7					7			
Inshore/sand–gravel	*Oncorhynchus gorbuscha*	22	16		5	9							18												20									
	Salvelinus malma	66	33	6	3	6	2						11												42						2			
	Gadus macrocephalus	112	2	17		6		1									2		1	1					58	5	4	5		1	9	33	7	
	Theragra chalcogramma	48	0																						6						4	4		
	Trichodon trichodon	9	4	11																					11									
	Ammodytes hexapterus	1*	0																															
	Pleurogrammus monopterygius	73	5	1	1	1	1					27			1										30		5			26	30	8		
	Gymnocanthus galeatus	76	13	21		18	3	3				7			1	1									51			3			7			
	Hippoglossus stenolepis	69	23	3		1						1				6					1				22		14	1			14	1	19	
	Lepidopsetta bilineata	16	4	83			6	6				6				6									88	6		6			6			
Inshore/rock–algae	*Bathymaster caeruleofasciatus*	3	18		33			33																	33	33		67			67			
	B. signatus	2	0																															
	Sebastes ciliatus	20	8	5																					15									
	Hexagrammos lagocephalus	787	1	25		27	3	3	2	2	7		1			2	1					16	1		80	63		18	18	1	53	3		
	Blepsias cirrhosus	4	0								50														50									
	Hemilepidotus hemilepidotus	110	7	9		9	3	31			3			2	2				1	1					67	8	4	8	4		16	4	3	
	Myoxocephalus polyacanthacephalus	37	11	19		30																			51	3					3			
	Agonus acipenseriuus	15	0				27																		40							20		
	Aptocyclus ventricosus	4	25	25																					75							75		
Intertidal	*Polypera greeni*	2	0	50				50																										
	Anoplarchus purpurescens	4	0	25									25	25											100			50			50	50		
	Pholis lacta	6	0	50		75							17	17											100									
	Clinocottus acuticeps	2	0																						100	33		50			50			
	C. embryum	3	0																															
	Liparis callyodon	8	0											13											13						13			

Fish community	Fish species	Prey items: Lithodid crabs, *Lithodes*, *Paralithodes*, and *Hapalogaster*	All decapods, including unidentified	Gammarid, caprellid, and hyperiid amphipods	Mysids	Calanoid and harpacticoid copepods	*Stenobrachius leucopsarus*	*Ammodytes hexapterus*, including larvae	*Bathylagus stilbius*	*Nectoliparis pelagicus*	*Chauliodus macouni*	*Electrona arctica*	*Gadus macrocephalus*	*Theragra chalcogramma*	*Bathymaster* sp.	*Anoplarchus purpurescens*	Unidentified cottids	*Blepsias cirrhosus*	*Clinocottus* sp.	*Gymnocanthus galeatus*	*Hemilepidotus hemilepidotus*	*Myoxocephalus polyacanthacephalus*	*Sebastes* sp., including juveniles	*Clupea harengus pallasii*	*Agonus acipenserinus*	*Hippoglossus stenolepis*	*Lepidopsetta bilineata*	*Hexagrammos lagocephalus*	*Aptocyclus ventricosus*	*Eumicrotremus orbis*	*Liparis* sp.	All fish, including unidentified
Epipelagic	*Oncorhynchus keta*			11		11																										11
	O. nerka			80			20																									20
	Alepisaurus ferox																				50			50						50		100
Mesopelagic	*Bathylagus stilbius*					38																										13
	Chauliodus macouni			25																												
	Diaphus theta			24		35																										
	Electrona arctica			25		25																										
	Stenobrachius leucopsarus		2	5		51																										
	Coryphaenoides acrolepis		25		50		50			25	25	25																				100
Offshore demersal/rock—sponge	*Gadus macrocephalus*		100	25				25													50											75
	Theragra chalcogramma		9	32			5		5														5									32
	Sebastes alutus			61		40																										8
	Hemilepidotus hemilepidotus		83	50																												
	Mallacocottus kincaidi	6	28	61													6															25
	Myoxocephalus polyacanthacephalus	50	100																													
Offshore demersal/sand—gravel	*Bathymaster signatus*																															100
	Atheresthes stomias		25	25													25															25
	Hippoglossus stenolepis		53	16										2			4			5												68
	Lepidopsetta bilineata			29																												
Inshore/sand—gravel	*Oncorhynchus gorbuscha*			77	41			5														5										45
	Salvelinus malma			50	48			12									3						3									27
	Gadus macrocephalus		47	51	27	2		7												19	4		2					2				75
	Theragra chalcogramma		13	35	90	13		2									2					2					2					21
	Trichodon trichodon			44	67			11																								11
	Ammodytes hexapterus			100		100																										
	Pleurogrammus monopterygius		12	36	48	30		3																								10
	Gymnocanthus galeatus		4	55	18	1		4																								17
	Hippoglossus stenolepis	6	32	20	3			29					7	3			3		1	7		1	3			1	22					74
	Lepidopsetta bilineata		6	88	6																											
Inshore/rock—algae	*Bathymaster caeruleofasciatus*			67																												
	B. signatus			100																												
	Sebastes ciliatus			40	60	10		5																								15
	Hexagrammos lagocephalus		7	83	19	3									1	1		1	1		1	1						1			1	12
	Blepsias cirrhosus			100	25																											
	Hemilepidotus hemilepidotus		19	80	8	2		1					1				7			1	3	1					1					25
	Myoxocephalus polyacanthacephalus			89				3																	1							11
	Agonus acipenserinus		33	100	7																											13
	Aptocyclus ventricosus		75	100	25																											50
Intertidal	*Polypera greeni*		50	100																	3								50			50
	Anoplarchus purpurescens			50																												
	Pholis laeta			100																												
	Clinocottus acuticeps			100																												
	C. embryum			33		100																										
	Liparis callyodon			100				13																								13

*Includes nonquantitative observations.

Table 5—Percentage Composition by Biomass and Percentage Occurrence (in Parentheses) for General Prey Taxa of Important Species Occurring in Both Offshore and Inshore Communities

Predators	No.	Prey						
		Fish	Decapods	Molluscs	Amphipods	Mysids	Copepods	Miscellaneous
Pacific cod								
Offshore	4	85.5	10.8	0.1	0.4	0.0	0.0	3.2
		(75.0)	(100.0)	(25.0)	(25.0)	(0.0)	(0.0)	(75.0)
Inshore	112	66.1	16.5	0.3	4.0	2.5	0.1	10.5
		(76.8)	(48.2)	(8.9)	(51.8)	(27.7)	(1.8)	(58.9)
Walleye pollock								
Offshore	22	8.3	86.8	2.6	2.2	0.0	0.0	0.1
		(31.8)	(95.5)	(13.6)	(31.8)	(0.0)	(0.0)	(4.6)
Inshore	48	14.6	0.7	0.0	10.5	70.8	2.7	0.7
		(20.8)	(4.2)	(0.0)	(35.4)	(89.6)	(12.5)	(6.3)
Great sculpin								
Offshore	4	0.0	100.0	0.0	0.0	0.0	0.0	0.0
		(0.0)	(100.0)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)
Inshore	37	55.2	0.0	0.1	34.3	0.0	0.0	10.4
		(10.8)	(0.0)	(2.7)	(89.2)	(0.0)	(0.0)	(51.4)
Red Irish lord								
Offshore	6	0.0	72.0	0.0	8.9	0.0	0.0	19.1
		(0.0)	(83.3)	(0.0)	(50.0)	(0.0)	(0.0)	(50.0)
Inshore	110	10.8	18.9	2.7	39.0	0.5	0.0	28.1
		(24.5)	(19.1)	(16.4)	(80.0)	(8.2)	(0.0)	(67.3)
Pacific halibut								
Offshore	57	64.9	31.9	0.8	0.2	0.0	0.0	2.2
		(68.4)	(52.6)	(3.5)	(15.8)	(0.0)	(0.0)	(17.5)
Inshore	69	68.1	24.6	4.7	0.2	*	0.0	2.4
		(74.0)	(31.9)	(14.5)	(17.4)	(2.9)	(0.0)	(21.7)
Rock sole								
Offshore	4	0.0	0.0	0.0	0.0	0.0	0.0	100.0
		(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(100.0)
Inshore	16	0.0	3.9	0.2	15.9	0.2	0.0	79.8
		(0.0)	(6.3)	(6.3)	(87.5)	(6.3)	(0.0)	(87.5)

*Less than 0.05%.

The offshore demersal/rock—sponge community includes four fishes that are also found in inshore communities: (1) Pacific cod, (2) walleye pollock, (3) great sculpin, and (4) red Irish lord (Table 5). Cod inshore and offshore are equally piscivorous, but offshore they feed exclusively on red Irish lord and Pacific sand lance whereas inshore they prey on armorhead sculpins more than on any other fish. Inshore, shrimp were prominent in their diets, and squid and octopus had replaced *Erimacrus*. Pacific cod in both inshore and nearshore habitats seem not to exploit the abundant benthipelagic amphipods. Although walleye pollock in the offshore community appear to be characteristically associated with the Pacific cod and sculpins along the bottom, benthic organisms are not dominant in their diet. Instead, the walleye pollock apparently move up off the bottom diurnally to exploit mesopelagic euphausiids (contributing 87% of the stomach contents biomass), shrimp, squid, octopus, and fishes (northern lampfish, California smoothtongue, and juvenile rockfish, *Sebastes*).

Offshore cottids also differ from their inshore counterparts in their food habits (Table 5). Red Irish lord feed selectively on horse crabs with supplemental contributions by shrimp, amphipods, and polychaete annelids. Large adult great sculpins feed exclusively on the two large decapods, the horse crab (*Erimacrus*) and the tanner crab (*Chionoecetes* sp.). The blackfin sculpin, an abundant cottid exclusive to this habitat, is a benthiphage that preys on polychaete annelids, ophiuroids, bivalves, gastropods, squid, octopus, deepwater isopods (*Arcturus setusus*?), horse and tanner crabs, amphipods, shrimp, and unidentified cottids, the more important prey being polychaete annelids, amphipods, and the fishes.

The dominant fish of the deepwater rockfish niche, the Pacific ocean perch, is planktivorous, concentrating on the euphausiid (86% composition by weight) and hyperiid amphipod (6% composi-

tion by weight) components of the coastal zooplankton with incidental exploitation of mesopelagic fishes—Pacific viperfish and lanternfishes—and demersal cottids. A large bathypelagic calanoid copepod (*Calanus cristatus*) and the chaetognath [*Sagitta planctonis* (?)] also appear in the Pacific ocean perch diet. This diet composition generally agrees with the findings of Lyubimova (1963), Paraketsov (1963), Skalkin (1964), and Chikuni (1975), who found crustaceans to be the major prey items with planktonic [calanoids (*C. cristatus*), euphausiids, and hyperiids] and nektobenthic (mysids, amphipods, and shrimps) organisms predominating. These investigators also found some squids and small fish in the rockfish stomachs.

Mesopelagic fishes include planktivorous lanternfishes and bathylagids and their predators, the Pacific viperfish and roughscale rattail. Calanoid copepods and hyperiid amphipods constitute the major food sources of the lanternfishes with supplemental input from euphausiids (*Thysanoessa longipes, T. inermis,* and *Euphausia pacifica*), chaetognaths (*Sagitta* sp.), squid and pteropods, and carid shrimp (*Sergestes similis*). The viperfish and rattail prey selectively on the northern lampfish, the most abundant lanternfish of that fish community. The roughscale rattail also preys on its smaller competitor, the Pacific viperfish, and mesopelagic mysids (*Gnatophausia gigas*), isopods (*Arcturus* spp.), euphausiids, and squid (*Galiteuthius armata*). California smoothtongue prey on chaetognaths and calanoid copepods with a secondary contribution from euphausiids.

The maturing migrating sockeye and chum salmon of the epipelagic community are primarily piscivorous, preying on both the forage fish resident in that community (the Pacific sand lance) and the planktivorous northern lampfish of the adjacent mesopelagic community; the sockeye salmon probably captures these lanternfish during that prey's diurnal migration into the upper regions of the deeper habitat. Hyperiid amphipods and calanoid copepods contribute to the diets of both species of salmon, calanoid copepods being an important secondary component (25% composition) of the chum salmon diet. The piscivorous feeding habits of Amchitka's sockeye and chum salmon may well reflect the patchy seasonal abundance of fish [especially myctophids (lanternfishes)] occurring in the upwelling area of the offshore waters. Previous investigations (Andrievskaia, 1957; Allen, 1956a; 1956b; Foerster, 1968; Le Brasseur, 1959; and Synkova, 1951) have shown that the most common components in the diets of these salmon in the western Aleutians are euphausiids, hyperiid amphipods, and calanoid copepods with fish and squids forming only secondary food resources, indicating their seasonal patchy distributions around the North Pacific. Allen (1956b) further indicates that, where food is most abundant, both species become more selective in the feeding habits.

Longnose lancetfish are oceanic alepisaurs and were represented in the Amchitka collection by two fish that were blown ashore during stormy weather. Their stomach contents indicated that these fish are omnivorous predators that range through the epi- and mesopelagic water column and deeper, feeding on nekton resembling in composition that captured in our midwater trawling. Prey specifically includes Pacific spiny lumpsuckers, octopus (*Bolitaena heathi*), and squid (*Gonatus* sp.). Other minor components include polychaete annelids, Pacific herring (*Clupea harengus pallasi*), and juvenile cottids, possibly red Irish lords. This diet composition indicates that the longnose lancetfish feeds opportunistically on the slow-moving components of the nekton, neglecting the abundant but more mobile lanternfishes and other forage fishes (Pacific sand lance and juvenile hexagrammids) as well as the dense zooplankton populations, all apparently available within the fish's habitat. This conclusion conforms with Haedrich (1964), Haedrich and Nielson (1966), and Parin, Nesis, and Vinogradov (1968). Parin et al. described these fish as feeding at depths of 100 to 300 m, at the boundary of the epi- and mesopelagic regions. This depth in the Indian Ocean is in the lower levels of the upper isothermal layer and the upper levels of the principal thermocline.

Without a more thorough knowledge of the distributions and abundances of the prey organisms or quantitative evaluation of predator exploitation, a complete summary of the dynamics of the trophic relationships between the components of Amchitka's marine food web is not possible. Given the first-order semiquantitative results of these investigations, however, some important generalizations can be made.

The nearshore environment harbors a rich diverse community of marine organisms providing abundant food resources to resident and immigrant fishes. This is, in part, a result of the diverse macrophytic algal flora of the Amchitka littoral and inner sublittoral zones. The intricacy of this community appears to be in response to the predation pressure on herbivores from the system's top carnivore, the sea otter (Palmisano and Estes, Chap. 22, this volume). This complex algal community not only provides a diversity of habitats for benthic and benthipelagic macroinvertebrates but also provides considerable autotrophically accumu-

lated energy to the inshore marine food web through linkages to the abundant herbivorous molluscs, echinoderms, and crustaceans. Direct herbivory, however, is not as significant a mechanism of energy transfer in this system as indirect herbivory, as was indicated by the low trophic contributions of herbivorous organisms to inshore fish. Even the opportunistic benthophagous rock greenling fail to prey significantly on herbivores in areas where other prey are abundant. Specifically, the major herbivore of the system, the sea urchin (*Strongylocentrotus polyacanthus*) occurs only incidentally in fish diets. Again, the effect of sea otter predation on the inshore sea urchin populations is to severely limit the availability of urchins to other inshore predators (Palmisano and Estes, Chap. 22, this volume).

On the other hand, indirect energy transfer through the production of detritus does appear to be significant. Seasonal die-off and attrition, especially during the winter storm period, create large masses of detached macroalgae in the upper littoral region. Their decay releases great quantities of detritus and nutrients into the inshore waters and promotes prodigious amphipod and mysid populations in the inshore habitats. The trophic importance of these benthipelagic macroinvertebrates in the food web is evident. Amphipods contributed a mean 39% by weight to the diets of the 25 inshore fish, and their mean frequency of occurrence was 72%; mysids, not as widely distributed as the diverse amphipod taxa, contributed 13% by weight and 20% in frequency of occurrence. Energy transfer through breakdown of macroalgae is not limited to inshore amphipods and mysids. Palmisano and Estes (Chap. 22, this volume) indicate that kelp fragments collect around *Hedophyllum* holdfasts and thus provide detrital food supplies to the special communities of invertebrates associated within and under the holdfasts, especially the isopods *Idotea wosnesenskii* and *Exosphaeroma amplicauda*, which also contribute to the diets of rock greenling and great sculpin. Simenstad (1971a) suggested that inshore–offshore circulation along the bottom carries detached intertidal algae from the littoral bench into inner sublittoral habitats where fishes prey both on littoral invertebrates carried with this algae and on those sublittoral forms foraging on the algae. It was also demonstrated that the decaying masses of algae in the upper littoral zones support heavy populations of beach fly (*Diptera* sp.) larvae which are then available at high tides to foraging rock greenling, spotted snailfish, and Dolly Varden.

The pelagic trophic equivalent of the amphipod is the Pacific sand lance. Although this fish constitutes an unpredictable rapid-swimming resource, it contributes to the diets of 8 of the 10 species studied from the inshore/sand–gravel community. Its larval and prejuvenile forms are also in the diets of three fishes of the inshore/rock–algae community. This forage fish is the system's main means of energy transfer between zooplankton and the piscivorous fishes of the community. No predator can afford to prey selectively on sand lance since its occurrence is apparently not certain enough to guarantee a reliable food resource. However, when it does occur, it appears to be the selected preferred prey. Stomachs of predators were found to be unusually distended with sand lance whenever their schools were in the inshore waters. Even the rock greenling was observed to capture sand lance to distention during a large inshore influx of schools of sand lance in August 1973. Studies of the avian predators of Amchitka inshore fish have also noted the occurrence of sand lance in the diets of many species (Williamson, Emison, and White, 1972). Offshore the sand lance appears to suffer little predation pressure from epipelagic piscivores.

The relative importance of various components of the Amchitka inshore and offshore marine ecosystems can be further seen by enumerating and weighting the food-web links identified in Fig. 8. Table 6 shows the number of trophic contributions (arrows in Figs. 8a and 8b) in each of four categories of percentage relative biomass; the four percentage categories are weighted and added to provide a total weighted contribution of this prey to the ecosystem's fishes. Organisms in the 0 to 24% column were weighted 1, those in the 25 to 49% column were weighted 2, etc. Theoretically, in this simplistic approach the higher the total weighted contribution, the greater the role these prey resources play in the structure and energy-flow dynamics of the ecosystem. As indicated in Table 6, the most significant contributors are amphipods, mysids, polychaete annelids, and Pacific sand lance in the inshore ecosystem and amphipods, copepods, euphausiids, and northern lampfish in the offshore ecosystem.

Spatial heterogeneity of the habitats studied influences not only the structure of the associated animal communities but also the complexity of the food web involved. The homogeneous epipelagic portions of both offshore and inshore habitats have much simpler patterns of trophic links between the fishes and their food resources than the spatially heterogeneous inshore/rock–algae or offshore demersal/rock–sponge communities. This is assumed to be a result both of the greater diversity of food resource available in the heterogeneous

Table 6—Trophic Contributions by Percentages of Relative Biomass and Total Weighted Contributions of Prey Organisms to Inshore and Offshore Amchitka Marine Fishes

Prey organisms	Contribution and weighting factors*				Total	Weighted contributions
	0 to 24% (1)	25 to 49% (2)	50 to 74% (3)	75 to 100% (4)		
Inshore						
Amphipods	6	9	3	4	22	49
Mysids	2	4	3		9	19
Shrimps	4	1			5	6
Copepods	1			2	3	9
Isopods	3	1			4	5
Brachyuran crabs	2				2	2
Lithodid crabs	1				1	1
Cumaceans	1				1	1
Gastropods	3				3	3
Pelecypods	4				4	4
Amphineurans	1				1	1
Cephalopods	1				1	1
Ophiuroids	1	2			3	5
Polychaete annelids	7	1	1		9	12
Insects	3				3	3
Pacific sand lance	4	6			10	16
Armorhead sculpin		1	1		2	5
Rock sole	1	1			2	3
Red Irish lord		1			1	2
Offshore						
Amphipods	7	2			9	11
Mysids	1				1	1
Shrimps	5		1		6	8
Copepods	1	4	1	1	7	16
Isopods	1	1			2	3
Brachyuran crabs	1	1	2		4	9
Lithodid crabs	1		1		2	4
Euphausiids	5		1	1	7	12
Gastropods	1				1	1
Pelecypods	1				1	1
Cephalopods	5		1		6	8
Pteropods and heteropods	1				1	1
Ophiuroids	1			1	2	5
Polychaete annelids	1	2			3	5
Chaetognaths	2			1	3	6
Pacific sand lance		1	1		2	5
Armorhead sculpin		1	1		2	5
Red Irish lord	1				1	1
Northern lampfish	2	1		2	5	12
Pacific viperfish	2				2	2
Walleye pollock	1				1	1
Pacific ocean perch	1				1	1
California smoothtongue	1				1	1
Bigeye lanternfish	1				1	1
Pacific herring		1			1	1
Spiny lumpsucker	1				1	2
Sturgeon poacher	1				1	1
Tadpole snailfish	1				1	1
Unidentified cottids	1	1			2	3
Unidentified fish				1	1	4

*The factors used in weighting are given in parentheses.

communities and the concomitant more generalistic feeding behavior of the fishes there. The pelagic specialists (salmon, Pacific sand lance, and Atka mackerel) exclusively exploit the patchy abundance of planktonic prey, which enables them to maximize energy ingested per encounter with prey (copepods, pelagic amphipods, and mysids) concentrations.

The large specialist consumers of the demersal fish communities (great sculpins, arrowtooth flounders, and Pacific halibut) feed on large high-energy-per-item prey (fish and large crustaceans), which enables them to extract more energy per unit of feeding time than if they exploited the more common smaller prey available in their habitats (Schoener, 1969). The small specialists of the littoral community (pricklebacks and gunnels) feed on the abundant crustaceans. Their diets and opportunistic feeding behavior reflect the necessity for these species (small, territorial, and situated in a constantly fluctuating environment) to monitor prey, predators, competitors, and mates within a limiting habitat. Most of the generalists (rock greenling, red Irish lord, Pacific cod, walleye pollock, and blackfin sculpin) are species that occupy habitats with consistent heterogeneous concentrations of prey. These fishes are thus able to maximize energy consumed by feeding continuously on a diverse diet of prey organisms.

The benthipelagic amphipod and mysid populations appear to be the most universal prey and the principal converters of plant detritus energy into energy sources available to the secondary consumer level, and the offshore euphausiid populations play, to a lesser degree, a similar role; the principal energy importer apparently is the Pacific sand lance, the mobile populations of which continuously introduce energy derived from the zooplankton resources of the surrounding oceanic region into the Amchitka inshore ecosystem.

Other investigators (see Palmisano and Estes, Chap. 22, this volume) have documented the effect of the sea otter as a "keystone species" (Paine, 1969) and its herbivorous prey, the sea urchin, an influential "foundation species" (Dayton, 1972) in structuring the inshore biotic community. The role of this interaction, though indirect, in determining energy flow in the system's food web should not be ignored because it is the lower level conversion of energy that eventually determines the composition of the upper level consumers, such as the fish communities.

The lack of data on food sources of the prey organisms illustrated in Fig. 8 prevented us from extending corresponding linkages to lower trophic levels. Documentation of predation by Amchitka's avian and mammalian top carnivores is similarly limited. Williams (1938), Murie (1940), Lensink (1962), Burgner and Nakatani (1972), and Palmisano and Estes (Chap. 22, this volume) all report predation on marine fishes by the sea otter at Amchitka. Kenyon (1969) specifically identified the smooth lumpsucker, red Irish lord, Atka mackerel, and rock greenling as important constituents of sea otter diet at Amchitka in the 1960s, with the smooth lumpsucker occurring most frequently in the stomachs examined. As noted earlier, predation pressure may have sharply reduced the abundance of this species in recent times.

Williamson, Emison, and White (1972) have reported fish predation by littoral and pelagic feeding birds, among them the Red-throated Loon (*Gavia stellata*), Pelagic Cormorant (*Phalacrocorax pelagicus*), Red-faced Cormorant (*P. urile*), Red-breasted Merganser (*Mergus serrator*), Bald Eagle (*Haliaeetus leucocephalus*), Glaucous-winged Gull (*Larus glaucescens*), Arctic Tern (*Sterna paradisaea*), Aleutian Tern (*S. aleutica*), Common Murre (*Uria aalge*), Thick-billed Murre (*U. lomvia*), Pigeon Guillemot (*Cepphus columba*), Horned Puffin (*Fratercula corniculata*), and Tufted Puffin (*Lunda cirrhata*). The common prey of these birds was the Pacific sand lance, but the rock greenling, Atka mackerel, armorhead sculpin, red Irish lord, and spotted and lobefin snailfish were also represented in their diets. Pacific cod and rockfish species were also reported prey organisms, but it is suspected that these were scavenged from waste from a foreign fishing vessel offshore.

Impact of Amchitka Nuclear Tests on Marine Fishes

Principal interests of the U. S. Atomic Energy Commission in FRI's study of Amchitka's marine fishes were establishing pretest base lines of species occurrence and abundance and of ecological relationships so that posttest comparisons could be made to evaluate the impact of proposed underground nuclear tests at Amchitka. This information and information from the literature concerning shock effects were combined to provide inputs for the predictions and assessments by Battelle Memorial Institute and the AEC of the environmental impacts of the Milrow and Cannikin tests (Kirkwood, 1970; Merritt, 1970; Kirkwood and Fuller, 1971; 1972). In the establishment of these base lines, a great deal of new information was obtained about the marine fishes of Amchitka Island. This section summarizes the observed impact of the two tests (Milrow, Oct. 2, 1969;

Cannikin, Nov. 6, 1971) on Amchitka's marine fish communities.

A review of the literature from previous underwater explosions and related experiments or phenomena (Simenstad, 1971b; 1974) indicated that the shock wave from an underground nuclear explosion could inflict damage on marine organisms through several mechanisms. Directly, it could damage or kill individual organisms through the mechanical impact or pressure change produced when the shock wave passes through the water. It could also indirectly alter species composition, distribution, and/or abundance in the affected fish communities through the alteration of the marine habitat, which would affect changes in food resources, living space, and reproductive substrate. The hydrostatic changes imposed by the shock wave were considered, however, to be potentially the most damaging to individual fish. Two specific mechanisms are applicable in these circumstances: (1) Pressures over and under the ambient pressure and (2) bulk cavitation. The literature documents that, for low-frequency shock waves, such as those produced by the underground tests (10 to 15 Hz), the negative pressure phases of the hydrostatic pressure history would be the most damaging to fishes, more so to physoclistous* than to physostomous† and non-gas-bladdered species. Except for fast-rising shock waves incident on gas-bladdered fishes (as from dynamite explosions), compression or overpressure was not shown to be detrimental. A phenomenon that limits the maximum underpressure attainable, as a function of water depth, is cavitation, i.e., the reduction of pressure to the point of producing gas bubbles within the water. Cavitation of an organism's body fluids was thought to be an important mechanism of fish kill possible from the underground nuclear tests (Fig. 9). The observed effects of the Milrow and Cannikin events were evaluated with this background of direct and habitat-associated effects.

An underground nuclear test (Long Shot, Oct. 29, 1965) of 80 kt at Amchitka Island occurred prior to our investigations. A group of biologists from several organizations conducted surveys and experiments to evaluate the impact of this test on the fauna of Amchitka. Seymour and Nakatani (1967) reported no fish killed in live-boxes in the ocean as close as 1.6 km (Cyril Cove) to Long Shot surface zero (SZ).‡ The only dead fishes observed were two Pacific cod in the waters off Cyril Cove. On the basis of the live-box experiments and the observed fish kill, the damage to fish life caused by Long Shot was judged insignificant (Seymour and Nakatani, 1967).

Fig. 9—Aerial photograph of marine waters surrounding test site during Milrow test, Oct. 2, 1969, approximately 1.5 sec after the detonation. Note white water areas which are regions of cavitation caused by shock wave produced by the underground nuclear detonation. (Photograph courtesy of Edgerton, Germeshausen and Grier, Inc.)

With the background of the Long Shot experience, in the summer of 1967 FRI began studies at Amchitka, including base-line surveys of existing fish populations for pretest and posttest comparisons of species composition and abundance of fishes, and live-box experiments were conducted at Milrow test time. Surveys continued after the 1969 Milrow test through the period of preparation for the Cannikin test in 1971 and continued thereafter until the spring of 1973.

Nakatani and Burgner (1974) and Isakson (1974) have reported on the impact of the Milrow and Cannikin tests on the overall marine environment. Burgner, Isakson, and Lebednik (1971b) summarized the impact of the Milrow test on Amchitka's marine environment, including fishes. We repeat the major findings below.

Milrow. Fish surveys were conducted both inshore and offshore before and after the Milrow test. Studies were concentrated on the Rifle Range Point–Duck Cove area (Fig. 1). Analysis of the catch-per-unit effort (fish per hour) before and after the test for all gear types used revealed no significant or marked changes in fish abundance offshore or inshore (Burgner et al., 1971a).

Immediately prior to the test, three pairs (six total) of live-boxes containing rock greenling and

*Possessing no pneumatic duct between the gas bladder and the alimentary canal.

†Possessing an open pneumatic duct between the gas bladder and the alimentary canal.

‡That place at the island's surface where the emplacement hole was started.

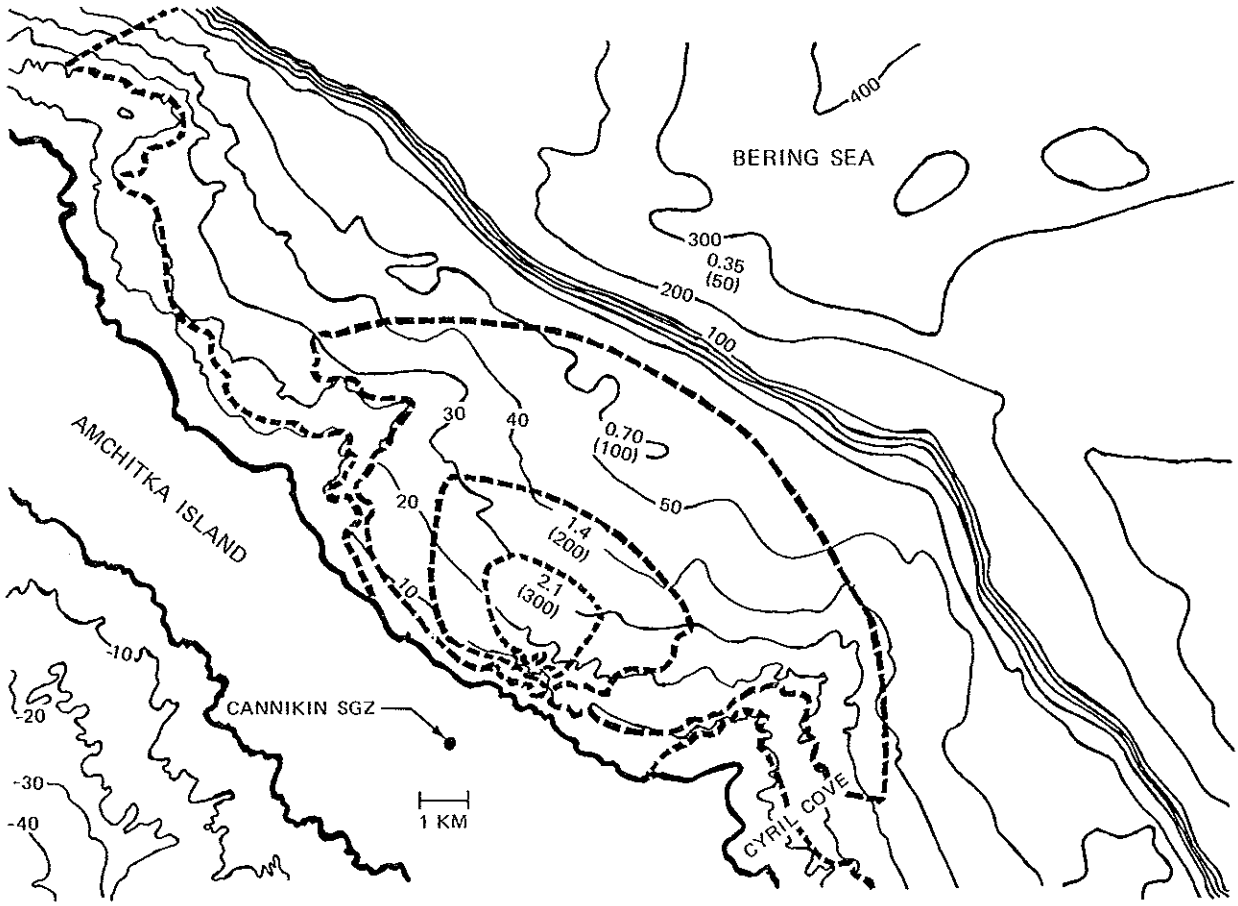


Fig. 10a—Predicted overpressure [in megapascals (pounds per square inch)] at bottom in Bering Sea adjacent to Cannikin SZ.

red Irish lord were placed in Duck Cove at distances from 2.6 to 4.0 km (8,500 to 13,000 ft) from Milrow SZ. These fishes were exposed to overpressures of 0.59 to 1.17 MPa (85 to 170 psi), underpressures of about −0.57 MPa (−83 psi), and accelerations of 2.5 to 5 *g* (Merritt, 1970; 1973). Other than two rock greenling, which apparently escaped, all fishes in the live-boxes survived. After the test these fishes were held for 4 weeks in seawater tanks and then released, no further or delayed injuries having been noted.

Three hours after the test, from a helicopter three unidentified and apparently injured fishes were seen thrashing on the ocean surface, two off Rifle Range Point, about 1.9 km (1.2 miles) southwest of Milrow SZ, and one off Crown Reefer Point, about 5.6 km (3.5 miles) north of Milrow SZ. These fishes could not be collected because the helicopter could not safely land. No other dead or injured fishes were seen during the posttest beach surveys.

Only rock greenling and red Irish lord were placed in the test-time live-boxes because they were the only species that survived the rigors of capture for the Milrow holding experiments. The three injured fishes seen after the test may have been Pacific cod or rockfish, which possess gas bladders.

No accurate estimate of fish kill by Milrow is possible from such insufficient information. We believe there may have been a small kill of marine fishes, but it could have had little impact because it was not detectable in pretest and posttest comparisons. Indirect effects related to disruption of marine fish habitat were not detected.

Cannikin. After Milrow, sampling effort was shifted to the Bering Sea adjacent to Cannikin SZ. Locations ranged from Petrel Point to Crown Reefer Point and also included a second area adjacent to Kirilof Point and Kirilof Bay.

The sampling design included both test-time live-box experiments and pretest and posttest surveys in the areas where fishes were thought most vulnerable to pressure changes. Sampling and live-box positions were established with the use of maps of peak water-pressure changes (Figs. 10a and 10b) predicted to occur during the test. The theory

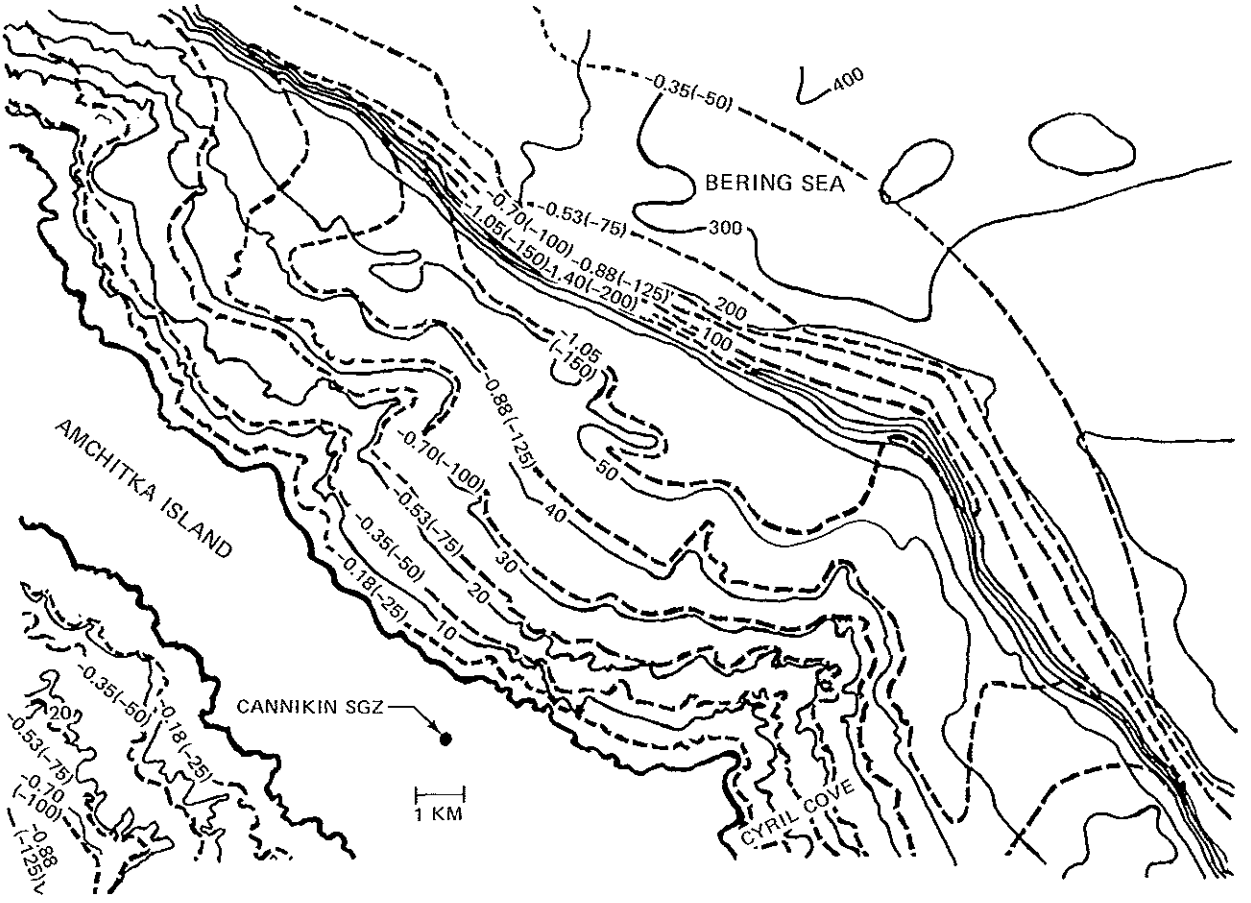


Fig. 10b—Predicted underpressure [in megapascals (pounds per square inch)] at the bottom in Bering Sea adjacent to Cannikin SZ.

and calculations behind these predictions resulted from the Milrow pressure–time data (Merritt, 1970; 1973; 1974; personal communication, 1971).

A severe storm, with winds of 110 km/hr, gusting to over 150 km/hr, throughout the day and night before the Cannikin test resulted in heavy seas, which prevented the placement of live-boxes as planned (Nakatani, Isakson, and Burgner, 1973, Appendix B; Isakson, 1974). Instead, 7.5 hr before the test a single live-box string was placed in 18-m(60-ft)-deep water in Constantine Harbor about 15 km (9 miles) from Cannikin SZ. A live-box at 16-m (52-ft) depth contained six rock greenling, four Pacific cod, three Pacific halibut, two red Irish lord, one rock sole, one great sculpin, and one dusky rockfish. Another live-box at 2-m (7-ft) depth contained 10 rock greenling and 6 Pacific cod. Three hours after the test, only one fish, a 67-cm (26 in.) Pacific cod, showed any abnormality, a "bubble" in the right eye and difficulty in equilibrium maintenance. Because no similar problems were seen in the other fishes, it was assumed that these symptoms were the result of handling, possibly during cage retrieval, rather than a test effect. All experimental fishes and control fishes were held for 8 days after the test, and no delayed mortalities or injuries were noted in the experimental fishes.

Immediately after the test, no dead or injured fishes were seen from a helicopter or from a ship. However, viewing was poor because of heavy seas.

Beginning about 4 hr after Cannikin and during daylight hours for 3 days after the test, biologists from several organizations surveyed the Bering Sea and Pacific Ocean coasts adjacent to the Cannikin SZ area. The areas surveyed and the fishes recovered are shown in Fig. 11. Almost all the dead fishes found were stranded on tidal benches or beaches uplifted as much as a meter. Otherwise, owing to the northwesterly winds prevailing during the test, fishes washed up on the shore were found mostly on the Pacific Ocean side of Amchitka.

Of the 295 fishes recovered during beach walks, the majority (277) were rock greenling that were stranded on uplifted intertidal benches and washed into coves on sand and cobble beaches. Autopsies by Dr. Robert Rausch (U. S. Public Health Service,

Alaska) of 23 rock greenling revealed that about half had hemorrhaged or sustained other damage in the brain cavity and/or the viscera as the result of water-pressure changes, acceleration while over the littoral bench, or in struggling once the beach had lifted.* The other autopsied rock greenling exhibited no noticeable injury.

The Pacific sandfish were found stranded in uplifted sandy beach areas and in drift zones of Sand Beach Cove (Fig. 11). This species commonly burrows upright in the sand of the littoral zone, and the fish were probably stranded there by the beach uplift during the test. Since longnose lancetfish are often washed ashore after storms, the one specimen found after Cannikin is assumed to be a result of the pretest storm and not the test.

The remains of Pacific cod and rockfish found on the Pacific shore had been stripped nearly to skeletons by amphipods. Because both of these fish species are physoclistous, they were probably killed by water-pressure changes, and a portion of those which surfaced were blown onto the shore. Cannikin being nearer the Bering Sea, greater pressure changes (both in magnitude and in area) were predicted there than in the Pacific Ocean (Figs. 10a and 10b), which implies that cod and rockfish should have been recovered off the Bering Sea coast but were not as a result of wind direction.

The only other marine fish recovered dead after the test was a dusky rockfish taken 3 days after the test in a bottom trawl (Fig. 11, haul No. 33) at 40 m (22 fm) in the Bering Sea about 6 km (4 miles) from Cannikin SZ. One expects fish captured by trawl to be killed or badly injured, but pale gills, pale external coloration, and amphipod predation indicated that this fish had been dead for some time. The recovery of this one individual suggests that other fishes killed by Cannikin also sank to the bottom, which further reduces the fraction of fish recovered.

Echo-sounding traces from along the Bering Sea coastline adjacent to Cannikin SZ indicated that the large schools of fish (probably rockfish and Pacific cod) normally present around submarine pinnacles before the test were not present afterward. Unfortunately these observations cannot be translated into quantitative estimates of fish kill and only represent general impressions.

Offshore, only the bottom trawl catches of rock sole declined significantly when actual or expected† posttest data were directly compared to pretest data for the same areas. The geometric mean catch of rock sole (average catch depth) significantly (t-test statistic, 2.52) declined from about 100 fish per hour pretest to a mean catch of about 31 fish per hour posttest. [See Nakatani et al. (1973) for further explanation of statistical catch comparisons.] Differences between Pacific halibut and total bottom trawl catches were statistically insignificant. Declines were observed for salmon species, Pacific cod, rockfishes (*Sebastes*), and midwater fishes, but occurrence and abundance of these species in the catches were too low to permit statistically valid comparisons of pretest and posttest catches. No decrease in catch of the more vulnerable physoclistous species (Pacific cod and rockfishes) was detected by this method, although the facts of dead cod having been found on the Pacific Ocean shore and greater pressure changes being expected on the Bering Sea side imply that some decrease might have been expected. This species is not a dominant of the fish community in the sampling area, however.

We estimate the size of the marine fish kill from Cannikin to be in the thousands (Kirkwood and Fuller, 1972), but such an estimate can be little more than a guess with the data collected. Even such an impact as this offshore fish kill on the marine environment was relatively small, highly localized, and short termed. Bottom trawl catches of rock sole about 1 year after the test (August–September 1972) equaled pretest catches. Repopulation was probably by immigration of adjacent rock sole populations into the affected region.

Concurrent with the November 1971 offshore fish-sampling program after Cannikin, nearshore fish sampling with trammel nets focused on rock greenling, which were observed killed in large numbers (277) by Cannikin. Net sets were short (less than 5 hr) during posttest sampling because of weather; thus many of the longer pretest sets could not be compared. The results of the pretest and posttest sampling for rock greenling, including the continuing effort through October 1972, are shown in Fig. 12. The short sets in November showed that there was a marked temporary decline in abundance of rock greenling from about 10 fish per hour to about 4 fish per hour. The two sets made in April 1972 averaged about 7 rock greenling per hour. Repopulation approached pretest

*Uplifts were as great as 1.1 m (3.6 ft) and accelerations as great as 10 *g* (Merritt, 1973).

†The data, transformed to the number of individual fishes caught per hour, were corrected to the mean pretest sampling depth [70.5 m (230 ft)] according to a positive relationship between catch (rock sole, Pacific halibut, and total catch) and sampling depth.

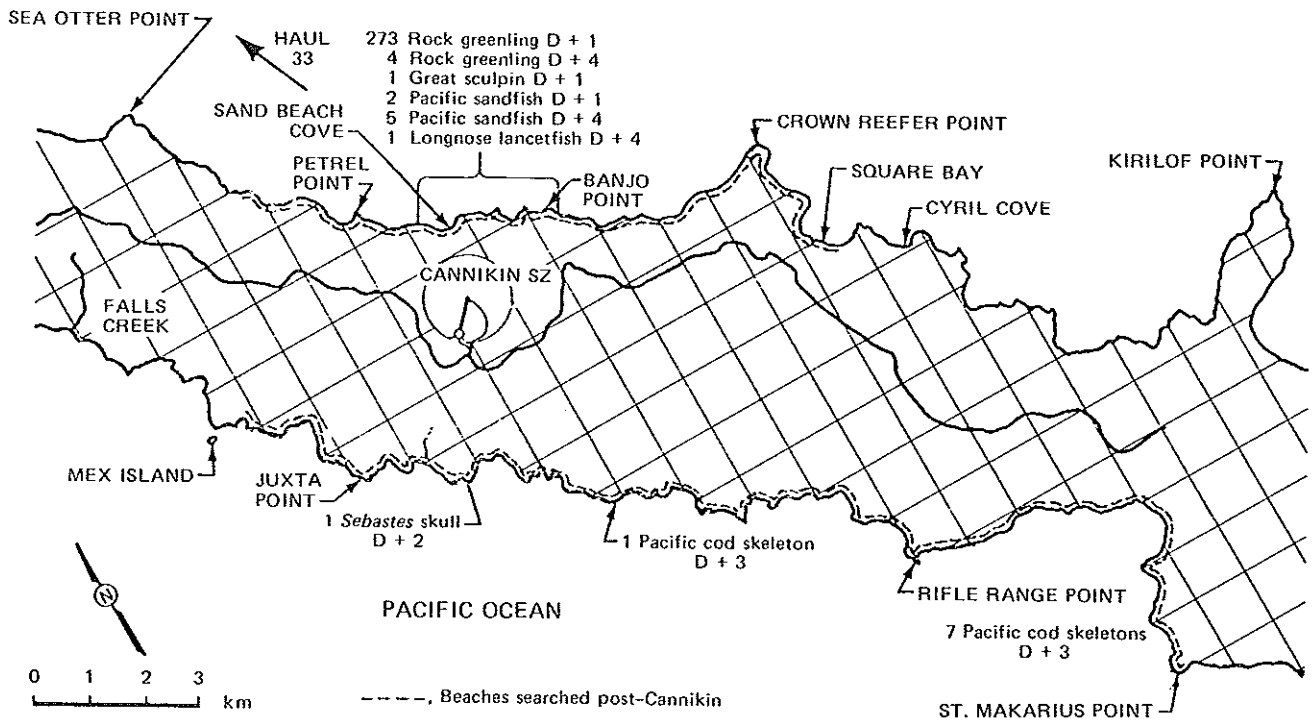


Fig. 11—Beaches searched post-Cannikin and locations of dead, injured, and stranded fishes and skeletons of fishes recovered from marine areas post-Cannikin. D+3 is 3 days after Cannikin. A 1000-m UTM grid is shown.

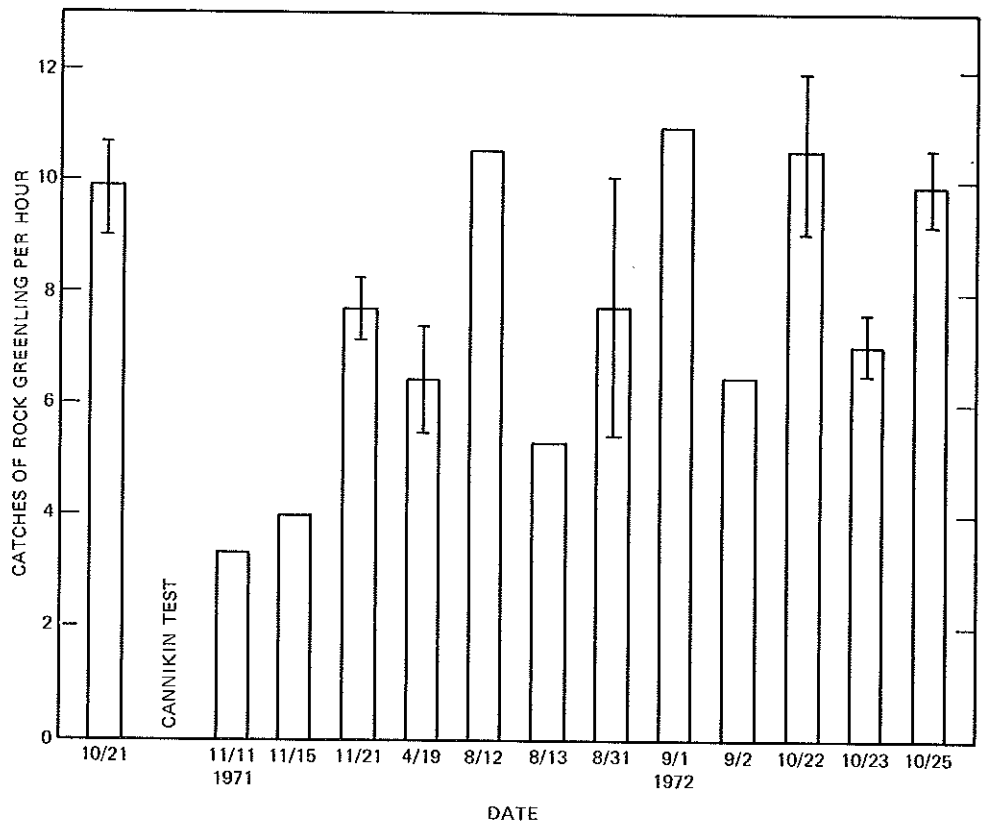


Fig. 12—Trammel net catches of rock greenling per hour, for short (<5 hr) sets in inshore/rock–algae fish community adjacent to intertidal sites IA-2 and IA-3, August 1971 through October 1972. A range is indicated where more than one set was made on a given day.

levels by fall 1972 when catches averaged about 8.5 rock greenling per hour (Fig. 12). As with the offshore rock sole, rock greenling repopulation was most likely by the immigration of rock greenling from nearby unaffected nearshore waters.

Finally, two anomalies were noted in the species composition in trammel net catches in the inshore fish communities before and after Cannikin. In the inshore/rock–algae community, four species (searcher, great sculpin, Pacific halibut, and Alaskan ronquil) were not captured after Cannikin; a few individuals of each of these species had been caught before. In the inshore/sand–gravel community, two species (Atka mackerel and dusky rockfish) were caught before but not after Cannikin. In both cases, considering seasonal differences, differences in the duration of sets, and the infrequent occurrence of these species in the area, the species composition and abundance are comparable (Nakatani and Burgner, 1974).

Summary of Impacts on Marine Fishes

In review, the data available from Cannikin experiments and observations do not permit precise quantification of the impact of that test on marine fish communities. Cannikin had both direct and indirect impacts on marine fishes inhabiting the Bering Sea littoral bench, which was uplifted during the test. These areas have been denied for some time, perhaps forever, as habitat for marine fishes, both those which are resident members of the community and those of adjacent communities which use the bench for feeding at high tide, e.g., the rock greenling. A precise quantitative assessment of fishes actually killed during the uplifting cannot be made with the data available; however, hundreds of dead fish were collected, which implies a significant short-term impact.

The direct impacts observed after Cannikin were not fully expected (Fig. 11). The majority of the dead fishes recovered were found on or near the uplifted Bering Sea littoral bench or along the Pacific Ocean coastline. One trawl in the Bering Sea, 6 km (4 miles) from Cannikin SZ, captured a dead rockfish, a significant datum since we have never before, in over 4 years of trawling about Amchitka, encountered an obviously dead fish in our catches. Comparison between pretest and posttest catches in the Bering Sea off Cannikin SZ showed marked declines in rock sole in offshore otter trawl hauls and rock greenling in inshore trammel net catches. These two species of fish recovered to pretest levels within a year after the test.

From these observations we conclude that Cannikin had a significant short-term prompt impact on Bering Sea and Pacific Ocean marine fishes within a 6-km (4-mile) radius of the test site. Complete detectable recovery of these populations, probably by immigration from unaffected areas, occurred after 1 year. Because of adverse weather conditions and the tendency for dead fishes to sink, few dead fish (Pacific cod and rockfish species) were recovered after the test, but the implications of our other data are that marine fishes numbering in the order of thousands were killed in the vicinity of Cannikin SZ. Although this may seem a major impact, its significance to the marine ecosystem of Amchitka Island must be considered as minor, especially when there was a documented recovery within a year or less.

The uplifting of a section of the littoral bench and consequent loss of habitat had only a slight indirect impact on inshore marine fishes. The uplifted area no longer available to these fishes is but a small percentage of the total littoral habitat of Amchitka. Again, as with fish kills, this impact was confined to the Cannikin SZ vicinity.

SUMMARY

Research on the marine fishes in the seas around Amchitka Island was conducted over a 7-year period, the primary objective being to evaluate the prompt and long-term impacts of nuclear testing on marine fish populations. Despite the mission-oriented nature of this research, which imposed some restraints on the scope of the investigations, the studies have led to new understandings of the role of the Amchitka marine fish fauna in the structure and functioning of the marine ecosystem surrounding the island. Information collected on the 92 fish species taken from marine waters around Amchitka has significantly expanded knowledge of Aleutian ichthyofauna. Collections demonstrated the presence at Amchitka of several fish species not previously reported beyond the eastern part of the North Pacific. The new information reinforces the concept of an Aleutian "filter bridge," which was suggested earlier by Wilimovsky (1964) and others. The Alaska Stream apparently serves both as the primary dispersal mechanism for pelagic eggs, larvae, and juveniles of indigenous fishes and as a barrier to eastward expansion of western Pacific species. However, this barrier is not an absolute one because we have tentatively identified larvae of typically Asiatic species in collections made off Amchitka. We can only speculate about possible exclusion mechanisms responsible for the occurrence of only larval forms of these species in the vicinity of Amchitka.

The structure of seven fish communities associated with specific epipelagic, midwater, and bottom habitats has been characterized in relatively broad and subjective terms. Recurrent group analysis of the data identified 13 species associations in five of the communities and provided additional understanding of the internal structure of the species groupings, especially with respect to some significant relationships between midwater predator species and their invertebrate prey.

Our sampling methods were not sufficiently precise to detect any statistically significant changes in community composition during the 7-year collection period. However, catch data revealed what appeared to be one population shift of considerable interest, which occurred after an intensive harvesting of Pacific ocean perch near Amchitka by foreign fisheries in the late 1960s. Following this intensive fishing effort, there appeared to have been a reversal of dominance in the demersal Pacific ocean perch—walleye pollock association, with walleye pollock becoming the dominant member of the assemblage.

Our studies indicate that the algae-based detritus component of the inshore marine ecosystem is largely responsible for the structure and energy flow in the food web of that ecosystem. Results of stomach analyses of fishes suggest that the extremely high densities of epipelagic crustaceans that use this food base (amphipods and mysids) support a large standing crop of benthipelagic-feeding fishes, most notably rock greenling and Atka mackerel. The whole question of the stability of this particular food-web structure takes on new dimensions when the role of the top carnivore of the system, the sea otter, in regulating herbivore populations is realized (Palmisano and Estes, Chap. 22, this volume).

As a major prey organism of nearshore fishes, the Pacific sand lance was second only to amphipods in the number of identified food-web links to inshore predators. Although we were unable to evaluate fully the abundance of the Pacific sand lance, we consider that the role of this planktivorous fish in importing biomass from offshore waters into the inshore ecosystem is an important feature of the inshore portion of the marine food web.

The effects of the underground nuclear testing program were very difficult to evaluate, but our efforts in documenting the impact of pressure pulses and shock waves on Amchitka marine fishes have contributed to the limited knowledge of the prompt effects of such perturbations on aquatic organisms. Bottom pressure changes of 300 psi over and 200 psi under ambient pressures in a shock wave of 10 to 15 Hz coupled with bulk cavitation of the marine waters in a relatively small area adjacent to the Cannikin test site resulted in the death of large numbers of several species of fish in offshore waters. This conclusion was based on an observed posttest decline in catches of rock sole, a fish that theoretically, by its lack of an air bladder, should be little affected by such pressure changes. Populations of more susceptible species, such as Pacific cod and several rockfish species, were assumed to have been affected also, although direct evidence to support this assumption is meager. A year after the test, catches of rock sole equaled pretest catches; reestablishment of the population was probably by immigration from nearby unaffected stocks.

In the littoral environment, catches of rock greenling declined sharply in Bering Sea waters adjacent to the Cannikin site immediately posttest. The decline was attributed to a substantial kill of rock greenling in the area resulting from a combination of forces generated by the Cannikin detonation. Catches posttest indicated that the affected population had begun to recover within 2 weeks after the detonation and had fully recovered by fall of the next year. Recovery was judged to have been by immigration of greenling from stocks outside the affected area.

Although both offshore and inshore fish populations in waters adjacent to the Amchitka test sites were adversely affected by the nuclear detonations, especially by the Cannikin test, the changes were short-term. Within a year after the Cannikin detonation, no effects on fish populations were detectable. Since the total area of marine habitat affected by the tests was such a small fraction of the total habitat around the island, the overall effect of the tests on the Amchitka marine ecosystem should be considered transitory and insignificant.

REFERENCES

Abakumov, V. A., 1964, On the Oceanic Period in the Life Cycle of the Lamprey *Entosphenus tridentatus* (Richardson), in Soviet Fisheries Investigations in the Northeast Pacific, Part II, translated from *Tr. Vses. Nauch.–Issled. Inst. Morsk. Ryb. Khoz. Okeanogr.*, Vol. 49, by Israel Program for Scientific Translations, TT67-51204, pp. 268-270.

Allen, G. H., 1956a, Food of Salmonid Fishes of the North Pacific Ocean. a. Food of Sockeye Salmon *(O. nerka)*, University of Washington, Department of Oceanography, Collection and Analysis of Oceanographic Data from the North Pacific Ocean, Fishery Report No. 1.

——, 1956b, Food of Salmonid Fishes of the North Pacific Ocean. b. Food of Chum Salmon *(O. keta)* (with Notes on the Food of Sockeye and Pink Salmon), University of Washington, Department of Oceanography, Collec-

tion and Analysis of Oceanographic Data from the North Pacific Ocean, Fishery Report No. 2.

American Fisheries Society, 1970, *A List of Common and Scientific Names of Fishes from the United States and Canada*, 3rd ed., Spec. Publ. No. 6.

Andrievskaia, L. D., 1957, [The Food of Pacific Salmon in the Northwestern Pacific Ocean.] Materialy po Biologii Morskogo Perioda Zhizni Dal'nevostochnykh Lososei, pp. 64-75, translated from *Tr. Vses. Nauch.–Issled. Inst. Morsk. Ryb. Khoz. Okeanogr.*, Fisheries Research Board of Canada Translation No. 182.

Andriyashev, A. P., 1954, Fishes of the Northern Seas of the USSR, translated from *Zool. Inst. USSR Acad. Sci.*, No. 53, by Israel Program for Scientific Translations, TT63-11160, 1964.

Bean, T. H., 1882a, Descriptions of New Fishes from Alaska and Siberia, *Proc. U. S. Natl. Mus.*, IV: 144-159.

——, 1882b, A Preliminary Catalogue of the Fishes of Alaska and Adjacent Waters, *Proc. U. S. Natl. Mus.*, IV: 230-272.

Burgner, R. L., and R. E. Nakatani, 1972, Amchitka Bioenvironmental Program. Research Program on Marine Ecology, Amchitka Island, Alaska, Annual Progress Report, July 1, 1970–June 30, 1971, USAEC Report BMI-171-144, Battelle Memorial Institute.

——, et al., 1971a, Amchitka Bioenvironmental Program. Research Program on Marine Ecology, Amchitka Island, Alaska, Annual Progress Report, July 1, 1969–June 30, 1970, USAEC Report BMI-171-137, Battelle Memorial Institute.

——, J. S. Isakson, and P. A. Lebednik, 1971b, Observations on the Effect of the Milrow Nuclear Test on Marine Organisms at Amchitka, *BioScience*, 21(12): 671-673.

——, et al., 1969, Amchitka Bioenvironmental Program. Research Program on Marine Ecology and Oceanography, Amchitka Island, Alaska, Annual Progress Report, July 1, 1968–June 30, 1969, USAEC Report BMI-171-128, Battelle Memorial Institute.

Chikuni, S., 1975, *Biological Study on the Population of the Pacific Ocean Perch in the North Pacific*, Far Seas Fisheries Research Laboratory, Bulletin No. 12.

Clemens, W. A., and G. V. Wilby, 1961, *Fishes of the Pacific Coast of Canada*, Fisheries Research Board of Canada, Bulletin 68 (second edition).

Cody, M. L., 1968, On the Methods of Resource Division in Grassland Bird Communities, *Amer. Natur.*, 102: 107-147.

Dall, W. H., 1877, On Succession in the Shell-Heaps of the Aleutian Islands, in *Tribes of the Extreme Northwest*, W. H. Dall, J. Furuhelm, and George Gibbs, Contributions to North American Ethnology, Vol. 1, pp. 41-91, U. S. Geographical and Geological Survey.

——, 1874, Explorations on the Western Coast of North America, Annual Report to the Board of Regents, Smithsonian Institution, pp. 417-418.

Dayton, P. K., 1972, Toward an Understanding of Community Resilience and the Potential Effects of Enrichments to the Benthos at McMurdo Sound, Antarctica, in *Proceedings of the Colloquium on Conservation Problems in Antarctica*, B. C. Parker (Ed.), pp. 81-95, Allen Press.

Evermann, B. W., and E. L. Goldsborough, 1907, The Fishes of Alaska, *Bull. U. S. Bur. Fish.*, 26: 219-360.

Fager, E. W., 1957, Determination and Analysis of Recurrent Groups, *Ecology*, 38(4): 586-595.

Foerster, R. E., 1968, *The Sockeye Salmon, Oncorhynchus nerka*, Fisheries Research Board of Canada, Bulletin 162.

Gilbert, C. H., 1895, The Ichthyological Collections of the Steamer *Albatross* During the Years 1890 and 1891, U. S. Commission on Fish and Fisheries, Report of the Commissioner for the Year Ending June 30, 1893, Part 19, pp. 393-476.

Gorbunova, V. N., 1962, Spawning and Development of Greenlings (Family Hexagrammidae), in Greenlings—Taxonomy, Biology, Interoceanic Transplantation, T. S. Rass (Ed.), pp. 121-183, translated from *Acad. Sci. USSR, Trans. Inst. Oceanol.*, Vol. 59, by Israel Program for Scientific Translations, 1970.

Gordeeva, K. T., 1954, Pitanie Paltusov v Beringovom More (Food of Halibut in the Bering Sea), *Izv. TINRO*, Vol. 39.

Greenwood, P. H., D. E. Rosen, S. H. Weitzman, and G. S. Myers, 1966, Phyletic Studies of Teleostean Fishes, with a Provisional Classification of Living Forms, *Bull. Amer. Mus. Natl. Hist.*, 131(4): 341-955.

Guryanova, E. F., 1935, The Commander Islands and Their Marine Littoral Fauna and Flora, *Priroda*, 11: 64-72.

Haedrich, K. Z., and J. G. Nielson, 1966, Fishes Eaten by *Alepisaurus* (Pisces, Iniomi) in the Southeastern Pacific Ocean, *Deep-Sea Res.*, 13: 909-919.

Haedrich, R. L., 1964, Food Habits and Young Stages on North Atlantic *Alepisaurus* (Pisces, Iniomi), *Breviora*, No. 201.

Hart, John L., 1973, *Pacific Fishes of Canada*, Fisheries Research Board of Canada, Bulletin 180.

Hartt, A. C., 1966, *Migrations of Salmon in the North Pacific Ocean and Bering Sea as Determined by Seining and Tagging, 1959–1960*, International North Pacific Fisheries Commission, Bulletin 19.

Isakson, J. S., 1974, Biological Effects of Underground Nuclear Testing on Marine Organisms. II. Observed Effects on Amchitka Island, Alaska, in Proceedings of the First Conference on the Environmental Effects of Explosives and Explosions, White Oak, Md., May 30–31, 1973, George A. Young (Comp.), Report NOLTR-73-223, pp. 98-106, Naval Ordnance Laboratory.

——, C. A. Simenstad, and R. L. Burgner, 1971, Fish Communities and Food Chains in the Amchitka Area, *BioScience*, 21(12): 666-670.

Jochelson, W., 1925, *Archaeological Investigations in the Aleutian Islands*, Publication No. 367, Carnegie Institution of Washington.

Jordan, D. S., and C. H. Gilbert, 1899, The Fishes of the Bering Sea, in The Fur Seals and Fur-Seal Islands of the North Pacific Ocean, Part 3, pp. 433-492.

——, and C. H. Gilbert, 1883, Synopsis of the Fishes of North America, *Bull. U.S. Natl. Mus.*, 16: 1-1018.

——, and E. D. Starks, 1904, A Review of the Cottidae or Sculpins Found in the Waters of Japan, *Proc. U.S. Natl. Mus.*, 27: 231-335.

Kenyon, K. W., 1969, *The Sea Otter in the Eastern Pacific Ocean*, U. S. Department of the Interior, Bureau of Sport Fisheries and Wildlife, North American Fauna, No. 68.

Kirkwood, J. B., 1970, Amchitka Bioenvironmental Program. Bioenvironmental Safety Studies, Amchitka Island, Alaska, Milrow D+2 Months Report, USAEC Report BMI-171-126, Battelle Memorial Institute.

——, and R. G. Fuller (Comps.), 1972, Amchitka Bioenvironmental Program. Bioenvironmental Safety Studies, Amchitka Island, Alaska, Cannikin D+2 Months Report, USAEC Report BMI-171-147, Battelle Memorial Institute.

——, and R. G. Fuller, 1971, Amchitka Bioenvironmental Program. Bioenvironmental-Effects Predictions for the Proposed Cannikin Underground Nuclear Detonation at Amchitka Island, Alaska, USAEC Report BMI-171-141, Battelle Memorial Institute.

Le Brasseur, R. J., 1959, Marine Ecology of Pacific Salmon. A. A Description of the Food, Fisheries Research Board of Canada, Biology Station, Nanaimo, B.C.

Lensink, C. J., 1962, The History and Status of Sea Otters in Alaska, Ph. D. Thesis, Purdue University, Xerox University Microfilms, Ann Arbor, Mich.

Lyubimova, T. G., 1963, Basic Aspects of the Biology and Distribution of Pacific Rockfish (*Sebastodes alutus* Gilbert) in the Gulf of Alaska, in Soviet Fisheries Investigations in the Northeast Pacific, Part I, P. A. Moiseev (Ed.), pp. 308-318, *Tr. Vses. Nauch.--Issled. Inst. Morsk. Ryb. Khoz. Okeanogr.*, Vol. 48.

MacArthur, R. H., and J. W. MacArthur, 1961, On Bird Species Diversity, *Ecology*, 42: 594-598.

Makarova, R. V., 1975, *Russians on the Pacific, 1743–1799* (translated and edited from the 1968 Russian original by R. A. Pierce and A. S. Donnelly), Limestone Press, Kingston, Ontario (Materials for the Study of Alaska History, No. 6).

McAlister, W. B., 1971, Oceanography in the Vicinity of Amchitka Island, Alaska, *BioScience*, 21(12): 646-651.

McCann, J. A., 1963, A Summary of Biological Field Work done on Amchitka Island, Aleutian Islands National Wildlife Refuge, Cold Bay, Alaska, unpublished.

Merritt, M. L., 1974, Characteristics of Shock Waves in Water Near Underground Explosions, in Proceedings of the First Conference on the Environmental Effects of Explosives and Explosions, White Oak, Md., May 30–31, 1973, George A. Young (Comp.), Report NOLTR-73-223, pp. 78-85, Naval Ordnance Laboratory.

——, 1973, Pressures in Water on and Near Amchitka Island, Milrow and Cannikin, USAEC Report SC-RR-720547, Sandia Laboratories.

——, 1970, Physical and Biological Effects: Milrow Event, USAEC Report NVO-79, Nevada Operations Office.

Murie, O. J., 1940, Notes on the Sea Otter, *J. Mammalogy*, 21(2): 119-131.

Nakatani, R. E., and R. L. Burgner, 1974, Amchitka Bioenvironmental Program. Research Program on Marine Ecology, Amchitka Island, Alaska, Annual Progress Report, July 1972 Through September 1973, and Summary Report, 1967 Through 1973, USAEC Report BMI-171-156, Battelle Memorial Institute.

——, J. S. Isakson, and R. L. Burgner, 1973, Amchitka Bioenvironmental Program. Research Program on Marine Ecology, Amchitka Island, Alaska, Annual Progress Report, July 1, 1971–June 30, 1972, USAEC Report BMI-171-150, Battelle Memorial Institute.

Nelson, E. W., 1887, Field Notes on Alaska Fishes, with Additional Notes by Tarleton H. Bean, in *Report Upon Natural History Collections made in Alaska Between the Years 1877 and 1881*, Henry W. Henshaw (Ed.), pp. 295-322, Arctic Series Publications No. 3 Issued in Connection with the Signal Service, U. S. Army.

Novikov, N. P., 1964, Basic Elements of the Biology of the Pacific Halibut (*Hippoglossus hippoglossus stenolepis* Schmidt) in the Bering Sea, in *Soviet Fisheries Investigations in the Northeast Pacific*, Part II, Vol. 19, pp. 175-219.

Orians, G. H., 1969, The Number of Bird Species in Some Tropical Forests, *Ecology*, 50: 783-801.

Paine, R. T., 1969, A Note on Trophic Complexity and Community Stability, *Amer. Natur.*, 103: 91-93.

Pallas, P. S., 1811–1842, Zoographia Rosso-Asiatica, Sistens Omnium Animalium in Extenso Imperio Rossico et Adjacentibus Maribus Observatorum Recensionem, Domicilia, Mores et Descriptiones Anatomen Atque Icones Plurimorum, 3 Vols., St. Petersburg.

Paraketsov, I. A., 1963, On the Biology of *Sebastodes alutus* of the Bering Sea, in Soviet Fisheries Investigations in the Northeast Pacific, Part I, P. A. Moiseev (Ed.), pp. 319-327, *Tr. Vses. Nauch.--Issled. Inst. Morsk. Ryb. Khoz. Okeanogr.*, Vol. 48.

Parin, N. U., K. N. Nesis, and M. Ye. Vinogradov, 1968, Data on the Feeding of *Alepisaurus* in the Indian Ocean, Problems in Ichthyology, pp. 418-427.

Pulliam, H. R., 1974, On the Theory of Optimal Diets, *Amer. Natur.*, 108(959): 59-74.

Quast, J. C., and E. L. Hall, 1972, List of Fishes of Alaska and Adjacent Waters with a Guide to some of Their Literature, NOAA Technical Report NMFS SSRF-658.

Rapport, D. J., 1971, An Optimization Model of Food Selection, *Amer. Natur.*, 105: 575-587.

Scheffer, V. B., 1959, Invertebrates and Fishes Collected in the Aleutians, 1936–1938, in *Fauna of the Aleutian Islands and Alaska Peninsula*, Olaus J. Murie, pp. 365-406, with Notes on Invertebrates and Fishes Collected in the Aleutians, 1936–1938, U. S. Department of the Interior, Bureau of Sport Fisheries and Wildlife, North American Fauna, No. 61.

Schoener, T. W., 1971, Theory of Feeding Strategies, *Annu. Rev. Ecol. Syst.*, 2: 369-404.

——, 1969, Optimal Size and Specialization in Constant and Fluctuating Environments: An Energy–Time Approach, in Symposium on Diversity and Stability in Ecological Systems, Upton, N. Y., May 26–28, 1969, USAEC Report BNL-50175, pp. 103-144, Brookhaven National Laboratory.

Schultz, Leonard P., 1939, A New Genus and Two New Species of Cottoid Fishes from the Aleutian Islands, *Proc. U. S. Natl. Mus.*, 85(3038): 187-191.

Seymour, A. H., and R. E. Nakatani, 1967, Long Shot Bioenvironmental Safety Program, Final Report, USAEC Report TID-24291, University of Washington.

Shmidt, P. U., 1904, *Pisces Marium Orientalium*, St. Petersburg.

Shubnikov, D. A., and L. A. Lisovenko, 1964, Data on the Biology of Rock Sole of the Southeastern Bering Sea, in Soviet Fisheries Investigations in the Northeast Pacific, Part II, P. A. Moiseev (Ed.), pp. 220-226, *Tr. Vses. Nauch.–Issled. Inst. Morsk. Ryb. Khoz. Okeanogr.*, Vol. 49.

Simenstad, C. A., 1974, Biological Effects of Underground Nuclear Testing on Marine Organisms. I. Review of Documented Effects, Discussion of Mechanisms of Damage, and Predictions of Amchitka Test Effects, in Proceedings of the First Conference on the Environmental Effects of Explosives and Explosions, White Oak, Md., May 30–31, 1973, George A. Young (Comp.), Report NOLTR-73-223, pp. 86-97, Naval Ordnance Laboratory.

——, 1971a, The Feeding Ecology of the Rock Greenling, *Hexagrammos lagocephalus*, in the Inshore Waters of Amchitka Island, Alaska, M.S. Thesis, University of Washington.

——, 1971b, Biological Effects of Nuclear Test-Imposed Shock Waves on Marine Organisms in the Vicinity of Amchitka Island, Alaska, Fisheries Research Institute, University of Washington.

Skalkin, V. A., 1964, Diet of Rockfish in the Bering Sea, in Soviet Fisheries Investigations in the Northeast Pacific,

Part II, P. A. Moiseev (Ed.), pp. 159-174, *Tr. Vses. Nauch.–Issled. Inst. Morsk. Ryb. Khoz. Okeanogr.*, Vol. 49.

——, 1963, Diet of Flatfishes in the Southeastern Bering Sea, in Soviet Fisheries Investigations in the Northeast Pacific, Part I, P. A. Moiseev (Ed.), pp. 235-250, *Tr. Vses. Nauch.–Issled. Inst. Morsk. Ryb. Khoz. Okeanogr.*, Vol. 48.

Stejneger, L., 1936, *Georg Wilhelm Steller: The Pioneer of Alaskan Natural History*, Harvard University Press, Cambridge, Mass.

Synkova, A. N., 1951. [On the Food of Pacific Salmon in Kamchatka Waters], *Izv. TINRO*, 39: 105-121 (Fisheries Research Board Translation No. 415).

Tanner, Z. L., 1892–1896, Report Upon the Investigations of the U. S. Fish Commission Steamer *Albatross* for the Year Ending June 30 (1889–1894), U. S. Commission on Fish and Fisheries, Reports to the Commissioner for (1888–1894), Part XVI, pp. 395-512; Part XVIII, pp. 207-342; Part XIX, pp. 305-341; Part XX, pp. 197-278.

Turner, L. M., 1886, *Contributions to the Natural History of Alaska*, Results of Investigations Made Chiefly in the Yukon District and the Aleutian Islands; Conducted Under the Auspices of the Signal Service, United States Army, Extending from May 1860 to August 1881, Arctic Series Publications No. 2 Issued in Connection with the Signal Service, U. S. Army.

U. S. Bureau of Fisheries, 1907, Dredging and Hydrographic Records of the U. S. Fisheries Steamer *Albatross* for 1906, Bureau of Fisheries Document 621.

Whittaker, R. H., 1970, *Communities and Ecosystems*, The MacMillan Company, London.

Wilimovsky, N. J., 1964, Inshore Fish Fauna of the Aleutian Archipelago, in *Proceedings of the 14th Alaska Science Conference*, pp. 172-190.

——, 1958, Provisional Keys to the Fishes of Alaska, U. S. Fish and Wildlife Service, unpublished.

——, 1954, List of the Fishes of Alaska, *Stanford Ichth. Bull.*, 4(5): 279-294.

Williams, C. S., 1938, Notes on Food of the Sea Otter, *J. Mammalogy*, 19(1): 105-107.

Williamson, F. S. L., W. B. Emison, and C. M. White, 1972, Amchitka Bioenvironmental Program. Studies of the Avifauna on Amchitka Island, Alaska, Annual Progress Report, July 1, 1970–June 30, 1971, USAEC Report BMI-171-134, Battelle Memorial Institute.