The Distribution and Biogeography of *Zostera marina* (Eelgrass) in Alaska[1]

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Although innumerable botanists have visited Alaska to record and study its flora, most accounts terminate at the high-tide line. Consequently, the marine vegetation, especially that of the most northern coasts of Alaska, has received little attention and the distributions of many species are sketchily known. *Zostera marina* Linnaeus, the common eelgrass, has probably received more interest than most, because of its importance as a waterfowl food. In spite of this, the distribution outlined by Hultén (1941:95, 1960:69, 1964:256) and other published sources (Anderson, 1959:48; Porsild, 1932:90–94; Polunin, 1940:40–41; Setchell, 1920:563–579, 1935:560–577; Murie and Scheffer, 1959:396) is very incomplete in the light of recent surveys of the coast. By compiling the results of personal efforts and communications over the past few years, I can now document in detail the distribution of this species in Alaska.

An additional result of searching and studying the distribution of *Zostera* in Alaska has been a review of the mechanisms of dispersion that have established and maintained this distribution. These aspects of the study of *Zostera* have in turn led to considerations of the biogeography of the species which can be reconstructed from distribution records and dispersion mechanisms.

Distribution Survey

The genus *Zostera* contains 11 species of shallow-water, soft-bottom marine plants (Setchell, 1935). The most widespread species of the genus, *Zostera marina*, occurs discontinuously throughout the boreal Northern Hemisphere from the seas of Okhotsk and Japan to the Baltic and Mediterranean (Setchell, 1935: 571). On the Pacific coast of North America *Z. marina* extends from Port Clarence, 65° N (Porsild, 1932:90) to Agiabampo Lagoon, 26° N, in the Gulf of California (Steinbeck and Ricketts, 1941:254).

In Alaska, *Zostera* forms a distinct subtidal zone in protected bays, inlets, and lagoons along the coast from Bering Strait south (Hultén, 1941:95). During 1967 I was able to survey many miles of the Alaska coast to locate and examine the *Zostera* beds. These surveys included Southeast Alaska, Prince William Sound, the Cold Bay region of the Alaska Peninsula, parts of the Seward Peninsula near Nome and Teller, the coast of the Chukchi Sea between Kivalina and Cape Thompson, and the vicinity of Point Barrow. The observations from these field trips have been combined with the published records and personal observations of several people to present a detailed listing of the locations of *Zostera* beds on the coast of Alaska (Fig. 1 and Table 1).

In Southeast Alaska, the Alexander Archipelago, *Zostera* is found in most of the bays and inlets of the outer coast, but it is absent from many of these on the inside waters (Fig. 1 and Table 1). This is apparently due to the turbid effluent of glaciers. No plants were found in any of the areas receiving large amounts of glacial runoff although other environmental conditions appeared quite suitable for their growth. For example, in Doty Cove and Limestone Inlet in Stephens Passage (near Juneau) the absence of *Zostera* is enigmatic in winter months when ambient waters are clear; but in summer the problem is solved by the presence of very turbid water from nearby Taku Inlet. In bays and inlets receiving quantities of the turbid glacial water the subtidal zone of soft bottoms usually occupied by *Zostera* is devoid of all macrophytes.

The coast from Cross Sound to Prince William Sound is rugged and exposed to the open sea; most of the existing bays harbor glaciers or glacial streams. *Zostera* has been reported only in Yakutat Bay (Setchell, 1920:567; Fig.

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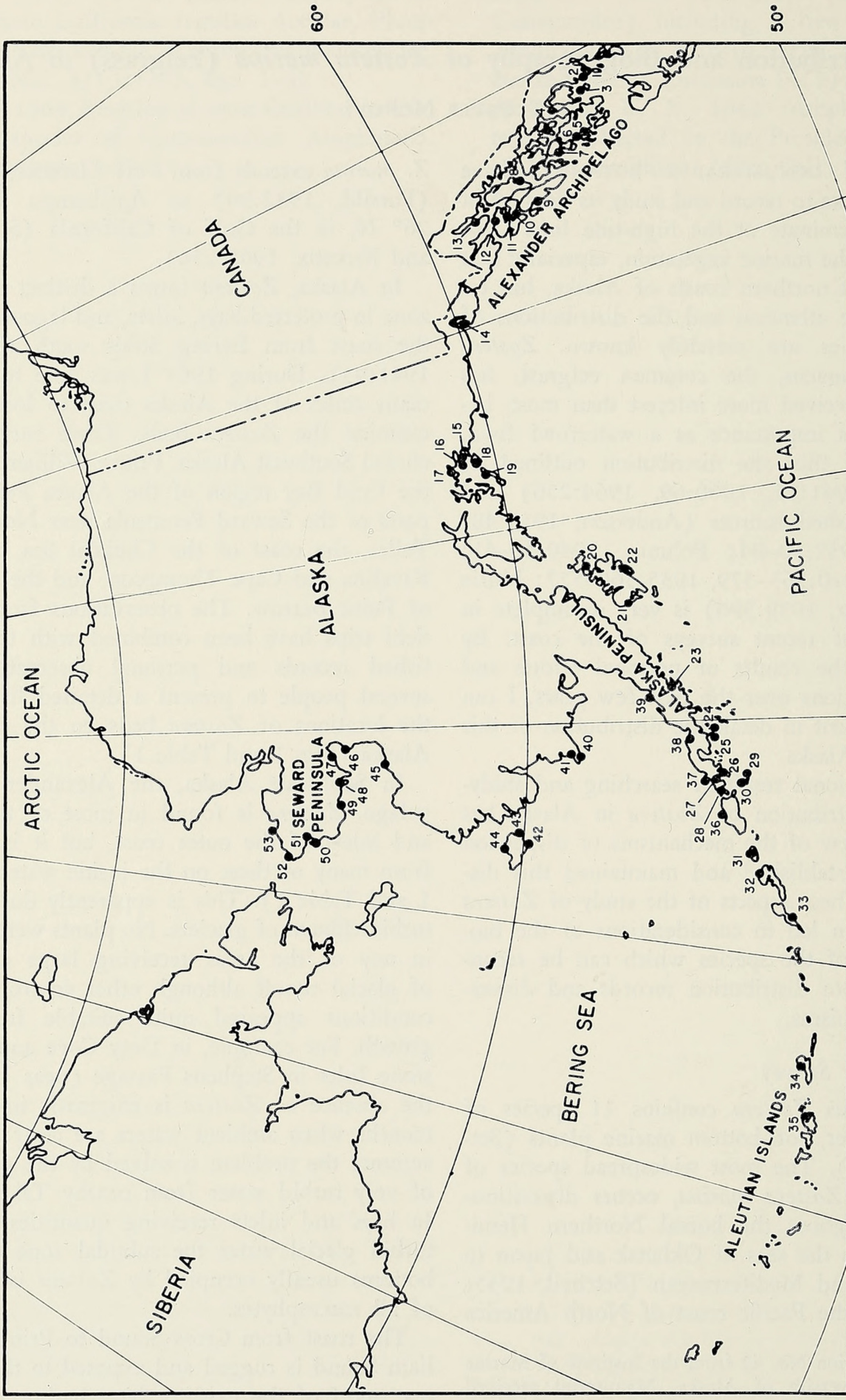

FIG. 1. Chart of Alaska showing the location of records of *Zostera marina* on the coast. Numbers refer to locations given in Table 1.

TABLE 1
RECORDS OF *Zostera marina* IN ALASKA

CHART NUMBER*	LOCATION	SOURCE
Alexander Archipelago		
1	Foggy Bay	Hultén, 1941
2	Cape Fox	Hultén, 1941
3	Gravina Lake	Hultén, 1941
4	Yes Bay	Hultén, 1941
5	Craig	Hultén, 1941
6	Klawak	McRoy, this study
7	Calder Bay	McRoy, this study
8	Pybus Bay	McRoy, this study
9	Sitka	Hultén, 1941
10	Hoonah Sound	McRoy, this study
11	Tenakee Inlet	McRoy, this study
12	Port Frederick	McRoy, this study
13	St. James Bay	Palmer, 1941
Cross Sound to Prince William Sound		
14	Yakutat Bay	Setchell, 1920
Prince William Sound		
15	Olsen Bay	Johansen, 1965
16	Redhead Lagoon	McRoy, this study
17	Sawmill Bay	McRoy, this study
18	Port Etches, Hinchinbrook Island	Johansen, 1965
19	Stockdale Harbor, Montague Island	Johansen, 1965
Kodiak Island, Alaska Peninsula and Aleutian Islands		
20	Afognak Island	Beals, 1941
21	Sturgeon River	Hultén, 1941
22	Port Hobron, Kodiak Island	Hultén, 1941
23	Chignik Bay	Hultén, 1941
24	Popof Island	Hultén, 1941
25	Unga Island	Hultén, 1941
26	King Cove	Hultén, 1941
27	Cold Bay	McRoy, this study
28	Morshovi Bay	McRoy, this study
29	Caton Island	Beals, 1941
30	Sanak Island	Beals, 1941
31	Akun and Akutan islands	Beals, 1941
32	Dutch Harbor	Beals, 1941
33	Vsevidof Island	Murie and Scheffer, 1959
34	Atka Island	Jones, 1965
35	Adak Island	Jones, 1965
36	Unimak Island	Hultén, 1941
Bering Sea		
37	Izembek Lagoon	McRoy, 1966
38	Herendeen Bay	McRoy, 1966
39	Port Heiden	McRoy, 1966
40	Nanvak Bay	King, 1963
41	Chagvan Bay	King, 1963
42	Ingrimiut, Nunivak Island	King, 1963
43	Ikongimuit, Nunivak Island	King, 1963
44	Mekoryuk, Nunivak Island	King, 1963
45	St. Michaels	Porsild, 1932
46	Malikfik Bay, Norton Sound	Porsild, 1932
47	Kwiniuk Inlet, Norton Sound	Porsild, 1932
48	Golovin Bay	Porsild, 1932
49	Safety Lagoon	Burns, 1967
50	Port Clarence	Kjellman, 1883
51	Grantly Harbor	McRoy, this study
Bering Straits		
52	Lopp Lagoon	Burns, 1967
53	Ikpek Lagoon	Burns, 1967

* Numbers refer to the geographical locations shown in Figure 1.

1 and Table 1). Isolated populations in other more inaccessible areas are of course possible. Prince William Sound contains many *Zostera* beds (Fig. 1 and Table 1), but their distribution was altered by the earthquake of March 1964. Johansen (1965:93–94) lists nine localities where he found dead *Zostera* attributable to the seismic uplift of the region. In June 1967 I revisited many of Johansen's stations. In several of these, the most striking being the vicinity of Cordova, no new *Zostera* was seen; in other places, such as Redhead Lagoon, reduced populations were evident.

The outer coast of the Kenai Peninsula is a glaciated region where no *Zostera* has been reported, nor has any been found in Cook Inlet, which might be expected from the turbidity and currents in the Inlet. There are, however, unconfirmed reports of *Zostera* in Kachemak Bay.

Several bays on Kodiak and Afognak islands, on the Alaska Peninsula, and in the Aleutian Islands contain *Zostera* beds (Hultén, 1941:95; Beals, 1941; Fig. 1 and Table 1). The western limit of the species in North America was Vsevidof Island (Murie and Scheffer, 1959: 369). This limit can now be extended to Atka and Adak islands (Jones, personal communication, 1965). The plants on Adak are evidently a result of transplantation experiments by the

U.S. Fish and Wildlife Service. No plants are known to occur in the western Aleutian Islands, probably due to the lack of protected bays. Plants are known from Kamchatka Peninsula and Bering Island on the Asian side of the Bering Sea (Hultén, 1926:75, 1960:69).

In the Bering Sea *Zostera* forms extensive meadows in the numerous coastal lagoons of the Alaska Peninsula (Fig. 1 and Table 1). The meadows in Izembek Lagoon on the Peninsula are the largest known single stand of the species (McRoy, 1966:103). Farther north, *Zostera* occurs in Nanvak and Chagvan bays and in many of the lagoons at the mouths of rivers on Nunivak Island (King, personal communication, 1963). No other *Zostera* beds have been found between King Salmon and St. Michael.

Porsild (1932:90–94) recorded the northern distribution of *Zostera* from St. Michael to Port Clarence (Fig. 1 and Table 1). Kjellman (1883:53) first observed *Zostera* in Port Clarence, the accepted northern limit in Alaska. Recently, *Zostera* has been seen beyond Bering Strait in the lagoons (Lopp and Ikpek) of the north coast of the Seward Peninsula (Burns, personal communication, 1967). I have also extended surveys to portions of the coast between Kotzebue and Barrow, but have not uncovered any other *Zostera* producing areas.

Mechanisms of Dispersion

The distribution of *Zostera* in Alaska and elsewhere in the Northern Hemisphere is the result of dispersion by several mechanisms. Oceanic currents appear to be the most effective means of long range dispersion, although there is some disagreement on this. Löve (1963:195) observes that saltwater plants are adapted to dispersal in sea water and cites as an example the seeds of *Zostera* with their corky appendages and bouyant vegetative parts. Sculthorpe (1967:358), on the other hand, considers Löve's view of dispersal an "unfortunate generalization," since the seeds of *Zostera* and other marine angiosperms either float for only a short time or sink immediately. The seeds of *Zostera* have a specific gravity of 1.17 (Arasaki, 1950:70–76), a value somewhat greater than the 1.025 average of the ocean (Von Arx, 1962:118) and so would be expected to sink. In fact, however, the seeds are released attached to a reproductive stem which has several leaves and is capable of floating for long distances. Mats of *Zostera* and other marine angiosperms have been seen at sea several hundred miles from the coast (Menzies, Zaneveld, and Pratt, 1967:112). There can be no doubt that dispersion on a large scale is accomplished through the seed-producing and perhaps vegetative plants that annually detach and drift with oceanic surface circulation.

The several species of waterfowl that feed on *Zostera* are another vehicle for dispersion. Löve and Sculthorpe concur. Arasaki (1950:70–76) demonstrated that ducks do not destroy the viability of all seeds they ingest. The coast of Alaska is a flyway for numerous species of waterfowl that annually transport seeds over at least short distances and probably farther. This is a mechanism for dispersion in a direction opposite to that of the coastal oceanic currents.

In a local area *Zostera* extends its cover principally by vegetative growth from rhizomes, a process quantitatively more important than the growth of new seed plants. Again, Arasaki (1950:70–76) has shown that a single plant will cover 30 cm^2 the first year, 1 m^2 the second, and 2 m^2 the third. At this rate, it would not take long for a population to develop in a new area once a plant has been introduced.

Biogeographical Considerations

The global distribution of this species is discontinuous circumboreal. The other species of the seagrasses, with few exceptions, are tropical or subtropical and are considered to have originated in the Indian Ocean (Setchell, 1935:564–572). The genus *Zostera*, however, has no tropical representatives and apparently arose in the western Pacific Ocean, dispersing into the Northern and Southern hemispheres at a time when the tropics were less tropical. This history is supported by the present distribution of the 11 species of *Zostera* (Setchell, 1935:572) and the locations of fossils of *Zostera* ancestors in Japan (Koriba and Miki, 1930:165–204; Miki, 1932:774–778).

If the origin of *Zostera marina* was the western Pacific, then migration could have taken either of two routes. In the first case, dispersion could have moved in two directions from the origin, populating both sides of the Pacific Ocean in one direction and through the Indian Ocean and the Mediterranean Sea to both sides of the Atlantic Ocean in the other. Setchell (1935:572) suggested that a route of this sort could have occurred at a time, probably in the early Tertiary, when the Tethys Sea covered much of the Northern Hemisphere. The other possibility for dispersion is a one-way movement. This is really an argument for a one-way dispersion route through the Pacific Ocean rather than through the Indian Ocean. This path would result logically in the present distribution of the species. The theory demands that the Atlantic and its adjacent seas were populated by migration through the Arctic during a prehistoric milder climate, which should be entirely possible, for, as the distribution in Alaska illustrates, *Zostera marina* is a cold-tolerant species. If continuity through the Arctic once existed, relict populations would be expected along the Arctic coast. These do exist in the White Sea, the Barents Sea, the Kara Sea, and Hudson Bay (Zenkevitch, 1963:195–198; Blinova, 1962:150; Setchell, 1920:567; Porsild, 1932:91). Ekman (1953:160–164) describes similar patterns for many species of marine invertebrates and vertebrates that have discontinuous distributions in the Pacific and Atlantic oceans. Additionally, Durham and MacNeil (1967:343) report that a large number of species, more than 125, of marine invertebrates have dispersed from one ocean to the other mostly in one direction—into the Arctic-Atlantic; they consider these migrations to have occurred during the late Cenozoic.

The evidence available indicates that *Z. marina* originated in the western Pacific and dispersed to the north along the coast of Asia and then around to North America. Its tolerance to low temperatures permitted it not only to cross the subarctic Pacific to North America, but also to populate the Arctic and move eventually to both shores of the Atlantic. Perhaps in times of cooler climates migration continued into the north coast of the Mediterranean Sea and its adjacent seas. No other species of *Zostera* has this widespread distribution, nor is there another one tolerant to low temperatures. The single closely related species that has a similar, but more restrictive, temperature tolerance is *Phyllospadix scouleri* Hook which is endemic to the temperate Pacific Ocean. This species provides an example of the limited distribution of a less cold-tolerant species originating in the same area; it never reached the Atlantic. The opposite situation is illustrated by the distribution of *Zostera nana* Roth, a species less tolerant to cold water but more so to warm water; it is limited to the western Pacific, but has also been able to move through the Indian Ocean to populate parts of Africa, the Mediterranean (both north and south) and parts of the southern Atlantic coast of Europe.

SUMMARY AND CONCLUSIONS

Zostera marina, eelgrass, is a common inhabitant of the Alaska coast, occurring from the lagoons on the north coast of the Seward Peninsula to the southern limit of Alaska and beyond. New records of *Zostera* in Alaska are from Adak and Atka in the Aleutian Islands, Chagvan and Nanvak bays and Nunivak Island, and Lopp and Ikpek lagoons on the Seward Peninsula. In Prince William Sound the distribution of *Zostera* was markedly altered by uplift associated with the earthquake of March 1964.

Zostera grows in the soft sediments of shallow, protected marine bays, inlets, and lagoons. It is excluded from large river deltas, glacial fjords, and arctic environments. The distribution in Alaska is disjunct, a result of environmental restrictions rather than a lack of dispersion mechanisms. Global dispersion is a result of oceanic circulation and waterfowl migrations. Vegetative growth is the most important means of extending coverage of a restricted area. In view of the present distribution of the species and the geological structure of the Alaska coast, no extensions of the range of *Zostera* are expected. Populations may exist, of course, in remote places along the coast.

Alterations in the present distribution are possible only with major geological or climatic changes. Seismic uplift or depression of the south coast of Alaska could eliminate a large portion of the present populations. On the other hand, amelioration of conditions in arctic waters by a change in ice conditions could permit further extension of the present range.

The circumboreal distribution of *Z. marina* is considered to be a result of dispersion from a western Pacific origin around the Pacific and through the Arctic into the Atlantic and its adjacent seas. That this was the path of migration is supported by the present distribution of the species, the location of its fossil ancestors, and similar dispersal patterns for marine invertebrates.

The migration and present distribution of *Z. marina* have resulted from the eurythermality of the plant. This feature probably also permitted survival during oscillating Pleistocene climates.

The *Zostera* communities on the Alaska coast are important contributors to all levels of production in the food web and provide refuges to innumerable species of organisms. Research is in progress on the ecology of these interesting communities.

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