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Effects of ice scour on the structure of sublittoral marine algal assemblages of St. Lawrence and St. Matthew Islands, Alaska

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ABSTRACT: Ice scour and gouging play a major role in the distribution and abundance of macroalgae and sessile invertebrates in the northern Bering Sea. Annual ice scouring and gouging create a gradient of disturbance, at one extreme removing the entire biota from horizontal rock surfaces in shallow water (< 12 m), with a transition to a rock slope area where the effects of disturbance are less intense and more intermittent in nature. This appears to restrict adult perennial algae such as *Laminaria dentigera*, *L. groenlandica*, *L. yezoensis*, and *Alaria crispa* to valleys and crevices protected from ice scour. Recruitment of young Laminariales was highest on the less severely scoured sloping rock surfaces between the adult populations and the ice scoured rock tops, possibly due to the gradient of disturbance. *Laminaria* spp. were abundant in shallow water, but below the depth of ice scouring (> 12 m), *Laminaria* spp. were less common, and *Agarum cribrosum*, which was rare in shallow water, became common. Contrary to other studies, the lower distribution of *A. cribrosum* is not related to grazing sea urchins, as urchins and other large herbivores are absent. The algal zone extended to a depth of ca 28 m, where sessile invertebrate cover became high. The marine benthos of St. Lawrence Island was characterized by a high cover of *Laminaria* spp., few understory algae, and sessile invertebrates such as barnacles, hydroids, mussels, sponges, and bryozoans, while St. Matthew Island had a high cover of *Laminaria dentigera*, abundant understory red algae such as *Ptilota asplenioides*, *Cirrulicarpus gmelinii*, and encrusting coralline algae, and fewer sessile invertebrates.

INTRODUCTION

The structure and organization of marine algal communities are poorly known in northern polar habitats. Although there are several excellent studies in the sea otter dominated kelp communities from the Aleutian Islands (Weinmann 1969, Estes & Palmisano 1974, Dayton 1975) exploration of algal communities in the northern Bering Sea is generally limited to taxonomic descriptions (Setchell & Gardner 1903, Shumway et al. 1964).

The northeastern Bering Sea is seasonally covered with ice as far south as the Pribilof Islands (Hood 1981). The ice begins to form in late November and break up in late May at St. Lawrence Island (LaBelle & Wise 1983). The ice breaks along pressure zones where surface ice is forced into pressure ridges and deep ice keels form underwater. When the ice cover breaks up, these deep keels often run into the seafloor gouging extensive bottom areas (Thor & Nelson 1981). Neushul (1965) directly observed the violent grinding and pounding of the ice on shallow rocky shores in the Antarctic.

The majority of the work associated with ice scouring and gouging in the Arctic has focused on its extent and location with particular reference to the possible effects on man-made structures that might be placed in these areas. Ice gouging on soft-bottom substrates generally occurs in water depths of up to 30 m, with single gouge widths of between 5 and 60 m, multiple parallel gouge widths of 50 m to several km, and gouge depths of up to 1 m in soft bottoms (Thor & Nelson 1981). Josenhans (1987) reports icebergs scouring the benthos to depths of 170 m on the Labrador Shelf.

The ecological effects of ice scouring and gouging on benthic communities is also poorly known from northern polar waters. In Newfoundland, ice scour is temporally and spatially patchy, and was found to remove *Alaria esculenta* (L.) Grev. (Keats et al. 1985), resulting in ice scoured patches that were colonized by annual

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algae. Intertidal organisms appear to have refuge from ice scour in crevices in the rock and in spaces beneath and between boulders in the Pribilof Islands (O'Clair 1981). Qualitative observations in the adjacent subtidal area indicated that larger plants were found only in crevices, and that the upper surfaces of ice scoured rock were primarily occupied by filamentous green algae and small recruits of the kelp *Alaria crispa* Kjellman. Ice scour effects were only apparent down to a depth of 4 m, and large perennial plants were common below that depth (O'Clair 1981).

In the Antarctic, severe ice scour has been suggested as the chief factor which controls the distribution and abundance of certain species in shallow water (Neushul 1965, DeLaca & Lipps 1976). Qualitative observations in scoured areas indicate that algae are stunted in growth, reduced to crusts, or restricted to cracks (Delepine et al. 1966, DeLaca & Lipps 1976, Moe & DeLaca 1976).

The ecological effects of anchor ice growth and uplift are well known from the studies of Dayton et al. (1969, 1970). Anchor ice disturbance is different from the scouring and gouging caused by ice grounding. Large ice platelets grow on the shallow seafloor and benthic organisms to depths of as great as 30 m. The resulting uplift causes a distinct zonation of benthic communities in McMurdo Sound (Dayton et al. 1969, 1970).

This paper describes benthic community patterns caused by ice scour and gouging in the northern Bering Sea, and presents the first quantitative description of the distribution and abundance of the common algae. A more complete taxonomic and floristic treatment of the algae will be presented elsewhere (Wynne & Heine unpubl.).

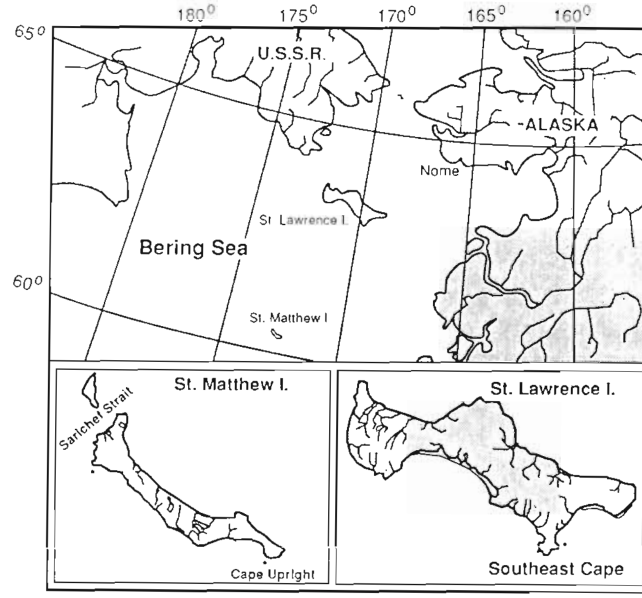

Fig. 1. Study sites at St. Lawrence and St. Matthew Islands in the Bering Sea, Alaska. Sites are marked •

MATERIALS AND METHODS

From 6 to 25 June 1986, 28 dives were made at a variety of benthic sites on St. Lawrence and St. Matthew Islands in the Bering Sea (Fig. 1). For the community profiles of St. Matthew Island, divers started at a depth of 27 m and swam a straight line towards the shoreline, collecting specimens and noting the distribution and abundance of orgnaisms and physical features.

Mean density of large brown macroalgae and percent cover of common macroalgae and invertebrate groups were determined by randomly placing 1 m^2 quadrats on the substrate. The number of large brown algae were counted and recorded. A random point contact (RPC) method was employed to determine the percent cover (see Foster 1975 for complete description). A 1 m long iron RPC bar with a string containing 5 knots on it was blindly dropped into the quadrat. The string was stretched out tightly and each knot successively placed onto the substrate. If an overstory plant intersected a 1 m long imaginary line above the point of contact, it was recorded as a hit. Any organisms that the knots were resting on were also recorded. Hence it was possible to exceed 100 % cover. Ten points were sampled per quadrat.

The density of adult and recently recruited brown macroalgae was sampled in several strata (N = 12 at each site): ice-scoured areas, rocky slopes, protected valleys, and sand channels. Divers randomly placed 1 m^2 quadrats in each area. The number of plants in each quadrat were counted and recorded.

Size frequency of the brown algae was determined in situ and in the laboratory. Adult plants were measured underwater using a fiberglass tape measure, and young recruited plants were collected from 1 m^2 quadrats and measured in the laboratory immediately after the dive. Total length was measured from the top of the holdfast to the tip of the terminal blade. Voucher algal specimens were preserved in a 5 % formalin solution, and later pressed. Invertebrates were fixed in 10 % formalin and later transferred to 50 % isopropyl alcohol.

Side-scan sonar was used to locate rocky habitats and obvious areas of ice gouging using a 100 kHz EGG 259-4 system (Fig. 2). The tow fish, which contains the underwater transducers, was towed at a depth of ca 5 m above the bottom, at a constant speed, from behind the RV 'Alpha Helix'. Recordings were made on the 50 m range scale (see Oliver & Kvitek 1984 for details).

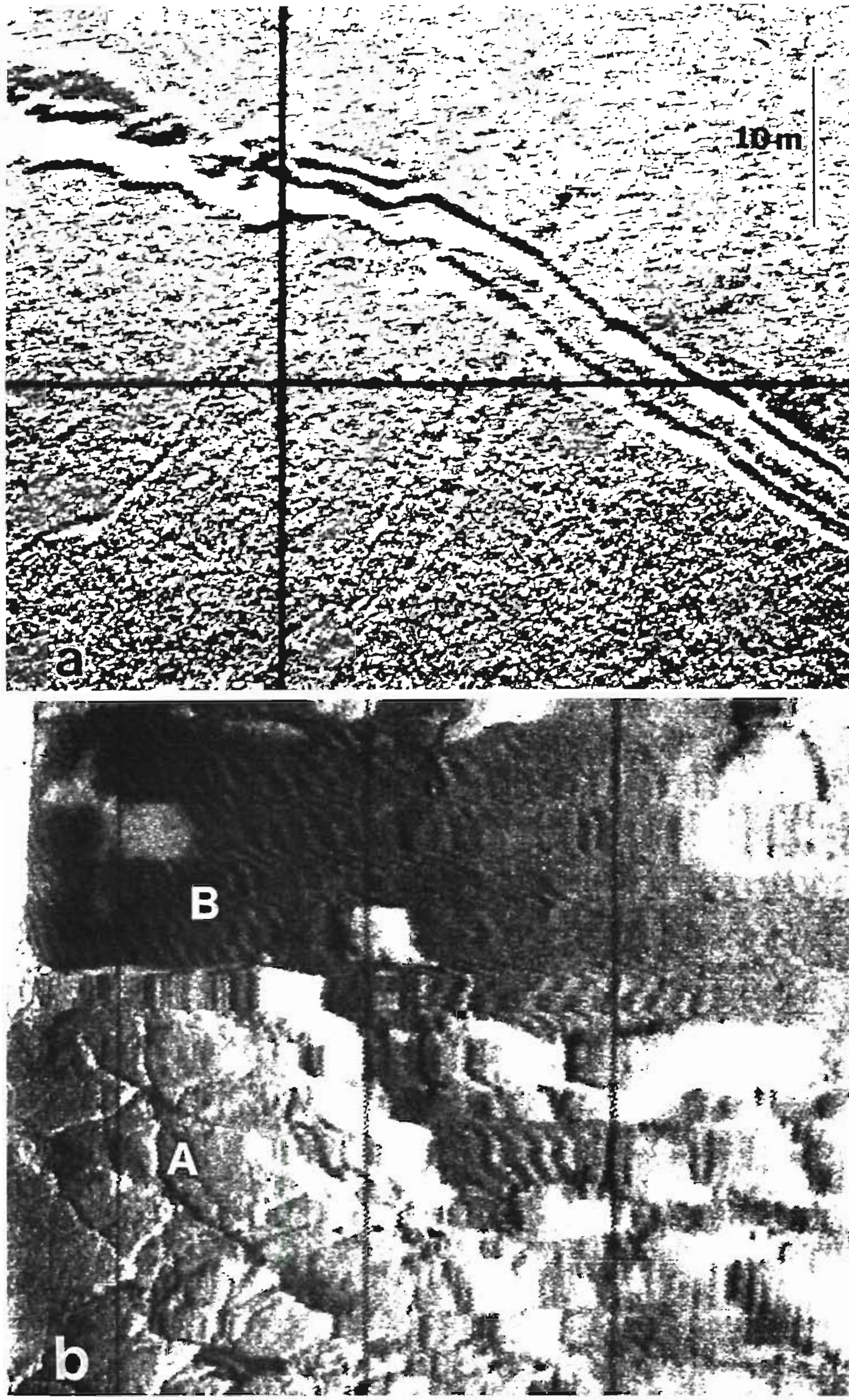

Fig. 2. (a) Side scan sonar record of ice gouging in soft bottom at a depth of 20 m. (b) Ice-scoured horizontal rock tops showing fractures (A), and adjacent ripple marked sand and gravel bed (B) at a depth of 15 m. From St. Matthew Island

RESULTS

Ice scour and gouging patterns

Ice scouring and gouging sheared, polished, and fractured rocks depending upon the severity of impact (Fig. 2b). Diver's observations revealed that flat rock tops, many 10 to 30 m^2 in area, were scoured clean of all growth, including encrusting coralline algae, at locations on each island. At St. Lawrence Island there were no recruits or adult *Alaria crispa* or *Laminaria dentigera* on ice scoured rock tops (Table 1). The same pattern was observed for *Laminaria dentigera* on ice scoured rock tops at St. Matthew Island. On rock slope areas adjacent to horizontal rock surfaces, ice scour appeared to be less severe, as divers observed the presence of encrusting coralline algae and remnants of algal holdfasts and stipes that had been sheared off.

The effects of ice scour were dramatic to a depth of 12 m (Fig. 3). At the Southeast Cape site on St. Lawrence Island, ice scouring was patchy and more severe compared to St. Matthew Island. Adult *Alaria crispa* were the only large brown algae that were abundant (mean density of 41.7 m^{-2}) near ice-scoured areas (Table 1). A very dense mixed bed of *Laminaria groenlandica* Rosenvinge plants (mean density of 86.1 m^{-2}) that contained recent recruits as well as individuals with up to 2 seasons growth (Wilce pers. comm.) was found in the rock slope habitat.

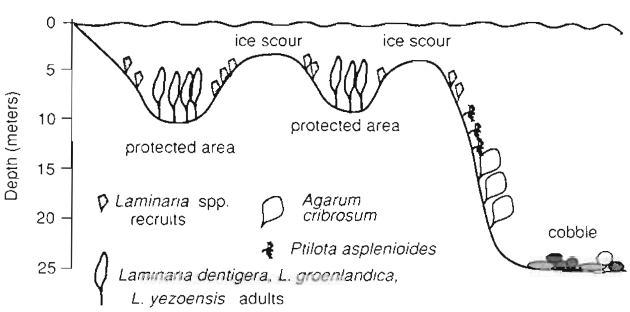

Fig. 3. Diagramatic representation of typical sublittoral habitat in areas of ice scour. Note, plant sizes are not to scale

At the Cape Upright site on St. Matthew Island a lush bed of *Laminaria dentigera* Kjellman (mean density of 15.0 m^{-2}) and few *Alaria crispa* were present in the protected valleys and crevices between the scoured areas (Table 1). The number of recently recruited Laminariales in these protected areas was low. On the sloping rock surfaces between the protected valleys and the heavily ice scoured and gouged rock surfaces, recruits of young Laminariales recently settled in very high numbers, with a mean density of 74.3 m^{-2}. Adult Laminariales were rare where recruitment was high on the rock slope.

Adult *Laminaria dentigera* from both islands showed a normal size distribution with the majority of the plants lengths between 100 and 200 cm (Fig. 4). A high percentage of the recruits ocurred in the smallest size category, and the percent frequency of occurrence decreased markedly with increasing size, indicating that the plants had just recently settled (Fig. 5).

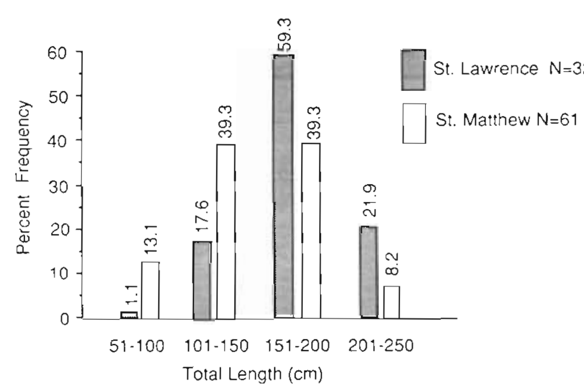

Fig. 4. *Laminaria dentigera*. Size frequency of adults from areas protected from ice scour

Table 1. Mean density m^{-2} (1 SD) of Laminariales adults and recruits in selected habitats. (1) Ice-scoured area on top of ice-scoured rocks, (2) rock slopes which were not ice-scoured but just below ice-scoured tops, (3) protected valleys, crevices, or depressions most protected from ice scour, and (4) sand channels. $N = 6$ for each sample

Site and species	Ice scoured rock	Rock slope	Protected valley	Sand channel
Southeast Cape, St. Lawrence Island				
Alaria crispa (adults)	0	0	0	41.7 (10.7)
Laminaria groenlandica (adults and recruits)	0	86.1 (27.4)	Habitat absent	0
Cape Upright, St. Matthew Island				
Laminaria dentigera (adults)	0	0.3 (0.5)	15.0 (4.4)	Habitat absent
Laminaria sp. (recruits)	0	74.3 (16.3)	0.8 (1.1)	Habitat absent

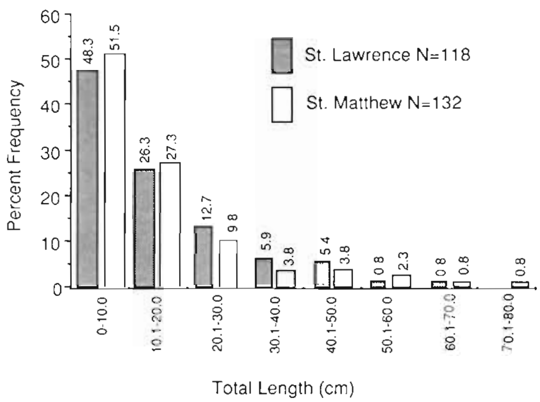

Fig. 5. *Laminaria* spp. Size frequency of recruits from areas adjacent to ice scour

Algal and invertebrate distribution and abundance

At the Southeast Cape site, adult *Laminaria dentigera* and *L. groenlandica* were numerous (mean density of 13.4 m^{-2}) and covered 91 % of the sea floor (Table 2). Recently recruited young Laminariales were less abundant (mean density of 5.1 m^{-2}), especially in areas with a dense overstory of adult plants. Other common algae included *Agarum cribosum* (Mertens) Bory (6 % cover), *Odonthalia dentata* (L.) Lyngb. (8 %), and encrusting coralline algae (29 %). Sessile invertebrate cover was high, consisting of barnacles (24 % cover), hydroids (17 %), mussels (11 %), and yellow sponge (9 %). Total cover was 198 % due to the layering aspect of the *Laminaria* spp. overstory.

Two water depths were surveyed in areas devoid of ice scour effects south of Sarichef Strait on St. Matthew Island. Adult *Laminaria dentigera* (and a few *Laminaria yezoensis* Miyabe) were much more abundant in shallower water (mean density of 8.8 m^{-2}) than at the deeper station (mean density of 1.8 m^{-2}) (Table 3). Recruits were rare in deeper water (mean density of 1.0 m^{-2}) and slightly more abundant in shallower water (mean density of 4.0 m^{-2}). *Agarum cribrosum* had a cover of 23.7 % at the deeper station, but was not present in the shallow zone. The understory red algae

Table 2. Mean density m^{-2} (1 SD) and percent cover of common macrophytes and invertebrate groups at Southeast Cape, St. Lawrence Island, at a depth of 8 m, with little or no ice gouging. --: no data

Species	Density (N = 25)	Percent cover (N = 10)
Laminaria dentigera and L. groenlandica	13.4 (5.7)	91.0
Laminariales recruits	5.1 (4.8)	1.0
Agarum cribrosum	1.4 (2.2)	6.0
Odonthalia dentata	–	8.0
Encrusting coralline algae	–	29.0
Barnacles	–	24.0
Hydroids	–	17.0
Mussels	–	1.0
Yellow sponge	–	9.0
Bryozoan	–	2.0
Total cover		198.0 %[a]

[a] Total cover exceeds 100 % because of layered canopy

Table 3. Mean density m^{-2} (1 SD) and percent cover of common macrophytes and invertebrate groups at Sarichef Strait, St. Matthew Island, in areas with little or no ice gouging. Deep site is at a depth of 14 m, and shallow site is at a depth of 8 m

Species	Density		Percent Cover	
	Deep (N = 8)	Shallow (N = 10)	Deep (N = 8)	Shallow (N = 8)
Laminaria dentigera	1.8 (2.9)	8.8 (5.7)	17.5	76.0
Laminariales recruits	1.0 (1.4)	4.0 (1.9)	0	1.2
Agarum cribrosum	4.0 (2.7)	0	23.7	0
Ptilota asplenioides			50.0	40.0
Cirrulicarpus gmelinii			10.0	7.5
Yendonia crassifolia			5.0	2.5
Callophyllis rhynchocarpa			2.5	6.2
Encrusting coralline algae			43.7	51.2
Articulated coralline algae			6.2	10.0
Yellow sponge			8.7	11.2
Orange sponge			1.2	
Tunicate			11.2	
Barnacles			10.0	
Total cover			189.7 %[a]	205.8 %[a]

[a] Total cover exceeds 100 % because of layered canopy

Ptilota asplenioides (Esper.) C. Ag., *Cirrulicarpus gmelinii* (Grunow) Tokida & Masaki, and encrusting coralline algae were abundant in both deep and shallow water. Sessile invertebrate cover was lower than that found at St. Lawrence Island. Tunicates and barnacles were present at the deeper station, but absent in shallower water (Table 3). Total cover was slightly higher in shallower water, and was comparable to that found at Southeast Cape, St. Lawrence Island (Tables 2 and 3).

Surveys at a depth of 27 m at the site south of Sarichef Strait, St. Matthew Island, indicated that this was below the depth of the foliose algal zone, with a high cover of pink alcyonacean soft coral, erect bushy bryozoans, hydroids on rock edges, and a low cover of encrusting coralline algae. At a depth of 20 m, *Agarum cribrosum* and foliose red algae became common (Fig. 3).

DISCUSSION

The distribution and abundance of macroalgae and sessile invertebrates in shallow water at St. Lawrence and St. Matthew Islands is strongly influenced by ice scour. Ice scouring and gouging at these sites removed the entire biota from horizontal rock surfaces at depths up to 12 m. Adult perennial algal species are restricted to protected valleys and crevices between the flat, ice scoured rocks. The same species recruit in large numbers on the rock slopes between the protected crevices and the ice scoured rock tops.

The obvious question is why did the recruits settle only on the rock slopes, and not on the ice scoured rock tops? There appears to be a gradient of disturbance from the severe scouring and gouging of the horizontal rock tops to the less intense, intermittent scouring of the rock slope. Since the ice cover had only recently broken up, the rock tops may have been subjected to ice scour when the propagules settled, prohibiting their survival.

In other studies, *Alaria fistulosa* P. et R. rapidly recruited into space provided by the removal of *Laminaria* spp. and *Agarum cribrosum* canopies (Dayton 1975), and into recently ice scoured areas (O'Clair 1981). Although *A. crispa* adults were abundant in nearby sand channels, recruits of this species were not found in the ice scoured areas in this study, which were dominated by juvenile *Laminaria* spp. This may be due to intergeneric differences in spore availability at the time of the disturbance, and more detailed observations during other periods of the year might reveal different recruitment patterns.

Laminaria dentigera was abundant in shallow water at St. Matthew Island. *Agarum cribrosum* was most abundant in deeper water, and was rare in the shallow zone dominated by the *Laminaria* spp. At southern Kodiak Island, *Laminaria dentigera* was also abundant in shallow water to a depth of 18 m (Calvin & Ellis 1978), and *A. cribrosum* was abundant only at the most protected sites, usually occurring in a band within the *Laminaria* spp. zone, but sometimes extending below it. Dayton (1975) reported a similar distribution pattern for these species, and suggested that *Laminaria* spp. suppresses the growth of *A. cribrosum* in shallow water, but that *A. cribrosum* was more successful in deeper water in the presence of sea urchins, which have been shown to dislike this species (Vadas 1968). As sea urchins were absent at the sites reported here, factors other than grazing must be influencing the distribution of these species.

The understory algal cover at St. Matthew Island was much more extensive than that at St. Lawrence Island, with a total combined cover of 117 %, and sessile invertebrate cover was low. This may be related to reduced ice formation and scour with decreasing latitude. Although there are no data available for seasonal variations in underwater light levels, our observations from past visits indicate that water visibility was consistently better at St. Matthew Island, averaging 5 to 10 m, and light levels were appreciable down to depths of 20 m.

The diversity of algae on St. Lawrence Island was relatively low. There was a distinct lack of understory foliose algae, a relatively low cover of coralline algae, and a high cover of sessile invertebrates. The more severe ice scour at this island may prevent the establishment of understory algal beds and favor the more resilient sessile invertebrate forms found. A similar pattern was observed in the Antarctic, where species diversity was higher in areas where ice scour sheared off the *Desmarestia menziesii* canopy, opening up space for red algae and invertebrates (DeLaca & Lipps 1976).

It is conceivable that ice cover and extended periods of darkness at the latitude of St. Lawrence Island prohibit the extensive development of a red algal understory. *Laminaria solidungula* grows most rapidly in complete winter darkness under the ice canopy by utilizing stored food reserves (Chapman & Lindley 1980, Dunton 1985). However, for other non-Laminarian algal species, no growth would be expected under snow-covered ice (Healy 1972). Although dredge samples in the more northerly Beaufort Sea have produced a variety of seaweeds (Mohr et al. 1957), algal stands are largely absent from the perimeter of the northern Bering Sea (Dall 1875). This may be due in large part to the sedimentation and silting effects of sea ice (MacGinitie 1955), which may hinder the establishment and development of sporophytes.

Below the depth of ice gouging (>12 m), algae were more common on horizontal surfaces, and sessile invertebrates covered vertical walls. Below the algal zone (ca >27 m), some rocky areas were characterized by large (up to 30 m^2) patches of pink alcyonacean soft coral, erect bushy bryozoans, hydroids, and sponges. Motile invertebrates and fishes were absent, except a few sea stars and king crabs. This conspicuous lack of grazers suggests that the lower limit of algal distribution may be influenced by a lack of light and by competition for space with sessile invertebrates (Foster & Schiel 1985).

The kelp forests of Amchitka Island, which are inhabited by sea otters that effectively remove many of the large herbivores, are characterized by a surface canopy of *Alaria fistulosa* and subsurface canopies of *Laminaria* species and *Agarum cribrosum* (Dayton 1975). Competitive effects on the distribution of these large kelps have been demonstrated experimentally. Dayton (1975) also suggests that the lower distribution of these kelps appears to be primarily limited by sea urchin grazing. As sea urchins and other herbivores were not found in this study, the lower limit of distribution of the kelps is most likely determined by the lack of light.

A gradient of disturbance exists on both a latitudinal and microhabitat scale. General observations indicated that ice scouring and gouging was more severe to the north at St. Lawrence Island, where algal diversity was low, and less severe to the south at St. Matthew Island, where diversity was higher, supporting current disturbance theory (Connell 1978, Sousa 1984). Ice gouging also limits the distribution of adult *Laminaria* spp. and *Alaria crispa* to protected microhabitats. *A. crispa* does not form a surface canopy (pers. obs.), and a more distinct separation of *Laminaria* spp. and *Agarum cribrosum* populations exist. Whereas *Alaria fistulosa* was characterized as a fugitive species which rapidly colonized areas artificially cleared of the dominant *Laminaria* spp. canopy at Amchitka (Dayton 1975), this was not the case in the natural clearing caused by ice gouging in the northern Bering Sea.

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