Distribution, population structure and feeding of subtidal seastars in the northern Gulf of St. Lawrence

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ABSTRACT: The distribution and size-structure of seastar populations in the Mingan Islands, northern Gulf of St. Lawrence, were examined using quantitative sampling by SCUBA. *Asterias vulgaris* and *Leptasterias polaris* are the most abundant seastars. In both species, individuals measuring 1 to 5 cm in diameter are concentrated in the rocky subtidal zone, at a slightly greater depth for *A. vulgaris* (4 to 7 m) than for *L. polaris* (0 to 3 m). With increasing size and probably the onset of sexual maturity, both species aggregate near the low tide level and join concentrations of several earlier year classes. This shift in distribution is most marked for *A. vulgaris*. Finally, adults measuring > 15 to 20 cm in diameter are associated with mixed and sediment substrata at greater depths. The aggregation in shallow water upon attaining 5 cm in diameter probably occurs because the seastars are attracted to the mussel beds in this zone, whereas the shift to habitats at greater depths at size 15 to 20 cm may be caused by a change in food preference towards larger prey which are concentrated in the sediment zone (e.g. large bivalves). *Crossaster papposus* and *Solaster endeca* are rarer species and also show different patterns of size partitioning related to depth and substratum. Seastars appear to be the dominant predators in the northern Gulf and probably play an important role in determining community structure. A variety of interactions (competition, predation, facilitation) exist between *A. vulgaris* and *L. polaris*, and between these seastars and the most abundant benthic carnivore, the whelk *Buccinum undatum*.

INTRODUCTION

The primarily carnivorous feeding habits of seastars have long been recognized (Boolootian 1966, Mauzey et al. 1968) and during the past 20 to 30 yr seastar predation has been shown to be a major factor in structuring many marine benthic communities (Menge 1982, Duggins 1983). The most detailed studies are those made in the intertidal zone. For example, Paine (1974) demonstrated that the seastar *Pisaster ochraceus* is the key predator in rocky intertidal communities on the Pacific coast of North America. Its removal shifts the abundance of organisms in lower trophic levels, particularly of species which monopolize space, and markedly changes community structure. One would expect predation by seastars to be particularly important in the subtidal zone, where their activities are less limited by physiological stress. However, with the exception of the studies of seastar *Acanthaster planci* on coral reefs (Glynn 1976, Birkeland 1982), relatively few studies have quantified the impact of asteroid

predation in the subtidal zone. A major problem in predicting the impact of seastars is the lack of understanding of the dynamics of seastar populations and in particular of factors determining recruitment intensity and juvenile survival. These processes are poorly understood even for *Asterias rubens* and *Asterias vulgaris*, the species which are often taken as models for asteroid biology (Boolootian 1966). For example, the causes of the periodic massive aggregations of seastars which decimate molluscan stocks are unknown (Galtsoff & Loosanoff 1939, Hancock 1955, Brun 1968, Sloan & Aldridge 1981, Dare 1982). Recruitment and juvenile survival in asteroids are largely determined by subtidal processes, and consequently both Sloan (1980) and Menge (1982) emphasized the need for more detailed studies of the population structure and foraging of asteroids in the subtidal zone.

Studies of subtidal communities in the northern Gulf of St. Lawrence, Canada, have only recently appeared in the literature (Himmelman et al. 1983a, b, Drouin et al. 1985, Himmelman & Lavergne 1985, Brault &

Bourget 1985, Himmelman 1991). Here, urchin-dominated communities are widespread and persistent (Himmelman et al. 1983a, b, Himmelman & Lavergne 1985), in contrast to subtidal communities in the Canadian Maritime provinces, where transformations between urchin-dominated and algal-dominated states occur periodically (Miller & Colodey 1983, Chapman & Johnson 1990, Elner & Vadas 1990). Within the rocky zone of the northern Gulf, a few browsers of algal films, chiefly limpets and chitons, and many species of filter feeders, including holothuroids, ophiuroids, small bivalves, ascidians, sponges and cnidarians, are present among the numerous urchins (Drouin et al. 1985, Himmelman & Lavergne 1985, Jalbert et al. 1989, Himmelman 1991). On sediment bottoms below the rocky zone, the conspicuous animals are filter feeders, such as large clams *(Mya truncata, Spisula polynyma, Clinocardium ciliatum, Chlamys islandica)*, and sand dollars *Echinarachnius parma*. There are 4 main types of subtidal predators exploiting these food resources: (1) whelks, mainly *Buccinum undatum*; (2) 4 seastars, *Leptasterias polaris, Asterias vulgaris, Crossaster papposus (= Solaster papposus)*, and *Solaster endeca*; (3) 2 crabs, *Cancer irroratus* and *Hyas araneus*; and (4) a number of benthic fishes (Jalbert et al. 1989, Himmelman 1991). Whereas *B. undatum* is the most abundant carnivore, the large size and high abundance of seastars, as well as their frequent predatory activity, suggests that they are the dominant predatory guild (Himmelman 1991). Decapod crustaceans and fishes are considered to be the major predators in the Maritimes; however, their reduced numbers in the northern Gulf, coincident with the increased importance of seastars and whelks, suggests major differences in community organization compared to the Maritimes (Himmelman 1991).

Asterias vulgaris is the best studied of the 4 common seastars in the northern Gulf of St. Lawrence. It occurs from southern Labrador, south to North Carolina (Bousfield 1960), and is probably synonymous with *Asterias rubens* in European waters (Tortonese 1963, Nichols & Barker 1984). *A. vulgaris* and *A. rubens* spawn in the spring, producing planktotrophic larvae which settle in mid summer to early autumn (Smith 1940, Lacalli 1981, Barker & Nichols 1983). In Prince Edward Island, Smith (1940), from records of shifts in size distributions over time and the growth of individuals in cages, indicated that *A. vulgaris* attains ca 3.5 cm in diameter at 1 yr and ca 6 cm at 2 yr. In Newfoundland, *A. vulgaris* recruiting on mussel culture nets in summer 1979 reached 6 to 8 mm in ray length (ca 1.2 cm in diameter) by May 1980 (O'Neill et al. 1983). In Europe, *A. rubens* has a similar growth rate, even though hydrographic conditions differ from those in eastern Canadian waters. For example, observations by Nichols & Barker (1984) over a 3 yr period showed that the mean diameter at 1 yr varies from 2.8 to 4.2 cm, and at 2 yr from 5.2 to 5.8 cm.

Crossaster papposus and *Solaster endeca* extend to greater depths than *Asterias vulgaris* and *Leptasterias polaris* (Franz et al. 1981) and occur in both the northern North Atlantic and North Pacific (D'Yakonov 1950). Both produce lecithotrophic larvae in late winter (Gemmill 1912). Hancock (1958) reports that *C. papposus* recruitment precedes that of *A. rubens*, that 1 yr old individuals measure 1.8 to 4.0 cm in diameter, and that there is a 2 cm annual growth increment during the following few years.

Leptasterias polaris, which occurs along North American shores of the North Atlantic and in the Arctic (Grainger 1966), is abundant in Newfoundland and the northern Gulf of St. Lawrence but rare in the southern Gulf of St. Lawrence (Himmelman pers. obs.). In contrast to the above asteroids, *L. polaris* spawns in autumn, and the females brood their embryos through winter and spring (Himmelman et. al. 1982, Boivin et al. 1986). There is no published information on its growth or population biology.

Given the abundance of seastars and their likely importance in structuring the subtidal community, the present study examines the use of spatial and food resources by the 4 common seastars in subtidal communities of the northern Gulf of St. Lawrence. Specifically, we used SCUBA to (1) quantify their distribution and size-structure in relation to depth and substratum, (2) determine the distribution of potential prey species, (3) examine their use of prey resources in relation to habitat and prey distribution, and (4) consider the potential impact of seastars in the subtidal community.

METHODS

Our study was conducted at Cap du Corbeau in the Mingan Islands in the northern Gulf of St. Lawrence, eastern Canada (Fig. 1). This is a moderately exposed site with a gradation in substratum from bedrock and boulders in shallow water to sand and mud at greater depths. The size structure and diet of the seastars was quantified by examining 1 × 2 m quadrats placed at 1 m intervals along both sides of permanent transects running perpendicular to the shore. Transects extending from the low interidal zone to 20 m below lowest water of spring tides (LWST) were made at 6 points, each at 100 m intervals from the preceeding point along the perimeter of Cap du Corbeau (Fig. 1).

All observations made for each quadrat were recorded underwater on a plexiglass writing pad with attached ruler For seastars, the diameter of each individual was recorded in 1 cm size classes. Further, we
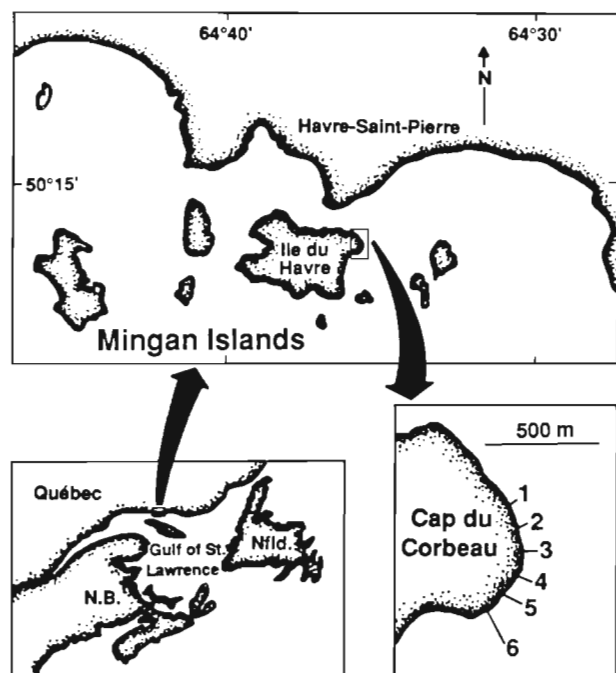
Fig. 1. Location of the 6 transects at the study site, Cap du Corbeau, in the Mingan Islands, Gulf of St. Lawrence, Canada

noted the occurrence of feeding and identified prey being eaten. Feeding individuals were readily identified because their arms were wrapped around their prey, the stomach was everted, or the central disc was swollen. In the latter case, pressure was applied to the aboral surface to expulse food materials from the cardiac stomach. The distribution of potential prey species was also quantified. Urchin abundance was noted as percentage cover. The abundance of other prey species was ranked as follows: 0 = absent, 1 = present, 2 = common, 3 = abundant, and 4 = very abundant. Very abundant was used only when the species completely covered the surface, for example a mussel bed. Percentage cover was used to quantify the abundance of algae and of 5 categories of substratum: sand/mud (< 0.02 cm), pebbles (0.02 to 64 cm), cobbles (64 to 256 cm), boulders (> 256 cm), and bedrock (adapted from Wentworth 1922).

The same 2 divers made all the observations. Between 10 July and 18 August 1984 practice runs were made along 4 transects to standardize the technique and minimize differences in the estimates of the 2 observers. The final run of the entire 6 transects was made between 20 August and 14 September 1984. Only data from the final run (932 quadrats of 2 m²) was used to calculate the distribution and size structure of the various seastar populations and to determine the proportion of individuals feeding, but observations from the preliminary runs were included in the examination of seastars diets. For each transect, on 3 occa-

sions at low tide depth measurements were recorded at each meter along the transect. Further, on 3 dates the depth was measured at a specific point along each of the transects during the same low tide. These measurements were used to calculate the depth of each quadrat related to LWST. The maximum difference in corrected depth measurements on different occasions was 0.3 m.

RESULTS AND DISCUSSION

Distribution and population structure of seastars

In the quantitative sampling at Cap du Corbeau during 20 August to 14 September, *Asterias vulgaris* and *Leptasterias polaris* were the most abundant seastars (1137 and 1032 individuals observed, respectively), *Crossaster papposus* was such less abundant (39 observed) and *Solaster endeca* was rare (6 observed). The depth distributions of *A. vulgaris* and *L. polaris* were similar, both attaining a maximum density at 0 to 2 m below LWST and showing a progressive decrease in abundance with depth (Fig. 2). The density decreased from 1.71 m^{-2} at 0 to 2 m to 0.01 m^{-2} at 16 to 18 m for *A. vulgaris* and from 2.10 m^{-2} at 0 to 2 m to 0.03 m^{-2} at 16 to 18 m for *L. polaris*. The abundance of both species also decreased sharply towards the lower intertidal zone (Fig. 2).

Both *Asterias vulgaris* and *Leptasterias polaris* showed distinct size partitioning related to depth which was similar for the 2 species (Fig. 2). *A. vulgaris* measuring 0 to 5 cm diameter formed a distinct group at 0 to 12 m below LWST and a second group measuring between 5 and 15 to 20 cm occurred mainly in the low intertidal and upper subtidal zones. Based on previous reports on the growth of *A. vulgaris* in eastern Canada (Smith 1940, O'Neill et al. 1983), and on the growth of *A. rubens* (= *A. vulgaris*) in Europe (Nichols & Barker 1984), the first group represented recruits from the previous year, 1983. Our sampling technique (the observation of 2 m² quadrats) did not permit us to search for the very small individuals (< 0.5 cm) which would be the 1984 recruits (These may not have been present during our sampling, since recruitment occurs in September and October in Newfoundland; O'Neill et al. 1983). The 5 to 20 cm *A. vulgaris* probably represent several subsequent year classes, since 2 yr old individuals measure > 5 cm in diameter and the growth rate of *Asterias* decreases sharply after the first year (Smith 1940, Nichols & Barker 1984). *A. vulgaris* and *A. rubens* attain sexual maturity in the second year at ca 5 cm in diameter (Smith 1940, Nichols & Barker 1984). Thus, individuals in the 5 to 20 cm group in shallow water were probably sexually mature. Individuals > 20 cm in diameter were only found below
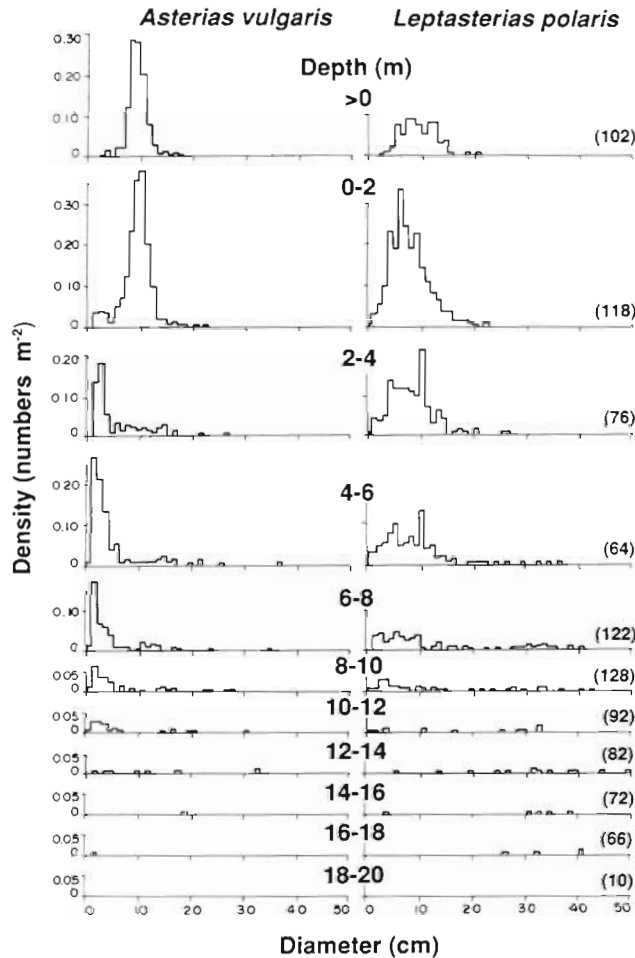
Fig. 2. *Asterias vulgaris* and *Leptasterias polaris*. Size structure for each 2 m depth interval between the low intertidal zone and 20 m depth at Cap du Corbeau. The number of 2 m² quadrats observed at each 2 m depth interval is indicated in parenthesis to the right

2 m in depth. The large size attained by *A. vulgaris* in the Mingan Islands (> 35 cm), coupled with the probable low growth rates due to low water temperatures, suggest that individuals may attain a considerable age (> 20 yr).

Although we observed 1984 recruits of *Leptasterias polaris* (< 3 mm in diameter) under some females, which were still brooding during June and July 1984, we did not quantify their density in different habitats. One broad group of individuals, measuring from 1 to 20 cm in diameter, was present in shallow water during our sampling in late summer. The lack of defined cohorts was expected because of the prolonged spawning and brooding periods of *L. polaris* (Himmelman et al. 1982, Boivin et al. 1986). No information exists on the growth of *L. polaris*. Nevertheless, it is likely that the 1 to 20 cm group represents a number of recent year classes. The size at sexual maturity for *L. polaris* is

unknown, although Boivin et al. (1986) indicate that individuals > 10 cm in diameter have fully developed gonads. Thus, gonads probably develop at a somewhat smaller size.

To facilitate comparing the 2 species, we divided the size data for *Asterias vulgaris* and *Leptasterias polaris* into 3 classes. The first measured 0.5 to 5 cm in diameter and will be referred to as juveniles as they are the youngest individuals. For *A. vulgaris*, as indicated above, this size group probably represents the 1983 cohort. The second group measured 5 to 20 cm and we will refer to them as small adults. As indicated above, probably all *A. vulgaris* and most *L. polaris* in this group should have developed gonads (Smith 1940, Nichols & Barker 1984, Boivin et al. 1986). The third group measured 20 to 50 cm and will be called large adults. For *A. vulgaris*, juveniles were clearly separated from small adults (Figs. 2 & 3), whereas this was not the case for *L. polaris*. For both species, the discontinuity in

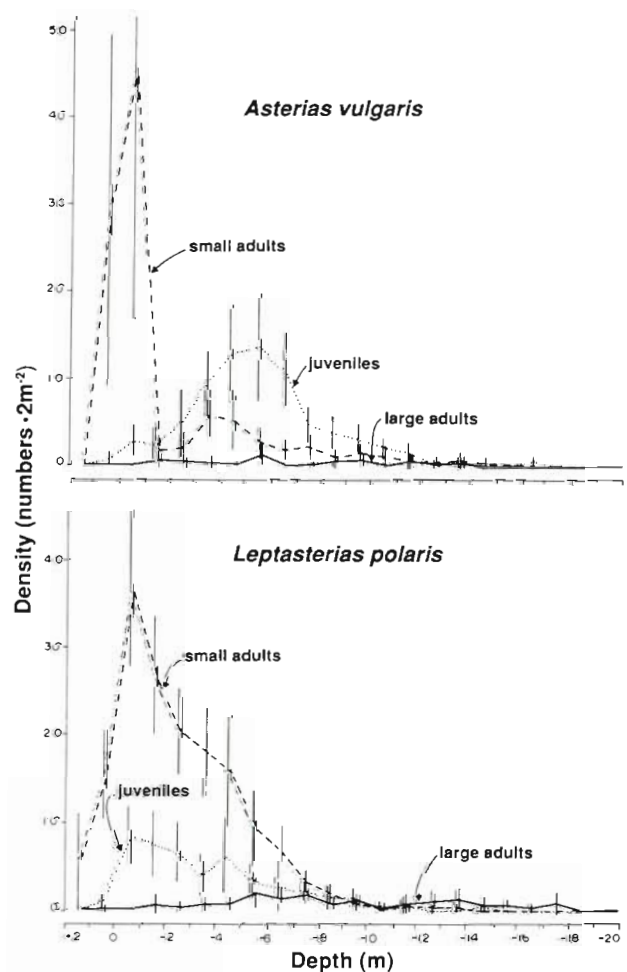
Fig. 3. *Asterias vulgaris* and *Leptasterias polaris*. Densities of juveniles (< 5 cm in diameter), small adults (5 to 20 cm) and large adults (> 20 cm) in relation to depth. Vertical lines indicate 95% confidence intervals

the distribution of small and large adults with depth justified considering them separately (Fig. 2).

Juvenile *Asterias vulgaris* attained a maximum abundance of 1.0 to 1.3 2m^{-2} at 4 to 7 m in depth (Fig. 3). By contrast, juvenile *Leptasterias polaris* were abundant in shallower water; they attained a peak of 0.8 2m^{-2} at 0 to 1 m and then decreased gradually with depth to virtually 0 at about 10 m (Fig. 3). Small adults of both species were most abundant near low water level, although the preference for this zone was not marked for *A. vulgaris*. Thus, the density of *A. vulgaris* dropped sharply between 0 to 1 and 1 to 2 m in depth, whereas *L. polaris* showed a more gradual decrease with depth. Large adults of both seastars were absent in shallow water (< 2 m) and present in low numbers at greater depths.

A separation of the samples according to substratum revealed a distinct association with particular substrata for the 3 size groups of *Asterias vulgaris* and *Leptasterias polaris* (Fig. 4). Juvenile *A. vulgaris* were practi-
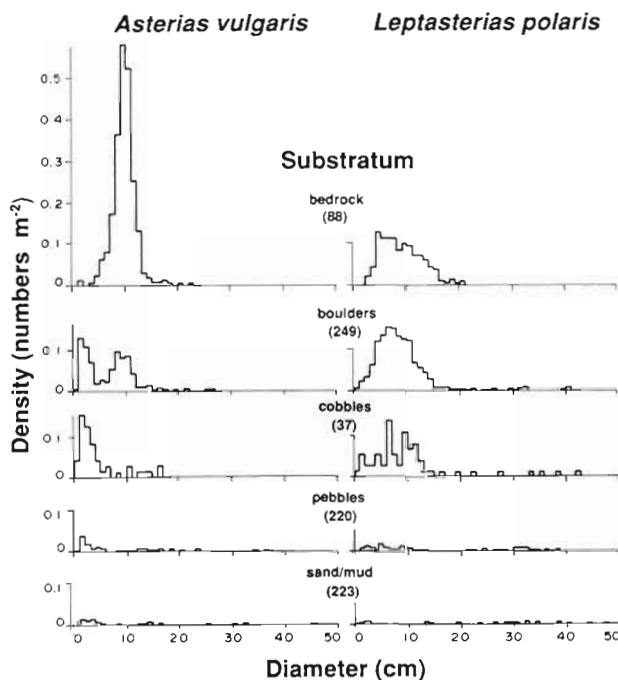

Fig. 4. *Asterias vulgaris* and *Leptasterias polaris*. Size structure in relation to substratum. Only the data from quadrats in which > 50 % of the surface area was one substratum type was used in calculating these distributions. The number of 2 m^2 quadrats observed for each substratum is indicated in parenthesis

cally only found in quadrats where the principal substatum was boulders or cobbles, small adults were by far the most abundant on bedrock and secondly on boulders, and large adults were only encountered mainly on pebbles and sand/mud. Juveniles and small adult *L. polaris* were concentrated on bedrock, boul-

ders and cobbles, and large adults were virtually absent on bedrock and presents on the other substrata.

An examination of the quadrat data organized in 2 m depth classes showed that *Crossaster papposus* was absent in the low intertidal zone down to 4 m and varied in density from 0.04 and 0.09 m^2 at greater depths. Its size structure contrasted with that of *Asterias vulgaris* and *Leptasterias polaris* (Fig. 5). The
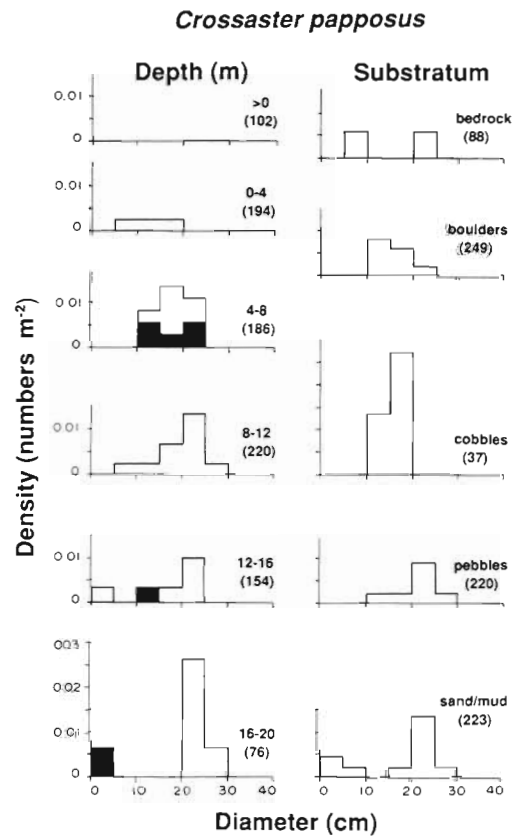

Fig. 5. *Crossaster papposus*. Size structure in relation to depth and substratum. Black regions of the size distributions to the left indicate individuals which were feeding. The number of 2 m^2 quadrats observed for each substratum is indicated in parenthesis

mean size of > 5 cm individuals showed a progressive increase with depth, and the largest individual found measured 28 cm in diameter (Fig. 5). Only 2 individuals < 5 cm in diameter were encountered and these were from below 13 m deep on sand/mud bottoms. According to Hancock (1958) the latter are 1 yr old individuals. A preference for sediment bottoms by juvenile *C. papposus* was also indicated by an earlier semiquantitative study in the Mingan Islands (Himmelman 1991); out of 299 individuals encountered, all 5 individuals measuring < 5 cm in diameter were found on sand or pebble bottoms below 11 m in depth.

Of the 6 *Solaster endeca* observed in our study, one

3.5 cm individual occurred at 17 m deep on mud bottom, and the others, measuring 6 to 31 cm in diameter, were found between 4 and 7 m on more rocky substrata. In our previous semiquantitative survey, 109 *S. endeca* were encountered (Himmelman 1991) and the size structure pattern was symmetrical with the mode at 20 to 25 cm in diameter: no individuals < 10 cm were observed.

Distribution of other species at Cap du Corbeau

To further understand the partitioning of different-sized seastars in different subtidal habitas, we examined the distribution of other organisms, in particular potential prey species. Two distinct zones were evident at Cap du Corbeau, a dense algal fringe near low water level and an extensive urchin-dominated community at greater depths. The sudden drop in algal abundance on rocky substrata within the first few meters in depth coincided with a sharp increase in the abundance of urchins (Fig. 6A, B). Algae susceptible to sea urchin grazing – *Alaria esculenta, Laminaria* spp. and *Develaria ramentacea* – predominated in the

fringe. Urchin grazing prevents their colonization at greater depths (Himmelman et al. 1983b, Himmelman & Nédélec 1990). All of the algae below 2 m in depth at Cap du Corbeau were grazing-resistant species, notably *Ptilota serrata, Phycodrys rubens, Turnerella pennyi* and *Agarum cribrosum*, and coralline algae (Himmelman & Nédélec 1990). The above pattern observed at Cap du Corbeau is characteristic of the subtidal zone over much of the northern Gulf of St. Lawrence and Newfoundland regions (Himmelman et al. 1983b, Himmelman 1985, Keats et al. 1985).

Most potential prey of seastars were concentrated in particular habitats. The mussel *Mytilus edulis* formed dense beds from the low intertidal region down to near the lower limit of *Alaria esculenta*, and then disappeared abruptly (Fig. 6). The limpet *Acmaea testudinalis* was most abundant on bedrock near low water level and decreased progressively in abundance with depth. A number of prey were associated with rocky substrata and their abundance increased to a peak between 2 and 6 m in depth, and then decreased at greater depths as rocky substrata became less frequent. These included the burrowing bivalve *Hiatella arctica*, the chitons *Tonicella* spp., the ophiuroid *Ophiopholis*
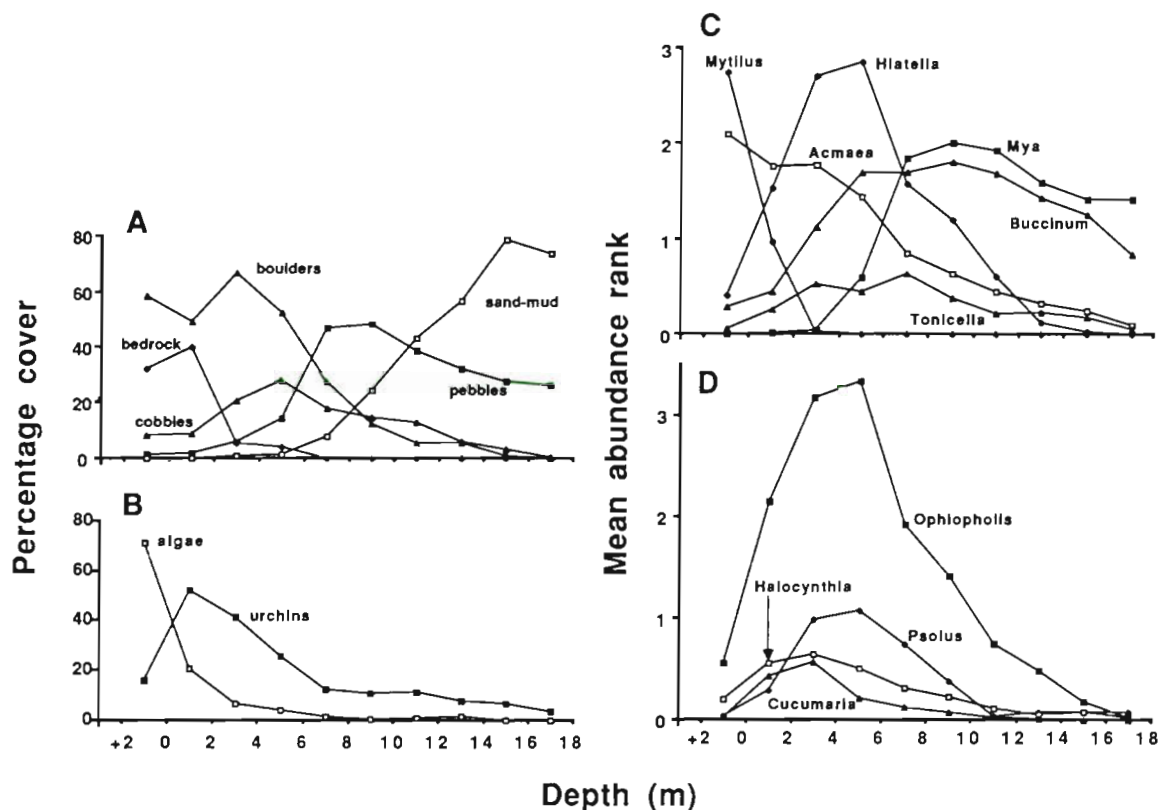

Fig. 6. Distribution of predominant subtidal organisms in relation to depth and substratum. Percentage cover was used to quantify the abundance of different substrata (A) and of macroalgae and urchins (B), whereas an abundance rank was used for the various other invertebrate species (C, D). Species in (C, D): *Mytilus edulis, Hiatella arctica, Acmaea testudinalis, Mya truncata, Buccinum undatum, Tonicella* spp., *Ophiopholis aculeata, Halocynthia pyriformis, Psolus fabricii, Cucumaria frondosa*

aculeata, the sea cucumbers *Psolus fabricii* and *Cucumaria frondosa*, and the ascidian *Halocynthia pyriformis* (Fig. 6C, D). Conversely, the most abundant clam species, *Mya truncata*, sharply increased in abundance between 2 and 6 m coinciding with the transition from rocky to sediment bottom (Fig. 6C). Other common sediment bottom invertebrates, such as *Clinocardium ciliatum*, *Spisula polymyna* and *Echinarachnius parma* (not shown in Fig. 6), were less abundant (mean abundance ranks of < 0.4 for all 2 m depth intervals) but nevertheless clearly associated with the sediment bottom below 6 m in depth.

Use of prey resources by seastars

In the intertidal zone, where mussel beds were common on bedrock and boulders, *Mytilus edulis* was the diet of *Asterias vulgaris* 99 % of the time and the diet of *Leptasterias polaris* 74 % of the time, and *Hiatella arctica* was a secondary prey for the 2 asteroids (Table 1). Virtually all of the seastars in this zone measured 5 to 20 cm in diameter (Fig. 2). With increasing depth to between 4 and 8 m, the diets of *A. vulgaris* and *L. polaris* showed a decrease in *M. edulis* and an increase in *H. arctica*, corresponding to changes in the abundance of these prey (Fig. 6C). In addition other species appeared. *Buccinum undatum* and *Mya truncata* were present in the diet of *L. polaris*, and *Tonicella* spp. and *M. truncata* in the diet of *A. vulgaris*. The clams *Clinocardium ciliatum*, *M. truncata*, *Serripes groenlandicus* and *Macoma* sp. became an important part of the diet of large adults of both seastars encountered below 8 m in depth. These changes in diet with depth strongly reflected changes in the prey available (Fig. 6C, D).

For *Asterias vulgaris*, the percentage of individuals feeding varied markedly with size (Fig. 7). It increased from 4.4 % for juveniles (< 5 cm) to ca 80 % for 5 to 15 cm individuals and then dropped to between 10 and 11 % for large adults measuring > 20 cm. The percentage feeding of the size groups between 0 and 20 cm was significantly higher at < 2 m in depth, where mussels were present, than at greater depths where mussels were absent (G-tests, p < 0.05). *Leptasterias*

Table 1 *Asterias vulgaris* and *Leptasterias polaris*. Proportion of different prey diets at different depths. Only a few individuals were encountered below 16 m in depth and none were feeding

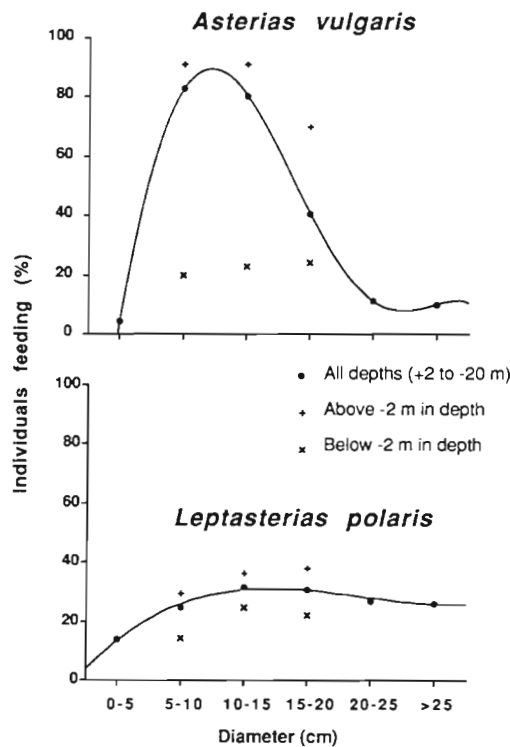| Prey species	< 0 m	0–4 m	4–8 m	8–12 m	12–16 m
Asterias vulgaris					
Acmaea testudinalis	0	0.3	0	0	0
Tonicella sp.	0	0	6.7	0	0
Mytilus edulis	99.0	92.1	6.7	0	0
Hiatella arctica	0.5	0.8	13.3	10.0	50.0
Mya truncata	0	0	6.7	0	0
Macoma spp.	0	0	0	10.0	0
Clinocardium ciliatum	0	0	6.7	20.0	0
Ophiopholis aculeata	0	0.8	0	0	0
Strongylocentrotus droebachiensis	0	0.3	0	0	0
Unidentified	0.5	5.7	53.3	60.0	50.0
Total feeding	197	367	11	10	2
Leptasterias polaris					
Acmaea testudinalis	0	0.9	0	0	0
Buccinum undatum	0	1.3	4.8	15.4	0
Littorina sp.	0	0.4	0	0	0
Margarites sp.	0	0.4	0	0	0
Tonicella sp.	0	0	1.6	0	0
Mytilus edulis	73.6	48.9	0	0	0
Hiatella arctica	5.7	17.9	42.9	38.5	0
Mya truncata	0	0.9	9.5	7.7	40.0
Mya arenaria	0	0.4	0	0	0
Macoma spp.	0	0.4	0	7.7	0
Clinocardium ciliatum	0	0	0	0	20.0
Serripes groenlandicus	0	0	0	7.7	0
Pectinaria granulata	0	0.4	0	0	0
Ophiopholis aculeata	0	0	1.6	0	0
Halocynthia pyriformis	0	1.3	1.6	0	0
Unidentified	20.8	26.6	38.1	23.1	40.0
Total feeding	53	229	63	13	5

Fig. 7. *Asterias vulgaris* and *Leptasterias polaris*. Proportion of individuals feeding in relation to size, for data from all depths, as well as for data from shallow water (< 2 m) and deeper water (> 2 m) treated separately. All individuals measuring > 25 cm in diameter were found below 2 m in depth

rians and tunicates; *S. endeca* was observed feeding only on echinoderms, mainly sea cucumbers (Dutil 1988, Himmelman 1991).

Mechanisms determining the distribution of seastars

Prey preferences vary markedly for different seastar species and further many seastars vary their prey selection as they increase in size (Sloan 1980). For example, Hancock (1955) showed that young *Asterias rubens* (< 5 cm) feed preferentially on small mussels and barnacles whereas larger individuals select larger prey such as oysters. The present study and those of Dutil (1988) and Himmelman (1991) show that the 4 common seastars in the northern Gulf of St. Lawrence also have distinct prey preferences. Since most prey species are strongly localized in their distribution (Fig. 6), changes in dietary preferences as seastars grow could be a major factor leading to the partitioning of different sized individuals related to depth and substratum. Dutil (1988) shows that *A. vulgaris, Leptasterias polaris, Crossaster papposus* and *Solaster endeca* are highly mobile; for example, large individuals can readily cover distances of > 5 m in 12 h. Since, at Cap du Corbeau, distances between the extremes in habitat (i.e. from bedrock in shallow water to sand and mud at 15 to 20 m depth) are relatively short (50 to 150 m), they can probably be traversed by seastars in a short period. Even if the search for prey is random, reduced movement while feeding on preferred prey could explain the aggregation of seastars in zones where preferred prey occur. Although distance chemodetection is weak in seastars (Sloan & Campbell 1981), any such ability would tend to enhance aggregation of seastars near their prey. Distance chemodetection has been demonstrated for *A. vulgaris* (Smith 1940, Zafiriou et al. 1972) and *C. papposus* (Sloan & Northway 1982).

Upon attaining 5 cm in diameter, and probably coincident with attaining sexual maturity, *Asterias vulgaris* and *Leptasterias polaris* show a marked shift in distribution to shallow water. This change appears to be related to the abundance of mussels in this zone, since most of these shallow water individuals were actively feeding on mussels (Fig. 7, Table 1). This shift, whether due to directed or random movements, resulted in aggregations of small adults at the lower limit of the mussel zone (Fig. 8A). Although we did not directly observe seastars moving to shallow water (and this would be difficult to follow using SCUBA in this cold water subtidal region), movements of *A. rubens* to the low edge of bivalve beds in the intertidal zone have been documented in Britain (Sloan & Aldridge 1981, Dare 1982). In several situations, where there were extensive mussel beds covering gently sloping bot-
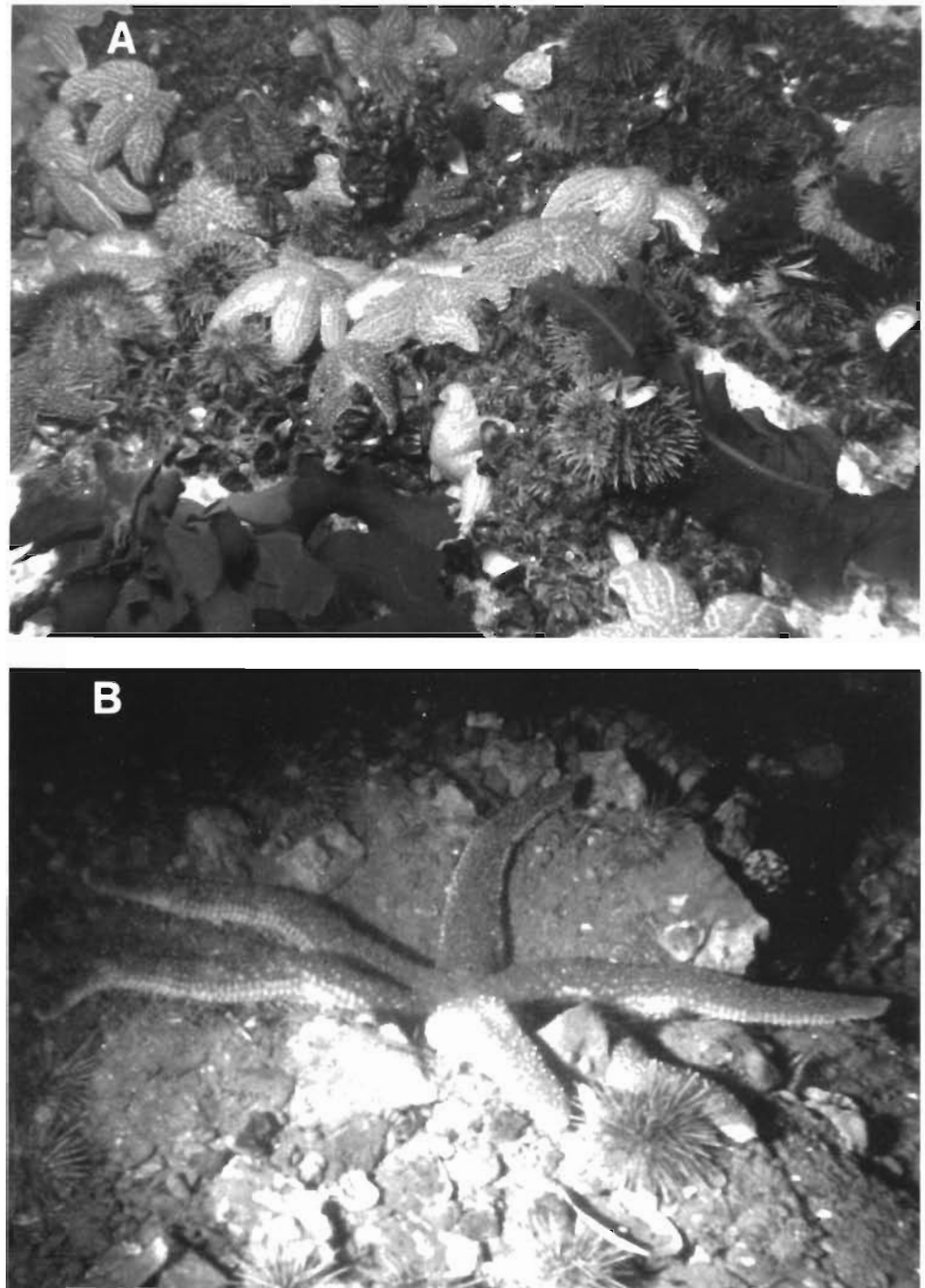
polaris showed a different relationship between feeding activity and size (Fig. 7). There was only a 2.3-fold increase between the 0 to 5 and 10 to 15 cm size groups (*G*-test, p > 0.01), and the proportion of individuals feeding did not decrease for larger individuals (*G*-test, p > 0.05). The proportion of small adults feeding tended to be higher above 2 m in depth, compared to below 2 m, and this difference was significant for the 5 to 10 and 10 to 15 cm size groups (*G*-test, p < 0.05). For juveniles, the proportion feeding was virtually the same for individuals above and below 2 m in depth. The proportion of > 20 cm individuals feeding was 2-fold greater for *L. polaris* than for large *A. vulgaris* (*G*-test, p < 0.05).

Crossaster papposus were observed feeding only 10 times; the urchin *Strongylocentrotus droebachiensis* was the prey 4 times, and the other times the prey could not be identified. *Psolus fabricii* was the prey in the one feeding observation for *Solaster endeca*. For *C. papposus*, 18 % (10/39) of individuals encountered were feeding, compared to 17 % (1/6) for *S. endeca*. During other studies in the Mingan Islands, *C. papposus* was also found to prey on urchins most frequently, but it was also observed consuming numerous other invertebrates, including other echinoderms, bivalves, cnida-

Fig. 8. (A) Aggregation of *Asterias vulgaris* and *Leptasterias polaris* at the lower edge of the mussel zone just below LWST In the same area urchins are grazing on *Alaria esculenta*. (B) Large *Leptasterias polaris* digging for a clam (probably *Mya truncata*) in a mixed substratum area at ca 9 m depth

toms, foraging fronts, with a mean density of > 100 seastars m^{-2}, measured > 10 m in width. Such aggregations were observed advancing through mussel beds at a rate of > 150 m mo^{-1}. Similar movement of *A. vulgaris* and *Asterias forbesi* into the intertidal zone have been reported by Menge (1979, 1982) at locations on the New England, USA, coast. These observed movements of *Asterias* spp. into shallow water occurred during summer, and a return to deeper water was noted in the autumn. Our study indicates that it is

the 5 to 15 cm individuals which move into shallow water whereas smaller *A. vulgaris* and *L. polaris* remain at intermediate depths in the rocky subtidal zone.

Large *Asterias vulgaris* and *Leptasterias polaris*, measuring 15 to 20 cm in diameter, aggregate at greater depths where mixed and sediment substrata predominate. We hypothesize that the gains from feeding on small mussels decrease with increasing size (mussels at Cap du Corbeau rarely exceeded 2 cm in length), and as a consequence there is a change in

dietary preference for larger prey. This hypothesis is supported by the observation of O'Neill et al. (1983) that the ingestion rates of *A. vulgaris* feeding on mussels (grams of mussels consumed per gram of seastar) decrease as the seastar increases in size. Our observations of predation at greater depths show that large *L. polaris* are well adapted to feeding on the larger organisms associated with sediment bottoms. Using their podia they dig holes to capture the large clams buried in the sediments (Fig. 8B). We have also observed large *A. vulgaris* and *L. polaris* preying on large gastropods such as *Buccinum undatum* and *Aporrhais occidentalis*, which were concentrated in the sediment zone (Table 1; Himmelman 1991).

Observations in the present study (Fig. 5) and in that of Himmelman (1991) indicate that small *Crossaster papposus* (< 5 cm in diameter) are only found on sediment bottoms below 11 m depth, suggesting that recruitment occurs in this habitat. Individuals > 5 cm in diameter occur over a wide depth range and showed an increase in mean size with depth (Fig. 5). We postulate that on attaining 5 cm in diameter, *C. papposus* migrate to shallow water (4 to 8 m) and then, with increasing size, move gradually to greater depths. The proportion of individuals feeding was highest at 4 to 8 m depth (42 %), which corresponds to the zone of transition from rocky to sediment substrata (Fig. 5). This suggests that food resources were more available there. The diverse diet of *C. papposus* (Himmelman 1991) may explain why particular size groups (except for juveniles) are not strongly associated with specific habitats.

Potential species interactions

A strong impact of seastar predation is suggested by the abrupt drop in numbers of mussels in the first few meters depth where aggregations of small adult *Asterias vulgaris* and *Leptasterias polaris* become abundant (Figs. 2 & 8A). Mussels were limited to a few meters in depth even though the subtidal zone is a favourable environment for their settlement and growth. For example, they are abundant on substrata, such as navigation buoys, which are not accessible to seastars (Fradette & Bourget 1980). In a study in the St. Lawrence Estuary, Brault & Bourget (1985) showed that mussels heavily colonize artificial substrata at 5 m deep, but an accidental entry of *L. polaris* during their study caused heavy mortalities. Our observation of many small adult *A. vulgaris* and *L. polaris* actively feeding at the low edge of the mussel zone suggests that this predation limits mussels to shallower depths. Similarly, Menge (1979) reported that seastar predation limits mussels to shallow water along the New England

coast, although in this region *A. forbesi* and *A. vulgaris* are the asteroid predators.

The high degree of overlap between *Asterias vulgaris* and *Leptasterias polaris* in their vertical distribution and use of spatial and food resources indicates that they may be competing. Intraspecific competition among young *A. vulgaris* feeding on mussels has been indicated by O'Neill et al. (1983) and similar competition may exist between young *A. vulgaris* and *L. polaris* feeding on mussels near low water level. Large adults of the 2 species may also compete for molluscan prey in the deeper sediment zone. However, caution must be taken in concluding that competition is occurring based on ecological overlap, since factors other than resource limitation may limit populations. For example, Menge (1979) indicates that, in spite of a high degree of ecological overlap between populations of *A. vulgaris* and *A. forbesi* in New England, competition is probably weak or sporadic. He suggests that disease and heavy storms probably maintain these populations below the resource-determined equilibrium. A facilitative interaction also exists between *A. vulgaris* and *L. polaris* in the Mingan Islands, since we have often observed *A. vulgaris* preying on remains of clams left by *L. polaris*, and in a few instances *A. vulgaris* was found crawling under the arms of *L. polaris* to steal its prey (Dutil 1988).

Asterias vulgaris and *Leptasterias polaris* probably also interact with the whelk *Buccinum undatum*, the most abundant of the benthic carnivores in the Mingan Islands (Jalbert 1986). These 3 large species potentially compete for prey, given their sympatry in the subtidal zone and their shared preference for bivalves (for diet of *B. undatum* see Caddy & Chandler 1968, Nielsen 1975). In addition, seastars prey on whelks. In our sampling, *B. undatum* was the second and third most important prey of *L. polaris* at depths between 0 and 12 m (Table 1). We did not observe *A. vulgaris* preying on whelks in this study, but this was documented by Himmelman (1991). A predatory interaction between seastars and *B. undatum* is further indicated by the strong escape response (violent twisting) of *B. undatum* to *A. vulgaris* and *L. polaris* (Thomas & Himmelman 1988). Since small whelks only display a fleeing response when exposed to *L. polaris* (Harvey et al. 1987), they are probably more vulnerable to seastar predation. During our study, we recorded *L. polaris* preying on *B. undatum* 8 times. In 7 of these attacks the whelks measured < 3 cm in length and in 5 of them the seastar measured 7 to 13 cm in diameter. The one attack on a larger whelk (7 cm) was by a large adult *L. polaris* (42 cm). This suggests that the predatory interaction is mainly between small adult *L. polaris* and small *B. undatum*. The well-developed escape response of large *B. undatum* to *L. polaris* probably reduces its vulnerability to seastar attacks. Surpris-

ingly, in the sediment zone where large whelks and seastars are concentrated, groups of large *B. undatum* are sometimes found near *L. polaris* feeding on clams. In this situation, the escape response appears to be inhibited or subservient to the feeding stimulus. *B. undatum*, like *A. vulgaris*, feeds on prey remains left by *L. polaris*, and is sometimes found with its proboscis deep within sediments which had been recently disturbed by the digging activities of *L. polaris* (Dutil & Himmelman unpubl.). These observations suggest a facilitative interaction (sensu Duggins 1981) between *B. undatum* and *L. polaris*. The inhibition of the whelk's escape response when the seastar is feeding may be advantageous in that it permits whelks to profit from the seastar's foraging activities.

In conclusion, our study shows a distinct spatial partitioning of different size groups of *Asterias vulgaris* and *Leptasterias polaris* in the subtidal zone and we postulate that this is largely brought about by the aggregation of particular size groups in habitats where their preferred prey are concentrated. Juveniles of these asteroids are found in the upper subtidal zone (at a slightly greater depth for *A. vulgaris* than for *Leptasterias polaris*), and upon attaining about 5 cm in diameter they move towards the low intertidal zone to feed on mussels. This aggregation in shallow water is most pronounced for *A. vulgaris*. The predation by these small adults likely determines the lower limit of mussel beds. Finally, upon attaining 15 to 20 cm in diameter, the seastars shift their distribution to sediment bottoms in deeper water where larger prey are abundant. *Crossaster papposus* and *Solaster endeca* are less abundant seastars. The prey resources they exploit differ from those used by *A. vulgaris* and *L. polaris*. The abundance and frequent predatory activity of seastars in the northern Gulf of St. Lawrence suggests they are an important predatory guild, but given the spatial partitioning of different size groups within the subtidal zone the impact of their foraging is probably a function of the specific habitat.

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