Distribution and feeding ecology of the seastars *Leptasterias polaris* and *Asterias vulgaris* in the northern Gulf of St Lawrence, Canada

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Extensive field observations were made in the Mingan Islands, northern Gulf of St Lawrence, to evaluate spatial and temporal variations in the use of habitat and prey resources by two major subtidal predators, the seastars *Leptasterias polaris* and *Asterias vulgaris*. Although both seastars have similar size structures and generally overlapped in their spatial and temporal distribution, the degree of overlap varied in different sites and appeared to be related to prey abundance, substratum type and slope. Three general patterns were observed: (1) both species aggregating in shallow water and decreasing in numbers with depth; (2) the two species showing inverse depth distributions; and (3) both seastars occurring in low numbers across the subtidal zone. Temporal changes in availability of the preferred prey of the two seastars, the mussel *Mytilus edulis*, appeared to be a major factor affecting their abundance and distribution. The two seastars occurred together in dense aggregations on mussel beds in shallow water. They consume similar-sized mussels until the number of mussels becomes reduced when *A. vulgaris*, but not *L. polaris*, begins to select larger mussels. Once a mussel bed is decimated, the seastars appear to move away, possibly in search of other beds. Intensive seastar foraging limits the distribution of mussels to a few metres in depth. Below the mussel zone, the two seastars are spatially segregated at a small spatial scale (1 m² quadrat) and select different alternative prey, *L. polaris* feeding mainly on the crevice-dwelling clam *Hiatella arctica* and *A. vulgaris* on the ophiuroid *Ophiopholis aculeata*. The size partitioning of the preferred prey in shallow water, and spatial segregation and selection of different alternative prey at greater depths may reflect mechanisms permitting the two seastars to coexist.

INTRODUCTION

The distribution and abundance of species are determined by a combination of factors including biogeographical history, environmental conditions (e.g. temperature, salinity, storms), availability of spatial and food resources, rates of reproduction, mortality and migration, and intra- and interspecies interactions (e.g. presence of predators or competitors). At a local scale, the availability and use of resources and interactions with other individuals are key factors regulating the morphology and behaviour of individuals and these in turn affect populations (Branch, 1975; Brown et al., 1979; Underwood, 1988; Hopkins & Gartner, 1992; De'ath & Moran, 1998).

The seastars, *Leptasterias polaris* (Müller & Troschel, 1842) and *Asterias vulgaris* (Verrill, 1866), are major predators in the subtidal community in the northern Gulf of St Lawrence (Himmelman, 1991; Himmelman & Dutil, 1991). *Leptasterias polaris* is common in the north-western North Atlantic and Canadian Arctic regions (Grainger, 1966) and attains its southern limit in the southern Gulf of St Lawrence. This species or a subspecies may also be found in the Beaufort, Chukchi and Bering Seas (Hoberg et al., 1980; H.M. Feder, personal communication). In contrast, *A. vulgaris* (possibly synonymous with *Asterias rubens* in Europe, Nichols & Barker, 1984)

extends from southern Labrador south to North Carolina (Bousfield, 1960). Thus, the two seastars overlap geographically in the Gulf of St Lawrence. Moreover, in the northern Gulf of St Lawrence, both species have similar vertical distributions, juveniles and small adults occurring in high densities on hard substrata in shallow water and large adults mainly found on soft bottoms at greater depths (Jalbert, 1986; Himmelman & Dutil, 1991).

Recent studies of *L. polaris* and *A. vulgaris* have focused on large adults (>20 cm in diameter) and considered their distribution and abundance (Himmelman & Lavergne, 1985; Jalbert, 1986; Jalbert et al., 1989; Himmelman, 1991; Himmelman & Dutil, 1991), activity patterns (movement, feeding and reproduction; Himmelman et al., 1982; Boivin et al., 1986; Dutil, 1988; Himmelman & Dutil, 1991; Rochette et al., 1994; Hamel & Mercier, 1995) and interspecific interactions (Morissette & Himmelman, 2000a,b). Dutil (1988) and Himmelman & Dutil (1991) suggest that *L. polaris* and *A. vulgaris* are competing because of their overlap in space and food utilization. Large adults of both species feed principally on large infaunal bivalves, such as *Mya truncata* (Linnaeus, 1758), *Spisula polynyma* Stimpson, 1860 and *Clinocardium ciliatum* (Fabricius, 1780) and secondarily on echinoderms and polychaetes. At times *A. vulgaris* kleptoparasitizes (steals) prey from *L. polaris* (Morissette & Himmelman,

2000a,b). In addition, *L. polaris* is sometimes preyed upon by *A. vulgaris* and exhibits a distinct escape response to *A. vulgaris* (Dutil, 1988; Himmelman, 1991; Morissette & Himmelman, 2000b). Although the above studies focused on large adults, the interactions between juvenile (0–5 cm) and small adult (5–20 cm) *L. polaris* and *A. vulgaris* could be more intense as they occur in high densities in the rocky subtidal zone and feed principally on the bivalves *Mytilus edulis* Linnaeus, 1758 and *Hiatella arctica* (Linnaeus, 1767) and the brittlestar *Ophiopholis aculeata* (Linnaeus, 1767) (Dutil, 1988; Himmelman & Dutil, 1991). The existing information on juveniles and small adults is scarce and limited to observations during one summer at one site (Himmelman & Dutil, 1991). Although these observations indicate similar distributions and prey selection for the two seastars, such limited observations could be misleading. For example, marked inter-site and inter-annual shifts in abundance, distribution and prey use have been reported for a number of seastars (including *A. vulgaris*) in different geographical regions [Smith (1940) in eastern Canada, Menge (1979) in New England, Sloan (1980) in England]. Thus, detailed information is needed on the use of space and prey resources for the two seastars over different sites and years, to better evaluate the degree of niche overlap and possible mechanisms permitting coexistence.

Several mechanisms have been proposed to explain the coexistence of ecologically similar species in situations of strong overlap in the use of resources. These mechanisms may be external (e.g. predation) or may depend on the species interacting (e.g. partitioning, Schoener, 1974b). Possible external factors which may cause niche differentiation are selective predation or parasitism on the dominant species (Rathcke, 1976; Strong, 1982; Hixon & Menge, 1991), and environmental variability that keeps abundance below the carrying capacity of the environment (Roughgarden & Feldman, 1975; Wiens, 1977; Schoener, 1982). It is unlikely that the abundance and distribution of *L. polaris* and *A. vulgaris* are limited by predators or parasites. Predators of these seastars are uncommon and probably limited to other seastars (Dutil, 1988; Himmelman, 1991; personal observation). Although parasites have been described for these seastars (Hoberg et al., 1980; Grygier, 1986; Hamel & Mercier, 1994; Claereboudt & Bouland, 1994), they are not known to cause mortality. Massive mortality caused by storms or diseases, as observed for *Asterias* spp. in New England (Menge, 1979; Ojeda & Dearborn, 1989) has never been observed in the Mingan Islands.

Interacting species may evolve adaptations to partition resources to reduce overlap (Branch, 1984). Prey species or habitat use may be partitioned in space or time, or prey may be partitioned by species or size (e.g. Dodson, 1970; Sprules, 1972; Menge, 1974; Roughgarden, 1974; Fenchel, 1975; Arrontes & Underwood, 1991; Hopkins & Gartner, 1992). Dutil (1988) indicates that large adult *L. polaris* and *A. vulgaris* show a degree of prey species partitioning but no partitioning of prey by size. The overlap in the geographic and bathymetric distributions of the two seastars suggests that resources are not partitioned in space and there is also no evidence of partitioning over time. Both seastars feed actively throughout the summer (Himmelman, 1991; Himmelman & Dutil, 1991). Moreover,

as feeding bouts are generally prolonged (ingestion periods for large adults frequently exceed 24 h; Dutil, 1988), temporal partitioning of resources over daily or tidal cycles is unlikely. Further, the activity budgets of large adults of both species (relative time spent searching for, capturing and manipulating prey) are similar, and the time spent manipulating prey varies little with seastar size (Dutil, 1988).

Thus, the existing information (mainly on large adults) indicates that: (1) *L. polaris* and *A. vulgaris* share habitat and food resources; (2) there is no evidence that external factors (e.g. predation, storms, diseases) control their numbers; and (3) they show no apparent spatial or temporal partitioning of resources. This suggests that these seastars should interact strongly, especially juveniles and small adults that aggregate in high numbers in shallow water where mussels, their preferred prey, are abundant. The present study examines the distribution, abundance, and use of prey resources, of juvenile and small adult *L. polaris* and *A. vulgaris* over temporal (3 y) and spatial (11 sites) scales that should be adequate to evaluate factors determining their distributions and possible mechanisms permitting their coexistence in the rocky subtidal zone. The variety of sites we studied permitted accessing adaptations of the seastars to contrasting habitats (variations in slope, substratum, prey type and abundance, and abundance of inter- and conspecific seastars).

MATERIALS AND METHODS

The study was conducted in the Mingan Islands in the northern Gulf of St Lawrence, Canada (Figure 1). Subtidal communities in this area have been previously described by Himmelman (1991). Detailed field observations were conducted at three sites, Petite Ile au Marteau, Ile aux Goélands and Cap du Corbeau, located ~3–4 km from each other. At each site, the abundance, size structure, diet and feeding frequency of *Leptaterias polaris* and *Asterias vulgaris* were determined and also the distribution, abundance and size structure of their prey. At each site observations were made along six transects that ran perpendicular to the shore, from the lower limit of the intertidal zone to the end of rocky substratum (~8–14 m below lowest water of spring tides, LWST). The transects were spaced at 25 m intervals along the shore. Using 1 m² quadrats placed at 1 m intervals, alternating from one side to the other of each transect (the side of the first quadrat chosen at random), divers recorded: (1) depth; (2) percentage cover of different type of substrata (sand, pebbles, cobbles, boulders and bedrock; Himmelman & Dutil, 1991; Wentworth, 1922); (3) densities of major prey items (the mussel *Mytilus edulis*, the crevice-dwelling clam *Hiatella arctica*, the limpet *Acmaea testudinalis* (O.F. Müller, 1776), the chiton *Tonicella marmorea* (Fabricius, 1780), the whelk *Buccinum undatum* (Linnaeus, 1758) and the brittlestar *Ophiopholis aculeata*; (4) densities of each seastar species and individual size (radius=distance from the centre of the disc to the end of the longest arm; Barnes & Powell, 1951; we subsequently doubled the value to convert to diameter) of each seastar; (5) percentage of individuals feeding; and (6) species and size of prey consumed. We sampled at Petite Ile au Marteau and Ile aux Goélands in
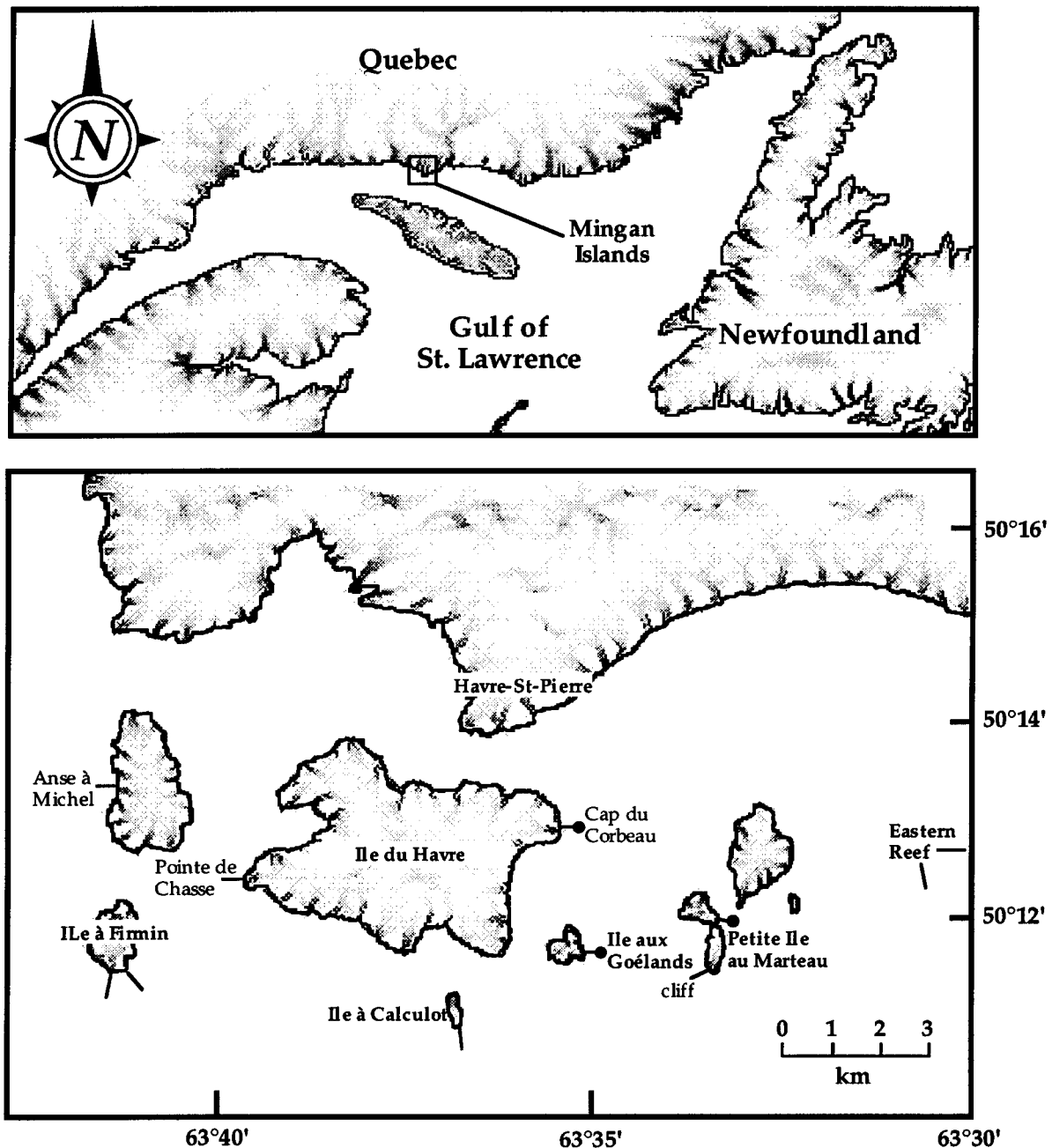
Figure 1. Location of the three intensively studied sites (●) and rapid transect sites in the Mingan Islands, northern Gulf of St Lawrence. The lines indicate position of transects.

late May to early June 1996, 1997 and 1998 and in August 1997, and at Cap du Corbeau in late May to early June in both 1996 and 1997.

To increase the number of observations of prey selection, we systematically crossed back and forth over a 300 m section along each site and recorded for each feeding asteroid encountered, the depth, its size, and the species and size of prey being consumed. This sampling was done in late May to early June and in August in 1996 and 1997 at Petite Ile au Marteau and Ile aux Goélands and in June and August 1996 and June 1997 at Cap du Corbeau.

From the quadrat sampling we calculated Yule's V coefficient of association (Kendall, 1947) as an index of prey selection relative to availability (Pearre, 1982). The V-selectivity index ranges from −1 to +1, with 0

values indicating that prey are consumed according to availability. To evaluate the overlap in diet between *L. polaris* and *A. vulgaris* we calculated both Morisita's C_λ index (recommended when different food alternatives exist within a habitat, Morisita, 1959; Horn, 1966) and the per cent overlap calculation of Menge & Menge (1974).

To evaluate the degree to which the three intensively studied sites were representative of the Mingan Islands, additional observations were made at eight other rocky bottom sites (Figure 1) using the 'rapid transect' method of Himmelman (1991). Briefly, two divers made observations along a ~3 m wide transect running perpendicular to the shore (from the intertidal zone to the lower end of the rocky zone) on the distribution and

diet of *L. polaris* and *A. vulgaris* and the distribution of potential prey. Rapid transect locations were chosen after preliminary dives to identify sites meeting the criteria of a rocky bottom and the presence of both seastar species. Of ~15 sites thus identified, eight were chosen for sampling. Transects were made at the southern and south-eastern side of Ile à Firmin, at the southern and eastern side of the Eastern Reef and at Ile à Calculot, Pointe de Chasse (Ile du Havre), Anse à Michel (Ile du Fantôme) and the western cliff of Petite Ile au Marteau.

Statistical analysis

Two-way ANOVAs were used to test the null hypothesis of no differences in density between seastar species and depth for each year at each site, and also to test the hypothesis of no differences between sampling dates and depth for each prey at each site. A three-way ANOVA was used to test for differences in the density of seastars between seastar species, depth and season (spring and summer) in 1997. A two-way ANOVA was used to test for differences in abundance between the two seastars in different years. Quadrats from the same 2 m depth intervals were used as replicates for the statistical analyses. Data were log transformed $(\ln(y+1))$ when necessary to obtain normality and homoscedasticity of the data. Normality was tested using the Shapiro–Wilk's test (SAS, 1991) and homogeneity of variances was tested using the Levene test (Snedecor & Cochran, 1989). When these assumptions were not met, ANOVAs were applied to both the raw and to rank transformed data, as suggested by Conover (1980) and the former was chosen for presentation when results were the same for the two analyses and the latter when they were not. A multiple pairwise comparison test (least square means) was used to test for specific differences within a significant source of variation (SAS, 1991).

Differences in percentage feeding were evaluated using a generalized linear model with a binomial distribution and an incomplete factorial design (McCullagh & Nelder, 1989) and multiple comparisons were made using Glimmix's macro (Littell et al., 1996).

The significance of the V prey selectivity index was evaluated using χ^2-tests with one degree of freedom applied to two-way contingency tables (Kendall, 1947; Sokal & Rohlf, 1981; Pearre, 1982).

Comparisons of the size of mussels selected relative to availability were made for different depth zones using χ^2-tests, using the adjusted residuals to identify specific differences between observed and expected values for each mussel size class (Steel & Torrie, 1985; Agresti, 1996). To test whether mussel size consumed was related to predator size, t-tests were applied to evaluate if Pearson correlation coefficients (r) were significant (Sokal & Rohlf, 1981; Steel & Torrie, 1985).

A principal component analysis (PCA, Joliffe, 1986) was applied to the data from the 571 quadrats sampled over the 3-y study to evaluate whether seastar density was associated with prey abundance, substratum type, slope, depth and the density of the other seastar. In addition, correlation analyses were made to quantify associations revealed by the PCA analysis. To evaluate the significance of Spearman rank correlation coefficients (r_s), t-tests were applied (Steel & Torrie, 1985).

RESULTS

Prey distribution and abundance

Prey abundance and distribution varied among the contrasting shore profiles at the three study sites (Figure 2). At Petite Ile au Marteau, a vertical bedrock wall extended from the intertidal zone down to a depth of ~8 m and was followed by a boulder and cobble talus down to 14 m where sand and mud substrata began (Figure 2). A narrow mussel (*Mytilus edulis*) bed was present in shallow water (0–2 m in depth, maximal abundance at 1 m), just below a belt of brown macroalgae. Mussel abundance decreased markedly over the study period, from ~3000 ind m^{-2} in 1996 to ~1700 ind m^{-2} in 1997 ($P=0.002$) and ~900 ind m^{-2} in 1998 ($P=0.06$; Figure 3). The crevice-dwelling clam, *Hiatella arctica*, was most abundant between 3 and 6 m and its density decreased, although not significantly, at the beginning of the boulder–cobble slope at greater depths (Figure 3). The brittlestar, *Ophiopholis aculeata*, was most abundant on vertical surfaces between 3 and 6 m (~300 ind m^{-2}) and its numbers dropped on the boulder–cobble slope ($P<0.001$; Figure 3). The limpet, *Acmaea testudinalis*, and chiton, *Tonicella marmorea*, were far less abundant (~20–50 ind m^{-2}) and their numbers were relatively constant along the depth gradient (Figure 3; $P>0.05$). A higher abundance of *A. testudinalis* was recorded at 1 m in 1996 and May 1997, however, the increase was not significant given the high variability of the data. The whelk, *Buccinum undatum*, first appeared at 3 m in depth and attained peak numbers in the lower boulder–cobble zone at 11–13 m (Figure 3).

At Ile aux Goélands the bottom was a gently-sloped bedrock platform (Figure 2). At ~11 m the platform gave way to a vertical wall which extended to ~20 m, where a sand–mud slope began. A mussel bed covered a ~5-m wide area from the intertidal zone to ~2 m in depth (Figure 2). As at Petite Ile au Marteau, the density of mussels decreased markedly from 1996 to August 1997 ($P=0.004$; Figure 3), but remained stable between 1997 and 1998 ($P=0.99$). In August 1997, empty shells due to seastar predation were as abundant as living mussels. Whereas there were only scattered kelp [*Alaria esculenta* (Greville, 1830) and *Laminaria* sp.] in the mussel zone in 1996 and 1997, a dense cover of macroalgae, mainly *A. esculenta*, was present in 1998. The algal colonization likely developed during the winter when urchins move to deeper waters due to increased wave action. The macroalgal cover may have protected the mussels from predation during the summer. There was a scarcity of organisms between 2 to 6 m, where the bedrock bottom was in places covered by pebbles (transition zone; Figure 2). Below the transition zone, *H. arctica* and *O. aculeata* were the most abundant prey (Figure 3). The abundance of *H. arctica* was relatively constant along the depth gradient (200–500 ind m^{-2}). In contrast to Petite Ile au Marteau, ophiuroid abundance increased with depth. The density of ophiuroids was <500 ind m^{-2} at 6–8 m (shallow ophiuroid zone), 500–1000 ind m^{-2} at 8–11 m (deep ophiuroid zone) and peaked at ~1700 ind m^{-2} on the vertical wall (Figures 2 & 3). *Acmaea testudinalis* was most abundant at 1 m and in low numbers at all greater depths. Its density at 1 m increased seven-fold from June 1996 to

August 1997 ($P < 0.001$; Figure 3). *Tonicella marmorea* had a similar depth distribution and also increased in density from 1996 to August 1997 at 1 m ($P = 0.004$). As at Petite Ile au Marteau, the abundance of *B. undatum* increased with depth to a maximum at 11 m (Figure 3) and then dropped on the vertical wall.

Finally, the medium-sloped bottom at Cap du Corbeau supported a gradation in substrata, from boulders to cobbles and then sand (Figure 2). In 1996, mussels were extremely scarce (~ 3 ind m^{-2}) compared to the other sites and were mainly found in the first 3 m, where kelp was abundant. However, large numbers ($\sim 10,000$ m^{-2}) of mussel recruits (< 2 mm in shell length) were observed under macroalgae in 1997. There were also increases in *A. testudinalis* and *T. marmorea* from 1996 to 1997 (recruits measuring < 4 mm represented ~ 80–90% of the individuals of both species in 1997; Figure 3). As at Petite Ile au Marteau, *B. undatum* density increased as finer substrata became more abundant at greater depths.

Most of the eight rapid transect sites generally resembled one of the three intensively studied sites. At seven of the eight sites (all except Anse à Michel) a mussel bed was found within the first metres, associated with a zone of kelp and at Ile à Calculot and at both Eastern Reef sites, the mussel bed extended to 4 m in depth. The Ile à Firmin and Ile à Calculot sites were

gently-sloped bedrock platforms, as at Ile aux Goélands, and sandy bottoms began at ~ 20 m in depth and 300 m from the shore. The Eastern Reef sites consisted of a series of bedrock steps from ~ 2 to ~ 18 m in depth, the southern side was exposed to the predominant westerly winds and the easterly side to eastern winds during storms. At the western cliff of Petite Ile au Marteau a bedrock platform, similar to that at Ile aux Goélands, extended to ~ 15 m, and then a vertical wall extended to ~ 40 m. At Pointe de Chasse a rocky face extended from 0 to ~ 10 m and was followed by a steep bedrock slope down to ~ 20 m, where sand began. As observed for mussels, *A. testudinalis* was most abundant in shallow water. *Hiatella arctica* and *O. aculeata* were found mainly on bedrock, the former was abundant at all depths and the latter at greater depths. Anse à Michel resembled Cap du Corbeau, having a medium-sloped bottom with a gradation in substrata (fine sediments began at ~ 6 m), no mussel bed and a low abundance of other prey.

The Ile à Calculot and Eastern Reef sites were unusual in that there were extensive beds and patches of large mussels (~ 4–6 cm in length) at depths of ~ 6 m. In June 1997 these mussels were being preyed upon by large aggregations of *Leptasterias polaris* and *Asterias vulgaris* (~ 3 times more *L. polaris* than *A. vulgaris*). Observations at Ile à Calculot in August 1997 showed that many mussel
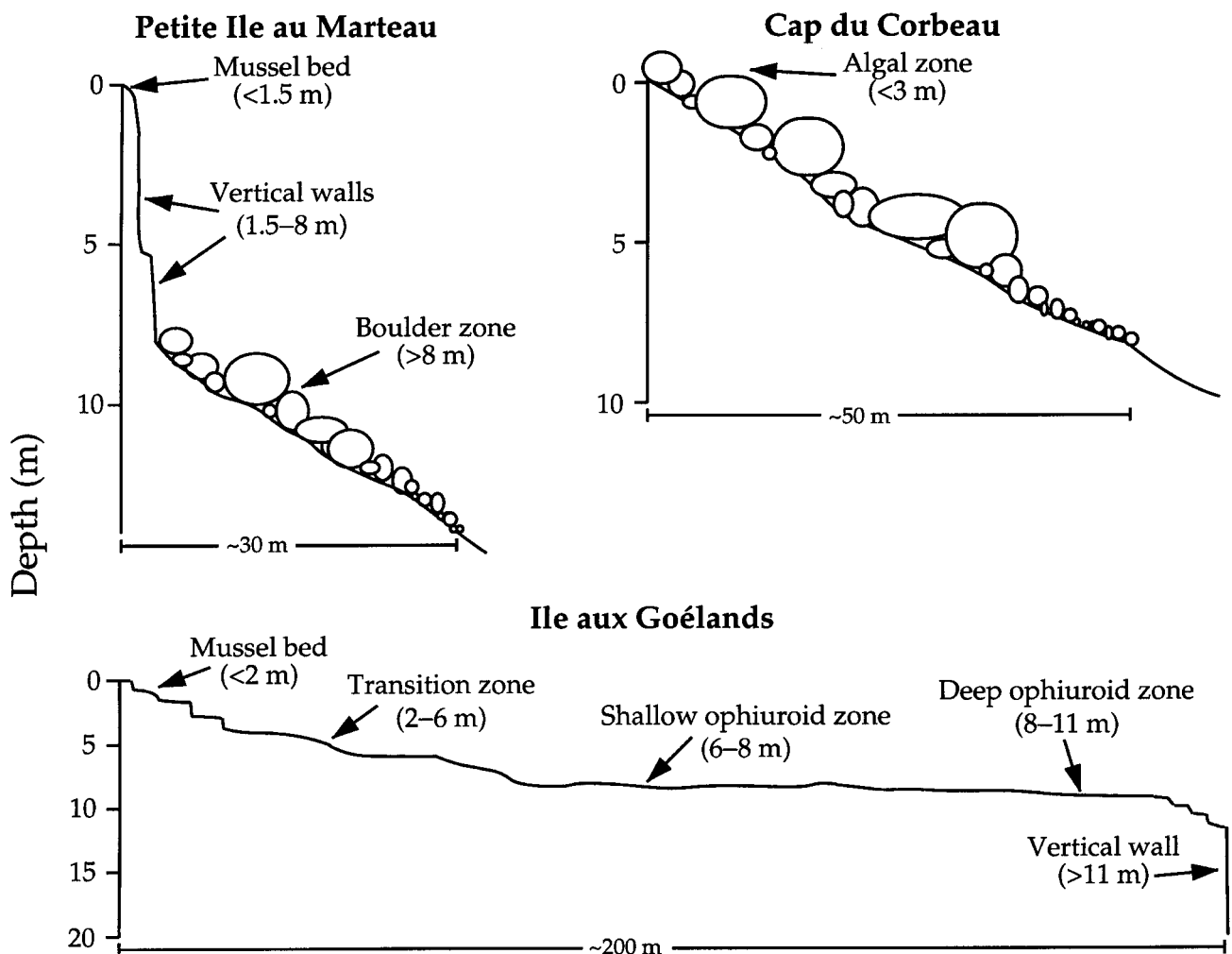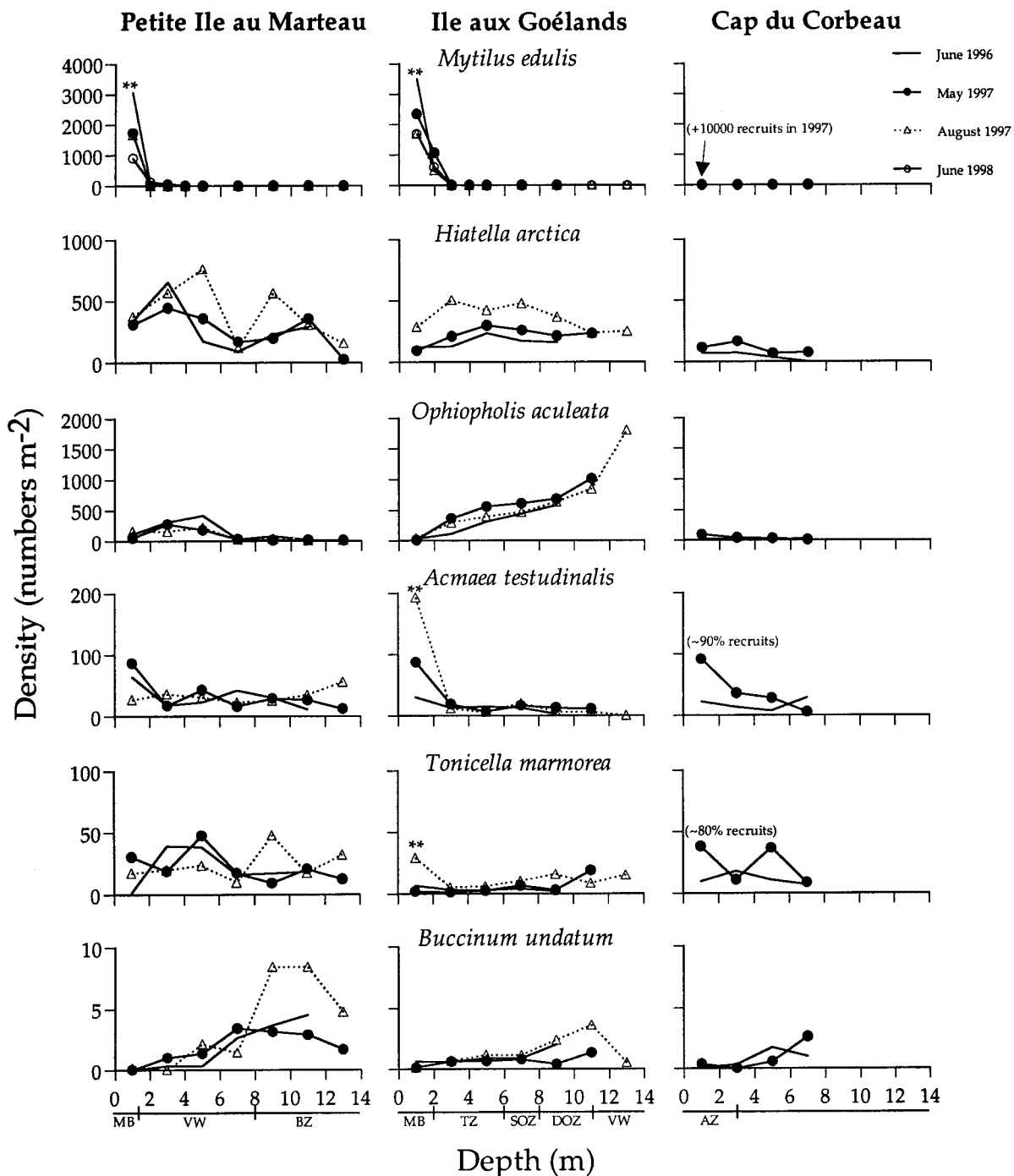

Figure 2. Bathymetric profiles for the three intensively studied sites.
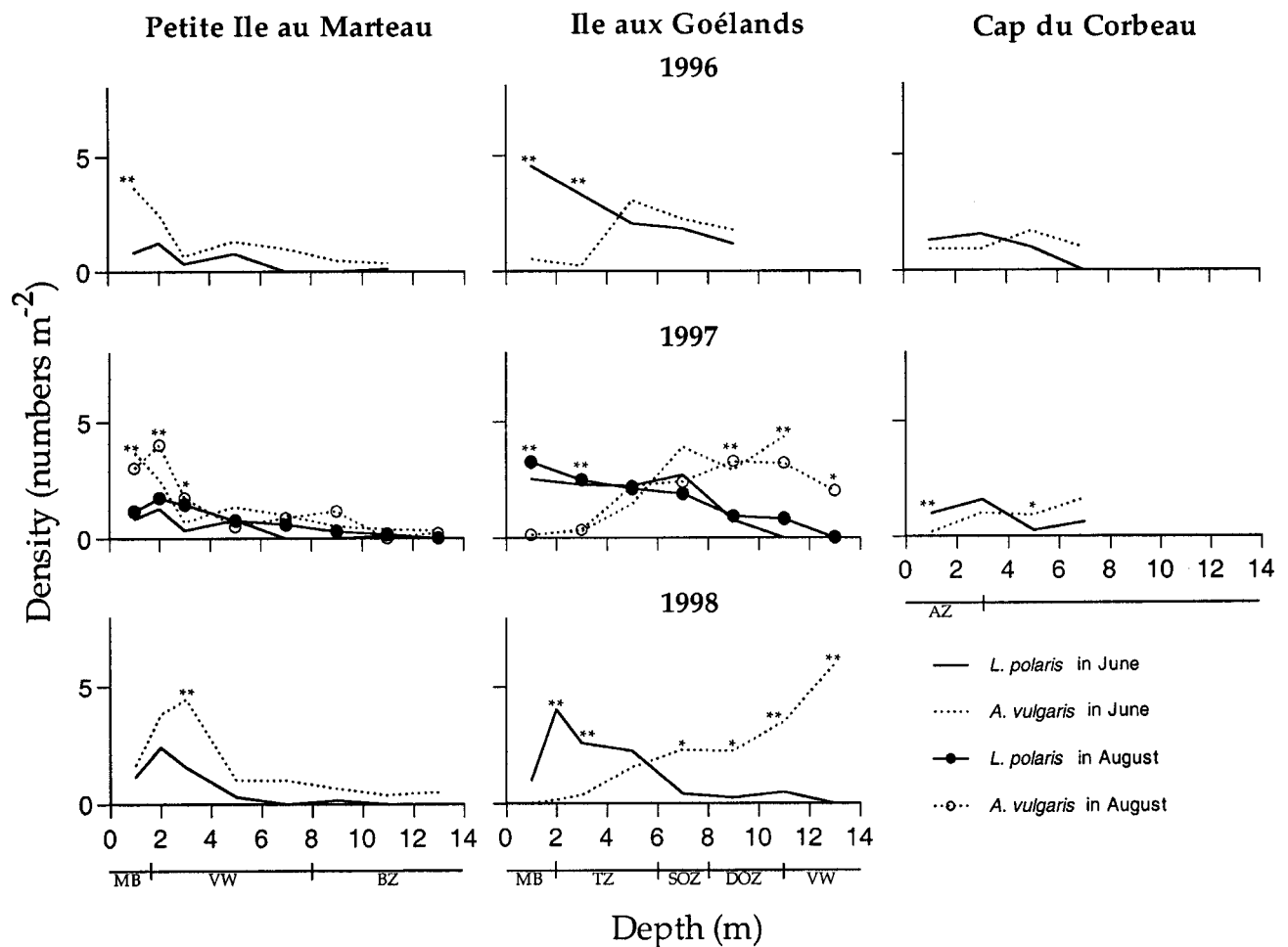
Figure 3. Prey abundance at Petite Ile au Marteau and Ile aux Goélands in June 1996, May 1997 and August 1997 (+June 1998 for mussels), and Cap du Corbeau in June 1996 and May 1997 (some lines are not visible due to overlap). **, difference in abundance of *Mytilus edulis* between June 1996 and May 1997, and in abundance of *Acmaea testudinalis* and *Tonicella marmorea* between August 1997 and the other sampling dates, both at 1 m in depth ($P < 0.01$). Error bars are not shown to enhance clarity of presentation. MB, mussel bed; VW, vertical wall; BZ, boulder zone; TZ, transition zone; SOZ, shallow ophiuroid zone; DOZ, deep ophiuroid zone; AZ, algal zone.

patches had been consumed by seastars and by 1998 ~90% of the deep mussel bed had disappeared. At the Eastern Reef sites the mussel bed was reduced by ~60% between 1997 and 1998 due to seastar predation.

Distribution and abundance of seastars

The distribution and abundance of seastars varied markedly within and among sites and over time (Figure 4).

At Petite Ile au Marteau both *Leptasterias polaris* and *Asterias vulgaris* were most abundant (and formed aggregations) in the first 3 m (peak at 2 m) which corresponded to the mussel bed and the beginning of a vertical wall (Figure 2). Below 3 m, their densities were low and uniform (Figure 4). In all three years, the density of *A. vulgaris* was greater than that of *L. polaris* at all depths ($P < 0.001$). The major inter-annual changes were a decrease from 1996 to 1997 in the abundance of *A. vulgaris*

Figure 4. Abundance of *Leptasterias polaris* and *Asterias vulgaris* at Petite Ile au Marteau, Ile aux Goélands and Cap du Corbeau in different sampling periods in 1996, 1997 and 1998. *, depths where the density of the two seastars is different (**, $P<0.01$; *, $P<0.05$). Error bars are not shown to enhance clarity of presentation. MB, mussel bed; VW, vertical wall; BZ, boulder zone; TZ, transition zone; SOZ, shallow ophiuroid zone; DOZ, deep ophiuroid zone; AZ, algal zone.

at 2 m ($P<0.001$) and 3 m ($P<0.05$) and an increase from 1997 to 1998 at 3 m ($P<0.05$; Figure 4). No changes in densities were detected between June and August in 1997 for either *L. polaris* or *A. vulgaris* ($P=0.57$).

At Ile aux Goélands *L. polaris* occurred in peak numbers (aggregations) in the first metres and decreased in abundance with depth, whereas *A. vulgaris* increased in numbers with depth to a maximum at 11–13 m (Figure 4). This inverse depth distribution of the two seastars was observed in all three years. A major part of the depth related changes occurred between 2–6 m in depth in the transition zone, where a sharp decrease in *L. polaris* ($P=0.03$ for 1996, and $P<0.01$ for 1997 and 1998) coincided with an increase in *A. vulgaris* ($P<0.001$ for 1996 and 1997, and $P=0.01$ for 1998) (Figure 4). Prey were almost absent in this zone, although occasionally a few mussels were observed on dives following strong wave activity (presumably detached by waves). A major change between 1997 and 1998 was a shift in *L. polaris* to slightly greater depths, for example the density at 1 m decreased markedly ($P<0.05$; Figure 4). This coincided with the heavy colonization of the mussel bed by the kelp *Alaria esculenta* in 1998 (see above). Possibly the movement of

algal fronds repelled seastars as has been observed for sea urchins (Himmelman, 1969, 1985). Nevertheless, *L. polaris* were still common on a few patches of mussels not covered by algae. A similar phenomenon was observed at Ile aux Goélands in 1982 (J.H. Himmelman, unpublished data), further suggesting that periodic increases in algal cover can cause drops in seastar abundance. The high abundance ($\sim$5–6 ind m^{-2}) of *A. vulgaris* below 10 m in depth in 1997–1998 (Figure 4) was largely due to increases in 0.4–1.2 cm individuals (recruits), that accounted for $\sim$50% of the individuals. The recruits probably originated from the previous year's spawning. No differences were detected in either species between June and August 1997 ($P=0.55$). However, a seasonal migration of *A. vulgaris* was noted in December 1998 as *A. vulgaris* had virtually disappeared from between 0 to 6 m (J.-F. Raymond, personal communication), possibly as a result of the harsh conditions that develop in shallow water during the winter (e.g. strong waves). In late May to early June in 1996–1998, numerous *L. polaris* in the mussel and transition zones had scars on the aboral surface, possibly caused by ice abrasion. *Asterias vulgaris* observed at the same time and depth showed no signs of

abrasion, which further suggests that only *A. vulgaris* migrates to greater depths during the winter. Brooding *L. polaris* were observed in the mussel and transition zones at Ile aux Goélands in December 1998 (J.-F. Raymond, personal communication), and this activity is incompatible with migration since the embryos are attached to the substratum (Hamel & Mercier, 1995). The PCA, followed by correlation analyses to test for significant interactions between the abundance of seastars and prey, revealed a positive association between densities of *A. vulgaris* and *Ophiopholis aculeata* (r_s=0.46, $P<0.001$) and a negative association between *L. polaris* and *O. aculeata* (r_s=$-$0.19, $P<0.01$).

At Cap du Corbeau, the abundance of both seastars was low ($\sim$0.5–1 ind m^{-2}) compared to the above sites. The depth distributions of *L. polaris* and *A. vulgaris* tended to be inverse in 1996 (P=0.29; Figure 4) and this inverse pattern was significant in 1997 ($P<0.01$; Figure 4). The
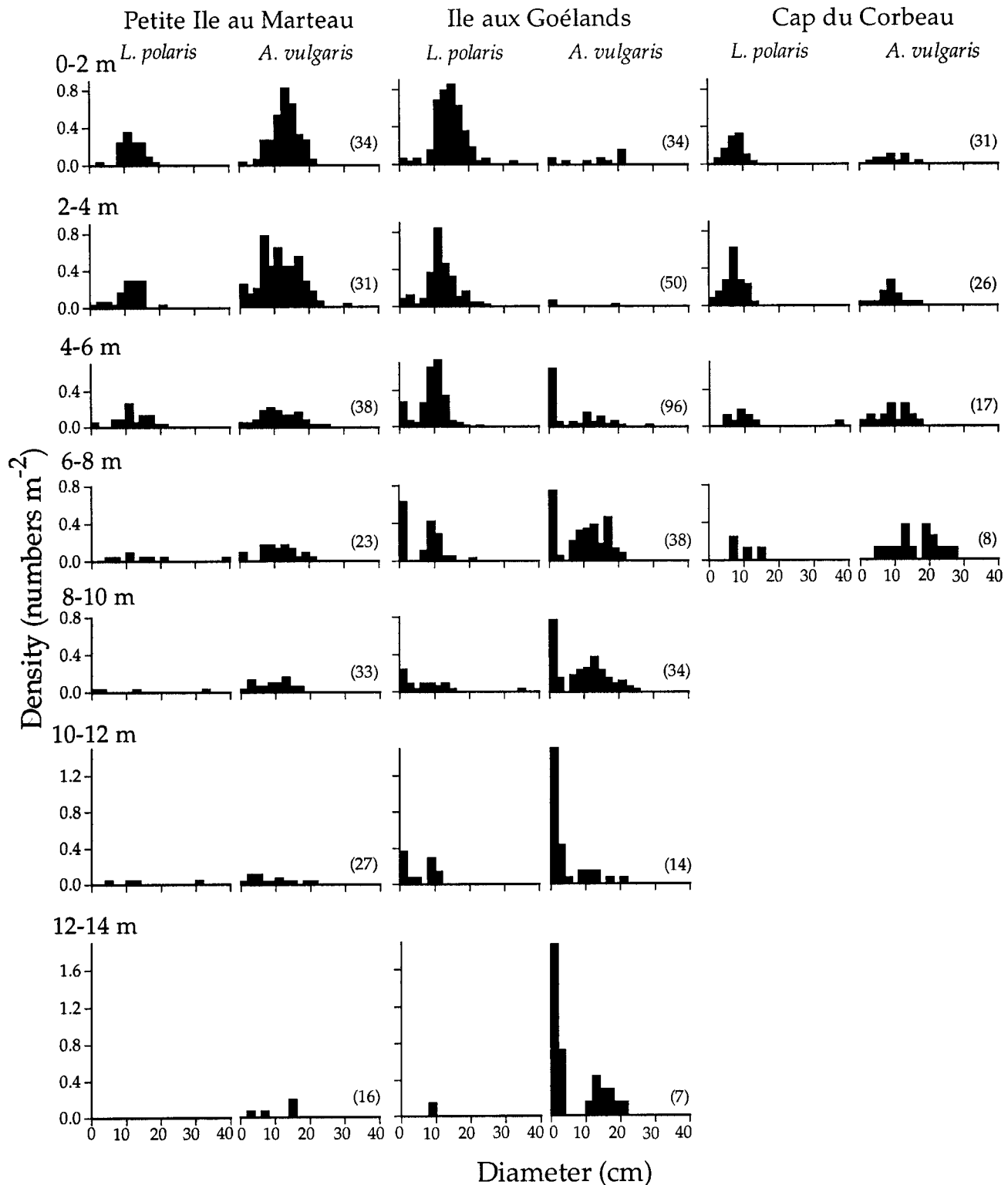
Figure 5. Size structure by depth of *Leptasterias polaris* and *Asterias vulgaris* at Petite Ile au Marteau, Ile aux Goélands and Cap du Corbeau. Numbers in parentheses indicate the number of quadrats observed at each 2-m depth interval.

PCA and correlation analyses indicated an association between *A. vulgaris* and *O. aculeata* (r_s=0.25, P=0.03) but not between *L. polaris* and *O. aculeata* (r_s=$-$0.03, P=0.79).

Thus, three patterns were found at the three sites: (1) both *L. polaris* and *A. vulgaris* decreased in abundance with depth at Petite Ile au Marteau; (2) the two species showed inverse depth distributions at Ile aux Goélands; and (3) both seastars showed even but low numbers across the depth gradient at Cap du Corbeau.

Most of the rapid transects revealed patterns similar to those observed at the more intensively studied sites. On the Eastern Reef sites, the distribution patterns for *L. polaris* and *A. vulgaris* were similar to that found at Petite Ile au Marteau (both seastars decreased in abundance with depth and *A. vulgaris* was more abundant than *L. polaris*). At Ile à Firmin, Ile à Calculot and the western cliff of Petite Ile au Marteau the two seastars showed depth distributions similar to that at Ile aux Goélands (*L. polaris* attained maximal densities in the first metres and its numbers decreased with depth, and the density of *A. vulgaris* increased with depth). Both seastars were in low abundance throughout the subtidal zone at Anse à Michel as at Cap du Corbeau. A new pattern was observed at Pointe de Chasse, both species were absent in shallow water ($<$2 m), common at $\sim$9 m and scarce at greater depths. Also, *L. polaris* was more abundant than *A. vulgaris*.

As the size distributions for *L. polaris* and *A. vulgaris* were similar over the three years at each site, the distributions for different sampling dates were combined (Figure 5). The distributions were similar for the two seastars within each of the sites. At Petite Ile au Marteau, juveniles (0–5 cm in diameter) of both species were found mainly from 2 m in depth to the end of the rocky zone ($\sim$14 m), with peak numbers between 2 and 6 m on the vertical wall

(Figure 5). Small adults (5–20 cm) were concentrated at 0–4 m, which included the mussel bed and the beginning of the vertical wall (Figures 2 & 7). The size distributions of *L. polaris* and *A. vulgaris* at Ile aux Goélands varied markedly from those at Petite Ile au Marteau. Juvenile *L. polaris* were concentrated between 4 and 12 m in depth and peaked in numbers at 6–8 m (the shallow ophiuroid zone). Juvenile *A. vulgaris* were mainly found from 4 to 14 m and peaked between 12 and 14 m on the vertical wall ($\sim$2 ind m^{-2}) (Figure 5). Small adult (5–20 cm) *L. polaris* were concentrated from 0 to 6 m and small adult *A. vulgaris* from 6 to 10 m. This segregation of small adults with depth was largely responsible for the inverse depth–density relationship of the two seastars. At Cap du Corbeau, juveniles and small adults of both species were distributed throughout the rocky zone rather than being concentrated at particular depths as at the previous sites (Figure 5). Nevertheless, the size of small adult *A. vulgaris* increased with depth and was greatest near where the rocky zone gave way to soft substratum (Figure 5). Although the modal size was similar for the two species ($\sim$8–10 cm in diameter), *A. vulgaris* attained a larger size than *L. polaris* at every depth (Figure 5).

The previous patterns showed the macrospatial distribution of both seastars. However, at a microspatial level (1-m^2 quadrat), the PCA and correlation analyses showed that densities of the two seastars were inversely correlated at Cap du Corbeau (r_s=$-$0.36, P<0.001) and Ile aux Goélands (r_{rs}=$-$0.41, P<0.001), but not at Petite Ile au Marteau (r_{rs}=0.06, P=0.53). However, correlations were not significant when analyses were applied only to the mussel bed zones (r_s=$-$0.16, P=0.20; r_s=0.10, P=0.30; and r_s=0.23, P=0.17; respectively). Thus, below the mussel zone, the two seastars seemed segregated at a microspatial level. The correlation analyses also revealed
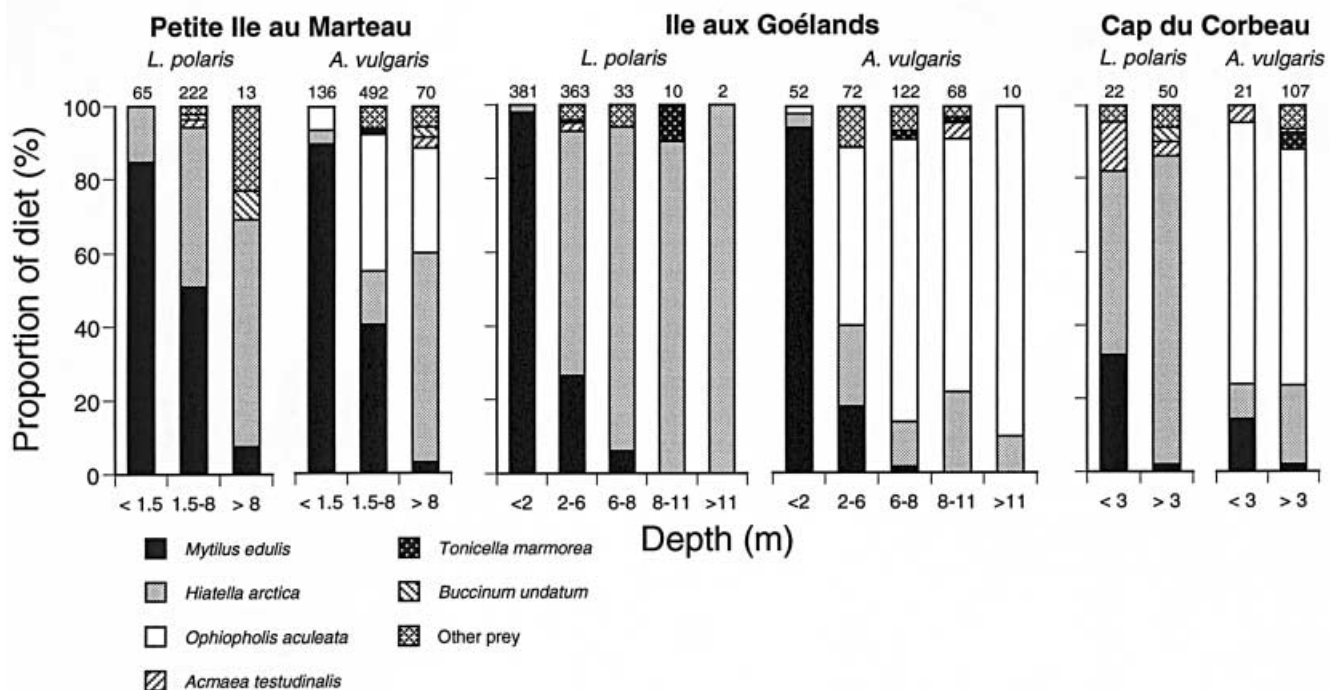
Figure 6. Prey species selection of *Leptasterias polaris* and *Asterias vulgaris* at different depths at Petite Ile au Marteau, Ile aux Goélands and Cap du Corbeau. Numbers at the top of each column indicate the number of observed prey being consumed at that depth.

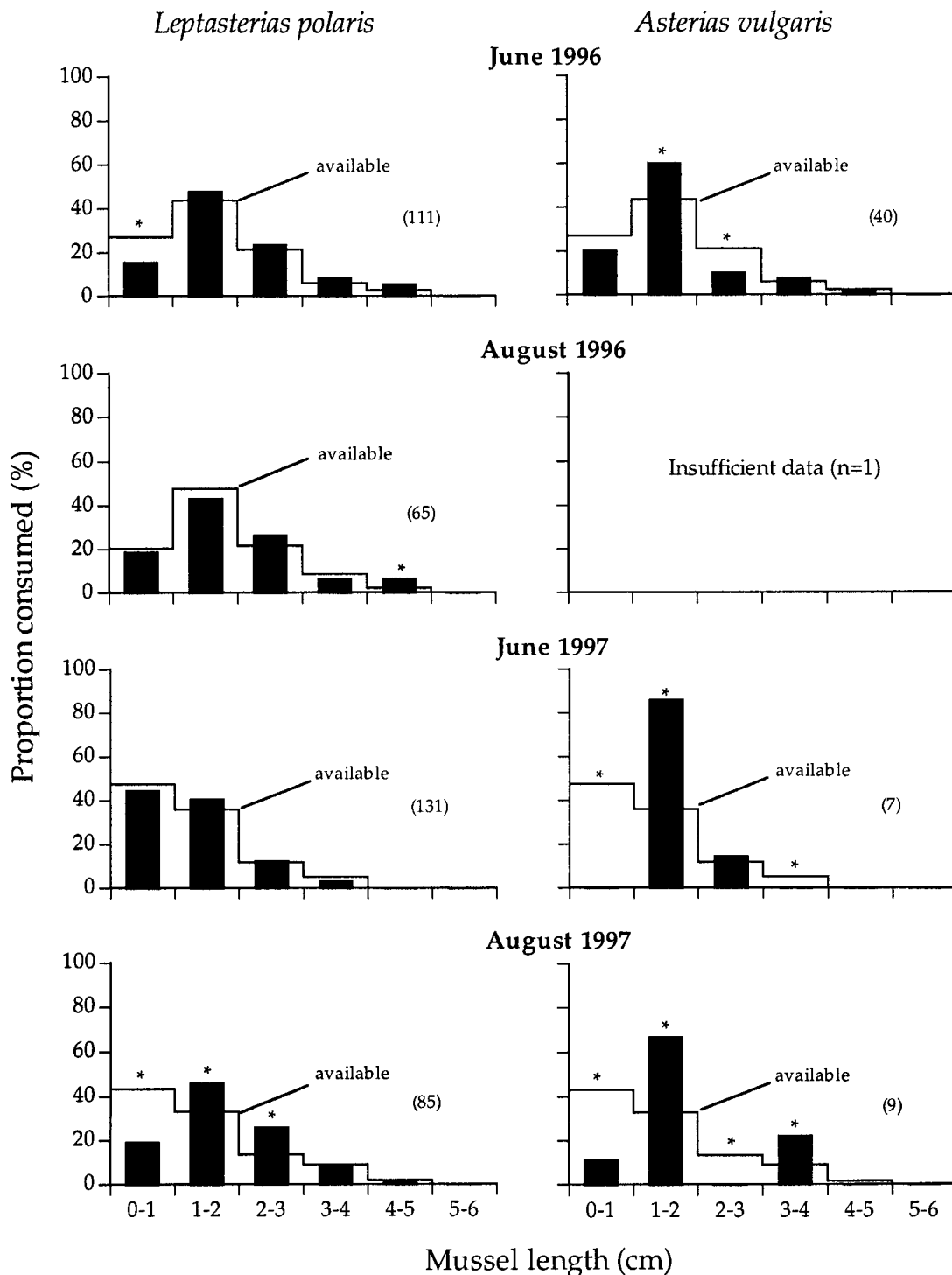*Journal of the Marine Biological Association of the United Kingdom (2001)*
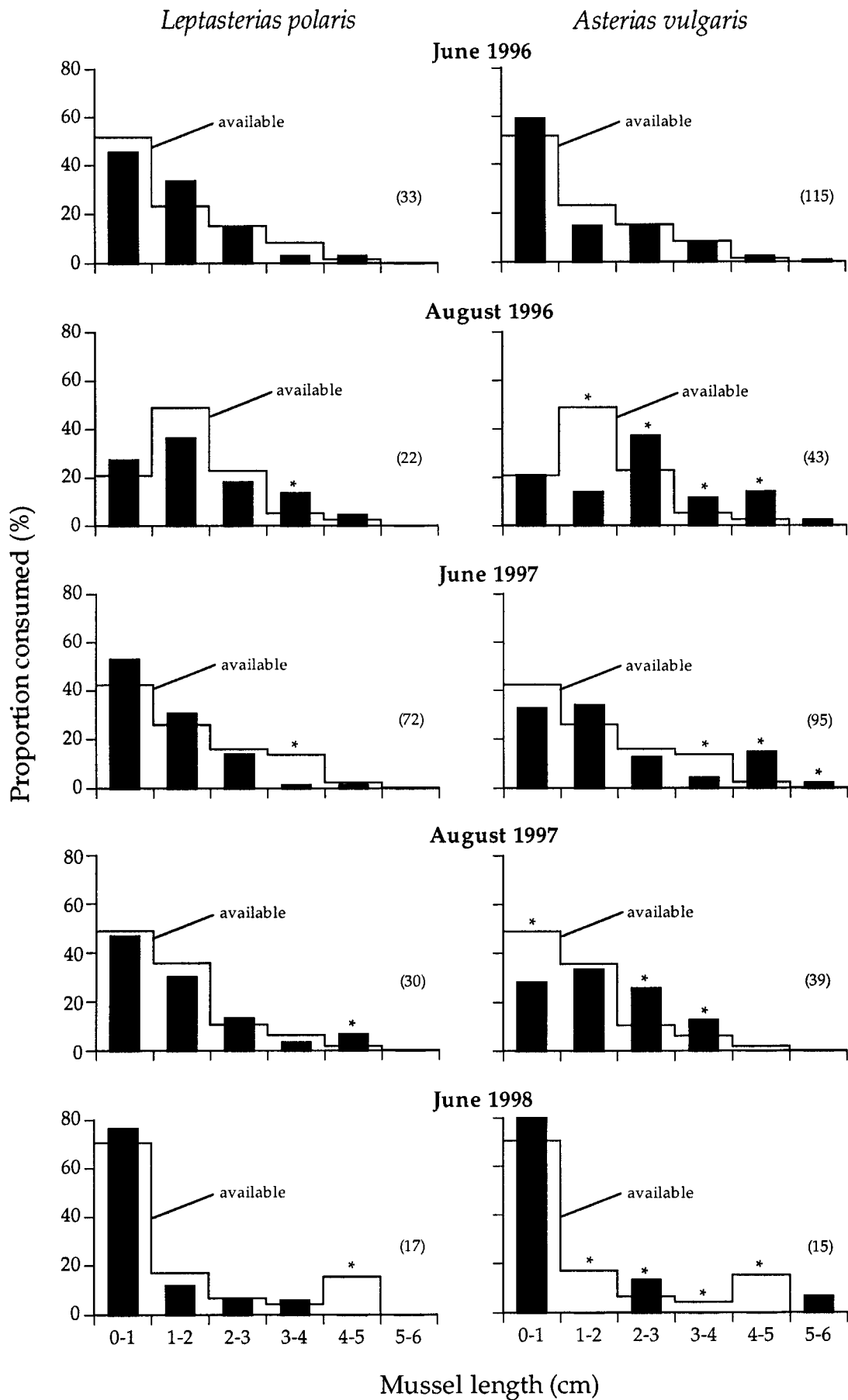
Figure 7. Mussel size selection of *Leptasterias polaris* and *Asterias vulgaris* in relation to availability at Petite Ile au Marteau during five sampling periods. *, significant differences between the size selected and that available ($P < 0.05$). Numbers in parentheses indicate the number of consumed mussels observed.

that at Petite Ile au Marteau *L. polaris* and *A. vulgaris* were concentrated on bedrock ($r_s=0.25$, $P=0.002$; and $r_s=0.33$, $P<0.001$, respectively) and on the steep bottoms ($r_s=0.32$, $P<0.001$; and $r_s=0.48$, $P<0.001$, respectively). At Ile aux Goélands, *L. polaris* was associated with gently sloped bottoms ($r_s=-0.28$, $P<0.001$) and *A. vulgaris* with steep bottoms ($r_s=0.46$, $P<0.001$). At all the sites (detailed studied and rapid transects), the abundance of seastars declined rapidly once rocky substrata gave way to pebbles and sand (Figures 2 & 4).

Prey species selection

For each seastar, prey species use was similar on the different sampling dates within each study site, so the data from different sampling periods were pooled

Figure 8. Mussel size selection of *Leptasterias polaris* and *Asterias vulgaris* in relation to availability at Ile aux Goélands during four sampling periods. Data for 1998 were too few to be plotted. *, significant differences ($P<0.05$) between the size selected and that available. Numbers in parentheses indicate the number of consumed mussels observed.

(Figure 6). In the shallow zone where a mussel bed was present at Petite Ile au Marteau and Ile aux Goélands, both seastars mainly consumed *Mytilus edulis* (∼80–100% of diet) (Figure 6). As mussel abundance decreased with depth, *Hiatella arctica* became the second most consumed prey for *Leptasterias polaris* and when mussels were absent, *H. arctica* became the most consumed prey (Figure 6). At Cap du Corbeau, where mussels were scarce, *H. arctica* was always the most consumed prey of *L. polaris*. Prey switching with depth and disappearance of mussels was different for *Asterias vulgaris* as *Ophiopholis aculeata* became the primary prey and *H. arctica* the second choice (Figure 6). However, the abundance of *O. aculeata* and *H. arctica* also influenced the diet of *A. vulgaris*. For example, *A. vulgaris* most often consumed *H. arctica* below 8 m in depth at Petite Ile au Marteau (Figure 6), where *H. arctica* was abundant (∼300–500 ind m^{-2}) and *O. aculeata* almost absent (Figure 3), whereas it mainly consumed *O. aculeata* at Ile aux Goélands (Figure 6), where *O. aculeata* was much more abundant than *H. arctica* (Figure 3). Similar prey use was observed in the rapid transects. Cannibalism was observed 21 times over three years for *A. vulgaris* and involved individuals already feeding.

The V-selectivity index indicated that *L. polaris* and *A. vulgaris* consumed mussels in proportion to their availability in the mussel bed at Petite Ile au Marteau (<1.5 m) but selected them at Ile aux Goélands (<2 m)

(Table 1). Both seastars selected mussels in the zone just below the mussel bed (Table 1). At all three sites, at depths where mussels were absent, *L. polaris* generally selected *H. arctica* and avoided *O. aculeata* whereas *A. vulgaris* selected *O. aculeata* and avoided *H. arctica* (Table 1). One exception to this pattern was at >8 m at Petite Ile au Marteau (Table 1) where *L. polaris* seemed to consume *H. arctica* and *O. aculeata* according to availability. This was probably due to the high abundance of *H. arctica* (75% of prey available) and low abundance of *O. aculeata*, (7% of prey available). Another exception was at >8 m at Ile aux Goélands, where the V indices indicated that *A. vulgaris* consumed *H. arctica* and *O. aculeata* according to availability. In this zone *H. arctica* and *O. aculeata* represented only 15–25% and 70–80%, respectively, of the prey available. *Acmaea testudinalis* and *Tonicella marmorea* were generally consumed according to availability, although at a few depths they were avoided or selected. *Buccinum undatum* was consistently selected by *L. polaris* at Petite Ile au Marteau (Table 1).

Both Morisita's overlap index (C_λ) and Menge's per cent overlap indicated strong overlap in prey species utilization by *L. polaris* and *Asterias vulgaris* in the mussel bed (at both Petite Ile au Marteau and Ile aux Goélands) and decreased overlap with depth and disappearance of mussels (Table 2). Little overlap was observed in areas in deeper water where mussels were absent. An exception

Table 1. *Yule's V prey selectivity index for* Leptasterias polaris *and* Asterias vulgaris *at different depths (m) at Petite Ile au Marteau, Ile aux Goélands and Cap du Corbeau.*
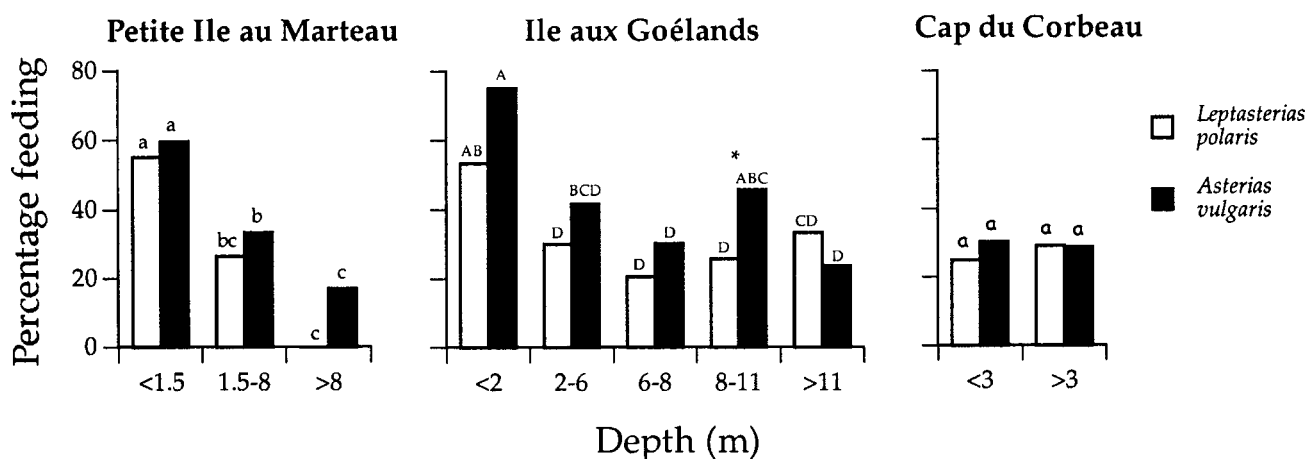
	Petite Ile au Marteau			Ile aux Goélands					Cap du Corbeau	
	<1.5	1.5–8	>8	<2	2–6	6–8	8–11	>11	<3	>3
Leptasterias polaris										
M. edulis	−0.060	0.138**	0.316**	0.019**	0.267**	0.254**	N.A.	N.A.	0.134**	0.024
H. arctica	0.011**	−0.019**	0.002	−0.008	0.031**	0.039**	0.025**	0.034**	−0.003	0.085**
A. testudinalis	−0.005	−0.004	−0.007	−0.015**	−0.007	−0.006	0.015*	−0.001	−0.015	−0.030
T. marmorea	−0.001	−0.012**	−0.007	−0.007	−0.001	−0.003	−0.002	−0.001	−0.010	−0.051*
B. undatum	−0.000	0.022**	0.017*	−0.001	0.003	−0.001	−0.001	−0.001	−0.003	0.038*
O. aculeata	−0.001	−0.039**	−0.006	−0.008	−0.071**	−0.04**	−0.028**	−0.032**	−0.014	−0.050**
Asterias vulgaris										
M. edulis	−0.001	0.161**	0.174**	0.008*	0.096**	0.132**	N.A.	N.A.	0.056**	0.031
H. arctica	−0.006	−0.078**	−0.020**	−0.005	−0.016**	−0.033**	−0.005	−0.005	−0.042**	−0.087**
A. testudinalis	−0.008	−0.015**	−0.011	−0.007	−0.007	−0.001	0.014*	−0.003	−0.025*	−0.064**
T. marmorea	−0.002	−0.013**	−0.017**	−0.003	−0.003	0.016**	0.002	−0.003	−0.010	−0.052**
B. undatum	−0.000	0.008	0.009	−0.000	−0.001	−0.002	−0.002	−0.001	−0.003	0.001
O. aculeata	0.073**	0.021**	0.053**	0.003	0.006	0.031**	0.001	0.007	0.101**	0.213**

**, $P<0.01$; *, $P>0.05$; N.A., no data available.

Table 2. *Overlap in diet of* Leptasterias polaris *and* Asterias vulgaris *at different depths (m) at Petite Ile au Marteau, Ile aux Goélands and Cap du Corbeau.*

	Petite Ile au Marteau			Ile aux Goélands					Cap du Corbeau	
Indexes	<1.5	1.5–8	>8	<2	2–6	6–8	8–11	>11	<3	>3
C_λ	0.99	0.71	0.88	1.00	0.48	0.16	0.30	0.11	0.22	0.31
% overlap	88.30	57.24	62.85	96.76	43.03	15.57	26.47	10.00	28.57	25.23

C_λ, Overlap index (Morisita, 1959; Horn, 1966); 0, no overlap; 1, total overlap; % overlap (Menge & Menge, 1974).

Figure 9. Percentage feeding of *Leptasterias polaris* and *Asterias vulgaris* at different depths at Petite Ile au Marteau, Ile aux Goélands and Cap du Corbeau. For each site, percentage values sharing the same letter are not significantly different ($P > 0.05$). The only difference between *L. polaris* and *A. vulgaris* was at 8–11 m at Ile aux Goélands (*).

was found at >8 m at Petite Ile au Marteau, where overlap increased because both seastars mainly consumed *H. arctica* (Table 2; Figure 6). At Cap du Corbeau, overlap was low at all depths, probably due to the scarcity of mussels.

Prey size selection

Both seastars showed size selection for their preferred prey species, *Mytilus edulis*. At Petite Ile au Marteau, the sizes of mussels consumed by *Leptasterias polaris* reflected availability and consisted mainly of 0–1 cm individuals (Figure 7). In contrast, *Asterias vulgaris* selected larger mussels on all dates except during June 1996, when mussels were most abundant (Figure 3) and consumed according to availability (Figure 7). Similarly, at Ile aux Goélands *L. polaris* consumed the most available size-class of mussels in 1996 (1–2 cm individuals) and June 1997 (>1 cm individuals) but in August 1997, when mussels were less abundant, *L. polaris* selected mussels larger than the most available size-class (thus mussels measuring >1 cm) (Figure 8). *Asterias vulgaris* selected larger mussels than the most available size, except when mussels were most abundant in June 1996 (Figures 3 & 8). Thus, at both sites, the two seastars generally partitioned mussels according to size when mussels became scarce. For both species, the size of mussels consumed generally increased with seastar size, even though large seastars still consumed some small mussels. Given the similar size structure of the two seastars (Figure 5), this would imply a similar use of prey size, and thus, increased overlap in prey use.

Percentage feeding

For each site, as percentage feeding was similar on most sampling dates, the data for the different dates were pooled (Figure 9). The only exception was the mussel bed at Ile aux Goélands, where percentage feeding decreased ($P < 0.05$) from ~60–70% in 1997 to ~30% in 1998, possibly because the increased algal growth had reduced access to the mussels. For each seastar, percentage feeding

varied with depth, prey availability and the prey being consumed. In the mussel beds at Petite Ile au Marteau and Ile aux Goélands, ~60–80% of *Leptasterias polaris* and *Asterias vulgaris* were feeding. At Petite Ile au Marteau, percentage feeding of both species decreased ($P < 0.001$) to ~30–40% on the vertical wall at 1.5–8.0 m, where *Ophiopholis aculeata* and *Hiatella arctica* were abundant, and further to 0–20% on the boulder–cobble zone at >8 m ($P < 0.05$) (Figure 9). At Ile aux Goélands, both species showed similar trends: percentage feeding decreased ($P = 0.0001$) from the mussel bed to 6–8 m and then remained relatively constant at greater depths (~20–30%, $P > 0.05$). The only exception was that percentage feeding by *A. vulgaris* increased in the deep ophiuroid zone (8–11 m, $P < 0.05$), where ophiuroids were more abundant. Percentage feeding of *A. vulgaris* decreased on the vertical wall ($P < 0.05$), where most of the individuals were recruits that were rarely observed feeding. At Cap du Corbeau, percentage feeding was low and constant at all depths (~20–30%, $P = 0.28$), reflecting the low abundance of mussels and other prey.

DISCUSSION

Whereas the observations of Himmelman & Dutil (1991) at one site in the Mingan Islands (Cap du Corbeau) in August 1984 indicated that the seastars *Leptasterias polaris* and *Asterias vulgaris* have similar depth distributions in the subtidal zone (both were most abundant in the first few metres and decreased in numbers with depth), our more extensive observations showed striking inter-site variations in the distribution of these seastars. Three general depth distribution patterns were observed: (1) both species aggregating in shallow water and decreasing in numbers with depth (as at Cap du Corbeau in 1984); (2) the two species showing inverse depth distributions; and (3) both seastars occurring in low numbers across the rocky subtidal zone. These variations in distribution were associated with a number of factors. Both seastars were generally most abundant on bedrock. The third pattern was only found at sites where

mussels, the preferred prey of the two seastars, were scarce at all depths. In contrast, the first two patterns were found at sites where mussels formed dense beds in the upper subtidal zone. Whereas the density of *L. polaris* was always greatest at shallow depths, the greatest density of *A. vulgaris* shifted to greater depths as the slope of the bottom decreased (Figures 2 & 4). Peak densities of *A. vulgaris* were also associated with the highest densities of its second most preferred prey, the ophiuroid *Ophiopholis aculeata*. As a result, on the steep slope at Petite Ile au Marteau where *O. aculeata* was most abundant in shallow water, both *A. vulgaris* and *L. polaris* were concentrated in shallow water. Depth distribution patterns were stable over the three years of our study, but, as discussed below, patterns can change over longer periods.

Distribution and abundance patterns may also be affected by interspecific interactions. Interactions between *L. polaris* and *A. vulgaris* appeared to depend mainly on the availability of mussels. When the two species co-occurred in areas of high mussel abundance (e.g. shallow depths at certain sites), they fed on the same prey species and the same size of prey, and similar proportions of individuals were feeding (60–80%). As mussels became scarcer at Petite Ile au Marteau and Ile aux Goélands in the second and third year of our study, differences between the two species developed, since *A. vulgaris*, but not *L. polaris*, began to select larger mussels (Figures 3, 7 & 8). Below the mussel zone, where the proportions of individuals feeding decreased for both seastars in all years, prey partitioning became evident. *Asterias vulgaris* fed extensively on *O. aculeata* and *L. polaris* fed on the crevice-dwelling clam *Hiatella arctica* and never on *O. aculeata*. Further, the two seastars were also segregated at small spatial scales (1 m^2 quadrats) below the mussel zone. As this segregation was not related to prey abundance (as the prey *H. arctica* and *O. aculeata* were not segregated at the scale of 1 m^2 quadrats), the two seastars were possibly avoiding one another in this zone. Nevertheless, we did not observe aggressive interactions between the two seastars, as reported for seastars in other systems (Menge & Menge, 1974), or escape responses as described by Dutil (1988) and Morissette & Himmelman (2000b) for large adults. Further, although Morissette & Himmelman (2000a) showed that large adult *A. vulgaris* kleptoparasitize (steal) prey from large adult *L. polaris* in sediment bottom habitats at greater depths, we did not observe such interactions in the rocky subtidal zone. Negative correlations in the abundance of predatory seastars have been considered to be a result of competitive interactions (Menge, 1972b; Menge & Menge, 1974). The spatial segregation detected in our quadrat sampling did not extend to larger scales, except for the inverse depth distributions of the two species at some sites (e.g. Ile aux Goélands). Large scale distribution seemed to be related to a combination of factors, such as prey abundance and the slope and type of the substratum.

Intraspecific interactions should be more important than interspecific interactions at sites where *L. polaris* and *A. vulgaris* show inverse depth distributions (e.g. Ile aux Goélands) and could lead to agonistic behaviours or cannibalism as documented in other systems (Wobber, 1975; Dayton et al., 1977; Harris et al., 1998). Laboratory

experiments on *A. vulgaris* by O'Neill et al. (1983) showed that intraspecific competition leads to selection of a broader size range of prey. Intraspecific competition could similarly explain why larger mussels were included in the diet of *L. polaris* as mussels became less abundant at Ile aux Goélands in August 1997. However, this needs to be substantiated experimentally. Although cannibalism has been frequently observed for *A. vulgaris* in New England when mussels are in short supply (Harris et al., 1998), during our studies we only occasionally observed cannibalism of *A. vulgaris* and never for *L. polaris*.

Seastar predation appears to control the lower limit of mussels in the Mingan Islands (Himmelman & Lavergne, 1985; Himmelman, 1991; Himmelman & Dutil, 1991; present study) and this is also the case in other regions (Paine, 1969, 1976; Feder, 1970; Menge, 1979; Sloan & Aldridge, 1981; Robles, 1987). In the Mingan Islands, persistent mussel beds only occur in the low intertidal and upper subtidal zones (extension of the mussels into the intertidal zone is greatly limited by the ice abrasion during winter). The survival of mussels near low water level is probably enhanced by the intolerance of the seastars to emersion (causing increased temperature variations and desiccation) and strong wave activity. Also, the establishment of macroalgae, especially *Alaria esculenta*, in the upper subtidal zone appears to enhance the effectiveness of this zone as a refuge from seastar predation (the movement of the algal fronds possibly disturbs seastars thus limiting their foraging). Finally, increased wave activity and ice in winter may cause seastars to move to deeper water, as indicated for *Asterias* spp. in New England (Menge, 1979, 1982) and for *Asterias vulgaris* in the present study. The lower limit of mussel beds can vary markedly in the Mingan Islands. For example, Himmelman & Dutil (1991) recorded a mussel bed (and intensive foraging by *L. polaris* and *A. vulgaris*) being present in the first few metres depth at Cap du Corbeau in 1984, but mussels were scarce at all depths at this site from 1996 to 1998. With the disappearance of the mussels, the depth distributions of the seastars changed from pattern 1 (both *L. polaris* and *A. vulgaris* being abundant in shallow water and decreasing in numbers with depth) in 1984, to pattern 3 (low numbers of both species at all depths) in 1996–1998. The time required to eliminate the mussels is unknown. We also documented several instances of dramatic declines in the abundance of mussels during our three-year study. For example, the density of mussels at Petite Ile au Marteau decreased by 50% between 1996 and 1997 and by another 50% between 1997 and 1998. In contrast, at Ile aux Goélands, mussels declined by 50% between 1996 and 1997, but remained constant between 1997 and 1998. The latter stabilization in mussel numbers coincided with extensive colonization by macroalgae, which may have limited seastar foraging.

The abundance of both seastars also declined after the disappearance of the subtidal mussel bed at Cap du Corbeau (from ∼2 m^{-2} in 1984 to ∼0.5–1 m^{-2} in 1996, personal observation), indicating that the low abundance of preferred prey may have caused the seastars to migrate to other sites. This suggestion is supported by numerous

reports of seastars migrating long distances in search of prey after decimating their food supply (e.g. *Mytilus edulis*) (Menge, 1982; Sloan, 1980; Sloan & Aldridge, 1981; Dare, 1982; McClintock & Lawrence, 1985; Robles et al., 1995). Distance chemoreception has been demonstrated for *A. vulgaris* (Zafiriou et al., 1972) and *L. polaris* (Rochette et al., 1994) and may be used in locating prey patches. Following the emigration of seastars, episodic recruitment of mussels (for example, as observed by Robles et al., 1995) usually results in re-establishment of mussel beds. The large numbers of small mussels ($\sim$10,000 m^{-2}) observed at Cap du Corbeau in 1997 (when seastars were in low abundance) showed that a major recruitment event was occurring.

Temporal changes in prey availability can be important in controlling seastar populations (Sloan, 1980), and our observations in the Mingan Islands indicate that prey availability is a major factor affecting the abundance and distribution of juvenile and small adult *L. polaris* and *A. vulgaris* in the rocky subtidal zone. *Leptasterias polaris* and *A. vulgaris* aggregate and forage intensively in zones or patches of high mussel abundance and then when the mussels become depleted, move away in search of other prey-rich sites. Such behaviours are likely to be important in producing the striking variations in seastar abundance in space and time. Variations in recruitment over space and time may further contribute to the variations in seastar populations. Unlike most seastars, *L. polaris* is a brooding species (Himmelman et al., 1982; Boivin et al., 1986). Consequently, local changes in reproductive output are likely to directly affect local recruitment. In contrast, *A. vulgaris* has long-lived (6–8 wk) planktotrophic larvae so that recruitment to local populations is likely to stem from larvae produced in other regions (Smith, 1940). *Asterias vulgaris* populations are thus said to be 'open' (*sensu* Caley et al., 1996) and recruitment is probably not coupled with reproductive success in a given local population. The recruitment of *A. vulgaris* is likely to be more variable than that of *L. polaris* due to vagaries in larval transport and survival. The fluctuations in *A. vulgaris* recruitment should eventually cause changes in the abundance of juvenile and small adult *A. vulgaris* and in turn affect interactions between *A. vulgaris* and *L. polaris*.

Our study illustrates differences between *L. polaris* and *A. vulgaris* in the size of the preferred prey selected and in the selection of alternative prey species when preferred prey become scarce or absent. We also found that the two seastars were spatially segregated at the scale of 1 m^2 quadrats in the zone where preferred prey are absent. These observations could reflect mechanisms permitting coexistence of these two subtidal predators. Although it is tempting to suggest that such differences are an evolutionary response to past competitive interactions (Connell, 1980), we do not have evidence for this. Experimental evidence is required to demonstrate the existence and consequences of potential competitive interactions between these two seastars (Reynoldson & Bellamy, 1971; Connell, 1983; Schoener, 1983; Underwood, 1986).

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