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Structural dynamics of a sea-star (*Marthasterias glacialis*) population

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The dynamics and feeding biology of a population of *Marthasterias glacialis* (Echinodermata: Asteroidea) was examined over a two-year period from 2000–2002 at Lough Hyne Marine Nature Reserve, Co. Cork, Ireland. A multivariate approach was used and both multiple factors and multiple interactions between factors were found to influence population structure. These included time of year, site, individual sea-star size, depth, and predator density. Individuals belonging to the smallest size-classes (0–50 mm and 51–100 mm) were most abundant amongst boulders in shallow water (0–1 m), while larger individuals were primarily found in water below 1 m in depth on finer grade substratum and shell debris. Dietary composition was also found to differ with depth; sea-stars in the immediate subtidal had an opportunistic diet, and fed on a variety of taxa, whilst those *M. glacialis* from 1–6 m were more selective and restrictive, feeding chiefly on bivalve prey. We propose that spatial partitioning of different size-classes and a generalist feeding strategy may account for the success of *M. glacialis* at Lough Hyne.

INTRODUCTION

The asteroid echinoderms (sea-stars) have been shown to play one of the most influential roles in benthic ecosystems on a variety of scales (Paine, 1966; Menge, 1972). The group is ubiquitous in many different marine environments, from deep abyssal depths to the intertidal zone and from the tropics to the poles. The strong influence that asteroids have on benthic communities may result from the wide range of trophic levels that members of this group can occupy (Guillou, 1996; Ellis & Rogers, 2000). Asteroids were some of the first marine predators to be experimentally manipulated in order to interpret the concept of 'keystone' species (Paine, 1966). Uniquely, asteroids can occupy keystone or pivotal roles in temperate (Paine, 1966), polar (Dayton, 1979) and tropical (De'ath & Moran, 1998) shallow marine benthos. As a result, aspects of diet and feeding biology, such as foraging rates, feeding stimuli, optimal foraging and prey selectivity have been extensively studied in many asteroid species (Dayton et al., 1977; Penney & Griffiths, 1984; Tokeshi et al., 1989; Arrontes & Underwood, 1991; Barbeau & Scheibling, 1994; Robles et al., 1995; De'ath & Moran, 1998; Gaymer et al., 2001).

Apart from those asteroid species known to occupy positions of pivotal importance within communities, other non-keystone asteroid populations may still exert a major structuring influence on benthic communities as a whole, particularly through their secondary consumption of benthic organisms. This is the role that the spiny sea-star, *Marthasterias glacialis* (Lamarck) is thought to play at Lough Hyne (Kitching & Thain, 1983). *Marthasterias glacialis* is a major shelf (littoral 180 m) predator of marine animals (including those of commercial importance such as *Paracentrotus lividus* (Savy, 1987) and *Choromytilus meridionalis* (Penney & Griffiths, 1984). Its range extends from north of Finland across the Mediterranean basin and the Adriatic Sea to the Guinean Gulf (Mortensen, 1927).

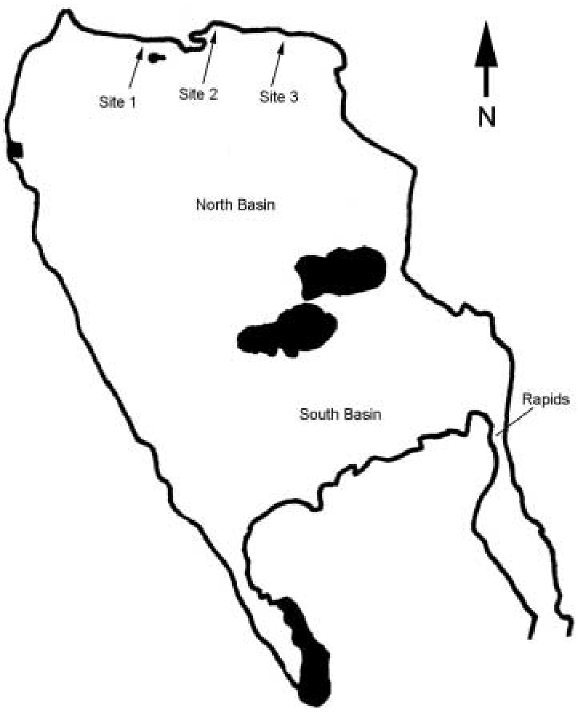

Figure 1. Map of Lough Hyne Marine Nature Reserve, Co. Cork, Ireland, showing study Sites 1, 2 and 3 along the north shore of the Lough.

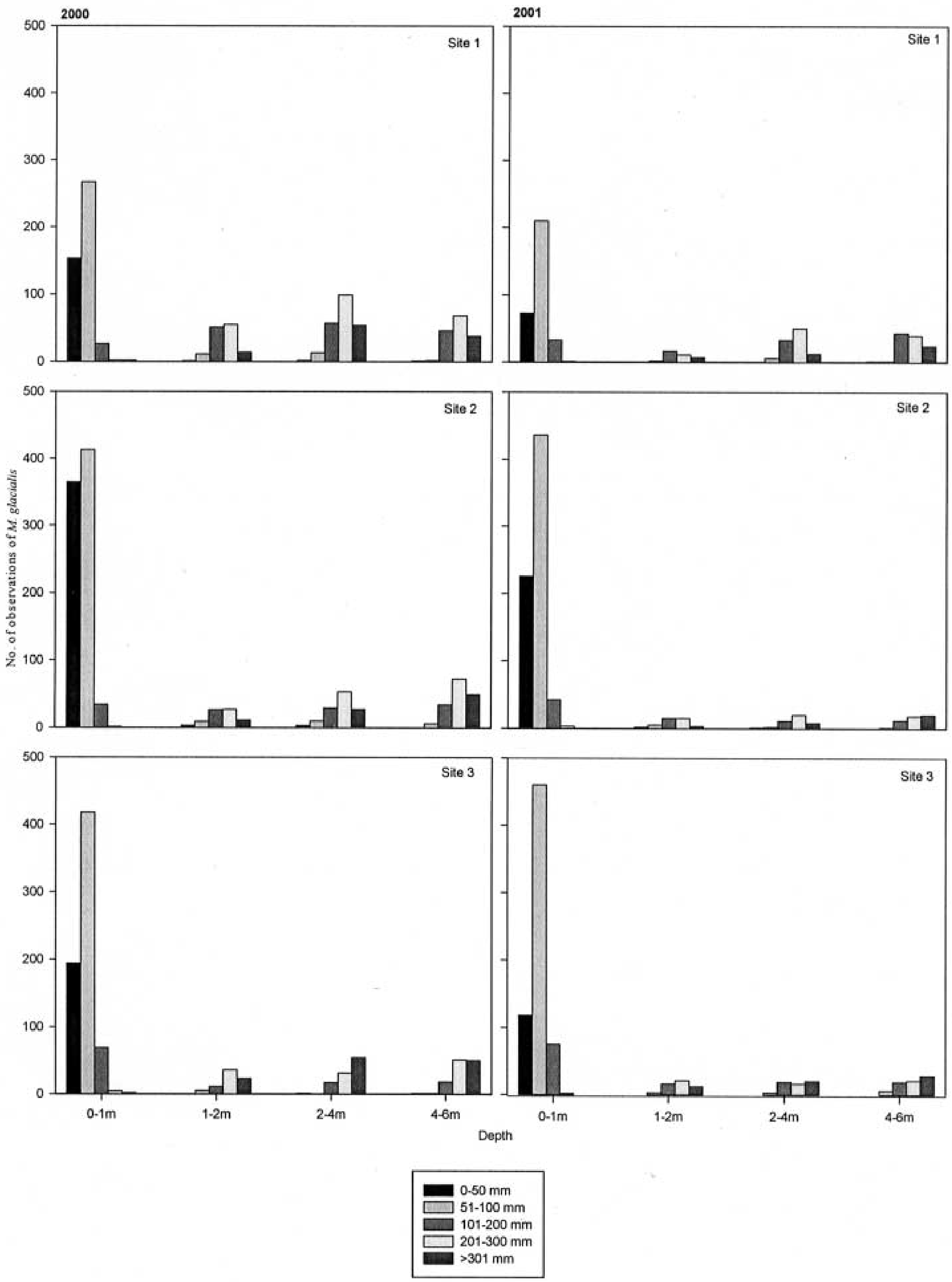

Figure 2. Number of observations of *Marthasterias glacialis* belonging to each size-class at each depth category for 2000 and 2001.

Despite the wide-ranging distribution of *M. glacialis*, and its role as a predator of commercial species, published studies of the ecology and population dynamics of this asteroid are rare. Some short-term studies have revealed diel activity patterns of *M. glacialis* (Ebling et al., 1966; Magennis, 1981; Savy, 1987). There is, however, a particular paucity of long-term data in relation to other potentially important aspects of asteroid ecology such as the effect of abiotic factors on spatial distribution, density, and size structure. The reproductive biology of *M. glacialis* has been examined in a number of studies (Barker & Nichols, 1983; Minchin, 1987). However, as is the case for many asteroid species, studies investigating feeding biology of *M. glacialis* dominate the literature (Ebling et al., 1966; Valentincic, 1973; Magennis, 1981; Kitching & Thain, 1983; Penney & Griffiths, 1984; Savy, 1987; Frid, 1992). To date these studies have been mostly qualitative and of short duration and have shown *M. glacialis* to be dietary non-

Table 1. *Analysis of factors affecting the population and size structure of* Marthasterias glacialis *at Lough Hyne. Four-way fixed factor ANOVA (year (two levels), site (three levels), depth (four levels) and size (five levels)). Variances were homogenous, Levene's test P>0.05).*

Source	DF	*F*	*P*
Year	1	4.46	0.035
Site	2	3.23	0.040
Depth	3	269.74	0.000
Size	4	37.13	0.000
Year×Site	2	2.97	0.052
Year×Depth	3	4.8	0.003
Year×Size	4	5.74	0.000
Site×Depth	6	15.43	0.000
Site×Size	8	11.32	0.000
Depth×Size	12	256.13	0.000
Year×Site×Depth	6	1.59	0.145
Year×Depth×Size	12	1.62	0.080
Year×Site×Size	8	0.64	0.743
Site×Depth×Size	24	3.23	0.000
Year×Site×Depth×Size	24	0.77	0.773

Table 2. *The density of* Marthasterias glacialis *at 0–1 m at Lough Hyne. Results of two-way ANOVA using log-transformed data. Variances were homogenous (Levene's test P>0.05).*

Source	DF	*F*	*P*
Site	2	17.37	0.000
Year	1	1.71	0.197
Site×Year	2	0.22	0.806
Error	48		
Total	53		

specific. The saddle oyster, *Anomia ephippium* (Ebling et al., 1966), barnacles and detritus (Magennis, 1981), sea urchins, such as *Paracentrotus lividus* and *Echinus esculentus* (Savy, 1987; Penney & Griffiths, 1984) and algae *Audinella floridula* (Frid, 1992) are all known prey items of *M. glacialis*. At Lough Hyne Marine Nature Reserve in Ireland, *M. glacialis* had a super-abundant potential food source in the echinoid *P. lividus* for decades (Kitching & Thain, 1987), but with the collapse of this sea urchin population, *M. glacialis* has become the most dominant and widespread echinoderm in the Lough (Greenwood et al., 1999; Barnes et al., 2002). The importance of *M. glacialis* within benthic communities has therefore been postulated, but the paucity of medium-term data and absence of long-term data has made evaluation of its role difficult.

In this study, a population of *M. glacialis* was observed *in situ* over a 24-month period at Lough Hyne. The ecology, hydrography and other physical attributes of this study area have been well described in previous studies (e.g. Kitching & Thain, 1987). At the north shore of Lough Hyne, *M. glacialis* is most abundant above 6 m depth, with smaller individuals (<100 mm) being found in shallow water (0–1 m), and larger individuals (>100 mm) existing at all depths (Frid, 1992; Greenwood et al., 1999). Such a pattern, which also exists amongst other asteroid species such as *Leptasterias polaris* (Himmelman & Dutil, 1991) could be influenced by a number of factors, including depth, food availability, predator density, and intraspecific competition. Little quantitative evidence however has been presented to demonstrate the relative importance of any of these factors in the case of *M. glacialis*. This study therefore aimed to answer a number of questions relating to the ecology of *M. glacialis* at Lough Hyne: (i) is depth is an important structuring factor of the *M. glacialis* population? (ii) Do crustacean predators affect *M. glacialis* densities and distribution? (iii) How does *M. glacialis* utilize the prey resources available at different depths? In this way, we were able to consider how the population dynamics of *M. glacialis* can directly influence the way in which they use their habitat, and can indirectly affect habitat utilization in marine benthic communities.

MATERIALS AND METHODS

Study site and species

Fieldwork was carried out *in situ* at Lough Hyne Marine Nature Reserve, Co. Cork, Ireland (51°70′N 9°40′W) (Figure 1). With six resident species, Lough Hyne is probably one of the sites of highest of asteroid diversity (of comparable area) in north-west Europe (Greenwood et al., 1999). Of the four most abundant species (*Asterina phylactica*, *Asterina gibbosa*, *Asterias rubens* and *Marthasterias glacialis*), *M. glacialis* is the most widely distributed asteroid within Lough Hyne (Greenwood et al., 1999). The Lough is diverse with respect to habitats and hydrographic conditions and is, therefore, an ideal place to study the effects of differing abiotic factors on populations. *Marthasterias glacialis* is found along much of the Co. Cork coast, but particularly so at the sheltered northern shore of Lough Hyne. *Marthasterias glacialis* typically occurs amongst rocky boulder scree on the shallow landward side, as well as on finer grade substrata sloping into the north basin of the Lough. Observations of *M. glacialis* were principally carried out from 0 to 6 m (the sea-star becomes less abundant below 6 m at this site (Greenwood et al., 1999)). Three sites along the north shore were chosen (Figure 1), and each was subsampled at four depth categories: 0–1 m, 1–2 m, 2–4 m, and 4–6 m. These depths were chosen because they represented four different habitats inhabited by *M. glacialis*. The shallowest category, 0–1 m, was a predominantly a boulder scree habitat. The 1–2 m, 2–4 m and 4–6 m categories, however, were dominated by finer grade (sand and gravel) substrata combined with shell fragments (making any *M. glacialis* present easily visible).

Data collection

All three study sites were sampled bimonthly over 24 months by means of a snorkelling survey from February 2000 to January 2002 (no data could be collected during the months of March and April 2001 due to restrictions imposed on Nature Reserves by the threat of an outbreak of Foot and Mouth Disease in Ireland). As *M. glacialis* are known to show diurnal rhythms of activity (Ebling et al., 1966), sampling was standardized such that data collection took place with the mid-point of each sampling period being midday. Data were collected using randomly

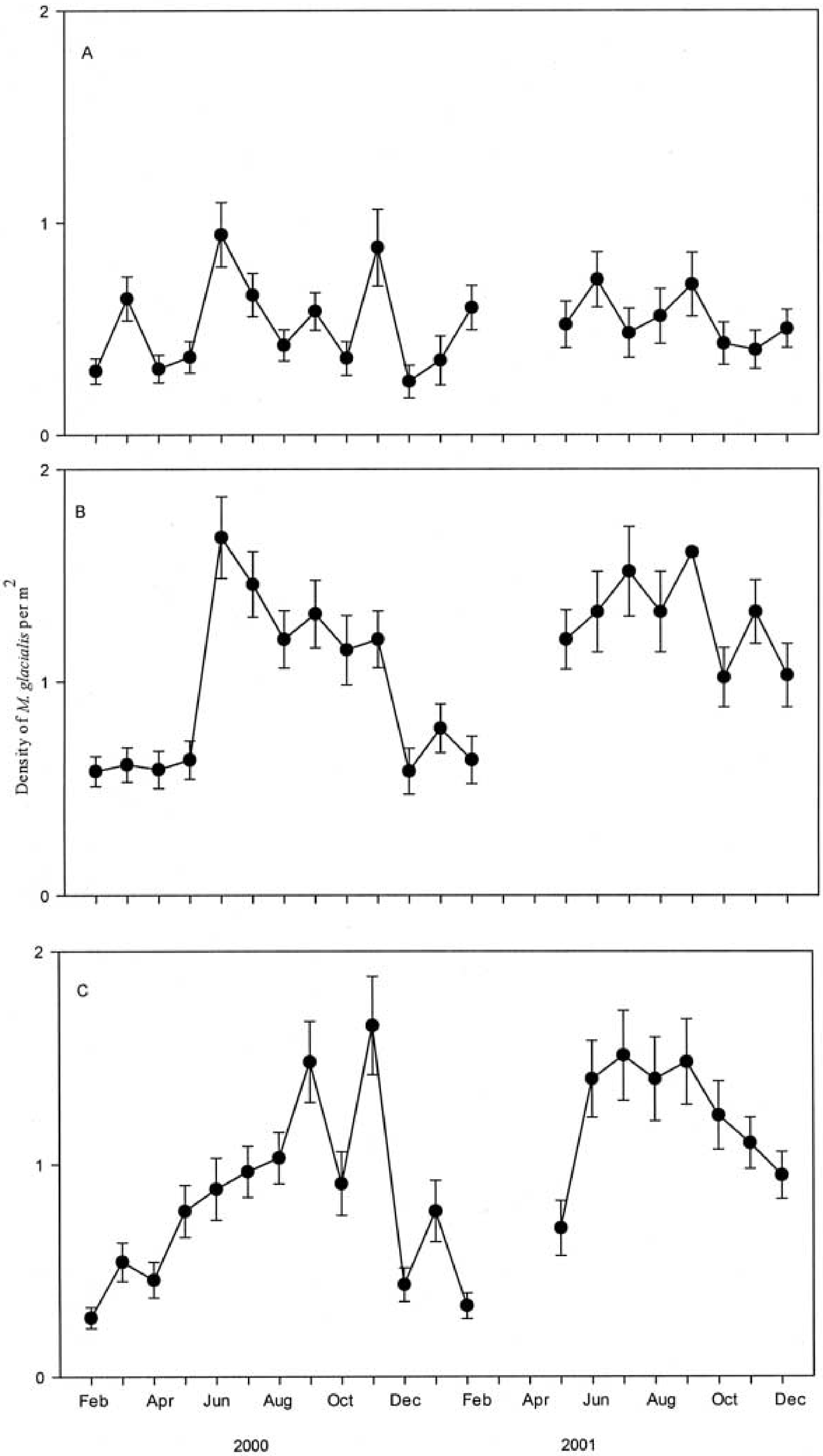

Figure 3. Mean (SE) monthly density per m^2 of *Marthasterias glacialis* at 0–1 m at Lough Hyne for Sites 1, 2 and 3. No data could be collected for March and April 2001 due to Foot and Mouth restrictions.

placed quadrats or transects, depending on the depth being sampled. In particular, for the 0–1 m depth, 30 randomly placed 1 m^2 quadrats were used in each of the three sites. Each quadrat was searched systematically by overturning every boulder, which maximized the likelihood of locating all *M. glacialis* individuals within the quadrat area. Due to the relatively low numbers of *M. glacialis* in deeper water, the sampling procedure was

Table 3. *Density of potential predators of* Marthasterias glacialis *at 0–1 m at Lough Hyne (*Carcinus maenas, Necora puber *and* Cancer pagurus*). Results of two-way ANOVA using log-transfotmed data. Variances were homogenous (Levene's test P>0.05).*

Source	DF	*F*	*P*
Site	2	1.71	0.192
Year	1	0.01	0.928
Site×Year	2	0.19	0.827
Error	48		
Total	53		

modified and transect sampling was used. At the 1–2 m, 2–4 m and 4–6 m depth categories, three $10\times1\,m^2$ transects were surveyed. A 10 m transect line was laid out on the bottom, and using a ruler, 50 cm on either side of the line was scanned, and the location of *M. glacialis* within the transect area was noted to the nearest metre. For each individual *M. glacialis* encountered, the following data were recorded for both quadrat and transect sampling:

1. *Size*: the maximum tip–tip diameter (arm-span) was measured in mm using Vernier callipers for individuals below 150 mm, and with a large flexible ruler for larger specimens. This is an accurate but time efficient methodology, and is believed to cause minimal disturbance to the animal (Barker & Nichols, 1983).
2. *Position*: the substratum on which *M. glacialis* individuals were found at the time of observation was divided into six types: boulders, cobbles, pebbles, gravel and sand (according to the Wentworth Scale) or shell fragments. In addition, the exact position of *M. glacialis* on the substratum was noted i.e. underneath or on top of boulders. This was only possible at 0–1 m, since boulders were not found in deeper water.
3. *Feeding*: *M. glacialis* feeds by extruding its stomach through the mouth to envelop its prey. In this study, individuals were recorded as 'feeding' when their stomach was everted, even if a prey item was not clearly visible. In cases where prey items were visible, they were identified to species level, wherever possible.
4. *Predator density*: the crustaceans *Necora puber*, *Carcinus maenas* and *Cancer pagurus* are potential predators of juvenile (<100 mm) *M. glacialis* at Lough Hyne, and have been observed feeding on *M. glacialis* during the course of this study (E. Verling, unpublished data). The numbers of these predators present within each m^2 quadrat and along each transect were also counted.

Data analysis

In order to establish which factors were most important in determining the size structure of the *M. glacialis* population, data were analysed using a four-way fixed factor ANOVA, with year, site, depth category and size-class as the four factors. Five size-classes were used in the analysis: 0–50 mm, 51–100 mm, 101–200 mm, 201–300 mm and >300 mm. Data were first log-transformed in order to

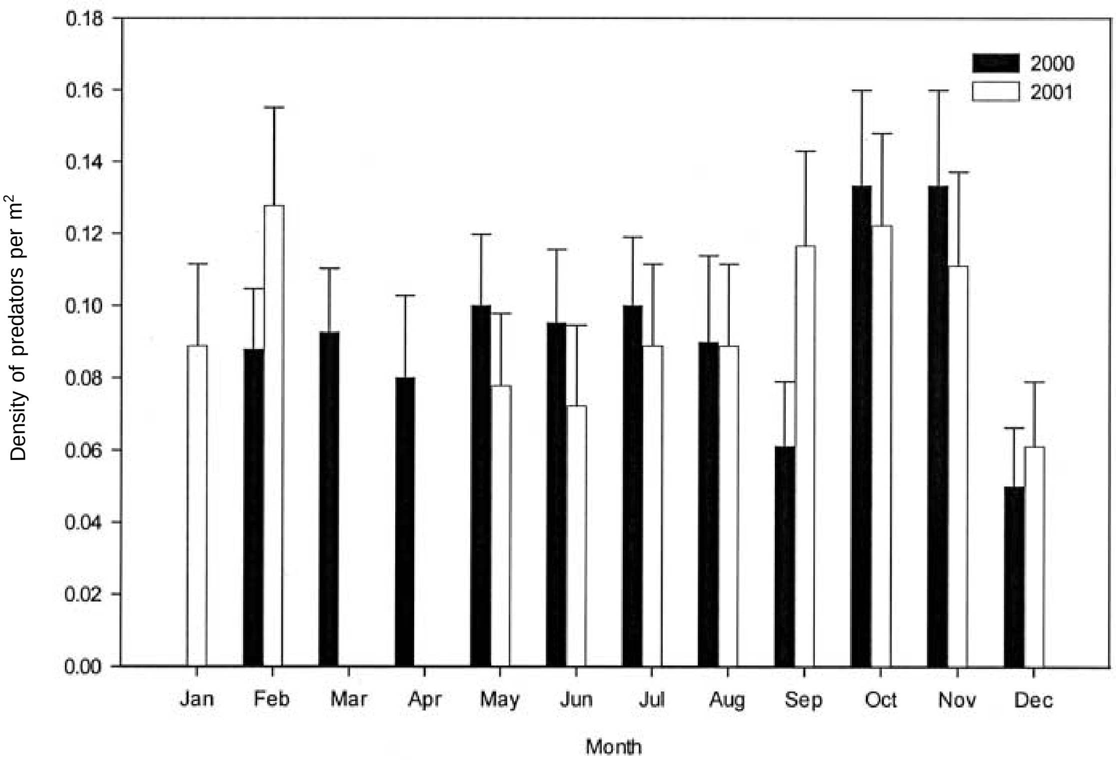

Figure 4. Mean (SE) monthly density per m^2 of potential crustacean predators of *Marthasterias glacialis* (*Carcinus maenas*, *Necora puber* and *Cancer pagurus)* at 0–1 m at Lough Hyne (pooled sites). No data could be collected for March and April 2001 due to Foot and Mouth disease restrictions.

Table 4. Marthasterias glacialis *diet at Lough Hyne at four different depths from 0–6 m for Sites 1, 2 and 3 (pooled data). Showing absolute numbers and percentages (in parentheses) of each prey type observed.*

	0–1 m			1–2 m			2–4 m			4–6 m		
Prey type	Site 1	Site 2	Site 3	Site 1	Site 2	Site 3	Site 1	Site 2	Site 3	Site 1	Site 2	Site 3
Mollusca												
Bivalvia	3 (3.7)	3 (2.4)	16 (13.0)	26 (74.3)	13 (76.4)	20 (66.7)	15 (45.0)	15 (68.0)	6 (31.5)	9 (37.5)	7 (33.4)	8 (35.0)
Gastropoda	6 (7.3)	6 (4.8)	44 (31.0)	0	1 (5.8)	2 (6.7)	0	0	1 (5.2)	0	0	0
Annelida												
Polychaeta (*Pomatoceras* sp.)	22 (26.8)	34 (27.6)	12 (10.0)	0	0	0	0	0	0	0	0	0
Echinodermata												
Echinoidea (*Paracentrotus lividus*)	4 (4.9)	4 (3.3)	1 (0.8)	0	1(15.8)	0	0	0	0	0	0	0
Asteroidea	2 (2.4)	2 (1.6)	0	0	0	0	0	0	0	0	0	0
Crustacea												
Malacostraca	8 (9.8)	17 (14.0)	7 (5.2)	0	0	0	5 (15.0)	4 (18.0)	5 (26.3)	7 (29.1)	5 (23.8)	6 (26.0)
Unidentified sp.*	37 (45.1)	57 (46.3)	52 (40.0)	9 (25.7)	2 (12.0)	8 (26.6)	12 (40.0)	3 (14.0)	7 (37.0)	8 (33.4)	9 (42.8)	9 (39.0)

*, Unidentified: prey items which were too decomposed or at too advanced a stage of digestion for accurate identification.

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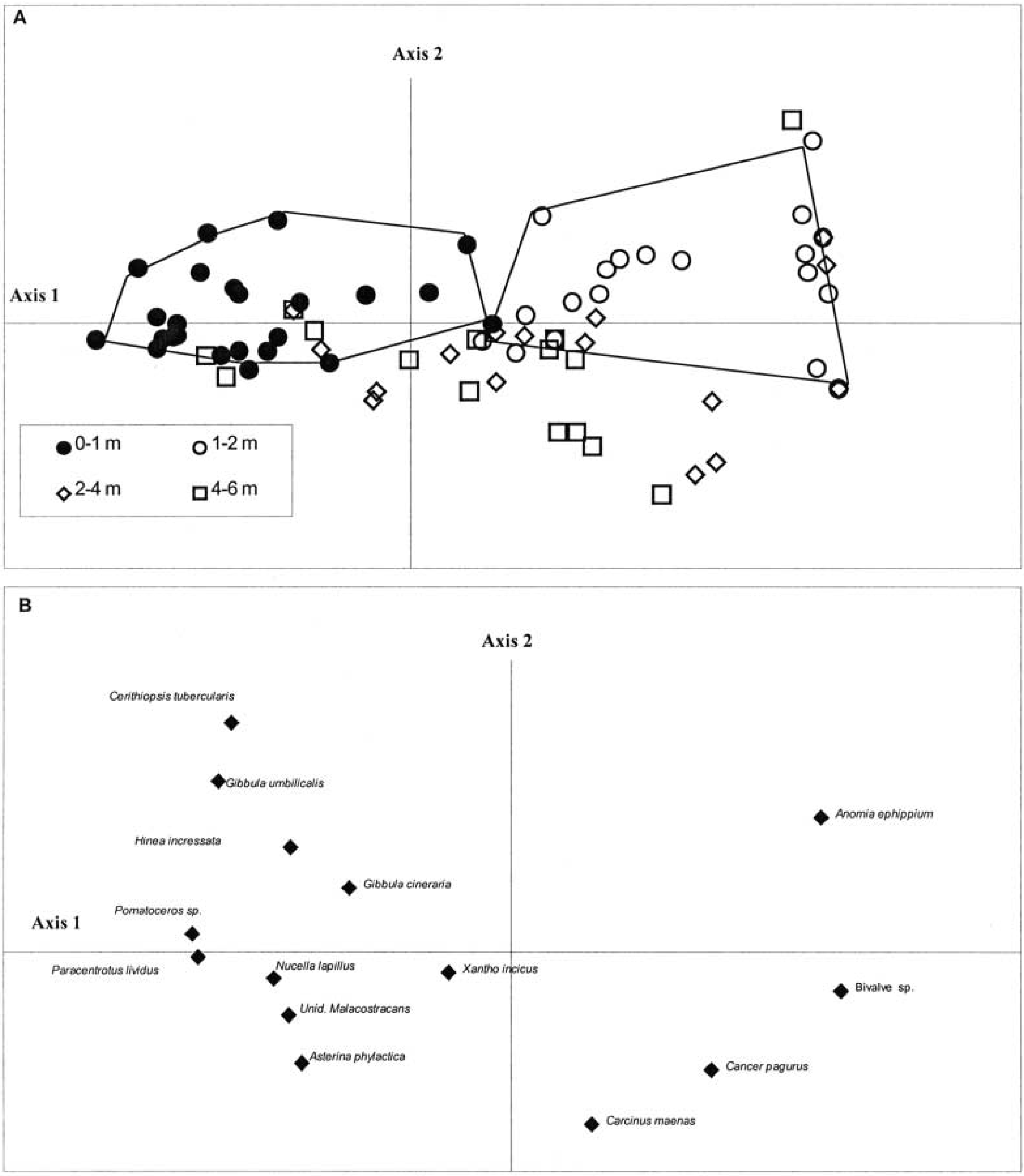

Figure 5. Correspondence Analysis (CA) to assess distinctness in the diet of *Marthasterias glacialis* observed at different depths. (A) scatter plot of sample scores for axis A plotted against axis B. Symbols for depths are shown in key insert; (B) scatterplot showing species scores for axis A plotted against axis B.

homogenize variances (Levene's test, $P > 0.05$). A two-way ANOVA tested for between-site and between-year variation in density of *M. glacialis* and of crustacean predators as a function of depth. In order to assess distinctness in diet composition as a function of depth, the raw data set (with year as a covariate) was tested with Correspondence Analysis (using CANOCO 4).

Since no data could be collected during March and April 2001, these months were excluded from all analysis for both 2000 and 2001.

RESULTS

Marthasterias glacialis *population demography and spatial organization*

The between-site, between-depth and between-size-class differences in *Marthasterias glacialis* population structure shown by Figure 2 were confirmed by multivariate statistical analysis. A four-way fixed ANOVA (Table 1) revealed population demography and bathymetric distribution to be complex, with multiple important factors as well as numerous two and three interaction effects. First, the variability of *M. glacialis* abundance with depth differed between site and between years. Second, the numbers of *M. glacialis* varied with individual size, which also varied with each of the other factors (year, site and depth). For example, the 51–100 mm sized sea-stars were more numerous at all three sites in 2001 (in total 417 observations) than in 2000 (in total 712 observations) but those belonging to each of the other four size-classes were not. Moreover, the number of sea-stars of the smallest size-classes differed considerably between sites whilst those of the largest did not.

The density of *M. glacialis* reached a maximum of 1.68 m^{-2} at 0–1 m in Site 2 in June 2000 and a minimum of 0.016 m^{-2} at 1–2 m in Site 1 in January 2000 and January 2001. A two-way ANOVA using log-transformed data found that there was a significant between-site variation in density at the 0–1 m depth category, whilst between-year variation was not significant (Table 2). This may be explained by the reduced number of *M. glacialis* observed at Site 1 compared with Sites 2 and 3 during both years. For the 0–1 m depth only, the overall density of *M. glacialis* was consistently lowest at Site 1 and no seasonal pattern of abundance was apparent there compared with Sites 2 and 3, where densities of *M. glacialis* reached a peak between June and October during both 2000 and 2001 at Sites 2 and 3 (Figure 3).

Predator density

During this study, crustacean predators (*Cancer pagurus*, *Carcinus maenas* and *Necora puber*) were observed to feed on juvenile *M. glacialis* amongst shallow water boulders. These predation events were observed approximately once per month over the sampling period. The mean density of these predators at 0–1 m was found to vary between a minimum of 0.05 m^{-2} at Site 3 during July 2001 and a maximum of 0.317 m^{-2} in at Site 2 during October 2001. No predators were recorded at 1–2 m, 2–4 m or 4–6 m depth categories. Between-site and between-year variability in predator density was not significant (Two-way ANOVA, Table 3), so all sites were pooled in order to give better resolution to between-year and between-month comparisons (Figure 4). Although between-year difference did not reach statistical significance (Two-way ANOVA, Table 3), there was evidence that a seasonal pattern existed, with highest densities of predators occurring between October and December during both years.

Feeding and dietary composition

The relative contributions of different items to the diet of *M. glacialis* are shown in Table 4. The composition of the diet varied between depths, but the pattern was similar across all three sites. The number of different prey items taken was significantly different between depths (Kruskal–Wallis test, df=3, H=8.81, P=0.03). Correspondence Analysis showed the dietary composition of *M. glacialis* at 0–1 m to be distinct from that of individuals found in deeper waters. The eigenvalues (which show how important the principal axes are) corresponding to the first two axes (as shown in Figure 5) were 0.4732 and 0.2951 respectively (the values for the third and fourth axes were 0.28 and 0.25 respectively). In particular, the diets of individuals at 0–1 m and 1–2 m appeared distinct from one another, whereas diets for individuals at 2–4 m and 4–6 m were broadly similar. There was some overlap between 0–1 m and 4–6 m, which may be due to the importance of crustacean prey at these depths compared with its relative unimportance at 1–2 m. At 0–1 m, prey items belonging to a number of different taxonomic groups were taken by small *M. glacialis*, with *Pomatoceros* sp. being the most common prey item at Sites 1 and 2 (composing 26.8% and 27.6%, respectively), but with gastropod prey being particularly important at Site 3 (31.0%). In contrast, at 1–2 m, 2–4 m and 4–6 m the composition of the diet was more restricted, and bivalve species (*Venus verrucos*, *Tapes rhomboides*, *Glycimeris glycimeris* and *Anomia ephippium*) were the most frequently observed prey item. Casual observations found ascidians to be a major component of the diet between 7 and 30 m, especially during the autumn months.

DISCUSSION

Despite the reputation of *Marthasterias glacialis* as a ubiquitous asteroid and a voracious predator, it has been the subject of surprisingly few quantitative ecological studies. Previous investigations have noted strong patterns of distribution with depth, and a wide dietary range (Magennis, 1981; Frid, 1992). Our data reveal that structure of the *M. glacialis* population at Lough Hyne appears to be controlled by multiple interacting factors. Changes in dietary preference with size may also be pivotal in restricting individuals differing in size to particular conditions of depth and substratum.

Given the partitioning of different sized individuals in space, the influence that *M. glacialis* exerts on the benthic communities of Lough Hyne is likely to change with habitat. We expected that increased recruitment of juveniles during summer months might influence the population structure, as previous investigations have indicated that *M. glacialis* spawns during the summer months, both within Lough Hyne (Minchin, 1987) and at other locations (Barker & Nichols, 1983; Savy, 1987). Abundances of juvenile *M. glacialis* observed at 0–1 m did increase during late summer for two of our three study sites in both 2000 and 2001. The lack of seasonality at Site 1 may be a result of reduced coverage of hard substratum. Boulders were less numerous at Site 1 (57%) than at either of Sites 2 or 3 (96% and 70%, respectively). Following settlement, survivorship of *M. glacialis* on hard boulder substratum may be greater than in more disturbed areas of finer substrata such as those that exist at Site 1. Another possibility is that the presence of boulders may have significant effects in terms of providing a suitable habitat for the prey items of juvenile sea-stars, thus leading to an increased survivorship of *M. glacialis* where boulders are abundant. Recruitment of *M. glacialis* did vary between our two study years; there were many more recruits in 2000 than there were in 2001. This may be due to reduced levels of *M. glacialis* larvae within the plankton, or to higher mortality amongst recently settled juveniles in 2001. As found in earlier years by Crook & Barnes (2001), the density of the crustaceans *Necora puber*, *Cancer pagurus* and *Carcinus maenas*, all potential predators of *M. glacialis*, was highest in autumn and winter at the North Shore of Lough Hyne. This may explain the reduced numbers of juvenile *M. glacialis* observed at 0–1 m during winter months.

Predation is considered to be important in shaping populations and assemblages in the marine environment (Lubchenco & Menge, 1978). In sheltered coastal environments like Lough Hyne, the role of predation is thought to be especially important (Paine, 1966). Maximum densities of *M. glacialis* and of crustacean predators, perhaps surprisingly, co-occurred in the immediate subtidal. However, we found that *M. glacialis*, like other juvenile asteroids behave cryptically in the structurally complex boulder environment (Tokeshi et al., 1989; Arrontes & Underwood, 1991; De'ath & Moran, 1998), with all juveniles being found in boulder interstices and crevices. Not only could such behaviour protect juveniles from large crustacean predators, but it may also serve to conceal them from overhead predators such as gulls. Ebling et al. (1966) suggested gulls to be significant as predators of *M. glacialis* in the shallow water of Lough Hyne, and we observed instances of gull predation during the course of this study. Avoidance of aerial predation may partially explain why larger *M. glacialis* were most commonly found in deeper water, where the risk of predation from gulls is considerably reduced.

Examination of diet can explain patterns of distribution of predator and prey (Sloan, 1980; Penney & Griffiths, 1984). In the case of extra-oral feeders, such as *M. glacialis*, examination of stomach contents is not possible, and *in situ* studies may be the most accurate way to estimate true feeding habits in the field (Mauzey et al., 1968; Sloan, 1980). Asteroids are considered to be opportunistic feeders, capable of exploiting and adapting to changes in prey availability (Menge, 1972). Our data support this in relation to *M. glacialis*; items that featured strongly in the diet at different sites and depths were also most abundant at those sites. The abundance of particular prey items (at particular sites or depths), such as *Anomia ephippium* was reflected in the diet of *M. glacialis*. This species did not, however, dominate the sea-star's diet, as has been suggested from experimental studies (Magennis, 1981; Kitching & Thain, 1987). We therefore support conclusions by Mauzey et al. (1968), which suggest that extrapolations drawn from experimental studies of asteroid biology may not reflect true patterns in nature.

There was little evidence to suggest that larger *M. glacialis* (>100 mm) exploited the variety of food resources found amongst shallow water boulders. These larger individuals, in particular those >200 mm chiefly fed on bivalve prey in the deeper water zones. This conformed to our expectations; other studies have shown that prey selection should be influenced by availability, energetic value and ease of manipulation (Gaymer et al., 2001). For the asteroids *Asterias vulgaris* and *Leptasterias polaris*, energetic gains from feeding on smaller prey items have been shown to decrease as the sea-star's size increased (Himmelman & Dutil, 1991). The time and effort involved in finding and subduing large bivalve prey may be counterbalanced by an associated high-energy gain. This may explain why the large *M. glacialis* are effectively restricted to deeper water once they reach a size large enough to manipulate large prey items. *Marthasterias glacialis*, in common with many other asteroids is a slow-moving predator, which relies primarily upon chemoreception and chance encounter to locate potential prey (Valentincic, 1973; Sloan, 1980). Despite this, mobile crustaceans such as *C. maenas*, *N. puber* and *Cancer pagurus* formed part of the diet for larger *M. glacialis*, in particular for individuals observed at 2–4 m and 4–6 m, where these crustaceans were not observed during sampling. This is likely to be a function of the sampling period (midday), since these crustacean species show crepuscular or nocturnal activity patterns. Although there is no way of being certain that crustacean prey was not already dead at the time of capture, it may be that *M. glacialis* obtains nocturnally active crustaceans when the latter migrate into deeper water at night. Alternatively, crustaceans in shallower water could be obtained during short foraging raids into boulder scree habitat by *M. glacialis*. These foraging raids may well occur at night, and previous studies have suggested that this is the case, both at Lough Hyne (Ebling et al., 1966; Frid, 1992). Elsewhere on the French Mediterranean coast, *M. glacialis* has been shown to carry out such feeding raids on the echinoid *Paracentrotus lividus*, which is estimated to constitute 50% of the diet of *M. glacialis* (Savy, 1987). A large population of *P. lividus* is resident amongst the boulder scree at 0–1 m at all three of our study sites at Lough Hyne, and it has been the subject of several previous studies (Crook et al., 1999; Crook & Barnes, 2001). Ebling et al. (1966) hypothesized that the unusual diurnally active nature of *P. lividus* at Lough Hyne (where sea urchins migrate to the tops of boulders during the day and below boulders at night) had evolved as a mechanism to avoid predation by nocturnally active *M. glacialis*. It is implicit in such a theory that predation pressure from *M. glacialis* must have been strong at some point in the past. This is not possible to prove, but our data do demonstrate unequivocally that throughout the two years of this study, *P. lividus* did not constitute a significant component of the diet of *M. glacialis*.

The spatial partitioning of different size-classes has been important in making *M. glacialis* the most widely dispersed asteroid within the Lough. Like other asteroids, such as *A. vulgaris* and *L. polaris* (Himmelman & Dutil, 1991), *M. glacialis* is a generalist feeder, and thus is capable of exploiting a wide range of prey resources. Though it is unlikely to occupy a keystone position in Lough Hyne, *M. glacialis* does emerge as a dominant benthic predator, and as such has the potential to exert a strong structuring influence on the benthic communities there. The asteroid's structuring influence may be particularly strong amongst shallow boulder scree, where it reaches peak densities and feeds on a number of different taxonomic groups. This may also be the case for *M. glacialis* populations in many other inshore habitats in north-west Europe.

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