

Dietary constraints on reproductive periodicity in two sympatric deep-sea astropectinid seastars

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Abstract. Examination of the diet of two sympatric species of seastar, *Bathybiaster vexillifer* and *Plutonaster bifrons* from ~2200 m depth in the Rockall Trough, NE Atlantic Ocean (~57° 18'N; 10° 28'W), suggested that diet may determine the different reproductive patterns found between these two species. In the non-seasonally breeding *B. vexillifer*, the diet showed a high Shannon-Wiener prey diversity index, the dominant prey being the irregular echinoid *Hemiaster expergitus* together with a variety of prosobranch gastropods and protobranch bivalves. By contrast, the prey diversity in the seasonally breeding *P. bifrons* was significantly lower than that of *B. vexillifer*. In addition, organic carbon content in the sediment residue in the stomachs of *P. bifrons* displayed a seasonal cycle, while no such seasonality was detected in *B. vexillifer*. The stomachs of *P. bifrons* also contained a higher proportion of scavenged material, including the seasonally available remains of mesopelagic blue whiting. These data, together with "Bathysnap" (time-lapse camera) observations of feeding behaviour in both species, suggest that *B. vexillifer* is a predator feeding deep in the sediment, whereas *P. bifrons* feeds close to the sediment surface where it is affected by the seasonal availability of phytodetritus and fish carcasses.

Introduction

Little is known of the dietary preferences of deep-sea seastars. Carey (1972) identified the gut contents of a number of species collected from the slope and abyssal plain off Oregon, NW America, and noted that diet changed from predominantly carnivory to omnivory with increasing depth. In the NE Atlantic, Khripounoff (1979) identified the main feeding type as omnivory amongst asteroids collected at depths of 2100 to 4600 m from six stations as part of the BIOGAS programme (Laubier and Monniot 1985). Nothing is known of any temporal variation of diet in deep-sea asteroids. This is in contrast to studies of species of the shallow-water astropectinid seastar *Astropecten*, which have revealed that their diet

varies with season. The main prey-species of this genus usually includes gastropods, bivalves and irregular echinoids (Christiansen 1970, Doi 1976, Ribí et al. 1977, Nojima 1988, 1989). Most species of *Astropecten* in shallow water are highly selective, the preferred diet being small bivalves, although when this prey is not abundant, their diet shifts to "non-selective detritus feeding" (Nojima 1989) or to scavenging on dead or moribund remains of the vernal copepod bloom (Franz and Worley 1982). Where two congeners of *Astropecten* compete for a food resource, the two species ingest prey of different size classes (Ribí et al. 1977). In addition, ontogenetic variation in the diet in *Astropecten latespinosus* has been described (Nojima 1989). In these studies the contribution of the organic matter associated with the sediment ingested with the prey was never quantitatively assessed.

The diet of astropectinids is of interest, as the gut structure of this group of seastars is very variable (Douchet 1981). Astropectinids appear to occupy a central position in the Asteroidea, between those with a "primitive" gut, where the pyloric caecum is little more than a sac off the stomach, and those with a more "advanced" structure, in which the pyloric caecum is a well defined structure attached to, but separate from, the pyloric stomach (Douchet 1981, Jangoux 1982). The size of the pyloric caecum in seastars is often related to the developmental state of the gonads. In many shallow-water asteroids, there is an inverse relationship between the pyloric caecum index and the gonad index. This has been interpreted as reflecting a storage of food in the pyloric caecum prior to transfer to the gonads in order to fuel their seasonal development (Barker and Nichols 1983) probably by means of the coelomic fluid (Ferguson 1982).

Seasonal reproduction is a common phenomenon in shallow-water astropectinids (Nojima 1979, Grant and Tyler 1984). In the deep sea, most asteroid (including astropectinid) species reproduce all the year round (quasi-continuously; i.e., non-seasonally: Pain et al. 1982a, b, Tyler et al. 1982), although at least two astropectinid species, *Plutonaster bifrons* and *Dytaster grandis*, are known

to have an annual reproductive periodicity (Tyler and Pain 1982, Tyler et al. 1990). This seasonality in reproduction (Tyler 1988) has been related to the increased flux of phytodetritus arriving at the seabed in this area of the deep-sea in the late spring and summer months (Billett et al. 1983, Lampitt 1985, Rice et al. 1986, 1991). This seasonally-pulsed downward flux may provide sufficient labile energy to fuel gametogenesis in the seasonally-breeding species.

To test the effect of diet on reproduction in deep-sea asteroids, we examined the stomach contents of two sympatric species of astropectinid seastar, the quasi-continuously breeding *Bathybiaster vexillifer* and the seasonally breeding *Plutonaster bifrons*. Specimens were obtained from a time-series sampling programme on the same station at 2200 m depth in the northern Rockall Trough. As the two species were collected from the same station, and often in the same trawl sample, we believe they have experienced similar environmental conditions. Thus, to test if differences in diet control the contrasting reproductive patterns in these two species, we examined three facets of their nutritive ecology: (i) is there variation in their diet? (ii) is there a seasonal cue in their digestive system? (iii) is there variation in their feeding behaviour? To this end, we examined, on a seasonal basis, the diet of both species and the variation, if any, in their pyloric caecum and gonad indices. We also examined photographs taken with the time-lapse camera system "Bathysnap" (Lampitt and Burnham 1983) and the Institute of Oceanographic Sciences epibenthic sledge (Rice et al. 1982) within the depth range of the two species in the Porcupine Seabight for evidence of their feeding behaviour.

Materials and methods

Samples of *Bathybiaster vexillifer* and *Plutonaster bifrons* were taken with a 3 m-wide Agassiz trawl from a depth of 2200 m, centred on $\sim 57^{\circ}18'N$; $10^{\circ}28'W$ (Station "M"; Gage and Tyler 1982) at the base of the Barra Fan in the northern Rockall Trough (NE Atlantic Ocean). The samples formed part of a megafaunal time-series inaugurated at this station by the Scottish Marine Biological Association in 1978 and sampled opportunistically to date (Table 1). Some of the samples used in this study had previously been used for the determination of reproductive patterns in these species (Tyler and Pain 1982, Tyler et al. 1982). Samples were sorted on deck, fixed in 10% buffered seawater formalin, and transferred after one week to 70% alcohol for long-term storage.

For the examination of gut contents and determination of organ indices, at least 10 individuals (where available) from each sample were examined (Table 1). For each specimen, the maximum arm radius (R) and interambulacral radius (r) (*sensu* Mortensen 1927) were measured. The entire dorsal surface was removed by incisions between the paxillar area and the dorsal marginal plates, which exposed the digestive system whilst leaving the gonads attached to the underside of the dorsal surface.

For the calculation of gonad indices, two pyloric caeca, two gonads and the intestinal caeca (the last present only in *Bathybiaster vexillifer*) were removed, wet-weighed, dried at 70°C overnight, reweighed and finally ashed at 550°C for 4 h, and then weighed to determine the ash-free dry weight (AFDW).

The gut contents were removed from the stomach and stored in 70% isopropyl alcohol. Gut contents were stained with 0.5% rose bengal in 70% alcohol overnight, and examined under a dissecting

Table 1. *Bathybiaster vexillifer* and *Plutonaster bifrons*. Samples used in this study

| Station; date | Depth (m) | n | |
|----------------------|-----------|----------------------|-------------------|
| | | <i>B. vexillifer</i> | <i>P. bifrons</i> |
| AT 144; 19 Apr. 1978 | 2 240 | 19 | 10 |
| AT 153; 15 Jan. 1979 | 2 200 | 17 | 16 |
| AT 154; 21 May 1979 | 2 264 | 8 | 5 |
| AT 167; 13 Aug. 1979 | 2 300 | 6 | 0 |
| AT 171; 03 Mar. 1980 | 2 225 | 5 | 15 |
| AT 177; 29 May 1980 | 2 220 | 4 | 9 |
| AT 181; 16 Sep. 1980 | 2 220 | 18 | 12 |
| AT 186; 12 Apr. 1981 | 2 170 | 7 | 19 |
| AT 195; 18 Aug. 1981 | 2 190 | 9 | 13 |
| AT 201; 09 May 1982 | 2 180 | 12 | 0 |
| AT 219; 03 Aug. 1982 | 1 991 | 8 | 15 |
| ES 232; 19 May 1983 | 2 195 | 11 | 0 |
| AT 256; 31 July 1983 | 1 705 | 8 | 9 |
| AT 394; 30 June 1990 | 2 190 | 12 | 0 |
| AT 400; 08 Sep. 1990 | 2 205 | 10 | 0 |
| AT 408; 14 Dec. 1990 | 2 240 | 8 | 0 |

microscope. All the recognizable, as well as stained unrecognizable, organic matter was removed and stored in 70% alcohol. The volume of the remaining sediment was noted and it was dried at 70°C overnight and ashed at 550°C for 6 h to determine the organic matter content. Dietary species diversity was calculated by the Shannon-Wiener index (Pielou 1977), treating the unrecognizable organic matter as a single species.

Photographic observations of feeding behaviour were conducted with the time-lapse camera "Bathysnap" (Lampitt and Burnham 1983) deployed at a depth of 2009 m at $51^{\circ}0.8'N$; $12^{\circ}54.4'W$ (Station 51418 #1, see Jackson et al. 1991).

Results

Gonad development

Examination of the gonad ash-free dry weight against time confirmed the conclusions of Tyler and Pain (1982) and Tyler et al. (1982) that *Bathybiaster vexillifer* is a continuous breeder and *Plutonaster bifrons* is a seasonal breeder (Fig. 1). To determine if these variations in gonad weight are related to season or age, the gonad ash-free dry weight was plotted against both Julian day and maximum radius (R). In *B. vexillifer* the gonad AFDW showed no clear variation with season, but did show a significant power relationship to size (R) (t -statistic = 12.96, $n = 131$) (Fig. 2A), suggesting that reproductive effort increases with increasing age. The gonad weight in *P. bifrons* also increased with R , but this regression was less significant (t -statistic = 3.81, $n = 155$) (Fig. 2B). There was a marked variation in the gonad AFDW as a function of season (Fig. 1B).

Pyloric caecum development

A similar, but less obvious, pattern to that observed in the gonad AFDW was seen in the pyloric caecum AFDW

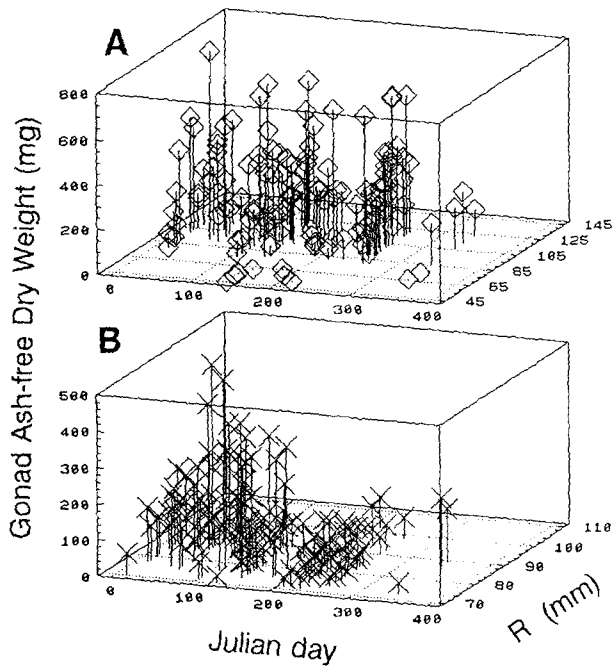


Fig. 1. *Bathybiaster vexillifer* (A) and *Plutonaster bifrons* (B). 3-D scatterplots of gonad ash-free dry weights as a function of Julian day and maximum radius (R)

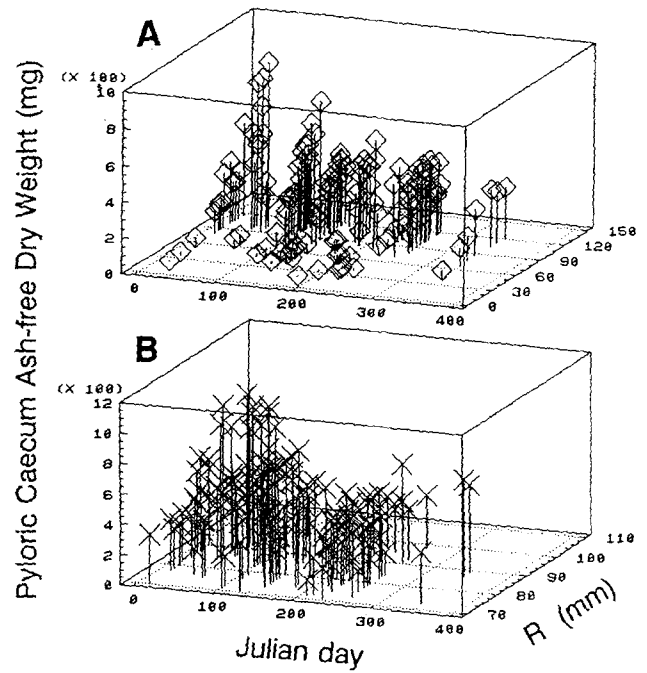


Fig. 3. *Bathybiaster vexillifer* (A) and *Plutonaster bifrons* (B). 3-D scatterplots of pyloric caecum ash-free dry weight against Julian day and maximum radius (R)

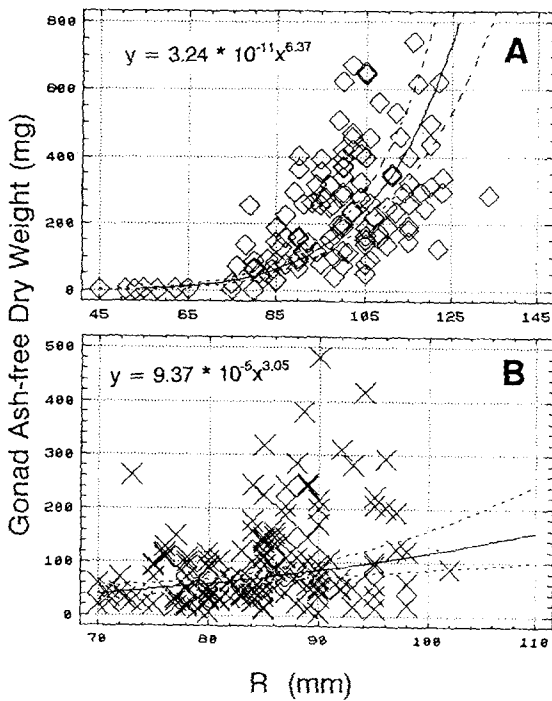


Fig. 2. *Bathybiaster vexillifer* (A) and *Plutonaster bifrons* (B). Regression of gonad ash-free dry weight on maximum radius (R). Dashed lines represent 95% confidence limits

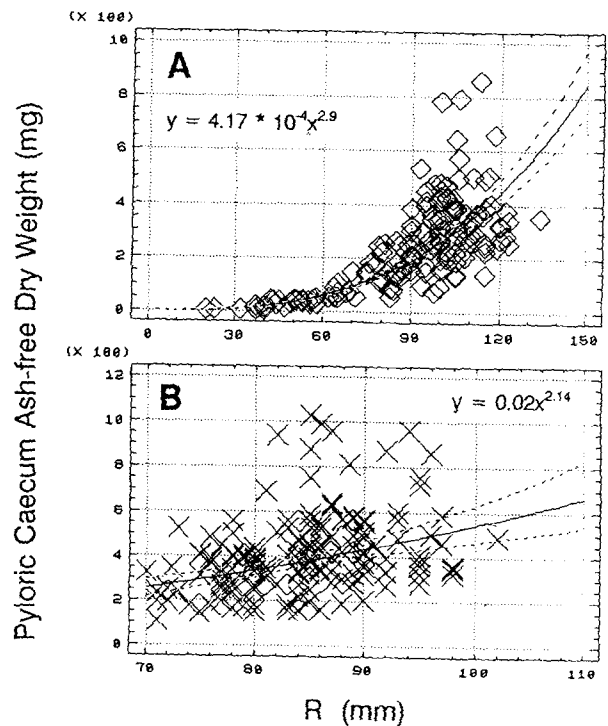


Fig. 4. *Bathybiaster vexillifer* (A) and *Plutonaster bifrons* (B). Regression of pyloric caecum ash-free dry weight against maximum radius (R). Dashed lines represent 95% confidence limits

in the two species. *Bathybiaster vexillifer* displayed no obvious seasonal variation (Fig. 3A), but did show a strong power regression as a function of size (t -statistic = 27.92, $P = < 0.001$) (Fig. 4A). In *Plutonaster bifrons*, on the other hand, there was a marked seasonal variation in pyloric caecum AFDW (Fig. 3B); although, in this

case, there was a significant regression with size that was weaker than that for *B. vexillifer* (t -statistic = 5.39, $P = < 0.001$) (Fig. 4B).

We compared the reproductive effort and nutritive storage of the two species on an annual basis. *Bathybiaster vexillifer* puts twice as much effort into reproduc-

Table 2. *Bathybiaster vexillifer*. Number of individuals examined during present study, numbers with food in their stomachs and prey items and prey-species diversity for samples at different times of the year. (Mean prey-diversity index = 2.55; SD = 0.61; mean evenness = 0.89; SD = 0.07)

| Species | Station, date, Julian Day, total number examined/number with food | | | | | | |
|-----------------------------------|---|--------------------------------------|---------------------------------------|---|--------------------------------------|---------------------------------------|--------------------------------------|
| | AT 153 15 Jan. 79 JD 15 17/12 | AT 171 29 Mar. 80 JD 62 5/3 | AT 186 12 Apr. 78 JD 102 7/6 | AT 144 19 Apr. 78 JD 109 19/16 | AT 201 9 May 82 JD 129 12/4 | AT 232 19 May 83 JD 139 11/9 | AT 154 21 May 79 JD 141 8/3 |
| Echinodermata | | | | | | | |
| <i>Hemiaster expergitus</i> | 6 | 2 | 6 | 10 | 6 | 4 | |
| <i>Ypsilothuria bitentaculata</i> | 1 | | | 2 | | | |
| ? <i>Pourtalesia</i> sp. | | | | | | | |
| Holothurian fragments | | | | 2 | | | |
| Ophiuroid arm | | | 1 | | | | |
| Gastropoda | | | | | | | |
| <i>Neverita (Natica) obtusata</i> | 6 | 1 | 1 | 7 | 1 | | |
| <i>Oenopota ovalis</i> | 1 | | | | | | |
| <i>Cylichna ?vortex</i> | 1 | 2 | | 2 | | | 1 |
| <i>Cylichna ?verrilli</i> | | | | | | | |
| <i>Benthonella tenella</i> | | | | | | | |
| <i>Ringicula nitida</i> | | | | | | | |
| <i>Mellanella</i> sp. | | | | | | | |
| <i>Cerithiella</i> sp. | | | | | | | |
| Unidentified archaeogastropod | | | | | | | |
| Gastropod operculum | | | | 1 | | | |
| <i>Scaphander punctostriatus</i> | | | 1 | | | | 1 |
| Bivalvia | | | | | | | |
| <i>Yoldiella jeffreysi</i> | 3 | 1 | | 2 | 1 | 1 | |
| <i>Yoldiella lucida</i> | | | | | | | |
| <i>Yoldiella inflata</i> | | | | | | | 1 |
| <i>Ledella pustulosa</i> | 1 | 2 | 2 | 4 | | 1 | 1 |
| <i>Silicula fragilis</i> | | | | | 1 | | |
| <i>Malletia johnsoni</i> | 3 | | 1 | 2 | | 6 | 1 |
| <i>Nuculoma</i> sp.A | | | | 1 | | | |
| <i>Limatula subovata</i> | | | | 1 | | | 1 |
| Scaphopoda | | | | | | | |
| | | | | | | 1 | |
| Polychaeta | | | | | | | |
| <i>Poecilochaetus cf fulgens</i> | | | | | | | |
| <i>Terebellides</i> sp.A | 1 | | | 1 | | | |
| <i>Diplocirrus</i> sp. | | | | 2 | | | |
| <i>Notomastus</i> sp. | | | | | | | 1 |
| <i>Axiothella</i> sp. | | | | | | | |
| Amphipoda | 1 | | | | | | |
| Isopoda | | 1 | 1 | 2 | | | |
| Cumacea | | | | | | | 1 |
| Nematoda | 1 | | | | | | |
| ?Sipuncula | | | | | | | |
| Allogromiid foram | | | | | 1 | | |
| Organic matter | | | | | 1 | 2 | |
| Species diversity | 3.04 | 2.42 | 2.13 | 3.63 | 1.71 | 2.5 | 2.25 |
| Evenness | 0.87 | 0.96 | 0.85 | 0.9 | 0.76 | 0.86 | 1.00 |

tion as *Plutonaster bifrons* (Student's *t*-test = 11.86; $P < 0.01$), whereas *P. bifrons* puts significantly more effort into nutrient storage than does *B. vexillifer* ($t = 7.42$; $P < 0.01$). There was a positive correlation between the gonad AFDW and the pyloric caecum AFDW in both species, with no evidence of the inverse relationship reported elsewhere (Barker and Nichols 1983) for asteroids (*Bathybiaster vexillifer*: $r^2 = 0.58$; $n = 132$; $P < 0.001$; *Plutonaster bifrons*: $r^2 = 0.55$; $n = 156$; $P < 0.001$) (Fig. 5).

Analysis of stomach contents

Stomach eversion in astropectinids is prevented, under natural conditions, by the gastric ligaments that attach the stomach wall to the ambulacral plates. Although none of the specimens examined in the present study had everted stomachs, several were empty and it is possible some material was voided from the stomachs during recovery from the great depth of capture (Tables 2 and 3).

Table 2 (continued)

| | | | | | | | | Totals |
|--------------------------------------|--|---------------------------------------|--------------------------------------|---------------------------------------|------------------------------------|--------------------------------------|------------------------------------|---------|
| AT 177 29 May 80 JD 149 4/2 | AT 394 30 June 90 JD 181 12/9 | AT 167 13 Aug. 79 JD 194 6/4 | AT 219 3 Aug. 81 JD 214 8/4 | AT 195 18 Aug. 81 JD 230 9/8 | AT 400 6 Sep. 90 251 10/9 | AT 181 16 Sep. 80 259 18/12 | AT 408 14 Dec. 90 339 8/6 | 154/107 |
| | | | 1 | 5 | | 6 | 2 | 50 |
| 1 | 1 | | 1 | 1 | | 4 | | 9 |
| | | | | | | 1 | | 1 |
| | | | | | 5?Kolga | 1 | | 3 |
| | | | | | | 1 | | 2 |
| | | | | | | 4 | 3 | 28 |
| | 1 | 1 | 1 | 3 | | | | 8 |
| | | 1 | | 1 | | 2 | | 4 |
| | 1 | | | 1 | 2 | | | 4 |
| | | | | 2 | 11 | | 7 | 26 |
| | 6 | | | 1 | | | | 0 |
| | | | | | | | | 0 |
| | | | | | | | 1 | 1 |
| 1 | | | | | 2 | | | 1 |
| | 2 | | | | | | 1 | 4 |
| | | | | | | | | |
| | 2 | 4 | | 4 | | | 1 | 19 |
| | | | | | | | 1 | 1 |
| | | | | | | | 2 | 1 |
| 1 | 1 | 1 | | 6 | | | | 22 |
| | | | | | | 5 | | 1 |
| | 1 | | | 2 | | | | 21 |
| 1 | | | 2 | 3 | | | | 1 |
| | | | | | | | | 7 |
| | | | | | | | | 1 |
| | 1 | | | | | | 1 | 3 |
| | | | | 1 | | 1 | | 3 |
| | | | | | | 1 | | 1 |
| | | | | | | 1 | | 1 |
| 1 | | 1 | | | | 3 | 1 | 7 |
| | | | | 1 | | 1 | | 6 |
| | | | | | | | | 1 |
| | | 1 | | | | | | 1 |
| | | | | | | | | 1 |
| | | | | | | | | 1 |
| 1 | 6 | 1 | 2 | 2 | 3 | 2 | | 27 |
| 1.94 | 2.65 | 2.65 | 3.49 | 2.17 | 2.65 | 2.65 | 3.49 | |
| 1.00 | 0.86 | 0.91 | 0.92 | 0.96 | 0.86 | 0.91 | 0.92 | |

The main recognizable food in samples of both species is listed in Tables 2 and 3. In *Bathybiaster vexillifer* the gut contents were dominated by the irregular echinoid *Hemiaster expergitus*. The individuals of this species removed from the gut were dominated by specimens estimated at <20 mm in length (Fig. 6). *H. expergitus* occurred singly in the stomach contents, except in five individuals of *B. vexillifer* in which 2 or 3 juvenile *H. expergitus* were found. In addition, 9 gastropod species were found, the most common being the prosobranchs *Never-*

ita (Natica) obtusata, *Benthonella tenella* and the opisthobranchs *Cylichna vortex* and *Scaphander punctostriatus*. The bivalves found in the gut contents included the protobranchs, dominated by *Yoldiella* spp., *Ledella pustulosa*, and *Malletia johnsoni*. In addition to these common species, other noteworthy prey include the holothurian *Ypsilothuria bitentaculata* and a wide variety of polychaete worms including *Poecilochaetus* cf. *fulgens*, *Terebellides* sp. A, *Diplocirrus* sp. and at least two species of maldanid. Peracarid fragments (particularly amphipods

Table 3. *Plutonaster bifrons*. Number of individuals examined during present study, numbers with food in their stomachs and prey items and prey-species' diversity for samples from different times of the year. (Mean prey diversity index = 1.49; SD = 0.36; mean evenness = 0.9; SD = 0.08)

| Species | Station, date, Julian Day, total number examined/number with food | | | | | | | | | | | | | | Totals |
|-----------------------------------|---|---------------------------------------|---|--|-------------------------------------|--------------------------------------|--------------------------------------|---------------------------------------|---------------------------------------|--|---|--|---|--|--------|
| | AT 153 15 Jan. 79 JD 15 16/8 | AT 171 29 Mar. 80 JD 62 15/9 | AT 186 12 Apr. 78 JD 102 19/10 | AT 144 19 Apr. 78 JD 109 10/8 | AT 201 9 May 82 JD 129 9/5 | AT 154 21 May 79 JD 141 5/3 | AT 177 29 May 80 JD 149 9/5 | AT 256 31 July 83 JD 210 9/6 | AT 219 3 Aug. 82 JD 214 15/5 | AT 195 18 Aug. 81 JD 230 13/8 | AT 181 16 Sept. 80 JD 259 12/8 | | | | |
| Echinodermata | 3 | 5 | 3 | 4 | 2 | 1 | 4 | 1 | 6 | 3 | | | | | 32 |
| <i>Hemiaster experegitus</i> | | | | | | | | | | | | | | | 0 |
| <i>Ypsilothuria bitentaculata</i> | | | | | | | | | | | | | | | 0 |
| ? <i>Pourtalesia</i> sp. | | | | | | | | | | | | | | | 0 |
| Holothurian fragments | | | | | | | | | | | | | | | 0 |
| Ophiuroid arm | | | | | | | | | | | | | | | 0 |
| Gastropoda | | | | | | | | | | | | | | | 0 |
| <i>Neverita (Natica) obtusata</i> | | | | | | | | | | | | | | | 0 |
| <i>Oenopota ovalis</i> | | | | | | | | | 1 | | | | | | 0 |
| <i>Cyllichna ?vortex</i> | | | | | | | | 2 | | | | | | | 7 |
| <i>Cyllichna ?verillii</i> | | 1 | | | | | | | | | | | | | 1 |
| <i>Benthonella tenella</i> | | | | | | | | | | | | | | | 0 |
| <i>Ringicula nitida</i> | 3 | | 3 | | | | | 1 | | | | | | | 7 |
| <i>Mellanella</i> sp. | | 1 | | | | | | | | | | | | | 1 |
| <i>Cerithiella</i> sp. | | | | | | | | | | | | | | | 0 |
| Unidentified archaeogastropod | | | | | | | | | | | | | | | 0 |
| Gastropod operculum | | | | | 1 | | | | | | | | | | 0 |
| <i>Scaphander punctostriatus</i> | | | | | | | | | | | | | 1 | | 0 |
| Bivalvia | | | | | | | | | | | | | | | 0 |
| <i>Yoldiella jeffreysi</i> | | | | | | | | | | | | | | | 0 |
| <i>Ledella pustulosa</i> | | | | | | | | | | | | | | | 0 |
| <i>Silicula fragilis</i> | | | | | | | | | | | | | | | 0 |
| <i>Mallieria johnsoni</i> | | | | | | | | | | | | | | | 0 |
| <i>Nuculoma</i> sp.A | | | | 2 | | | | | | | | | | | 2 |
| <i>Limatula subovata</i> | | | | | | | | | | | | | | | 0 |
| <i>Montacuta symmetricos</i> | | | | 1 | | | | | | | | | | | 1 |
| <i>Thyasira brevis</i> | | | | 1 | | | | | | | | | | | 1 |
| Scaphopoda | | | | | | | | | | | | | | | 1 |
| Polychaeta | | | | | | | | | | | | | | | 0 |
| <i>Poecilochaetus cf. fulgens</i> | | | | | | | | | | | | | | | 0 |
| <i>Terrebellides</i> sp.A | | | | | | | | | | | | | | | 0 |
| <i>Diplocirrus</i> sp. | | | | | | | | | | | | | | | 0 |
| <i>Notomastus</i> sp. | | | | | | | | | | | | | | | 0 |
| <i>Axiiothella</i> sp. | | | | | | | | | | | | | | | 0 |
| Amphipoda | | | | | | | | | | | | | | | 0 |
| Isopoda | | | | | | | | | | | | | | | 0 |
| Cumacea | | | | | | | | | | | | | | | 0 |
| Nematoda | | | | | | | | | | | | | | | 0 |
| ?Sipuncula | | | | | | | | | | | | | | | 0 |
| Fish scales | | | | | | | | | | | | | | | 0 |
| Fish fragments | | 2 fish | | | | | | | | | | | | | 4 |
| Organic matter | 6 | 2 | 3 | 4 | 2 | 2 | 3 | 5 | 6 | 2 | | | | | 40 |
| Species diversity | 1.45 | 1.61 | 2.16 | 2.02 | 1.47 | 0.89 | 1.48 | 1.11 | 1.27 | 1.48 | | | | | |
| Evenness | 0.94 | 0.83 | 0.96 | 0.9 | 0.96 | 0.91 | 0.97 | 0.72 | 0.83 | 0.97 | | | | | |

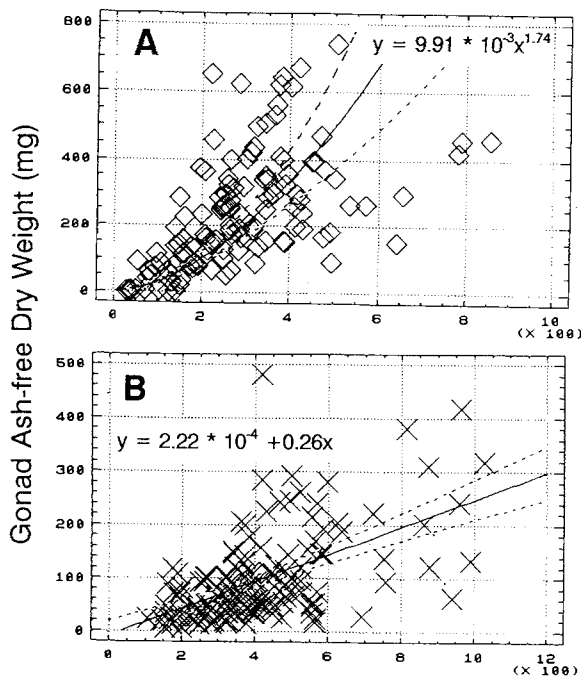


Fig. 5. *Bathybiaster vexillifer* (A) and *Plutonaster bifrons* (B). Relationship of gonad ash-free dry weight and pyloric caecum ash-free dry weight. Dashed lines represent 95% confidence limits

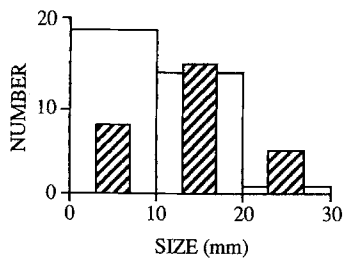


Fig. 6. *Bathybiaster vexillifer* (open histograms) and *Plutonaster bifrons* (hatched histograms). Size-frequency of dominant prey item, *Hemiaster expergitus*

and isopods) were found in a number of samples, but these were generally rare. Fragments of fish vertebrae and scales were also noted. Unrecognizable organic matter was found in a number of specimens but, except for one sample, these were in the minority. Calculation of Shannon-Wiener diversity of prey for each individual sample gave a range of 1.96 to 5.53 (\bar{x} = 2.55, SD = 0.61) (Table 2).

In *Plutonaster bifrons* the diet was dominated by *Hemiaster expergitus* (particularly fragments) and unrecognizable organic matter (Table 3). The size distribution of *H. expergitus* in the gut contents was dominated by individuals estimated to lie in the 10 to 20 mm length size-range (Fig. 6). There was a significant difference in the size distribution (χ^2 = 31.97; p < 0.01) of *H. expergitus* from *P. bifrons* and *Bathybiaster vexillifer*. Gastropods formed a minor element in the diet of *P. bifrons*, and only two specimens of a protobranch bivalve (both an undescribed *Nuculoma* sp.) and a single specimen of a polychaete were found. A notable finding was that two spec-

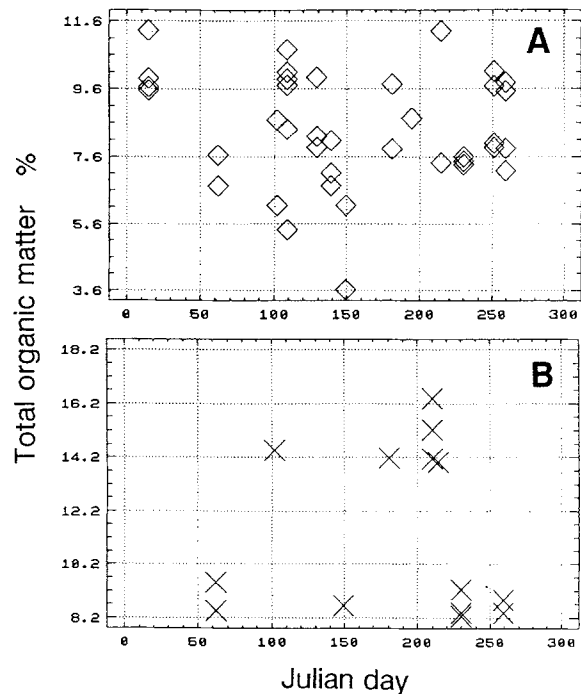


Fig. 7. *Bathybiaster vexillifer* (A) and *Plutonaster bifrons* (B). Scatterplots of total organic matter of stomach contents (%) against Julian day

imens of *P. bifrons* had partially ingested a badly decomposed specimen of blue whiting [*Micromesistius poutassou* (Risso)]. This was not a sampling artefact, as the fish had distorted the stomach of both seastars. In addition, fish scales and vertebrae were found in other specimens of *P. bifrons*. This rather limited diet of *P. bifrons* resulted in a dietary Shannon-Wiener diversity index varying from 1.11 to 2.16 (\bar{x} = 1.49, SD = 0.36).

Comparison of the dietary species' diversity of individual samples of the two seastar species revealed a significant difference (Student's t -test = 4.82; P = < 0.001). After the removal of empty stomachs and of recognizable prey items, only a limited number of specimens (38 *Bathybiaster vexillifer* and 14 *Plutonaster bifrons*) contained residual sediment. Analysis of the organic carbon content of this material from *B. vexillifer* revealed values of 3.6 to 11.3%, but with no apparent seasonal variation (Fig. 7A). Conversely, among the limited number of specimens of *P. bifrons* containing residual sediment, the organic carbon values ranged from 8.2 to 16.2% and displayed a seasonal cycle (Fig. 7B). Calculated as a percentage of the total organic remains, including recognizable species, *P. bifrons* contained significantly more unrecognizable organic matter than did *B. vexillifer* (t = 2.91; P < 0.001).

Seabed photographs of the two species in the Porcupine Seabight (see Rice et al. 1991) suggest a variation in feeding behaviour. This variation is clearly illustrated by a series of time-lapse (Bathysnap) photographs (Figs. 8, 9). "Bathysnap" was deployed on 1 April 1982 and recovered on 27 May 1982, having obtained photo-

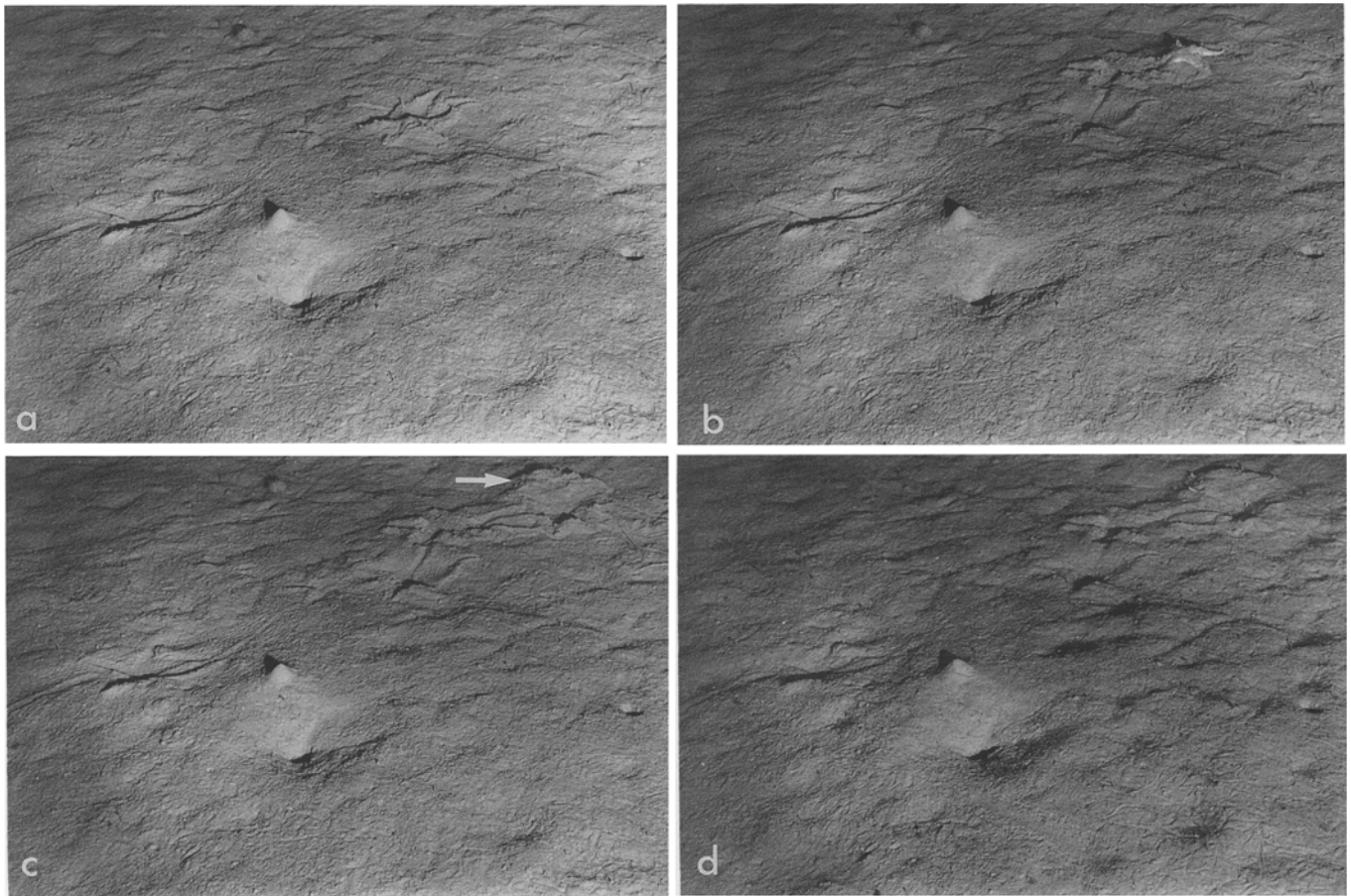


Fig. 8 a–d. *Bathyiaster vexillifer*. Time-lapse photographs from depth of 2 009 m in Porcupine Seabight, illustrating feeding behaviour. (a)–(c) Frames 539–541; 25 April 1982; (d) Frame 677, 1 May 1982. (See “Results – Analysis of stomach contents” for further details)

graphs at 64 min intervals, each covering an area of 2 m². Phytodetritus arrived on the seabed during the deployment, beginning on 29 April (cf. Fig. 8 a–c showing no phytodetritus on 25 April with Fig. 8 d showing small amounts of phytodetritus on 1 May and Fig. 9 showing much larger amounts on 2 May).

Fig. 8 a–c show successive frames of *Bathyiaster vexillifer* moving across the field of view from left to right, leaving extensive evidence of deep sediment penetration and finally disappearing from view beneath the sediment surface in the arrowed position on Fig. 8 c. The tips of the arms of this specimen began to emerge after 3 d, and it finally emerged completely and moved away from this feeding position 6 d after arrival (Fig. 8 d). Similar evidence of deep ploughing by *B. vexillifer* is shown in Fig. 9 c and d, this time with the seastar moving rapidly from the top-right to the bottom-left. This individual first appeared in the frame preceding that shown in Fig. 9 c (arrowed), while in the succeeding frame (Fig. 9 d) it has already left the photographed area. Thus, in the space of less than 3 h the seastar had traversed the area, leaving a very obvious trail with evidence of several deep feeding marks.

In contrast, Fig. 9 b shows the characteristic feeding posture of *Plutonaster bifrons* and the lack of an obvious trail as it moves across the seabed. During the previous

Table 4. Faunal dominants (>25 individuals in sample) in epibenthic sledge hauls ES176, ES184, ES197 and ES200, all from Station “M” (~57° 18' N; 10° 28' W)

| Echinodermata | Anthozoa |
|--------------------------------------|-------------------------------------|
| <i>Echinus affinis</i> | <i>Fungiacyathus marenzelleri</i> |
| <i>Ophiomusium lymani</i> | |
| <i>Ophiacantha bidentata</i> | Bivalvia |
| <i>Ophiura ljunghmani</i> | |
| Postlarval <i>Ophiocten gracilis</i> | <i>Limatula subovata</i> |
| <i>Amphilepis ingolfiana</i> | <i>Deminucula atacciana</i> |
| <i>Hymenaster membranaceus</i> | <i>Neilonella subovata</i> |
| <i>Benthopecten simplex</i> | <i>Pristoglossa nitens</i> |
| <i>Ypsilothuria bitentaculata</i> | <i>Malletia johnsoni</i> |
| | <i>Silicula fragilis</i> |
| Gastropoda | <i>Ledella pustulosa</i> |
| | <i>Yoldiella inflata</i> |
| <i>Benthonella tenella</i> | <i>Yoldiella jeffreysi</i> |
| <i>Oenopota graphica</i> | <i>Yoldiella lucida</i> |
| <i>Oenopota ovalis</i> | <i>Yoldiella curta</i> |
| <i>Ringicula</i> sp. | <i>Vesicomya atlantica</i> |
| <i>Torellia vestita</i> | <i>Thyasira (Axinulus) subovata</i> |
| <i>Skenia basistriata</i> | <i>Thyasira (Thyasira) obsoleta</i> |
| <i>Skenia</i> sp. | <i>Cuspida parva</i> |
| <i>Philine quadrata</i> | |
| <i>Scaphander punctostriatus</i> | |
| <i>Pulsellum affine</i> | |
| <i>Pulsellum lofotense</i> | |

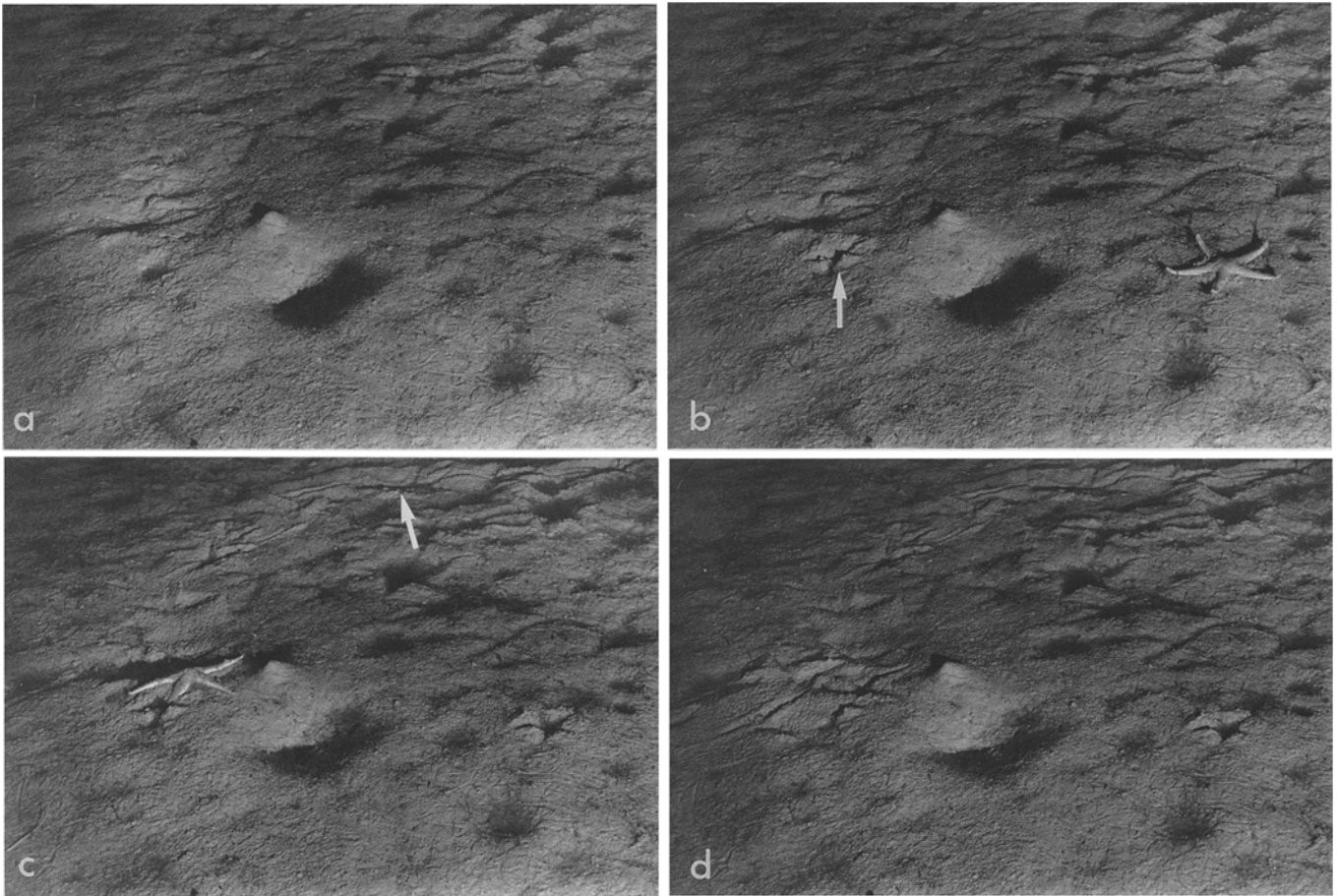


Fig. 9 a–d. *Plutonaster bifrons* (a) (b) and *Bathybiaster vexillifer* (c) (d). Time-lapse photographs from depth of 2 009 m in Porcupine Seabight, illustrating feeding behaviour. (a) (b) (c) (d) Frames 690,

691, 700 and 701, respectively (all 2 May 1982). (See “Results – Analysis of stomach contents” for further details)

hour, this individual had apparently fed once before within the photographed area, leaving its typical small, and apparently rather shallow, feeding trace (arrowed). In the preceding frame (Fig. 9 a), there is no sign of either the seastar or the feeding trace. Nine frames (almost 10 h) after its production, the left-hand *P. bifrons* feeding trace was destroyed by the passage of the *Bathybiaster vexillifer* (Fig. 9 c), but the right-hand trace had survived to act as a “trap” for phytodetritus, like other depressions in the seafloor (see Fig. 9 d).

These, and other similar photographs, suggest that *Bathybiaster vexillifer* causes a great deal of disturbance as it ploughs through the surface layers of the sediment and feeds at considerable depth, possibly several centimetres. *Plutonaster bifrons*, on the other hand, leaves no discernable trace except when feeding, and this activity is restricted to the superficial centimetre or so.

Benthic community at Station “M”

Although detailed analyses of the benthic community at Station “M” still require completion, we present here the dominant faunal elements for comparison with the gut contents in the two asteroid species under study. The

megafaunal dominants (inter alia) include *Ophiomusium lymani*, *Echinus affinis*, *Hymenaster membranaceus*, *Benthopecten simplex* and *Ypsilothuria bitentaculata*. Amongst the macrobenthic infauna, the dominant species belong to the gastropods and bivalves (Table 4). The polychaetes have not been included, since they were not identified beyond the family level.

Discussion

As *Bathybiaster vexillifer* and *Plutonaster bifrons* were collected at Station “M”, we make the assumption that both species were subjected to the same physico-chemical environment including temperature, salinity, pressure, local currents and the seasonal deposition of phytodetritus (Gage and Tyler 1982, Billett et al. 1983, Lampitt 1985, Rice et al. 1991).

Analysis of the gonad indices of *Bathybiaster vexillifer* and *Plutonaster bifrons* confirmed the reproductive pattern described previously for these species (Tyler et al. 1982, Tyler and Pain 1982). If the gonads constitute a significant target for the input of energy into these species (the others being growth and respiration) we might expect interspecific differences between the organ indices

that provide energy for reproduction. There is considerable interspecific variation in the gut structure between the two species (Tyler in preparation); analysis of the variation in the pyloric caecum in *B. vexillifer* and the stomach "pouches" in *P. bifrons* suggested that the non-seasonal pattern seen in the gonads of *B. vexillifer* and the seasonal pattern seen in the gonads of *P. bifrons* are reflected in the gut organ indices of both species.

Analysis of the diet of the two species also revealed distinct differences. *Bathybiaster vexillifer* is a predator taking a wide variety of benthic invertebrates. The prey species were dominated numerically by the irregular echinoid *Hemiaster expergitus*, the prosobranch gastropod *Neverita (Natica) obtusata*, and species of the proto-branches *Yoldiella*, *Ledella* and *Malletia*. The gastropod and bivalve species found in the gut contents of *B. vexillifer* are the dominant elements of the macrofauna at Station "M" (Table 4). However, *H. expergitus* is rarely taken in either epibenthic sledges or box cores from station "M", and it is possible that this apparent rarity may be a result of heavy juvenile predation by *B. vexillifer*. Nevertheless, juvenile *H. expergitus* can also be taken by epibenthic sledge (ES) and spade box corer (SBC). In relation to the background abundances of other prey species, *H. expergitus* seems rarer, implying that *B. vexillifer* is more efficient than the ES or SBC sampling (possibly since adults are fairly deeply burrowed) and/or takes more trouble to seek them out than other prey. Although polychaetes were found in the gut of *B. vexillifer*, they were not as abundant or in the same proportion as their presence in the sediment at station "M". (G.J.L.P. personal observation). Nematodes were absent from the gut of *B. vexillifer*, and for the most part peracarid crustaceans were rare. Unrecognizable organic matter was found in 27 of the 154 specimens examined (17.5%). This rises to 25% if only those with food in their gut are considered. Determination of the amount of organic matter in the sedimentary fraction in the gut of *B. vexillifer* revealed values varying between 3.6 and 11.2%, but showed no seasonal cycle.

The diet of *Plutonaster bifrons* is significantly less diverse than that of *Bathybiaster vexillifer*. *Hemiaster expergitus* (often crushed) was one of the few recognizable prey items, together with very few gastropods and only three bivalve specimens. Unrecognizable organic matter was more common than *H. expergitus* in the gut of *P. bifrons*, being found in 30.3% of all guts and in over 50% of those containing food. The organic carbon fraction of the gut contents was significantly higher than that in *B. vexillifer*, ranging from 8.2 to 16%, and displayed an apparent seasonal variation. These data suggest that detritus is a significant element in the diet of *P. bifrons*.

The results suggest an explanation of the variation in the reproductive pattern of the two species: *Bathybiaster vexillifer* exhibits the predation pattern typical of many shallow-water astropectinid seastars. This species has a diet dominated by the irregular echinoid *Hemiaster expergitus*, but it also preys upon gastropods and bivalves. Most of the prey species live burrowed within the sediment, with *H. expergitus* living as deep as 10 cm beneath the sediment-water interface. The photographic observa-

tions presented here, and elsewhere (Rice et al. 1991) have shown that *B. vexillifer* may burrow several centimetres into the sediment to feed. In doing so, it is likely to ingest "older" sediment in which there is no seasonal cue and with a generally lower organic carbon content than the superficial layers. The lack of a seasonal cue in the diet is transmitted through to the gonads and quasi-continuous breeding results.

Conversely, seafloor photographs suggest that *Plutonaster bifrons* feeds closer to the sediment surface. The gut contents of *P. bifrons* contained considerably fewer infaunal species than did *Bathybiaster vexillifer*. However, one of the infaunal bivalves, *Thyasira brevis*, is "thought to be deeply buried and largely static" (Payne and Allen 1991). If *P. bifrons* feeds mainly at the sediment surface, sediment ingested with material scavenged may well contain a seasonal cue derived from the seasonal downward flux of phytodetritus. However, only a small proportion (11.4%, see Table 3) of individuals of *P. bifrons* contained sediment. A second seasonal supply of organic matter may be in the form of "large" food falls. Fish scales and bones were found in a number of specimens of *P. bifrons*, and in two the remains of the blue whiting (*Micromesistius poutassou*) were found. This fish is a mesopelagic (<1000 m) shoaling species that migrates to the Rockall Trough area in large numbers to spawn in March/April of each year (Bailey 1982). Enough specimens of this species die and sink to the deep-sea bed to form a significant element (~25%) of the food intake of *Synaphobranchus kaupi*, *Histiobranchus bathybius*, *Nematonurus armatus* and *Antimora rostrata* (Mauchline and Gordon 1984). We may speculate that the remains of the dead blue whiting are readily scavenged by invertebrates, including *P. bifrons*, as well as by fish. If this is the case, a second seasonal influx of organic matter will occur immediately before the input of phytodetritus. This seasonal input to the diet of *P. bifrons* is transmitted through a seasonal cue in the pyloric caecum, resulting in seasonal reproduction in this species.

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