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The distribution, abundance and seasonality of pelagic marine invertebrate larvae in the maritime Antarctic

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A survey of pelagic larvae was undertaken between November 1992 and February 1995 at Signy Island, Antarctica (60°43′ S, 45°36′ W). A diver-towed net and hand-held plankton pump were used at five sites of varying depths (6–30 m) and benthic substrata, in a combination of monthly and fortnightly samples. Overall larval ecological diversity was much higher than expected, with 131 morphologically distinct larval forms collected, apparently representing most of the benthic phyla present. The species richness observed is comparable with levels recorded at temperate latitudes, and higher than Arctic data and the implications for Thorson's rule (the inferred cline of reduced pelagic larval diversity towards high latitudes) is discussed. Larval abundances were low (mean 2.6 individuals per m^3), which were two to six orders of magnitude lower than peaks in comparable data from temperate and tropical zones. We suggest that the low abundances recorded are a reflection of both slow developmental rates and a high dilution of larvae, reducing synchrony and spreading larvae over larger distances. Three seasonal periods, during which different larval types occur, have been identified. Summer, late summer and winter spawning strategies were discernible, and in some groups larvae occurred throughout the year.

Keywords: larva; Antarctic; diversity; abundance; seasonality; marine invertebrate

1. INTRODUCTION

Marine invertebrate larvae have fascinated observers since Aristotle and their ecology has been the object of study for many years (reviewed by Crisp 1984; Young 1990). The first, and arguably still the most comprehensive, categorization of larval developmental patterns was that undertaken by Gunnar Thorson (1946, 1950), though many subsequent workers have modified Thorson's original classification (Mileikovsky 1971; Chia 1974; Jablonski & Lutz 1983; Levin & Bridges 1995). There is now a generally adopted classification scheme based on four different criteria: (i) mode of larval nutrition (planktotrophy, lecithotrophy, osmotrophy, autotrophy); (ii) site of development (pelagic, demersal, benthic, parental brooding); (iii) disperal potential (time in the water column: teleplanic to non-planktonic); and (iv) morphogenesis (indirect, with larval stage; direct, no free-living larval stage). The diversity so evident in marine invertebrate reproductive strategies arises from the numerous possible combinations of these attributes.

There is no generally accepted definition of a 'larva'; McEdward & Janies (1993) have even reasoned that a meaningful definition would be impossible due to the evolutionary diversification of larval types and continuous nature of development. They did, however, provide a description that satisfactorily defines a larva for the purposes of the present study. They defined a larva as '. . . an intermediate stage in the life cycle that is produced by post-embryonic morphogenesis and is eliminated by the metamorphic transition to the juvenile . . .' A larval stage in the life history of benthic invertebrates enables the colonization of new substrata and the maintenance of genetic variation (Havenhand 1995). This is somewhat paradoxical because the larva usually is the most vulnerable stage in an organism's life cycle; larval mortalities prior to metamorphic competence typically are in excess of 95% and often greater than 99% (Strathmann 1985). The different environmental conditions existing in the world's seas and oceans might therefore be expected to influence strongly the reproductive strategies of the local fauna.

The extent to which reproductive strategy varies with latitude has been a source of discussion for many years. The seminal work of Thorson (1936, 1950) in Greenland and Denmark suggested that polar marine invertebrates tended to avoid a pelagic larval phase. This work, based mainly on molluscs, echinoderms and some annelids, formed the starting point for almost every subsequent debate in the literature. The term 'Thorson's rule' was coined by Mileikovsky (1971) to describe the inferred latitudinal cline in the proportion of species displaying pelagic larvae, from most species in the tropics to almost none in polar regions. The proposed latitudinal cline was

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based mainly on studies of prosobranch molluscs, and the trend was confirmed for Antarctic prosobranchs by Picken (1980). In contrast, studies of Antarctic echinoderms have shown pelagic lecithotrophy to be the dominant strategy, in apparent contradiction to Thorson's rule (Bosch & Pearse 1990; Pearse 1994). However, these are data from a single phylum, which, as with Mileikovsky's analysis of prosobranch molluscs, may bias opinion too far in the other direction (Pearse *et al.* 1991).

The currently accepted view that fewer species have pelagic feeding larvae in polar regions compared with lower latitudes (Clarke 1992, 1996) has mainly been deduced from observations of reproductive biology and egg size. We therefore felt it timely to conduct a year-round survey of the pelagic larvae present in Antarctic waters. These data add to the observations made at McMurdo Sound (77° S, 166° E) for one month's samples of spring zooplankton (Foster 1987) and periodically during a 15-month study on echinoderms (Bosch 1989), and in the Bellingshausen Sea (*ca.* 70° S, 85° W) over a two-month period (Shreeve & Peck 1995).

A two-year study was carried out at Signy Island, South Orkney Islands (60°43′ S, 45°36′ W) using simple, but repeatable, methods for both open-water and under sea-ice sampling. Reports of similar surveys at other latitudes are surprisingly scarce in the literature; most larval distributional data comprise either single-species surveys or have been undertaken as components of macrozooplankton collections. The survey of the waters near Helsingør and the island of Ven, between Denmark and Sweden (56° N, 12°E), and the subsequent monograph by Thorson (1946), remains one of the few surveys dedicated to collecting pelagic larvae of all taxa present, and is the only study that can be compared directly with the work reported here.

2. MATERIALS AND METHODS

(a) *Study sites*

Five sites were chosen in Borge Bay to represent the shallow littoral of Signy Island (figure 1). The water column above both hard rock and soft sediment substrata was sampled, at a range of depths between 6 and 28 m (figure 1). The other factor in selecting sites was accessibility, as SCUBA was used for all sampling, often in inclement weather. Billie Rocks (site 2) and Bare Rock (site 3) were closely located and were representatives of soft and hard substrata, respectively (White & Robins 1972; Barnes 1995*a*,*b*). They were therefore deemed primary sites and given the highest priority for sampling if weather or other factors limited diver access to the water. The five sites were visited regularly: collections were made at the two primary sites every two weeks, with monthly collections at the other three sites. Samples were collected from February 1993 to February 1995, a total period of 25 months.

Environmental variables including seawater temperature and salinity, sea-ice thickness and seasonal duration, chlorophyll standing crop and macronutrients (N, P, Si) have been continuously monitored for much of the past 30 years at Signy Island (Clarke *et al.* 1988; Clarke & Leakey 1996). During the 25-month period of this study the sea temperature varied between −1.88 °C and +0.78 °C and sea ice was present for a total of 332 days over two winters (between five and six months each year). Storms were typical of the area, with gale force winds recorded on 188 days.

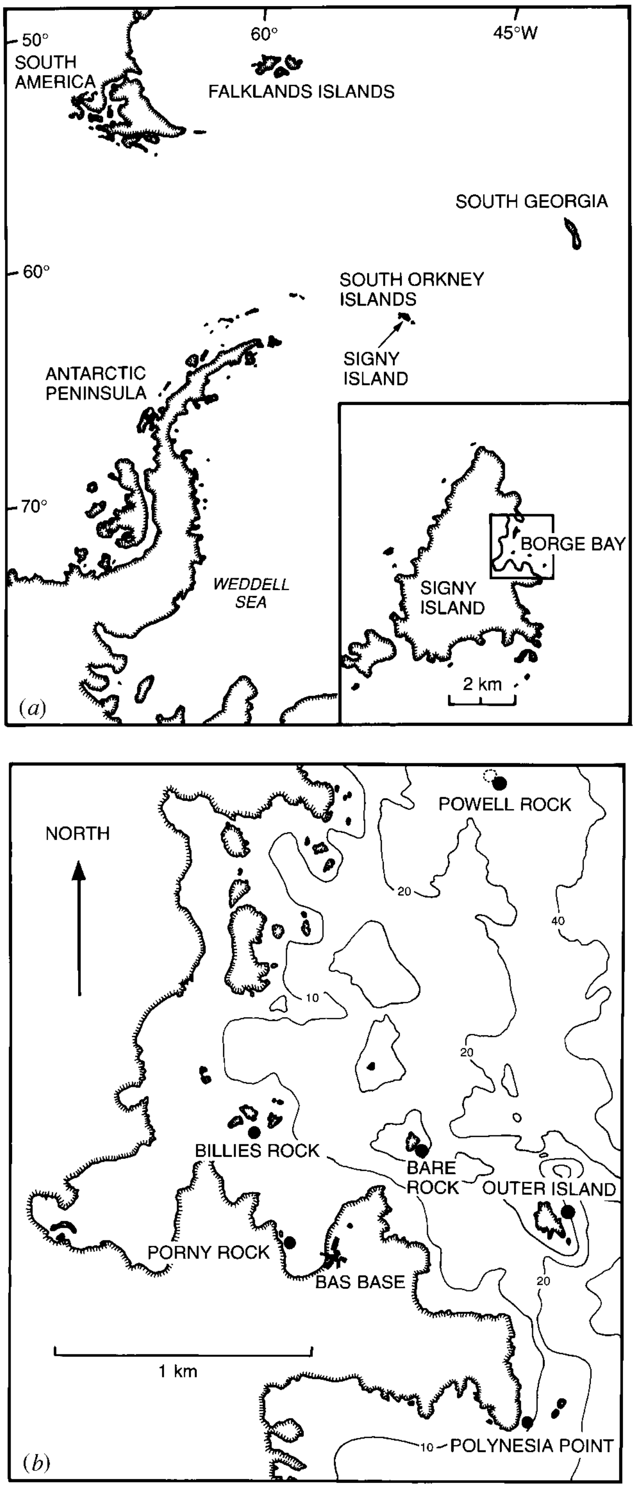

Figure 1. (*a*) Position of South Orkney Island group in the Maritime Antarctic. Inset shows Signy Island with Borge Bay marked. (*b*) Details of Borge Bay (● mark the study sites).

(b) *Pelagic larval sampling: diver-towed net*

The pelagic larval collections were taken by a diver-towed net of novel design (figure 2). Unlike boat deployment, SCUBA enabled the net to be used consistently in both open water and under sea ice. The optimal compromise between collecting a large sample volume and maintaining ease of use with two divers was found to be a net with a mouth area of 0.25 m^2. The drag induced by a net of this size was not beyond the capabilities of reasonably fit divers. The effort required to tow the net and the

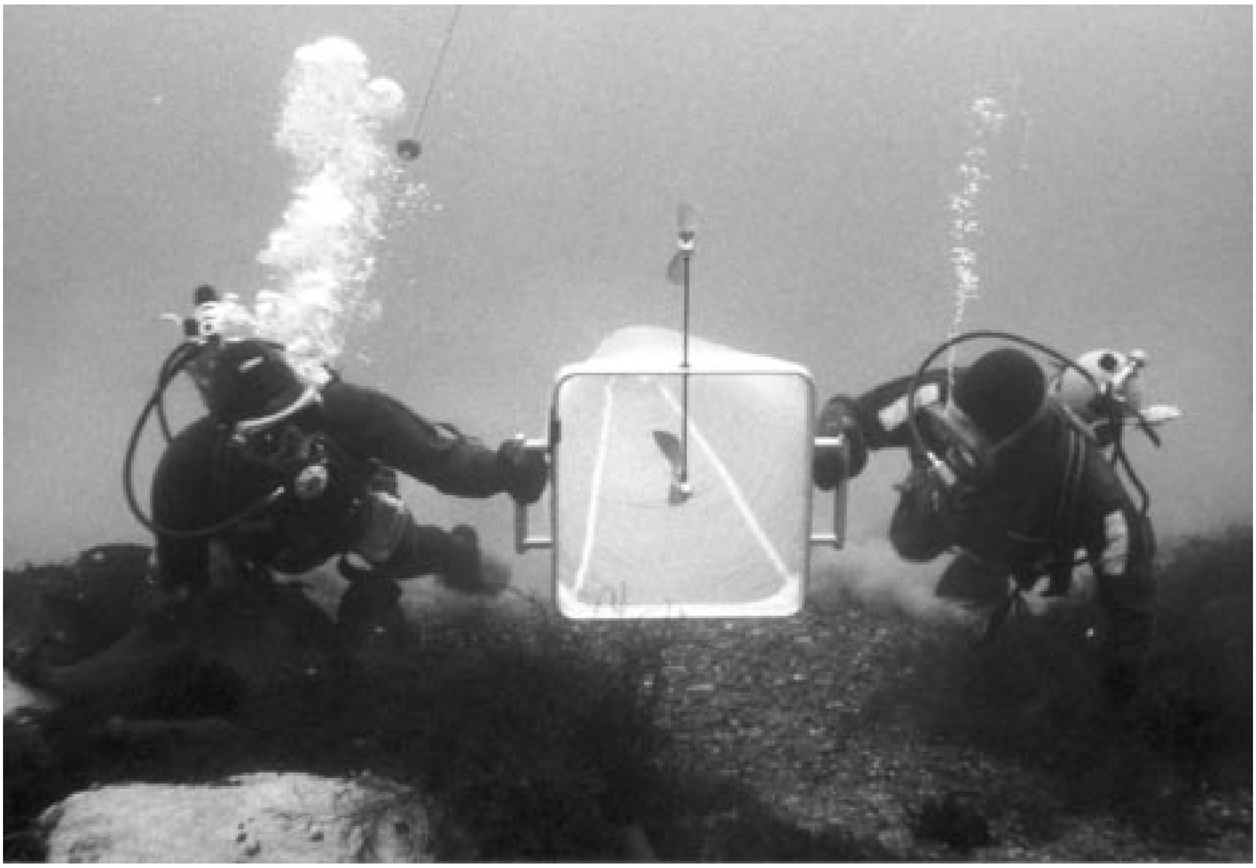

Figure 2. Photograph of collection net in use under sea ice. The divers could manipulate the net over the seabed and along sea-ice contours to maintain a consistent distance from the substratum. The two flowmeters are clearly visible, one inside the net and the other above it.

consequent build up of carbon dioxide in the breathing apparatus precluded sampling at depths more than 30 m. The use of a square net mouth, as opposed to the more usual circular designs (Siferd & Conover 1992), meant that it was possible to manoeuvre the net over the seabed at a constant height. A 100 μm mesh was used for all collections, with net evasion considered to be negligible for the size range of larvae captured (0.2–2 mm). Removable 1000-ml containers at the cod-end enabled consecutive discrete samples to be taken during a single dive.

Two General Oceanics 2030 R flowmeters were fitted to the net (figure 2). These were fitted with low velocity rotors, which had a threshold velocity response of 2 cm s^{-1}. Prior to use, the flowmeters were filled with 70% methylated spirit in tapwater to prevent freezing during transit to dive sites, because air temperatures often were below −25 °C. The flowmeter within the net allowed the volume of water filtered to be calculated, and the outer flowmeter enabled an estimation of the distance towed. Filtration efficiency was calculated as (volume filtered/(net mouth area × distance towed)), which equated to (inner flowmeter reading/outer flowmeter reading). Tows were made directly into the current flow during the few times when these were at sufficiently high velocities to affect flowmeter readings, thus minimizing erroneous measurements. There is a monotonic (and almost linear) positive relationship between filtration efficiency and tow speed up to velocities of about 1 knot (Tranter & Heron 1967), which is a realistic maximum speed for a diver-towed net. Care was taken to ensure as steady and reproducible a tow speed as possible to minimize variation in sampling efficiency; every collection dive involved the senior author (D.S.-S.).

Each collection dive consisted of two separate sample tows, both of approximately 50 m length. The first was 10–20 cm above the seabed and the second was 10–20 cm below the sea-surface, or under sea ice if it was present. During the peak of the austral summer phytoplankton bloom, the net was susceptible to clogging. To minimize this, the cod-end was replaced with a second sampling container halfway through each tow in the period December to February of both years of the survey.

(c) *Demersal larval sampling: plankton pump*

Because a net was unlikely to collect truly demersal larvae, a hand-held diver-operated plankton pump was constructed to sample close to the seabed. Several designs of this type of apparatus are described in the literature (Dixon & Robertson 1986; Powlik *et al.* 1991), although such surface-mounted pump systems are not suitable when winter sea ice was present. The device developed here (figure 3) was constructed around a 100 μm mesh conical net and an inexpensive Rule 500 bilge pump (12 V, 2.4 A, moving 23.5 l min^{-1}). Waterproof power plugs and 30 m of low-temperature cable connected the pump to an insulated gel lead-acid battery. Because of the severe attenuation of battery performance in extreme low temperatures (< −35 °C), an 85 Ah battery was used; this was much larger than would be necessary in tropical or temperate locations and was impractical to mount within the sampler as in a similar design from New Zealand (Taylor *et al.* 1995). The pump was primed by flooding prior to use and manipulated around and under rocks during each collection dive, which usually was of about 15 min duration. Longer sampling periods risked clogging the net and thus damaging specimens within it. At the end of sample collection the

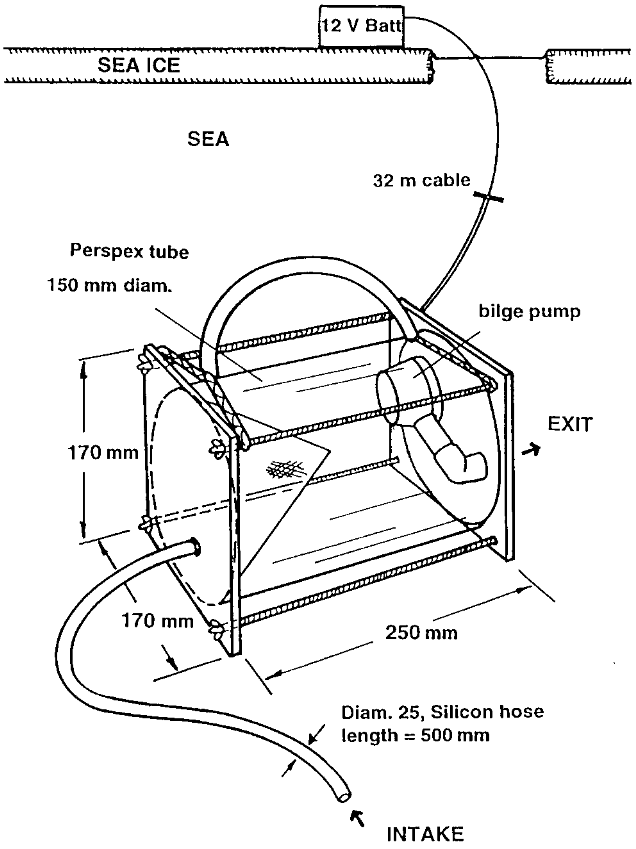

Figure 3. Diagram of pump sampler, all dimensions are in mm (not drawn to scale). Seawater was sucked into silicon hose 'intake', through the 100 µm mesh cone and out via the bilge pump through the aperture labelled 'exit'. Rubber gaskets sealed the cylinder to the endplates.

inlet and outlet were sealed and the whole apparatus returned to the laboratory for analysis. Quantification of larval abundance was not possible because of the difficulty of estimating the areas sampled in cryptic locations.

(d) *Analysis protocol*

The 1000-ml cod-end containers were returned to the station immediately after each collection dive and kept at ambient seawater temperature in the aquarium. The separate samples from both the net and the pump were sorted within 24 h to prevent degradation of delicate larval forms and damage from larval predators caught in the cod-end. The samples were filtered through a 100 µm mesh-lined cylinder, suspended in a seawater-filled beaker. The retained larvae and other planktonic constituents then were carefully washed into a Petri dish with 1.2 µm filtered (Whatman GF/C) seawater. They were examined at × 20 to × 80 magnification with a stereomicroscope. All novel forms were drawn, photographed, fixed in 2.5% EM grade gluteraldehyde and stored in a 4% sodium cacodylate buffer for examination by scanning electron microscopy (SEM) in the UK. A few drops of 1% propylene phenoxytol and 7.5% magnesium chloride were used to relax and immobilize active individuals.

Every individual larva in every sample was measured and recorded. Many of the larval forms were unidentifiable beyond class and sometimes (e.g. planulae) even phylum. There are no taxonomic sources available for Antarctic larvae and only a few larval forms could be related to adult taxa. The larvae collected in this study were therefore classified into morphologically defined operational taxonomic units (OTUs). The OTUs were then aggregated into larval functional groups (planulae, annelid trochophores and so on). These functional groups represented the highest taxonomic resolution that was consistently available. This two-level grouping of OTUs and functional groups allowed for statistical analysis at two distinct levels of taxonomic resolution. A compilation of identification drawings, light microscopy photographs and scanning electron micrographs of the larvae collected in the present study has been produced to aid identification by subsequent workers (Stanwell-Smith *et al.* 1997). All other planktonic components (e.g. diatoms or other phytoplanktonic taxa) were scored on a six-level nominal abundance scale, from occasional to very abundant.

The data were analysed with both univariate and multivariate statistical techniques: generalized linear models (GLM, Poisson distribution, log-link function) were applied to the data and principal component analysis (PCA) to the correlation matrix of log $(x+1)$ transformed data. Both analyses used routines in Genstat v. 5.3 (Payne *et al.* 1993). The data were also explored using ViSta (public domain software on the Internet at: http://forrest.psych.unc.edu), the visual statistics system for three-dimensional representation of multivariate analyses. In addition, ViSta was used to explore interactively a range of data transformations (Box–Cox transform function), with the log $(x+1)$ transformation giving the best approximation to normality.

3. RESULTS

(a) *Environmental seasonality*

The seawater temperature and chlorophyll concentrations in Borge Bay varied seasonally, both reaching maxima in the austral summers (figure 4). The size-fractionated measurements of phytoplankton chlorophyll enabled the amount of food available for larval feeding to be estimated. Microplankton chlorophyll (>20 µm) showed a single summer peak which generally exceeded 15 µg l^{-1} and a low winter standing crop. The data for 1993–94 are typical for this site, although an occasional (once in the last 14 years) distinct autumnal bloom occurred in February–March 1992 (Clarke & Leakey 1996). The nanoplankton chlorophyll (20–2 µm) also showed a clear seasonal variation, although the standing crop was an order of magnitude less than the microplankton, and the bloom was spread over a longer period. In winter (typically June–September), nanoplankton chlorophyll concentration usually exceeds that of microplankton (Clarke & Leakey 1996).

(b) *Seasonal larval distribution*

Over the 25 months of the survey, 317 net samples and 14 pump samples were successfully analysed. The mean tow length was 54.6 ± 0.9 (s.e.) m with a mean sampling efficiency of 42.3 ± 0.6%; therefore approximately 5000 l of seawater were filtered per tow (mean tow volume = 5736 ± 122 l). The larval counts for each tow were therefore corrected to a standard sampling volume of 5000 l.

The numbers of morphologically distinct forms (OTUs) in each of the functional groups are listed in table 1. In some cases these groups undoubtedly contain larvae from taxonomically unrelated adults, the most obvious example of this being the generally featureless

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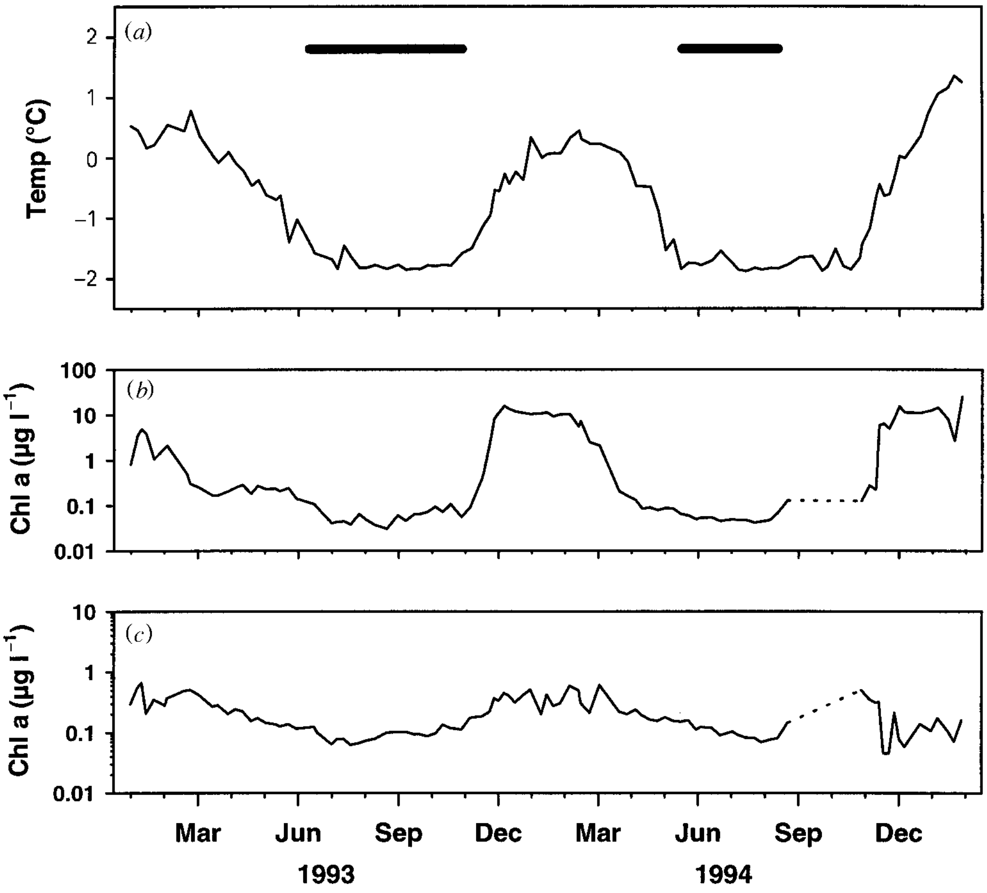

Figure 4. Environmental measurements made at 10 m depth in Borge Bay, Signy Island, 1993–95 (data from Clarke & Leakey (1996)). (*a*) Sea temperature, with the bars showing the period for which winter fast ice was present in the winters of 1993 and 1994. (*b*) Seasonal variation in seawater chlorophyll concentration ($\mu g\ l^{-1}$) at 10 m depth in Borge Bay, Signy Island, 1993–95; data for microplankton ($>20\ \mu m$). (*c*) Seasonal variation in seawater chlorophyll concentration ($\mu g\ l^{-1}$) at 10 m depth in Borge Bay, Signy Island, 1993–95; data for nanoplankton (20–2 μm). Note logarithmic axis for chlorophyll concentration. (The dotted lines show a three-month period for which data are missing.)

Table 1. *Taxonomic summary of the marine invertebrate larvae collected during a 25-month study at Signy Island, South Orkney Islands, Antarctica*

(Larvae were classified into morphologically defined OTUs, each identified to the lowest possible taxonomic level. The larval OTUs were then aggregated into functional groups.)

larval group	no. OTUs
planulae (sponges, octocorals)	22
nemertean pilida	8
annelid trochophores	11
annelid metatrochophores	9
annelid nectochaetes	12
annelid larvae	4
sipunculid pelagosphaeras	2
cirripede cyprids	5
molluscan trochophores	4
gastropod veligers	16
bivalve veligers	10
brachiopod larvae	3
echinoderm gastrulae	8
echinoderm bipinnaria	5
echinoid plutei	3
holothurian pentaculae	2
tunicate tadpoles	7
total	131

planulae. Although 22 morphologically distinct planulae were distinguished, these probably include larvae from octocorals and sponges (both of which are common benthic taxa at Signy Island) together, possibly, with platyhelminths. It is also possible that where larval functional groups represent different developmental stages, larval OTUs in more than one functional group may actually represent successive developmental stages of the same species. In such a case the total number of morphologically defined OTUs will exceed the real number of species involved. The converse problems of many related species having morphologically indistinguishable larvae results in the number of OTUs possibly underestimating the true species diversity.

The seasonal variations in abundance of the various larval functional groups are shown in figure 5, with data corrected to a standard volume of 5000 l. This figure pools data for all sites and also pools data from surface and demersal tows. Some differences were detected between sites and depths (see § 3c), but these generally were small. No larval types occurred in the qualitative pump samples that were not also seen in adjacent net collections, and the pump sample data were therefore not included in the analysis.

The planulae graph (figure 5*a*) pools the larvae from three phyla: Cnidaria, Porifera and Platyhelminthes. Planulae were present throughout the year, although higher numbers were caught in the early winter of 1993 than at other times of the survey. Barnacle cyprids also occurred in higher numbers in the 1993 winter. Winter larvae of both years comprised mostly echinoderm gastrulae and bipinnariae, and gastropod veligers (figure 5*b*). Nemertean pilidia were present in low numbers throughout the survey, with peaks in June. In contrast, annelids were strongly seasonal and were present mostly in the austral summer. Annelid larval number peaked in late summer (February–March), and formed a functional group separate from trochophores, metatrochophores and nectochaetes.

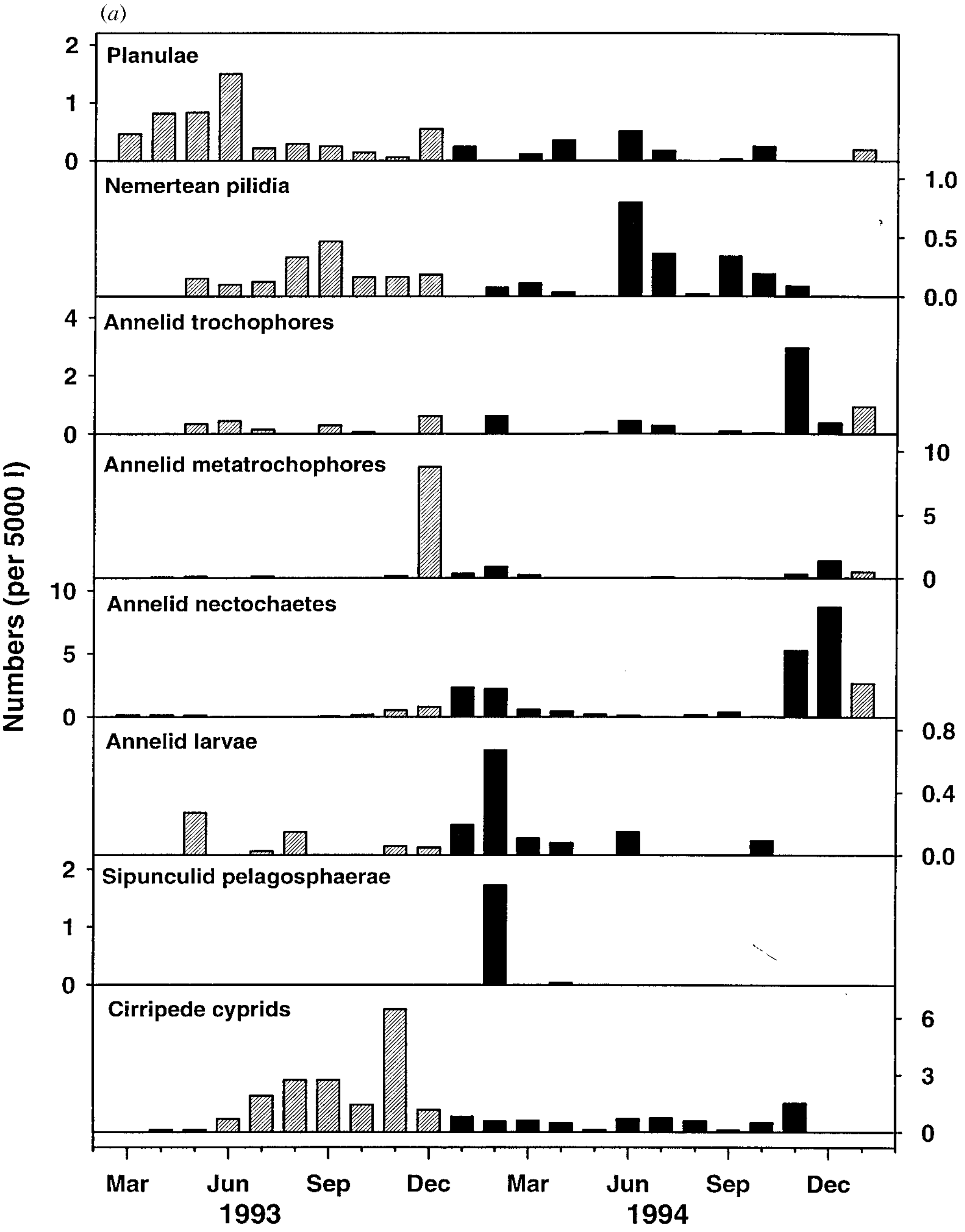

Figure 5. (*a*,*b*) Mean numbers of each larval group throughout the survey. The values have been corrected to a standard 5000-l collection tow. Note the black and hatched colour change in the bars to clarify inter-annual differences.

(c) *Generalized linear model* (*GLM*)

Univariate statistics were used to model the two years of results to gain a clearer insight into the ecological patterns displayed by each group of larvae. The numbers and relative proportions of larvae at different sites and different tow types (surface or benthic) are presented in table 2. Although some groups, such as brachiopod larvae, did not occur at all sites, most were ubiquitous. A peak of bivalve veligers occurred at site 2 (Billie Rocks, 14 m, soft sediment), consistent with the dense adult bivalve infauna at that site. Of the larval groups that showed distinct patterns, echinoderms clearly occurred more often in surface waters (approximately 1 m depth) than in benthic tows. Some of the annelid groups also tended to be surface dwelling.

The dominant ecological pattern, however, was the differing seasonality of the various larval groups. Variability in larval occurrence meant that repeated peaks over the two years might not have been clear visually in figure 5*a*,*b*. Seasonal patterns were therefore distinguished by fitting the GLM with deviances for each month indicating peaks of larval abundance (table 3). This model confirms the winter larval strategy of echinoderms, the peak in early winter of some planulae and, in contrast, the austral summer peak of annelids. A trend common to most larval groups was the presence of at least a few larvae throughout the year.

(d) *Principal components analysis*

Multivariate analyses were used to further dissect patterns in the occurrence of larval OTUs and relate these to the environmental variables. PCA was chosen because the biplots produced are conceptually simple to interpret. Analyses were hierarchical, with each

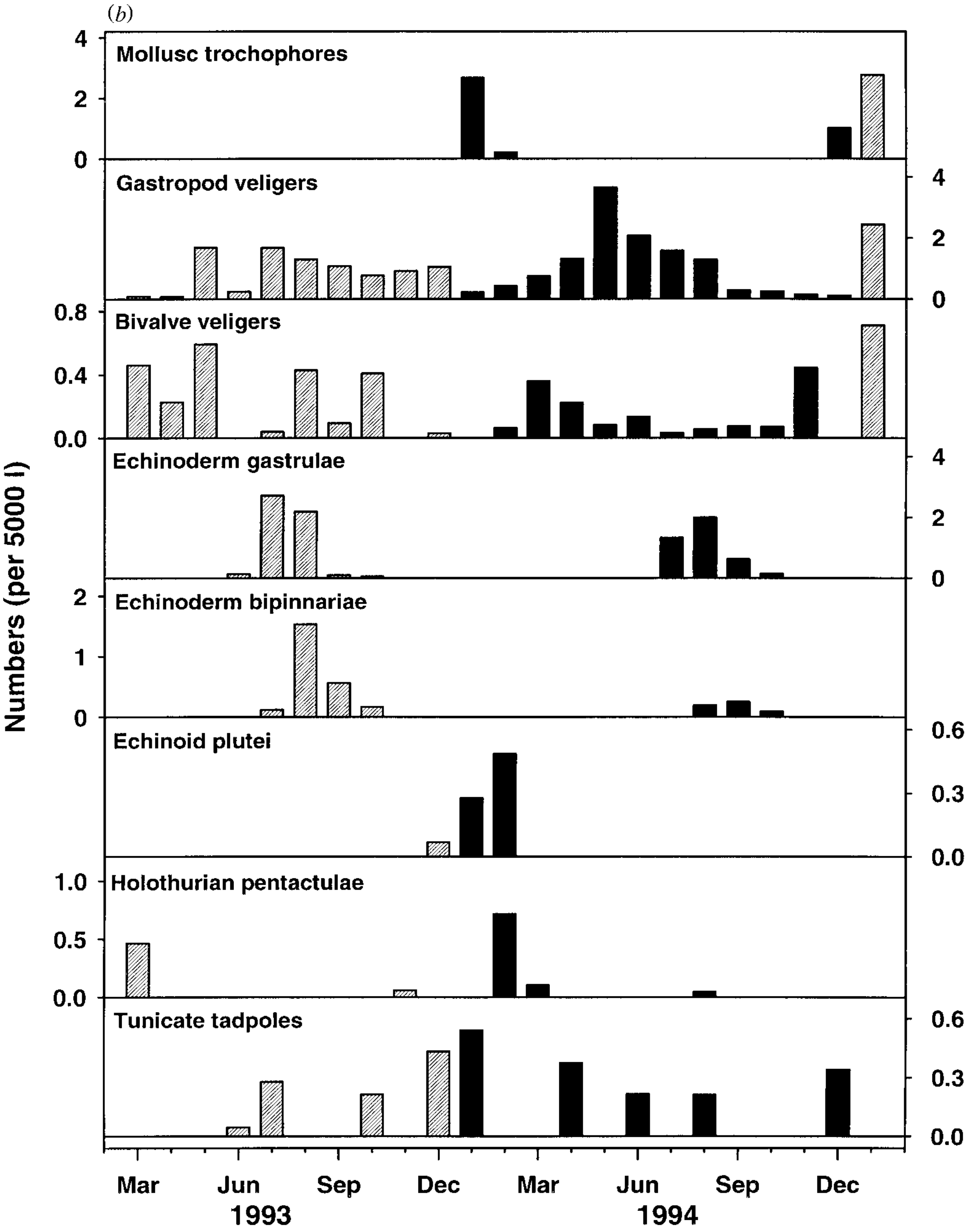

Figure 5. (*Cont.*)

successive analysis being conducted on increasingly aggregated data. First, each separate tow was considered. The differences between the five sites were found to be negligible, and so the five sites were pooled. Notwithstanding the above observations for echinoderms, the next analysis revealed only negligible differences between surface and benthic tows, and so these also were pooled. The results of a PCA analysis of the effect of season on the occurrence of larval OTUs are summarized in figure 6. This biplot shows that in contrast to the lack of separation for sites and depth, analysis of time of the year divided the larval functional groups into three clusters representing discrete periods of the year. The first five components accounted for 71% of the variance in the data, with the first two components explaining 42% (25% and 16%, respectively). This is a high value of explained variance considering the heterogeneous set of 317 tows and 17 larval groups, and the sparse nature of larval occurrence. The PCA has therefore succeeded in revealing the main features of the data set.

The biplot (figure 6) was interpreted as showing a clear divide (first principal component) between summer- and winter-occurring larvae. The summer larvae were further divided (second principal component) into early and late summer larvae. The relative lengths of the vectors radiating from the origin were considered analogous to the intensity of seasonality, such that shorter vectors indicated groups that tended to have a year-round presence, whereas longer vectors indicated sharp seasonal peaks of larval occurrence.

4. DISCUSSION

(a) *Diversity*

The current debate over the validity of Thorson's rule hinges on two phyla that show patterns of geographic

Table 2. *GLM model predictions for the depth preference and presence of larvae at different sites*

(Deviance values in bold indicate significance at $p \leqslant 0.05$ (depth n.s., not significant, $p > 0.05$). Bracketed deviance values show when the model was possibly in error, i.e. sparse data with high peaks. The black circles in the site column indicate larval presence (abundance level: low · → • → ● high).)

larval group	deviance (site)	site 1	2	3	4	5	deviance (depth)	depth preference
planulae (sponges, octocorals)	2.3	·	·	·	·	•	0.5	n.s.
nemertean pilidia	**6.8**	·	·	·	•		2.7	n.s.
annelid trochophores	**13.9**	●	•	·	·	·	**15.7**	surface
annelid metatrochophores	**19.5**	●	·	·	·	·	3.1	n.s.
annelid nectochaetes	**6.4**	·	●	●	·	·	1.5	n.s.
annelid larvae	**15.6**	·	·	·	·		**47.2**	surface
sipunculid pelagosphaeras	**(558.9)**	·	•	·		•	**(135.9)**	surface
cirripede cyprids	**3.0**	•	•	•	•		2.1	n.s.
molluscan trochophores	**22.4**	•	·	·	·	●	0.1	n.s.
gastropod veligers	**6.5**	•	•	•	●	●	3.7	n.s.
bivalve veligers	**2.7**	·	●	·	•	·	**8.7**	benthic
brachiopod larvae	**31.6**	·					**9.7**	surface
echinoderm gastrulae	**3.9**	·	·	●	•	•	1.7	n.s.
echinoderm bipinnaria	**9.6**	·	·	•	·	•	**42.9**	surface
echinoid plutei	**(168.8)**	·			·	•	**(139.6)**	surface
holothurian pentaculae	**16.4**	·	·	·		·	**108.6**	surface
tunicate tadpoles	**8.5**	·	·	·	·	•	3.1	n.s.

Table 3. *GLM model predictions for the presence of larvae throughout the year*

(All of the deviance values were significant at $p \leqslant 0.05$. Bracketed deviance values show where the model indicated possible error. The symbols refer to: (○) larval presence, (•) small peak and (●) large peak.)

larval group	deviance (month)	months J	F	M	A	M	J	J	A	S	O	N	D
planulae (sponges, octocorals)	4.2	○		○	○	○	●	○	○	○	○		○
nemertean pilidia	5.2		○	○	○	○	•	○	○	•	○	○	○
annelid trochophores	17.3	○	○			○	○	○		○		●	○
annelid metatrochophores	28.7	○	○	○	○			○				○	●
annelid nectochaetes	20.1	•	•	○	○	○			○	○	○	●	●
annelid larvae	12.7	○	•	○	○	○	○		○		○	○	○
sipunculid pelagosphaeras	(1050)		●		○								
cirripede cyprids	5.8	○	○	○	○	○	○	•	●	●	○	●	○
molluscan trochophores	40.9	●	○										
gastropod veligers	3.1	○	○	○	○	●	•	•	•	•	○	○	○
bivalve veligers	3.5	○	○	•	○	○	○	○	○	○	○	•	○
brachiopod larvae	25.9											○	•
echinoderm gastrulae	28.2						○	●	●	○	○		○
echinoderm bipinnaria	29.2							○	●	•	○		
echinoid plutei	(103.3)	•	•						○			○	
holothurian pentaculae	47.1		•	•					○		○		
tunicate tadpoles	12.7	•			○		○	○	○		○		•

variation in larval biology entirely different from each other. Thorson (1950) and Mileikovsky (1971) essentially based their argument on molluscs (especially prosobranchs), which they regarded as a model phylum for benthic invertebrate reproductive strategies (prosobranchs were referred to by Thorson as 'the barometer of the sea'). Among molluscs, a cline was found ranging from almost no pelagic larvae in Arctic regions to approximately 95% of species with a pelagic phase in tropical seas (Mileikovsky 1971). This was later supported by the work of Picken (1980) in the Southern Ocean, who showed that of 30 prosobranch species at Signy Island, most reproduced by direct development and only one species, the limpet *Nacella concinna*, produced a pelagic larva. Although the pattern established by Thorson and Mileikovsky has become the established paradigm, Pearse and colleagues have shown clearly that the echinoderms do not fit to the pattern established for prosobranch molluscs, with similar percentages of species with pelagic larvae in Antarctica (73%), California (75%) and Greenland (82%) (Pearse *et al.* 1991; Pearse 1994; reviewed by Clarke 1992). The real geographic distinction in echinoderm pelagic larvae is between feeding and non-feeding larvae: in California 20 (55%) out of 36 species produce feeding larvae, with eight species (22%) producing non-feeding larvae. In Greenland (high Arctic) and McMurdo Sound (high Antarctic) the proportions of feeding larvae are 17% (4 out of 23 species) and 22% (7 out of 32 species), respectively.

Several studies have reported high diversity in benthic fauna in southern polar latitudes (Dell 1972; reviewed by Arntz *et al.* 1994; Clarke & Crame 1998), although different groups vary in their contribution to overall diversity. Antarctic epifaunal suspension-feeding communities, in terms of total macrofaunal species richness within assemblages, have been compared to coral reefs (Gutt 1991). This is in contrast to the intertidal zone, which is a habitat characterized by high floral and faunal diversity in temperate and tropical locations, but almost devoid of life in polar regions because of ice scour (Barnes 1995*a*). Arntz *et al.* (1997) also highlight the disproportionate sampling intensity in the more easily accessible climatic zones, which impairs latitudinal comparisons between tropical, temperate and polar studies.

Nevertheless it is clear that there is a distinct cline in hard substratum epifaunal diversity in the northern hemisphere, due at least in the part to the low overall diversity of the high Arctic (Thorson 1957; Dayton 1990; Clarke 1992). The latter is probably related to the relative youth of the Arctic marine ecosystem (Dunton 1992), which is still undergoing active colonization (Vermeij 1991). In contrast, evidence for a similar latitudinal cline in the

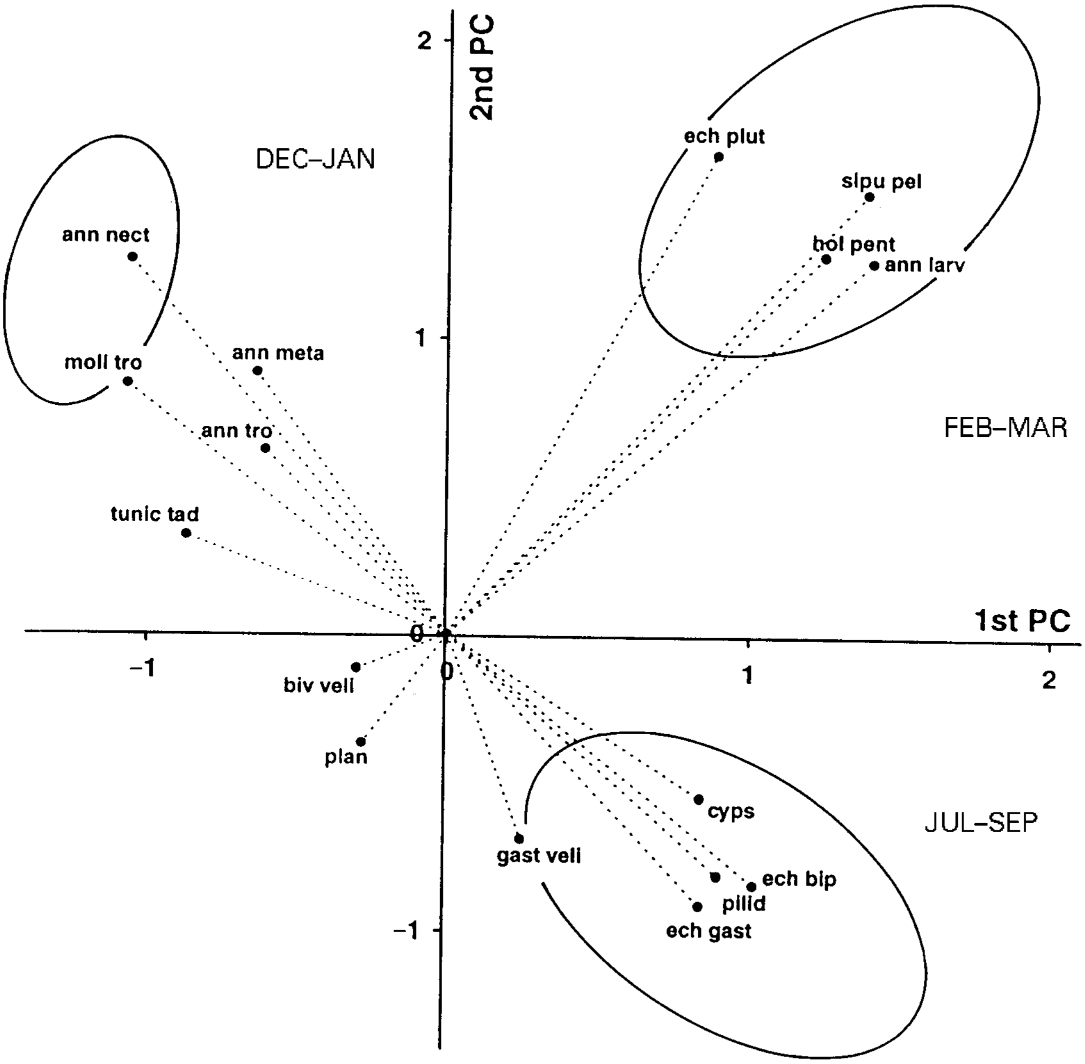

Figure 6. A biplot of the PCA of the larval data. The vectors represent the original variables, with the ellipses showing the area of the scores that fell in each quadrant of the biplot. The axis values are arbitrary units. ann nect, annelid nectochaetes; moll tro, molluscan trochophores; ann meta, annelid metatrochophores; ann tro, annelid trochophores; tunic tad, tunicate tadpoles; ech plut, echinoid plutei; sipu pel, sipuncolid pelagosphaeras; hol pent, holothurian pentaculae; ann larv, annelid larvae; biv veli, bivalve veligers; plan, planulae; gast veli, gastropod veligers; cyps, cirripede cyprids; ech bip, echinoderm bipinnaria; pilid, nemertean pilidia; ech gast, echinoderm gastrulae.

southern hemisphere is equivocal at best (Clarke 1992; Clarke & Crame 1998). Although some groups are missing (e.g. brachyuran crabs), or strikingly low in diversity (e.g. caridean decapods, teleost and cartilaginous fish), others are very diverse (Arntz *et al.* 1997; Clarke & Crame 1998). These differing patterns are of importance in interpreting the diversity of marine invertebrate larvae found in the Southern Ocean in this study.

The species richness of larvae in the present study was much higher than previously reported for other areas of the Antarctic. Research at McMurdo Sound has yielded 12 species with pelagic larvae, most of which were echinoderms (reviewed by Pearse *et al.* 1991). A survey of invertebrate larvae in the Bellingshausen Sea found 12 types of larvae from seven phyla (as distinct from species numbers, which were not determined because of taxonomic difficulties) (Shreeve & Peck 1995). The present study yielded 131 morphologically distinct larval forms (table 1). The shape of the species incidence curve (figure 7) indicates that this count is probably representative of the survey area (Sutherland 1996). We can therefore conclude that the total number of marine invertebrate species producing pelagic larvae in the maritime Antarctic probably is in the range 100–150.

A direct comparison with Thorson's (1946) study in Danish waters shows that although the total of molluscan larval types (*ca.* 70 species) was higher than at Signy Island, the annelids and echinoderms were similar (table 4). The total number of species collected by Thorson was also comparable (*ca.* 160), despite the large differences in larval development rates and environmental regime between the two regions.

There are very few reports in the literature for other parts of the world with which to compare the present data. To date, only two studies have been undertaken in the Arctic. A survey between 1958 and 1961 of the Norwegian and Barents Sea (74° N) found about 70 species of pelagic larvae (Mileikovsky 1968). Thorson (1936) inferred from surveys of adult benthic invertebrates in East Greenland (68–77° N) that approximately 12

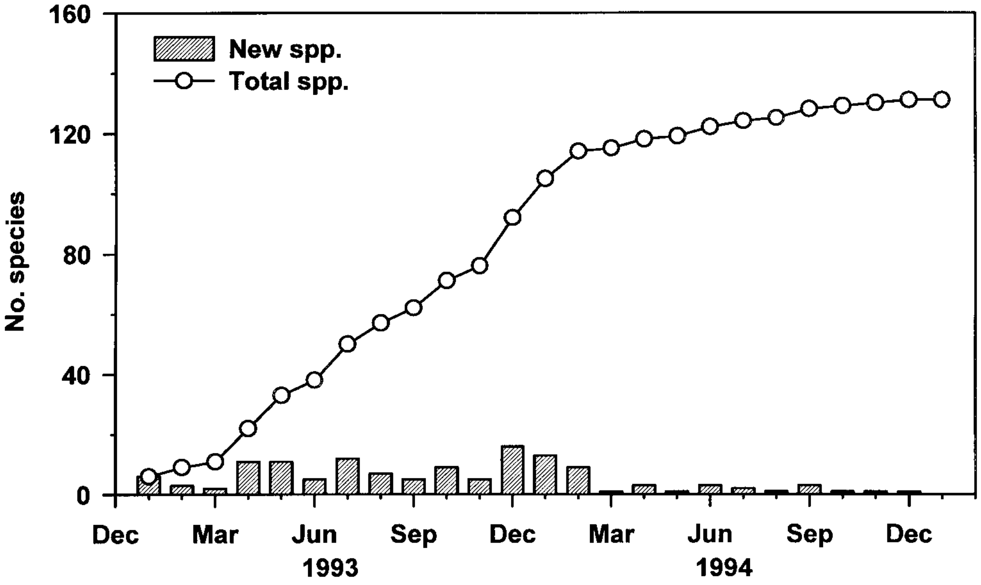

Figure 7. A cumulative species incidence curve of larval species collected throughout the survey. Hatched bars, new spp.; open circles, total spp.

species (comprising echinoderms, polychaetes, molluscs and one crustacean) developed with pelagic larvae. Although the data are sparse, we can draw the preliminary conclusion that whereas the maritime Antarctic (represented by Signy Island) has a diverse shallow-water benthic community and a diversity of larvae comparable with northern cold-temperate waters (as exemplified by Denmark), the Arctic is characterized by a low diversity of both adult taxa and larval forms. Geographic differences in the diversity of pelagic larvae are thus related to both variations in reproductive strategy and overall faunal diversity.

It is generally accepted that of the wide variety of benthic invertebrates that inhabit temperate seas, many have planktotrophic larvae. Thorson estimated the proportion to be 55–65% of the total number of species (Thorson 1950), but it is very difficult to find any other quantitative estimates in the literature. The most comprehensive compilation of the marine fauna of N. W. Europe (Hayward & Ryland 1995) describes some 1400 species. This would suggest that if Thorson's estimate is correct, over 800 different pelagic larvae (many of which would be closely related species, probably with morphologically indistinguishable larvae) must be present. In fact Thorson found only one-fifth of that number (table 4) in his survey of Øresund, Denmark (Thorson 1946). Thorson also suggested that 80–85% of tropical benthic invertebrates have planktotrophic, pelagic larvae (Thorson 1950). This estimate was based primarily on a study of prosobranch gastropods, and Thorson did recognize that the proportion of species releasing pelagic larvae might be lower in other taxa (Young & Chia 1987). As with the data for temperate regions, these estimates have been inferred from egg sizes in mature individuals rather than direct observations or surveys of larvae. Wickstead (1958) surveyed the zooplankton of the Singapore Straits, noting in passing that almost no year-round plankton sampling had been undertaken in the tropics. Unfortunately he did not record pelagic larvae, and today there is still a dearth of year-round data on larval diversity from almost anywhere in the world's oceans.

Table 4. *A comparison of the number of larval species found by Thorson (1946) and the present study*

(Difference in taxonomic grouping reflects the difficulties of identification of some taxa. The total of 159–164 larval taxa for Øresund comprises two studies: 121 larval taxa collected between August 1937 and August 1939, and 138 larval taxa between September 1941 and September 1942.)

location	Øresund, Denmark		Signy Island, South Orkney Islands	
description	sound between Baltic Sea and the Kattegut Sea		small rocky island in archipelago, on Scotia Arc	
depth	mostly 0–20 m deep channel at 40 m		inshore areas mostly 0–20 m, dropping off to 200 m (figure 1)	
water temperature	+2.6 °C (Feb) to +16.0 °C (Aug)		−1.9 °C (Jun–Nov) to +1.0 °C (Feb)	
latitude–longitude	(56° N, 12° E)		(61° S, 46° W)	
no. species				
	polychaetes	41	planulae	22
	prosobranchs	34	nemertean pilidia	8
	opisthobranchs	15	annelids	36
	lamellibranchs	28–33	molluscs	30
	decapods	12	decapods	0
	echinoderms	16	echinoderms	18
	other	13	tunicates	7
			other	10
	total	159–164	total	131

One important ecological feature noted by Thorson (1936) in his studies of the East Greenland fauna was the tendency for those few species which reproduced by pelagic larvae to be the most abundant. The correlation between pelagic larval development and high abundance in polar invertebrates has also been remarked upon for the Southern Ocean (Clarke 1992), with many of the common and numerically abundant species having pelagic larvae. This is highlighted by the dominance of the shallow-water Antarctic fauna by such species as the limpet *Nacella concinna* (Picken 1980), the cushion star *Odontaster validus* (Pearse 1965) and the nemertean *Parborlasia corrugatus* (Peck 1993), all of which reproduce by pelagic larvae.

(b) *Abundance*

In contrast to larval diversity, larval abundance seems to follow clear geographic clines. Anecdotal references to the paucity of marine invertebrate larvae in the Southern Ocean date back to the earliest expeditions (e.g. Thomson 1878; Hardy & Gunther 1935). Data from the present investigation concur with previous studies (Bosch 1989; Shreeve & Peck 1995) that the abundance of invertebrate larvae is very low in Antarctic waters (figure 5*a*,*b*). Thorson (1950) reported a maximum of 1400 larvae per 5000 l in samples taken near Ven, compared with the present maximum (mean monthly value) of only 13.7 larvae (all groups) occurring in the austral summer at Signy Island. A survey of the near shore waters of Porto Novo (S. E. India, 13° N) yielded a maximum larval density of $1.2\times10^5\,\mathrm{m}^{-3}$ (Srikrishnadhas *et al.* 1993), and conspicuous slicks of coral larvae observed on tropical reefs have reached densities of *ca.* $8\times10^6\,\mathrm{m}^{-3}$ (Babcock *et al.* 1986).

We were unable to find any other quantitative estimates of larval abundance in the literature. With the caveat that the available data are so scarce, it appears that there may well be a pattern of generally lower larval abundances at higher latitudes. However, as with any form of dispersal, the time spent in the water column will dictate the level of dilution (Okubo 1994). With warm temperatures and shorter development times, tropical pelagic larvae usually spend only a very short period in the water column. However, occasional larvae may well delay metamorphosis and spend long periods drifting up to thousands of kilometres. These teleplanic larvae (Scheltema 1971) incidentally result in gene dispersal over large tracts of ocean. As pointed out by Sammarco (1994), when ecological communities are faced with periodic heavy disturbance, the capability to initiate new colonies well away from the source of disturbance is highly advantageous. Sammarco modelled the dispersal of corals in relation to gross physical disturbances such as El Niño southern oscillation events and cyclones, and concluded that a combination of self-seeding with an additional input of a few long-distance dispersers was the optimal combination for the long-term persistence of reef communities (Sammarco 1994).

Antarctic benthic communities are subjected to regular and severe physical disturbances in the form of iceberg scour. In shallow waters and the intertidal area there also is intense scour and disruption from brash ice, fast ice and the winter ice foot (Barnes 1995*a*,*b*). The low temperatures increase development times perhaps up to 20-fold (Bosch *et al.* 1987; Peck & Robinson 1994; Stanwell-Smith & Peck 1998), but lower temperatures also reduce basal metabolic demands on larvae (Clarke 1983; Shilling & Manahan 1994). Taken together, these factors result in much-extended pelagic developmental periods. The extreme temperatures and the marked environmental seasonality in the Southern Ocean impose severe constraints on reproductive activity (Clarke 1988; Pearse *et al.* 1991). For example, in many species there is a narrow temperature window of spawning for species with external fertilization. Spawning aggregations to maximize reproductive success occur throughout the world's oceans, ranging from the tropics (Levitan 1991; Oliver & Babcock 1992) to the deep sea (Young *et al.* 1992). Spawning aggregations also occur in the Antarctic (Picken & Allen 1983), and a key factor here may be the reduction of distance between parents for high fertilization success as a result of the increased viscosity affecting sperm motility in cold water (Vogel 1994).

The longer larval lifetimes of Southern Ocean marine invertebrates would appear to confer an incidental advantage in terms of recolonization of habitat scoured by ice. In echinoids, Emlet (1995) found no relationship between time in the water column of larvae and species geographic range; rather he concluded that a strategy of pelagic larvae drifting for longer periods influenced geographic range indirectly by improving the chance of recovery from disturbance. Although many of the commonest and most widespread shallow-water marine invertebrates in the Antarctic reproduce by means of a pelagic larva, there is widespread occurrence of brooding or direct development in many molluscs and echinoids (Arnaud 1974; Picken 1980; Poulin & Féral 1996). This indicates that the existence of a free-swimming larva in the life history is not a prerequisite for successful colonization of habitats disturbed regularly by ice.

The low levels of larval abundance in the present study may be due to much greater dilution over a longer period, exacerbated by the island location of the present survey. This is supported by the similar density figures found for larvae several hundred kilometres offshore in the Bellingshausen Sea (Shreeve & Peck 1995). A consequence of long larval lifetimes in the plankton would be the potential for long-distance dispersal. This would suggest that in areas such as the Antarctic Peninsula, where a complex but effectively linear habitat is swept by an along-shore current, gene-flow through larval dispersal would lead to genetic homogeneity over a large geographic scale (Poulin & Féral 1996).

The low abundance of larvae with long lifetimes will be a driving factor in the year-round, albeit very slow, recruitment to settlement panels observed at Signy Island (Stanwell-Smith & Barnes 1997). It has been suggested for some environments that oceanographic control of larval availability might limit community development (Roughgarden *et al.* 1988; Grosberg & Levitan 1992). The data available from this study, although only from a single site, might suggest a very different pattern of community dynamics in the maritime Antarctic. Rather than large pulses of larvae, whose ability to settle and colonize new substrata is strongly influenced by oceanographic factors during their short lifespan, the Southern Ocean is characterized by a year-round but low abundance of long-lived, slow-developing larvae, with a consequent low level of year-round recruitment to new substrata.

(c) *Seasonality*

The major variability in the overall data set was attributable to seasonality rather than to site effects or the influence of depth. The dominance of seasonality over other factors might be explained by the long period of time that the larvae tend to spend in the water column, ensuring sufficient mixing within sites in the same locality. This was indicated by the presence of most larval types at all sites (table 2). Interestingly, most larval groups (even those with significant seasonal peaks) also occurred in low numbers throughout the year. This may be related to delayed metamorphosis, but over a longer time-scale (Todd & Doyle 1981), which would tend to smooth out the seasonality of larval occurrence even in species with a strongly seasonal pattern of spawning.

Within this framework, the multivariate analysis (figure 6) divided the larval groups into three main periods of occurrence. Annelids of different stages and molluscan trochophores tended to occur at the height of the phytoplankton bloom in mid-summer. This might suggest that these larvae are tied closely to the timing of the summer microphytoplankton bloom. Since this bloom increases in seasonality from the tropics to the poles, it may be a key factor in reducing the percentage of species reproducing by pelagic larvae in these groups. If this is the case, prosobranch molluscs would be one of the groups most affected, because they have the clearest latitudinal cline in reproductive strategy so far described (Thorson 1950; Mileikovsky 1971). The second 'season' of occurrence was that of echinoderms and nemertean pilidia whose peak occurrences are in the middle of winter. These larvae, although many are planktivorous, may also be the most adaptable in terms of other feeding strategies, such as osmotrophy (Manahan 1990) and bacterivory (Rivkin *et al.* 1986). They may also be able to feed selectively on the nanophytoplankton, because their occurrence in the water column coincides exactly with the period when flagellate chlorophyll (20–2 μm fraction) exceeds diatom chlorophyll (Clarke & Leakey 1996), and larvae of many temperate species are known to ingest particles in the nanophytoplankton range. This has been especially apparent in aquaculture systems (e.g. Webb & Chu 1981).

The third 'season' is one of a transitional nature, occurring in a period after the plankton bloom but before the temperatures drop to winter levels and sea ice forms. Larvae whose abundances peak in this period include echinoid plutei and sipunculid pelagosphaerae. Because these larvae tend to occur at a time of environmental transition, it is not at all clear what key environmental factors might be involved.

Although the multivariate analyses revealed the three distinct periods of seasonality discussed above, these groups may draw attention away from a fourth group; namely those larvae with no distinct seasonality. These larvae (e.g. the planulae) tend to be present year-round, but at low densities. Because larvae classified as planulae will have originated from a variety of adult taxa (22 morphologically distinct types were detected in this study), pooling all data as 'planulae' may have obscured distinctly seasonal occurrences of particular species of planulae. However, no group of planulae would be expected tightly associated with the summer phytoplankton bloom, because most planulae are lecithotrophic.

(d) *Conclusions*

The species-richness of pelagic larvae observed (131 morphologically distinct forms) is similar to that found in temperate waters. This diversity of larval types is much greater than has been found in the Arctic and runs counter to the hypothesis that a low diversity of larval types is a feature of polar habitats per se. Although some groups of organisms do contain fewer representatives reproducing by a pelagic larva at high latitudes (e.g. prosobranch molluscs and echinoids), the low diversity of larvae reported for the Arctic appears to be related primarily to the overall low diversity of the marine ecosystem at high northern latitudes. The Southern Ocean benthos overall is diverse, and the diversity of larvae detected in this study is comparable with cold-temperate rather than Arctic latitudes.

Densities of larvae found at any one time at high latitudes are reduced, which is probably related to protracted developmental periods resulting in greater dilution. This is clearly different from the common tropical strategy of synchronous mass release of gametes that form larvae and develop to metamorphosis, rapidly producing swarms of larvae in the water for short periods of time. Overall numbers of larvae may not be as divergent, but peak larval densities in polar waters may be lower because of dilution effects brought about by protracted development periods. At low temperatures the sensitivity of development rate to very small temperature changes may also make microhabitat factors important in increasing significantly the hatching period, further reducing local densities and dispersing larvae more widely. Seasonality of larvae is not as obvious as for other parts of the world with many larval groups occurring throughout the year. However, there were three distinct 'seasons' of larval peaks observed. Larval abundances were not correlated with site or depth for most groups, and there was little evidence of larvae being associated with sea ice or the epibenthos.

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