Polar Biol (2003) 26: 359–364
DOI 10.1007/s00300-003-0479-y

ORIGINAL PAPER

Theresinha M. Absher · Guisla Boehs
Angela R. Feijó · Andrea C. da Cruz

# Pelagic larvae of benthic gastropods from shallow Antarctic waters of Admiralty Bay, King George Island

Received: 3 January 2002 / Accepted: 30 December 2002 / Published online: 9 April 2003


**Abstract** The occurrence, distribution and summer variation of pelagic larvae of benthic gastropods in the shallow coastal area of Admiralty Bay were determined for the summers of 1993/1994, 1994/1995 and 1996/1997 from plankton samples taken at 15- to 30-m depths in 12 stations. Significant differences were found among years at the end of January and February. Results of Principal Component Analysis showed the inverse relation of high wind speed and abundance of gastropod larvae in the three austral summers sampled, and suggested that environmental conditions prevalent during 1994/1995 and 1995/1997 were similar and differed from those of 1993/1994, which may have influenced the number of larvae observed.

## Introduction

Marine invertebrates with a benthic-pelagic life history are among the most well dispersed in oceans. Reproductive patterns may include indirect development with planktotrophic or lecitotrophic larvae, or direct development with embryos incubated and hatching as juveniles (Thorson 1950). The occurrence of planktonic larvae depends on the temporal reproductive pattern and the life-cycle characteristic of the species, associated with environmental parameters (Giese and Pearse 1977). In marine gastropods, larval development may be direct or indirect. Many prosobranch gastropods display indirect development where the embryo hatches as a free-swimming planktonic larva whereas, in others, the gametes are discharged directly into the sea where fertilisation takes place (Hyman 1967). In both cases, a veliger larva develops and may be collected in plankton samples.

T. M. Absher (✉) · G. Boehs · A. R. Feijó · A. C. da Cruz
Centro de Estudos do Mar, Universidade Federal do Paraná,
Av. Beira Mar s/n Pontal do Sul, 83255-000 Paraná, Brazil
E-mail: tmabsher@cem.ufpr.br
Fax: +55-41-4551105

Despite numerous plankton-sampling programs in Antarctica (reviewed in Shreeve and Peck 1995), data on occurrence and distribution of larvae are incompatible with patterns of diversity in benthic molluscs of the Antarctic region (Perissinotto 1989; Nonato et al. 2000). The uncommon occurrence of planktonic larvae in Antarctic waters has been attributed to a predominance of brooding or direct development in molluscs and other Antarctic marine invertebrates (Thorson's rule) (Mileikovsky 1971), rather than a lack of adequate plankton sampling. However, numerous workers have argued that Thorson's rule should not be generalised to all Antarctic marine invertebrates (Foster 1987; Bosch and Pearse 1990; Pearse et al. 1991; Pearse 1994; Shreeve and Peck 1995). Many Antarctic echinoderms did not conform to the predictions of this rule (Bosch and Pearse 1990; Pearse et al. 1991), and recent studies have revealed increasing numbers of pelagic larvae from many taxa in Antarctic waters (Stanwell-Smith et al. 1997, 1999).

Zooplankton studies in Admiralty Bay, Antarctica have concentrated on seasonal succession, abundance and variability of holoplankton, and little attention has been paid to the presence of meroplanktonic invertebrate larvae (Dera and Weglenska 1983; Chojnacki and Weglenska 1984; Mensiienina and Rakusa-Suczczewski 1992; Freire et al. 1993; Santos 1995). In this paper, we analyse patterns of abundance and distribution of pelagic larvae of benthic gastropods as they relate to seasonal (austral summer) variations in a shallow coastal region of sheltered inlets of Admiralty Bay. We also examine correlations between these patterns of larval abundance and distribution with environmental factors, including salinity, seawater temperature, transparency, tidal cycles, and wind direction and speed.

## Materials and methods

Situated on King George Island, Admiralty Bay is open to the Bransfield Strait at south-southeast, comprising an area of 122 $km^2$ and a volume of 24.24 $km^3$ (Rakusa-Suszczewski 1980), and is divided into three inlets: Martel, Mackellar and Ezcurra. Depth increases rapidly from the shore to a maximum of 500 m in the centre of the bay. Tides are semidiurnal with diurnal inequalities (maximum range of 2.5 m) and play an important role in the bay's circulation (Pruszak 1980). Deep currents generated by tides, frequent upwellings, vertical mixing of the entire water column, and current velocities of 30–100 cm $s^{-1}$ in the 0- to 100-m surface layer are characteristic of the bay (Pruszak 1980; Rakusa-Suszczewski 1980).

Plankton samples were collected at four locations: Martel, Mackellar, and Ezcurra Inlets, and also in front of the Arctowski Polish Station, at 6 stations (1–3, 6–8) during the summer 1993/1994 (January to February) and at 12 stations (1–12) in summers 1994/1995 and 1996/1997 (December to February) (Fig. 1). A plankton net (50 cm diameter and 150 μm mesh size) was towed obliquely, from the sea bottom at 15–30 m depth, to the water surface, for 10 min at 2 knots. Each tow was considered as a sample. Plankton samples were preserved in 4% buffered formaldehyde. In the laboratory, the samples were concentrated, and examined using a counting chamber with a stereomicroscope. Total numbers of gastropod larvae in each net sample (= tow) were counted and corrected to a standard 100 $m^3$ collection tow. Data on seawater temperature, salinity, water transparency (Secchi disk), wind intensity ($m{\cdot}s^{-1}$) and direction and tidal cycles were also obtained. Data on wind direction and intensity were obtained from the Weather Station at "Comandante Ferraz Antarctic Station". An ANOVA was used to test for significant differences ($\alpha = 0.05$) in mean abundance and occurrence of gastropod larvae between years and stations at peak occurrence of larvae (end of January to February). A Least Significant Difference (LSD) test was used to verify significant differences a posteriori. Principal component analysis. (PCA), on a correlation matrix, was performed following log $(x + 1)$ transformation of the larval abundance data, in the peak period of each summer, combined with a suite of environmental variables (seawater temperature, salinity, transparency, tidal phase, wind direction and speed) likely to influence larval abundances at the sampling stations.

## Results

Of the 180 sampling tows collected, 47 (26%) contained no gastropod larvae. In the remaining 133 (74%), a total

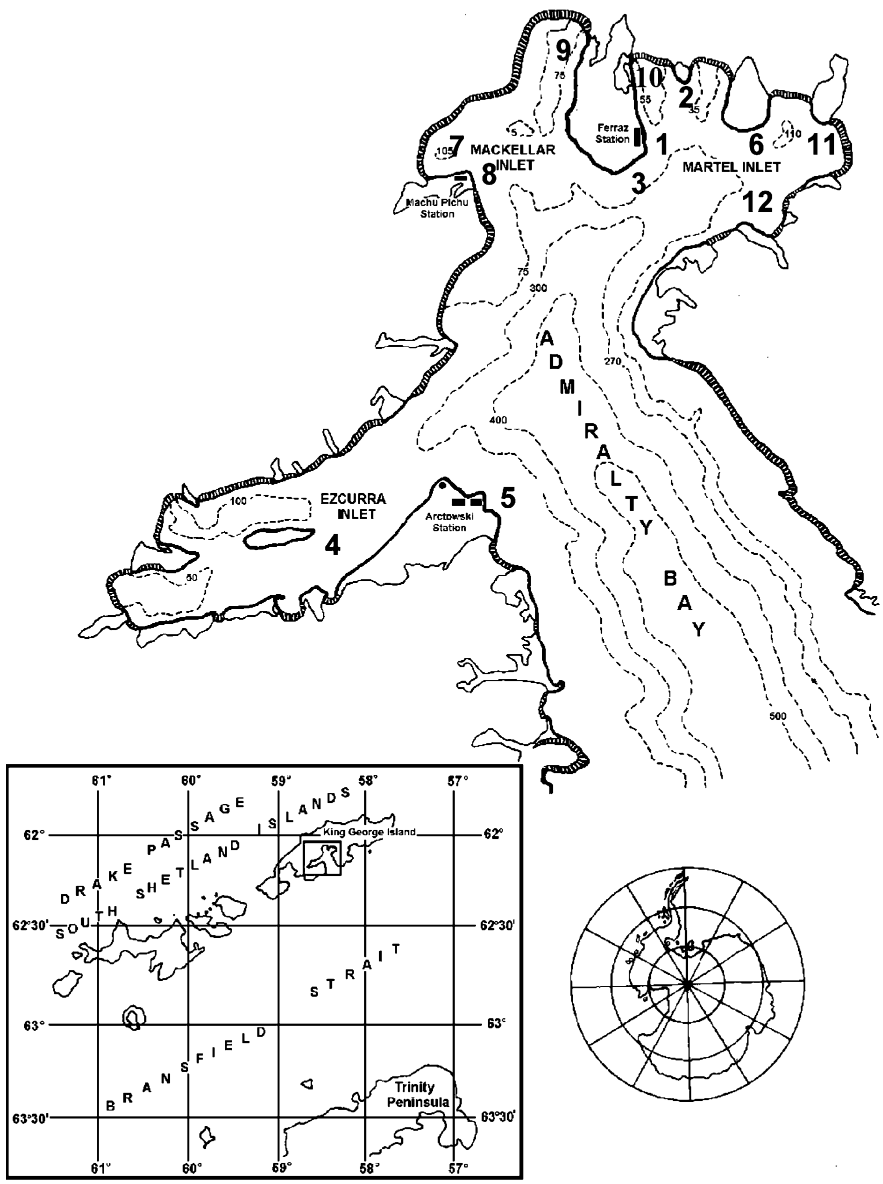



Fig. 1 Admiralty Bay, King George Island. Location of the 12 stations on Martel Inlet, Mackellar Inlet, Ezcurra Inlet and Arctowski

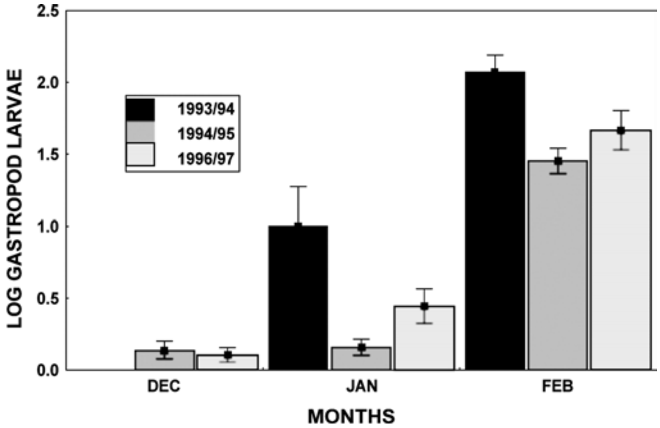



**Fig. 2** Log of total number of gastropod larvae collected in the three austral summers 1993/1994, 1995/1996 and 1996/1997 in December, January and February (mean ± SE)

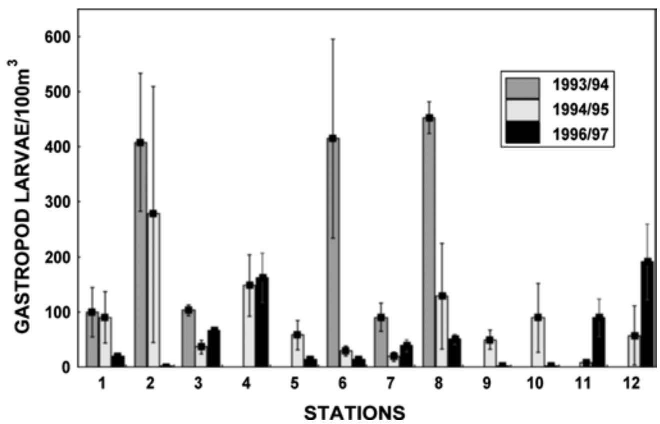



**Fig. 3** Density of gastropod larvae over three austral summers: 1993/1994, 1994/1995 and 1996/1997 at 12 stations in Admiralty Bay (mean ± SE)

of 18,519 gastropod larvae were counted (mean of 84.98 ± 15.05 (SE) larvae/100 $m^3$) Gastropod larvae were present in all three summers and at all stations at the end of January and February, with significant differences ($P < 0.05$) among years (Fig. 2). LSD tests indicated inter-annual abundance patterns of larvae at the end of January and all February were 1993/1994 > 1994/1995 = 1996/1997. Significant differences were also found among months in 1994/1995 and 1996/1997. LSD tests indicated February > January = December (Fig. 2). There was also a significant difference ($P < 0.05$) in larval abundances among stations (Fig. 3). LSD analysis indicated station 2 = 6 and 8 > remaining stations. In 2 consecutive tows, a total of 2,311 gastropod larvae (1,148 first tow and 1,163 second tow) were collected at station 6 (19/02/1994), while a total of 3,003 gastropod larvae (1,538 first tow and 1,465 second tow) were collected in consecutive tows at station 2 (22/02/1994), both located at Martel Inlet. Almost all gastropod larvae sampled were of the same type (99.15%); only 0.85% of the larvae were of two different

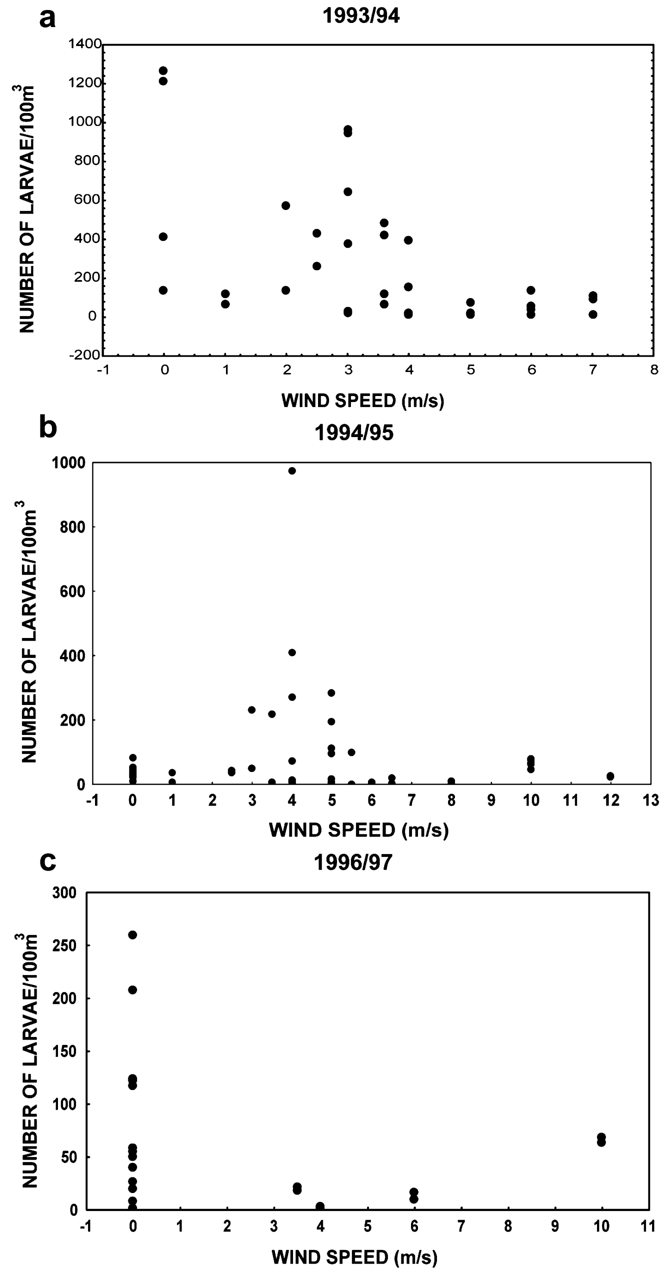
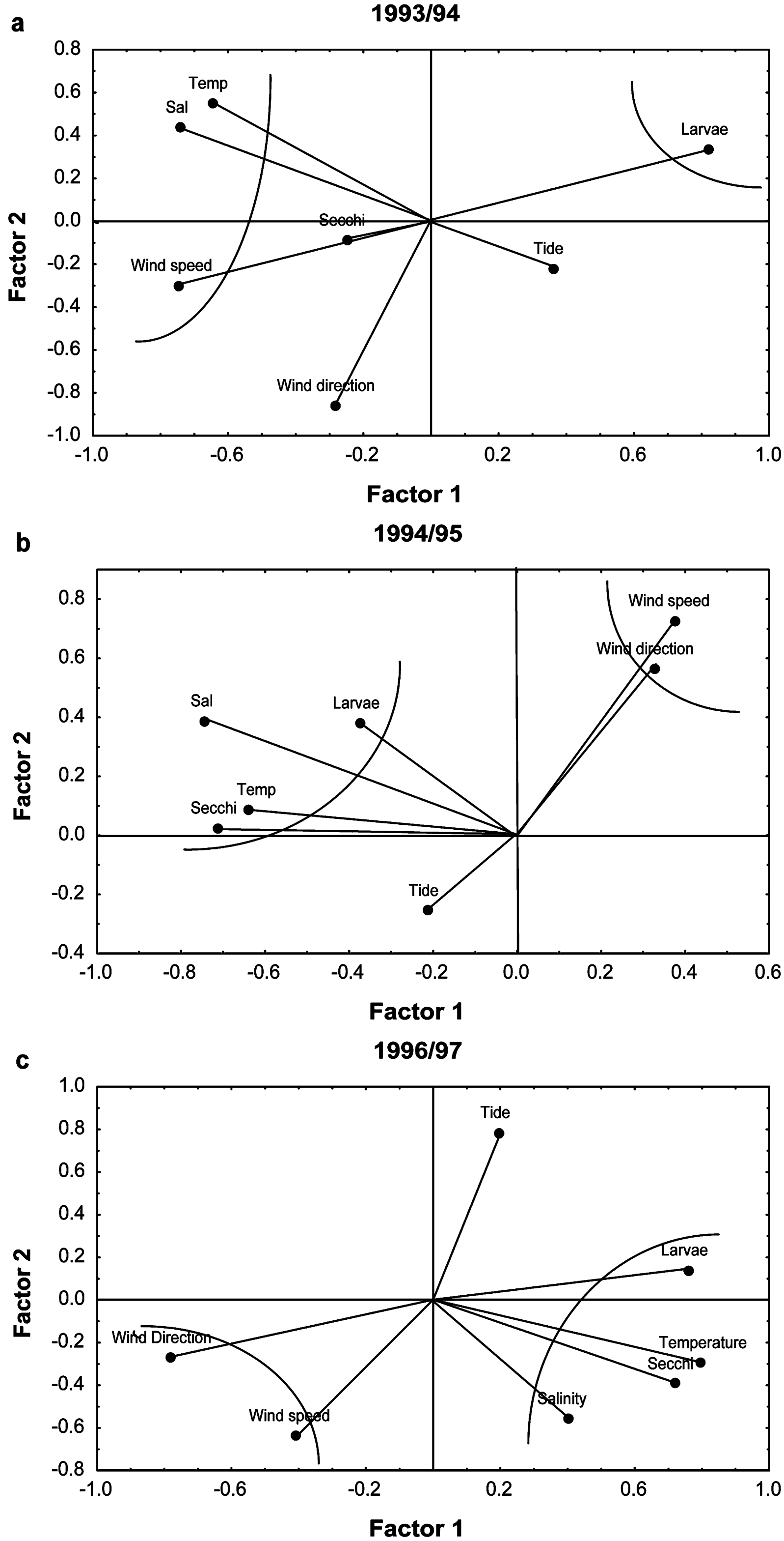



**Fig. 4a–c** Number of gastropod larvae in 100 $m^3$ under wind speed (m/s) in the three austral summers (1993/1994, 1994/1995 and 1996/1997)

kinds and started to appear at the end of February. There was little variation among years in seawater temperature or salinity. Values of salinity varied from 34.5 to 36.5 (1993/1994), and 33.0 to 36.0 (1994/1995 and 1996/1997), while water temperatures ranged from −1.0 to 2.5°C (1993/1994), −1.0 to 1.5°C (1994/1995) and −1 to 2.5°C (1996/1997). Water transparency, as measured by Secchi disk, showed greater levels of variation (3.1–6 m, 1993/1994; 1.2–8 m, 1994/1995; 0.6–10 m, 1996/1997). At the period of peak larval abundance (end of January and all February), wind direction during the 1993/1994 summer was predominantly from

**Fig. 5a–c** Principal Component Analysis: graphics of results of 1993/1994, 1994/1995 and 1996/1997, during peak abundances of gastropod larvae




the east, and in 50% of the days of sampling the wind speed was above 4 m $s^{-1}$ (Fig. 4a); the summer of 1994/1995, the main wind direction was from the southeast (76.30%) with speeds above 4 m $s^{1}$ (69.12%) (Fig. 4b); weak winds were observed in the 1996/1997 summer with speeds less than 4 m·$s^{-1}$ (66.66%) from the south (20.83%) (Fig. 4c).

PCA analyses, examining environmental factors and peak densities of larvae over the three austral summers, are shown in Fig. 5a–c. The first component of the three biplots for the summers of 1993/1994, 1994/1995 and 1996/1997 shows the influence of wind speed and direction over larval abundance during the 1993/1994, 1994/1995 and 1996/1997 summers. High larval abundance was favoured in waters under the influence of northeast winds with speed less than 4 m/s. The three first components of 1993/1994 accounted for 72% of the variance, with the first two components explaining 57% (35% and 22% respectively) (Fig. 5a), and indicated that environmental conditions prevalent during 1993/1994 favoured higher larval abundance at flood tide in seawater less saline and of lower temperature.

The three first components of the 1994/1995 summer explained 60% of the total variance, with the first two components explaining 45% (factor I = 27%; factor II = 18%) (Fig. 5b), and the first two components of the 1996/1997 summer (Fig. 5c) explained 62.2% of the variance (factor I = 38.6%; factor II = 23.6%). In both summers, environmental conditions were such that higher larval abundance were observed in seawater with higher salinity, higher temperature and less transparent waters.

## Discussion

According to Santos (1995), planktonic polychaete larvae are present in Admiralty Bay at both the beginning and end of austral summer. Similarly, Freire et al. (1993) recorded polychaete larvae towards the end of the austral summer in Admiralty Bay. We found gastropod larvae occurring at the end of the austral summer while being almost completely absent at the beginning of the summer. These results suggest that marine invertebrate larvae may occur over different periods of the summer, probably due to species-specific reproductive patterns selected by the most favourable environmental conditions.

Thorson's rule (Mileikovsky 1971), of avoidance of a pelagic larval phase in marine invertebrates, based mainly on gastropod reproductive strategy for high latitudes, cannot be confirmed, at least for one gastropod species of Admiralty Bay, as our results showed almost totality of gastropod larvae sampled in this study (99.15%) belong to one species.

The present study was carried out only during the austral summers, so the peak abundance of gastropod veligers in the austral winter, reported by Stanwell-Smith et al. (1999), in a survey over 25 months (1993/1994), could not be observed.

Inter-annual variation in larval abundance is a common phenomenon among marine invertebrates (Clancy and Cobb 1997; Powell 2001). PCA results, mainly factor I formation, suggest that environmental conditions prevalent during 1994/1995 and 1996/1997 were similar and differed from those of 1993/1994, likely influencing the numbers of larvae observed. Factor I of PCA analysis of 1994/1995 and 1996/1997 revealed the same pattern of larval abundance, with seawater temperature, salinity, transparency and tide in opposition to wind speed and direction. Among the physical factors likely to affect larval abundance, directly or indirectly, are tidal currents, and wind speed and direction. Freire et al. (1993) and Alder and Thompson (2000) emphasised the role of hydrographic processes on plankton dispersal in Antarctic waters. According to Pruszak (1980), the surface circulation of water under wind speeds greater than 4 m $s^{-1}$ is dependent on the distribution of wind direction in Admiralty Bay. Surface currents in Ezcurra, Martel and Mackellar Inlets, under the influence of strong winds (>4 m $s^{-1}$) from the SW-W or N, flow in that same direction and have prevalence over tidal flow. Wind from the north with speeds above 4 m/s would carry surface waters out of the inlets. The dynamics of surface currents, as proposed by Pruszak (1980), are in accordance with what we observed in both austral summers 1994/1995 and 1996/1997. PCA-component II of 1994/1995 revealed high abundances of larvae were present under high wind speed from the north, at ebb tide, with water flowing out of the bay. Freire et al. (1993) observed that surface waters, flowing out of the inlets towards Bransfield Strait, under a NW wind, contained higher plankton densities. The high densities of gastropod larvae we observed at stations 2, 6 and 8, situated in the inner portion of Martel and Mackellar inlets, may be due to the geomorphology of the inlets, which most probably determines the formation of eddies, and may contribute to larval retention in the area. The dilution effect observed by Stanwell-Smith et al. (1999) was not verified in the present study but, rather, a tendency for larval concentration in the innermost location of the inlets in Admiralty Bay, indicating the importance of local water dynamics in the concentration of larvae at those places.

The clear pulse of gastropod larvae verified in February of the three summers, together with the high densities of gastropod larvae sampled in consecutive tows in some days (19/02/1994; 22/02/1994) in the present study, suggest a similarity with synchronous reproductive strategy common in the tropics, contrary to what was postulated by Stanwell-Smith et al. (1999) for high latitudes. The stability of seawater temperature throughout the year observed in both regions may be responsible for this similarity, as seawater temperature plays a major role in the reproductive process.

Planktonic gastropod larvae are difficult to identify to species level. Nonetheless, the high densities we observed suggest they belong to a common gastropod species occurring in the region which possesses a broadcasting reproductive pattern. The most likely candidate is *Nacella concinna*, a nearshore prosobranch gastropod very abundant from shallow intertidal depths to ca. 80 m depth (Picken 1980; Rauschert 1991; Filcek 1993; Nonato et al. 2000). According to Powell (2001) *N. concinna* spawns in response to the spring phytoplankton bloom. In Admiralty Bay, primary production peaks at the end of January and February may be associated with the spawning events of *N. concinna* observed at that time of the year (Picken 1980). Ligowski and Kopczynska (1993) recorded peak phytoplankton numbers in Admiralty Bay at the end of February, with two smaller blooms occurring in the second half of January.

**Acknowledgements** We thank Professor John Pearse for his helpful comments and suggestions. We also thank two anonymous referees for their constructive criticism. This work was supported by a grant from CNPQ/PROANTAR (Conselho Nacional de Pesquisa e Desenvolvimento Tecnológico/Programa Antártico Brasileiro). Logistical support was provided by SECIRM (Secretaria da Comissão Interministerial para os Recursos do Mar-Marinha do Brasil).

## References

Alder VA, Thompson G (2000) Spatial and temporal distribution of tintinnids (Protozoa, Ciliata) in relation to frontal systems and the general hydrologic dynamics of the Southern Ocean (SW Atlantic Sector; 50°-64°S. 65°-49°W). In: Davison W, Howard-Williams C, Broady P (eds) Antarctic ecosystems: models for wider ecological understanding. Caxton Press, Christchurch, pp 203–214

Bosch I, Pearse JS (1990) Developmental types of shallow water asteroids of McMurdo Sound, Antarctica. Mar Biol 104:41–46

Chojnacki J, Weglenska T (1984) Periodicity of composition, abundance and vertical distribution of summer zooplankton (1977/1978) in Ezcurra Inlet, Admiralty Bay (King George Island, South Shetland). J Plankton Res 6:807–827

Clancy M, Cobb JS (1997) Effect of wind and tidal advection on distribution patterns of rock crab *Cancer irroratus* megalopae in Block Island Sound, Rhode Island. Mar Ecol Prog Ser 152:217–225

Dera J, Weglenska T (1983) Bioluminescence of zooplankton in the Antarctic fjord Ezcurra Inlet. Oceanology 15:185–207

Filcek K (1993) Patellidae. In: Rakusa-Suzczewski S (ed) The maritime Antarctic coastal ecosystem of Admiralty Bay. Polish Academy of Sciences, Warsaw

Foster BA (1987) Composition and abundance of zooplankton under the spring sea-ice of McMurdo Sound, Antarctica. Polar Biol 8:41–48

Freire AS, Coelho MJC, Bonecker SLC (1993) Short-term spatial-temporal distribution pattern of zooplankton in Admiralty Bay (Antarctica). Polar Biol 13:433–439

Giese AG, Pearse JS (1977) Reproduction of marine invertebrates, vol IV. Academic, New York

Hyman LH (1967) The invertebrates. Mollusca I, vol VI. McGraw-Hill, New York

Ligowski R, Kopczynska E (1993) Phytoplankton. In: Rakusa-Suszczewski S (ed) The maritime Antarctic coastal ecosystem of Admiralty Bay. Polish Academy of Sciences, Warsaw, pp 45–48

Mensiienina L, Rakusa-Suszczewski S (1992) Zooplankton changes during the year in Admiralty Bay (February 1990-January 1991). Pol Arch Hydrobiol 39:65–76

Mileikovsky SA (1971) Types of larval development in marine bottom invertebrates, their distribution and ecological significance: a re-evaluation. Mar Biol 10:193–213

Nonato EF, Brito TAS, Paiva PC, Petti MAV, Corbisier TN (2000) Benthic megafauna of the nearshore zone of Martel Inlet (King George Island, South Shetland Islands, Antarctica): depth zonation and underwater observations. Polar Biol 23:580–588

Pearse JS (1994) Cold-water echinoderms break "Thorson's Rule". In: Young CM, Eckelbarger KJ (eds) Reproduction, larval biology and recruitment of the deep-sea benthos. Columbia University Press, New York

Pearse JS, Mcclintock JB, Bosch I (1991) Reproduction of Antarctic benthic marine invertebrates: tempos, modes and timing. Am Zool 31:65–80

Perissinotto R (1989) The structure and diurnal variations of the zooplankton of the Prince Edwards Islands: implications for the biomass build-up of higher trophic levels. Polar Biol 9:505–510

Picken GB (1980) Distribution, growth, and reproduction of the Antarctic limpet *Nacella* (Patinigera) *concinna* (Strebel, 1908). J Exp Mar Biol Ecol 42:71–85

Powell DK (2001) Long-term reproductive cycles in Antarctic and sub-Antarctic free-spawning molluscs. VIII SCAR International Biology Symposium, August 27-September 1, Vrije Universiteit, Amsterdam, S3P64

Pruszak CZ (1980) Current circulation in the waters of the Admiralty Bay (region of Arctowiski Station on King George Island). Pol Polar Res 1:55–74

Rakusa-Suszczewski SS (1980) Environmental conditions and the functioning of Admiralty Bay (South Shetland Island) as part of the near shore Antarctic ecosystem. Pol Polar Res 1:11–29

Rauschert M (1991) Ergebnisse der faunistischen Arbeiten im Benthal von King George Island (Südshetlandinseln, Antarktis). Ber Polarforsch 76:1–75

Santos CC (1995) Relação entre fatores físicos e a comunidade zooplanctônica na Baía do Almirantado e regiões costeiras da Ilha Elefante (Antártica). MSc Thesis, Universidade Federal do Rio Janeiro

Shreeve RS, Peck LS (1995) Distribution of pelagic larvae of benthic marine invertebrates in the Bellingshausen Sea. Polar Biol 15:369–374

Stanwell-Smith D, Hood A, Peck LS (1997) A field guide to the pelagic invertebrates larvae of the maritime Antarctic. British Antarctic Survey, Cambridge

Stanwell-Smith D, Peck LS, Clarke A, Murray AWA, Todd CD (1999) The distribution, abundance and seasonality of pelagic marine invertebrate larvae in the maritime Antarctic. Philos Trans R Soc Lond 354:471–484

Thorson G (1950) Reproduction and larval ecology of marine bottom invertebrates. Biol Rev 25:1–45