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DISTRIBUTION AND ABUNDANCE OF GYMNOSOMATA (GASTROPODA: OPISTHOBRANCHIA) IN THE SOUTHWEST ATLANTIC

JOSÉ R. DADON and SILVINA F. CHAUVIN
Departamento de Ciencias Biológicas, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, 1428 Buenos Aires, Argentina
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ABSTRACT

The distribution and abundance of gymnosome gastropods in the Argentine Sea and Brazil—Malvinas Confluence during 1978–1979 and 1988 were studied. The collections analyzed included 768 quantitative samples obtained between 48°W and the coast, and from 35°S to 55°S. Two species were found. *Spongiobranchaea australis* was the most frequent and abundant (up to 730 per 1000 m^3); its presence in the area was associated with the core of the Malvinas Current. *Clione antarctica* was less abundant (maximum abundance: 230 per 1000 m^3) and was also associated with the Malvinas Current. The geographic ranges of both species in the area are wider than previously described. Since the range of *S. australis* in the area extends far from the range of its prey *Clio*, it is not clear whether *S. australis* can feed on the thecosomatous pteropod *Limacina* (and not only on *Clio*, as described in the bibliography) or it starves in that area. During the 1978–1979 annual cycle, the abundance of both species followed neither the abundance patterns of their prey nor of the total zooplankton, and differed from each other. The residence time of swarms of both gymnosomes were shorter than one month. As a general pattern, the aggregates are rapidly transported northward by the Malvinas Current and also penetrate the outer shelf water, but they remain there only during a short period and cannot preclude the final expatriation. So, the abundance of gymnosomes in the area depends on passive migration more than intrinsic population factors.

INTRODUCTION

The gymnosomes are perhaps the most poorly known of the holoplanktonic gastropods. Lalli & Gilmer (1989) summarized some of reasons for this bias. The gymnosomes are restricted to the pelagic environment and, probably due to their highly specialized carnivorous habits, they are rare. In addition, most specimens are obtained from oceanographic zooplankton samples preserved in formaldehyde, and, when preserved according to the standard methodology (that is, without prior anaesthetic), the animals contract into indistinguishable forms. The consequence is, in Lalli & Gilmer's words, that 'the formidable problems that arise when species identification must be based on the dissection of minute, contracted animals have discouraged many potential researchers'.

Most studies of gymnosomes have been conducted on populations from the northern hemisphere. In the southern hemisphere, only taxonomic lists can be found in the literature and the available information is very scarce. Twenty-four taxa (species and infraspecific levels) have been described for the South Atlantic and Antarctic (see review in Spoel & Dadon, in press). Data about gymnosome abundance can be found only in Ramírez & Viñas (1983), and Boysen-Ennen & Piatkowski (1988), who reported some local abundance estimates from Antarctic water.

The Argentine continental shelf and its surroundings are among the most thoroughly studied areas of the South Atlantic. Special attention must be given to the zooplankton communities of the continental shelf, since complete basic information is needed to understand the local fisheries dynamics, and also because the Argentine shelf seems to be a representative area of the cold temperate (or subantarctic) zone. Despite the interest in zooplankton, only two studies (Massy, 1932; Magaldi, 1981) dealt with the gymnosomes from the Argentine Sea and the surrounding area and their data can be briefly summarized as follows. In shelf water, *Spongiobranchaea australis* was found once at 43°46′S–56°57′W) and *Clione antarctica* three times (42°27′S–57°15′W; 42°22′S–56°59′W and 42°15′S–56°46′W; Magaldi, 1981). In the Brazil—Malvinas (Falkland) Convergence, three species were found: *Spongiobranchaea intermedia*, *Schizobrachium polycotylum* and *Thliptodon gegenbauri*, all of them from 41° to 43°S, and from 42° to 46°W (Massy, 1932). No quantitative estimates were given in either report. Subsequent reviews (Spoel, 1976; Spoel & Boltovskoy, 1981; Dadon & Boltovskoy, 1982) are based on these original data.

The object of this paper is to report the first quantitative estimates of gymnosome abundance in the South Atlantic; to delineate the geographical ranges of the species; and to identify the main factors which determine the distribution and abundance of the species in the Argentine Sea.

MATERIALS AND METHODS

Samples were collected during 18 cruises conducted over a complete annual cycle (April 1978–April 1979), in shelf and slope water off Argentina by the R/V 'Walther Herwig' and 'Shinkai Maru' (see Ciechomski, Ehrlich, Lasta & Sánchez, 1979; Cousseau, Hansen & Gru, 1979). For the Brazil—Malvinas Convergence, samples of two cruises were analysed: BIP 'Eduardo L. Holmberg' H04/83 (June 1983) and RTMA 'Evrika' (August–October 1988). In total, 768 samples obtained between 40°W and the coast, and between 35°–55°S, were studied.

Samples were collected during daytime and twilight with Bongo nets (mouth diameter, 60 cm; length, 330 cm) fitted with 330 or 505 mm mesh nets. On the continental shelf, oblique tows extended from the surface to approximately 20 m above the bottom; on the slope, from the surface to 100 m depth; in oceanic water, from the surface to 50 m. The maximal tow depth was estimated by the time-depth recorders. The nets were provided with digital flow meters in both mouth openings and were towed at 3.5 knots. In all cases, the volume of water filtered was 200–1000 m^3.

Samples were preserved in 5–7% buffered formaldehyde. For counting purposes, samples were either analyzed in their entirety or, when necessary, were divided into aliquots with a Folsom sample splitter.

Significant differences were tested for the two mesh sizes and for large volumes, but little or no significant differences were obtained either in the plankton volume or in the size composition of the zooplankters (Ciechomski & Sánchez, 1983).

RESULTS AND DISCUSSION

Geographic ranges of the species

Spongiobranchaea australis d'Orbigny, 1836 was the most frequent and abundant gymnosome of the study area. It was found in water ranging from 2.3 to 13.2°C and with salinity of 33.47–34.20. The abundance of the species peaked at 730 individuals/1000 m^3 (45°59'S–58°31'W), which is higher than maxima mentioned for other areas (190/1000 m^3 off South Georgia Islands: Ramírez & Viñas, 1983; < 1/1000 m^3 in the Wedell Sea: Boysen-Ennen, 1987; < 10/1000 m^3 in Croker Passage, Antarctic Peninsula: Hopkins, 1985).

Spongiobranchaea australis was recorded all along the continental slope up to 39°34'S (Fig. 1). This pattern shows that *S. australis* is clearly associated with the Malvinas (Falkland) Current. The Malvinas Current is a branch of the Circumpolar Current and its core flows along the continental slope off Argentina. This current is probably the only way for *S. australis* to enter the region, although the aggregates recorded seem to be rapidly expatriated northward (see below).

The horizontal range of *Spongiobranchaea australis* extends from the Antarctic coast to the northern limit of the Subantarctic water. In the Argentine Sea, it was present in the outer shelf water from 39° to 49°S (Fig. 1). The western limit for high concentrations of *S. australis* on the shelf coincided with the 100 m isobath, even though a few specimens were found west of this boundary. The observed range for the species was wider than previously described for the area (Spoel, 1976; fig. 197; Spoel & Heyman, 1983: fig. 120). According to the observed pattern, *S. australis* is not only oceanic but also a neritic tolerant species.

The other genus present in the studied area, *Clione*, occurs in both Arctic and Antarctic waters and it is commonly encountered in subpolar regions. This genus was described on the basis of specimens from the northern hemisphere. Some authors have considered that the southern and the northern populations belong to the same species, *Clione limacina* (Phipps, 1774), and that the southern population is a variety, form or subspecies. The latest review supporting this position is that of Spoel (1976), who mentioned it as *C. limacina* (Phipps, 1774) *antarctica* (Smith, 1902). Others considered that they belong to a separate species (*C. antarctica* Smith, 1902); the latest review taking this position is that of Gilmer & Lalli (1990). Herein, the southern *Clione* are considered as a separate species.

Clione antarctica was present in water with surface temperatures ranging from 2.3°C to 15.2°C, and with surface salinities from 33.12 to 35.43. These intervals include antarctic, subantarctic and transitional water, and their

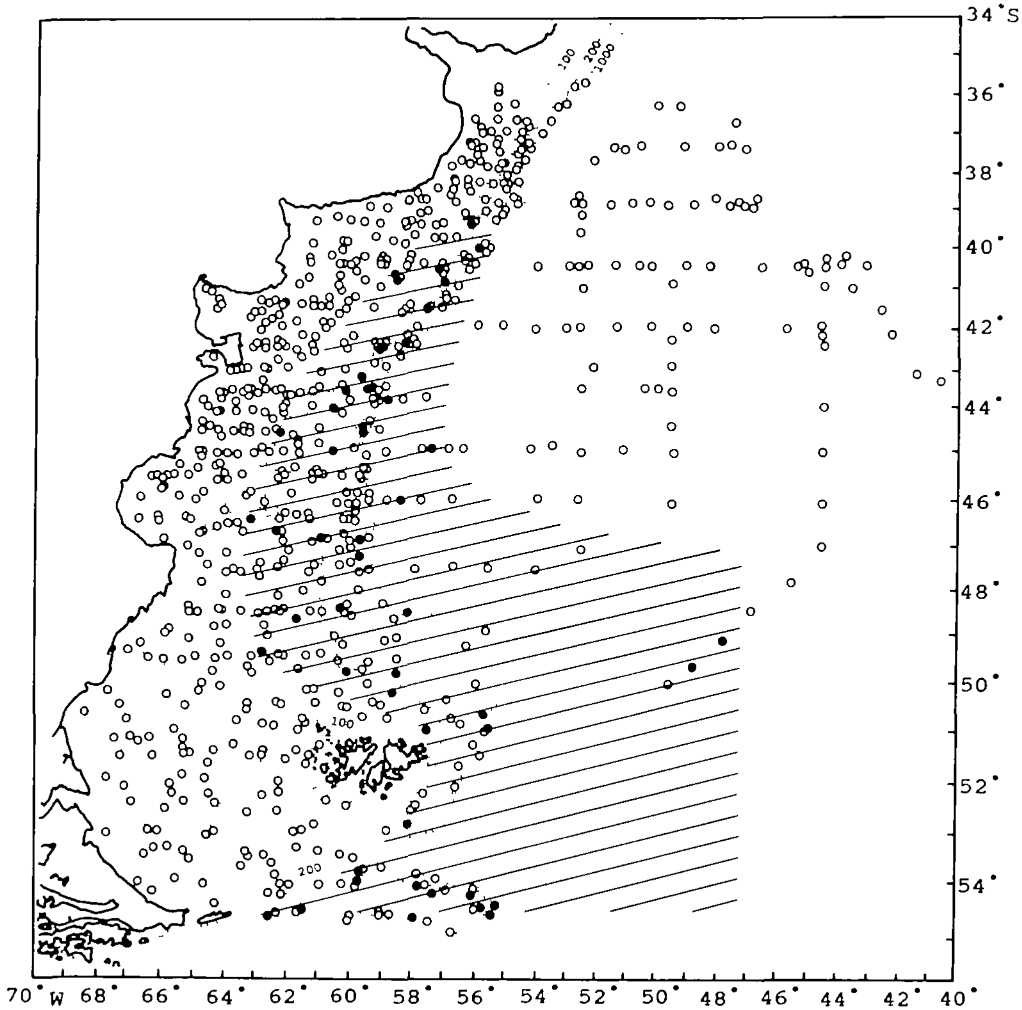


Figure 1. Geographical range of *Spongiobranchaea australis*. Symbols: ● = presence, ○ = absence.

extension is similar to the northern counterpart, *C. limacina* (Meisenheimer, 1905; Massy, 1920; Kramp, 1961). Laboratory experiments (Conover & Lalli, 1972) suggest that the feeding rate of *C. limacina* declines above 17°C. This temperature would be the upper limit of tolerance for this species, and, in fact, it is the maximum temperature recorded within its geographical range (Lalli & Gilmer, 1989). A similar mechanism may determine the distribution of *C. antarctica* in the southern hemisphere

Clione antarctica was more frequent in oceanic water, even though the maximum density (230 ind. per 1000 m^3) was registered in shelf water (45°31′S–61°31′W), in association with a swarm of *Limacina helicina*. This peak density is near the maxima mentioned in other southern areas: < 149 ind./1000 m^3 in the Weddell Sea (Boyssen-Ennen, 1987); < 60 ind./1000 m^3 near the South Sandwich Islands (Ramírez & Viñas, 1983).

The geographic range of *Clione antarctica* in the studied area (Fig. 2) was also wider than previously reported (Spoel, 1976: fig. 221; Spoel & Heyman, 1983: fig. 134). It is transported northward by the Malvinas Current and was recorded in slope water up to 35°45′S (fig. 4). In the Brazil—Malvinas Convergence, it was found as far as 41°12′S, associated at that point with transitional water. *C. antarctica* is also not only oceanic but a neritic tolerant

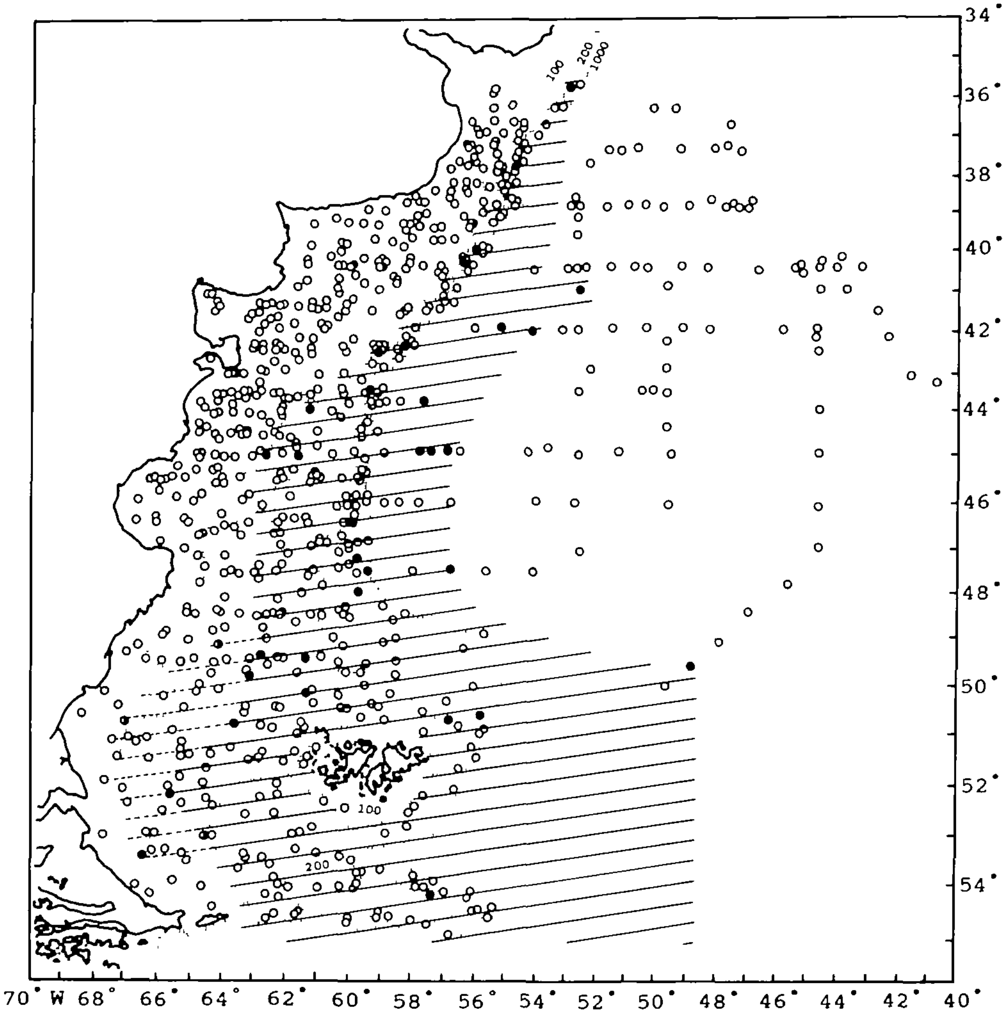


Figure 2. Geographical range of *Clione antarctica.* Symbols: ● = presence, ○ = absence.

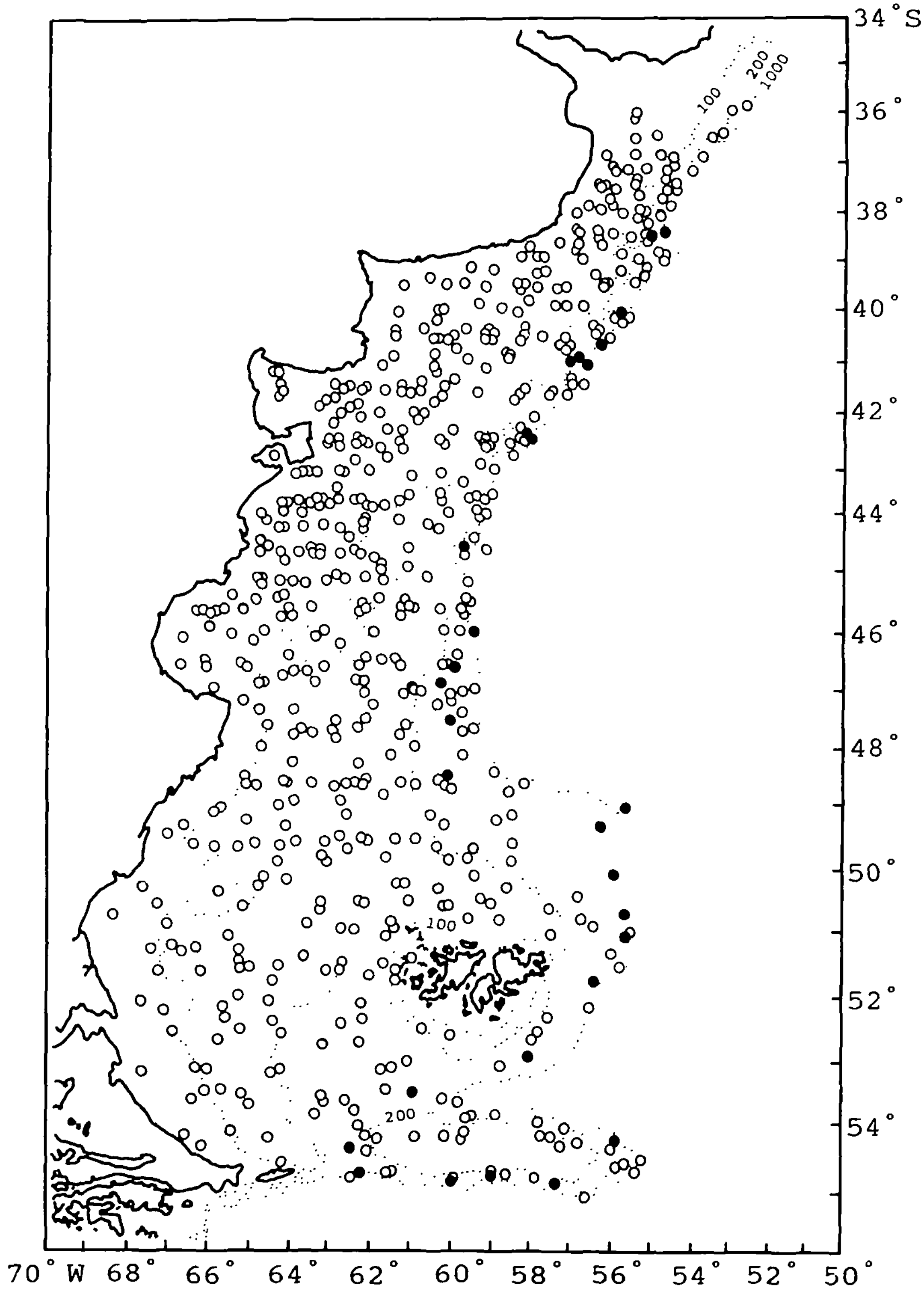
species. In the neritic area, it occurred between 42°–52°S; the western boundary of the range generally following the 100 m isobath, although exceptionally it reaches the 80 m isobath.

Feeding of Spongiobranchaea australis

The gymnosomes are highly specialized carnivores that feed on thecosomatous pteropods. Even though Pruvot-Fol (1924, 1954) suggested that some gymnosomes feed on zooplankton other than thecosomes, these reports have never been verified with living animals (Lalli & Gilmer, 1989). Present evidence suggests that most gymnosome species feed exclusively on one genus of thecosomes, with the diverse feeding structures of this group being adapted to the capture and extraction of specific shelled pteropods.

Manteufel (1937, in Spoel, 1976) established the strong correlation between the gymnosomes and the distribution of their prey, as a consequence of their food specificity. According to feeding experiments and analysis of gut contents, the thecosome *Clio* is the only known prey of *Spongiobranchaea australis* (Lalli, 1974;

Figure 3. Records of *Clio antarctica* in the South West Atlantic. Symbols: ● = presence, ○ = absence.


34°S
36°
38°
40°
42°
44°
46°
48°
50°
52°
54°
70° W
68°
66°
64°
62°
60°
58°
56°
54°
52°
50°
100
200
1000
100
200

Lalli & Gilmer, 1989). The only species of *Clio* present in the studied area is *C. antarctica* Dall, 1908.

In the analyzed collections, *Clio antarctica* occurred in only 17% of the samples taken in slope water. It was found usually in low densities (< 50 per 1000 m^3; exceptionally 120 per 1000 m^3, at 46°30'S, 60°09'W) (Dadon, 1989). Most of the specimens were embryonic and very small. According to Chen (1968), *C. antarctica* is exclusively oceanic and it seems to be restricted to subantarctic intermediate water between 200 and 800 m depth. Since the maximum sampling depth in slope water was only 100 m in the analyzed collections (see Materials and Methods), the presence of more developed specimens in deeper water cannot be ruled out.

Clio antarctica was absent in the analyzed samples taken in continental shelf water (Fig. 3), even when the water column was thoroughly sampled (see Materials and Methods). In fact, *C. antarctica* was never found in shelf water off Argentina (Dadon, 1989), where *Spongiobranchaea australis* was present.

Consequently, since the range of *Spongiobranchaea australis* extends beyond the range of *Clio*, the question arises about the feeding (and, consequently, the support) of *S. australis* in shelf water.

Analysis of alimentary tracts was performed to obtain data about the feeding of *Spongiobranchaea australis*. Only 31 well preserved specimens were found in the samples taken in shelf water. The body length of the specimens ranged from 0.5 mm to 15 mm. No remains of thecosomes from any of the alimentary tracts could be identified. This suggests that *S. australis* does not feed in shelf water. In fact, a similar situation was mentioned by Menteufel (1937, according to Spoel, 1976) for Arctic *Clione limacina*: the abundance of this species decreases as a result of the abrupt disappearance of the food species *Limacina helicina*. If this applies to *S. australis*, the presence of this species in the continental shelf would be only occasional and inevitably during a short period.

Another possibility should be considered. The absence of remains of thecosomes in the alimentary tract of the analyzed specimens is not in itself sufficient to discard an alternative prey species hypothesis.

At least one example has been recorded concerning gymnosomes feeding on more than one genus of prey. Feeding behaviour of the gymnosome *Pneumodermopsis paucidens* under laboratory and natural conditions differs considerably. In the laboratory, this species feeds on *Creseis* after a precise manipulation of the prey (Sentz-Braconnot, 1965). But in the North Atlantic, *P. paucidens* extends further north than any species of *Creseis* (Spoel, 1967, 1976) and has been reported feeding on *Limacina* (Spoel, 1976) and *Diacria* (Gilmer, unpubl. obs., in Lalli & Gilmer, 1989).

A similar pattern could occur in *Spongiobranchaea australis*; furthermore, taking in consideration that the range of the gymnosome extends farther west than that of *Clio*, this strongly suggests that *S. australis* may feed on other thecosomes.

Two thecosomes other than *Clio antarctica* are present in the studied area: *Limacina retroversa* (Fleming, 1823) and *L. helicina* (Phipps, 1774). *Limacina retroversa* is a subantarctic species. Even though it is an oceanic species, it can tolerate neritic conditions. In the Argentine Sea, *L. retroversa* was found in high numbers (see below) in slope water and in outer shelf water (Dadon, 1990). The western limit for massive occurrence of *L. retroversa* on the shelf coincided with the 100 m isobath to the south of 41°S (Dadon, op. cit.).

Limacina helicina has been reported from Antarctica to the Subtropical Front. Its distribution area in the Argentine Sea is similar to that of *L. retroversa*, but *L. helicina* is less abundant (Dadon, 1989).

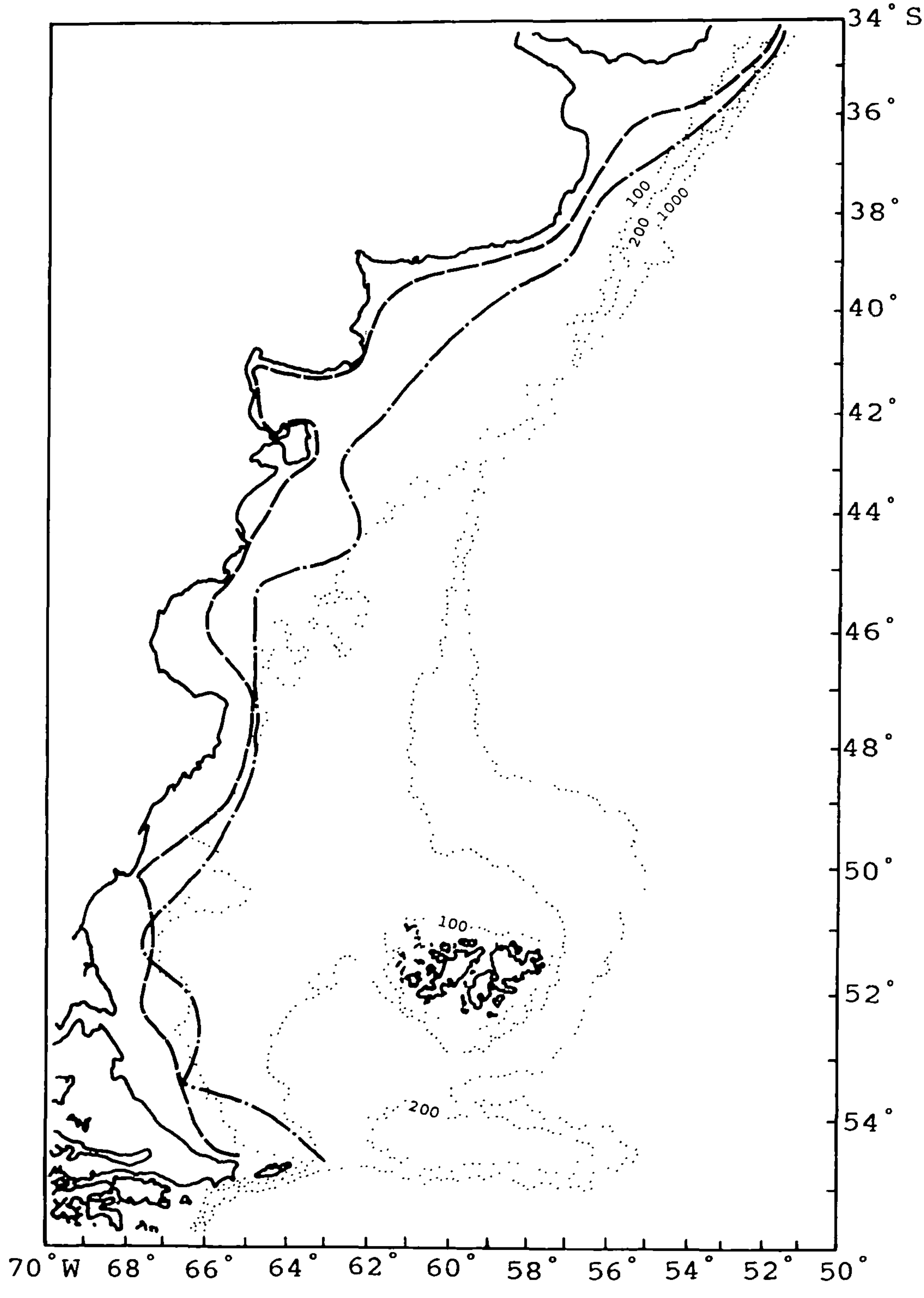
The geographic ranges of *Limacina helicina* and *L. retroversa* in the Argentine Sea overlap and extend beyond the range of *Spongiobranchaea australis* (Fig. 4). In the analyzed collections, *L. retroversa* was present in 91% of the stations where *S. australis* occurred, and *L. helicina* in 56%. These comparisons suggest that *L. retroversa* and/or *L. helicina* may be potential prey of *S. australis*.

Even when the available data are not enough to reject the starvation hypothesis or the alternative feeding hypothesis, either of these two alternatives modify our previous knowledge about *Spongiobranchaea australis*.

Seasonal variations in abundance, April 1978–April 1979

The Argentine continental shelf is broad, with a gradual slope. The slope zone is dominated

Figure 4. Western limit of the geographical range of *Limacina retroversa* (western line) and *L. helicina* (eastern line) in shelf water.


34° S
36°
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52°
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70° W
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66°
64°
62°
60°
58°
56°
54°
52°
50°

by the subantarctic water of the Malvinas Current, the core of which runs close to the 200 m isobath. The slope water is faster, colder and has higher nutrient concentrations than the shelf water. Because of the environmental differences, the production cycle is different in both zones. Slope water shows high biological production and little seasonality along the annual cycle. In contrast, a marked seasonality pattern is observed in shelf water. A pulse of high primary production begins in the northern continental shelf in September and it displaces southward, reaching the southern extreme in November (Carreto, Negri & Benavides, 1981). A pulse of high zooplankton production follows the phytoplankton peak. During the 1978–1979 cycle, the highest zooplankton densities were registered in November (spring) in the northern zone (42–44°S) and in summer in the southern zone (51–53°S). A secondary peak of zooplankton was observed on the northern shelf during late summer, but it did not develop in the southern portion (Ciechomski & Sánchez, 1983).

The abundance of gymnosomes also seems to be different in slope and neritic zones. *Spongiobranchaea australis* and *Clione antarctica* occurred in slope water throughout the 1978–1979 cycle, but in shelf water they were present only in November (*S. australis*), March (*C. antarctica*) and June (both species) (Fig. 5). Only the November peak coincided with the production maximum for zooplankton in the area.

The mean monthly densities of *Spongiobranchaea australis* and *Clione antarctica* were independent of each other in both the neritic and the slope areas (Spearman rank correlation coefficient r_s = 0.19 and 0.09, respectively; $P > 0.05$). Abundance of the two species and abundance of their prey (all possible combinations) were also independent ($-0.36 < r_s < 0.50$; $P > 0.05$). The swarms of gymnosomes were smaller and less dense than those of their

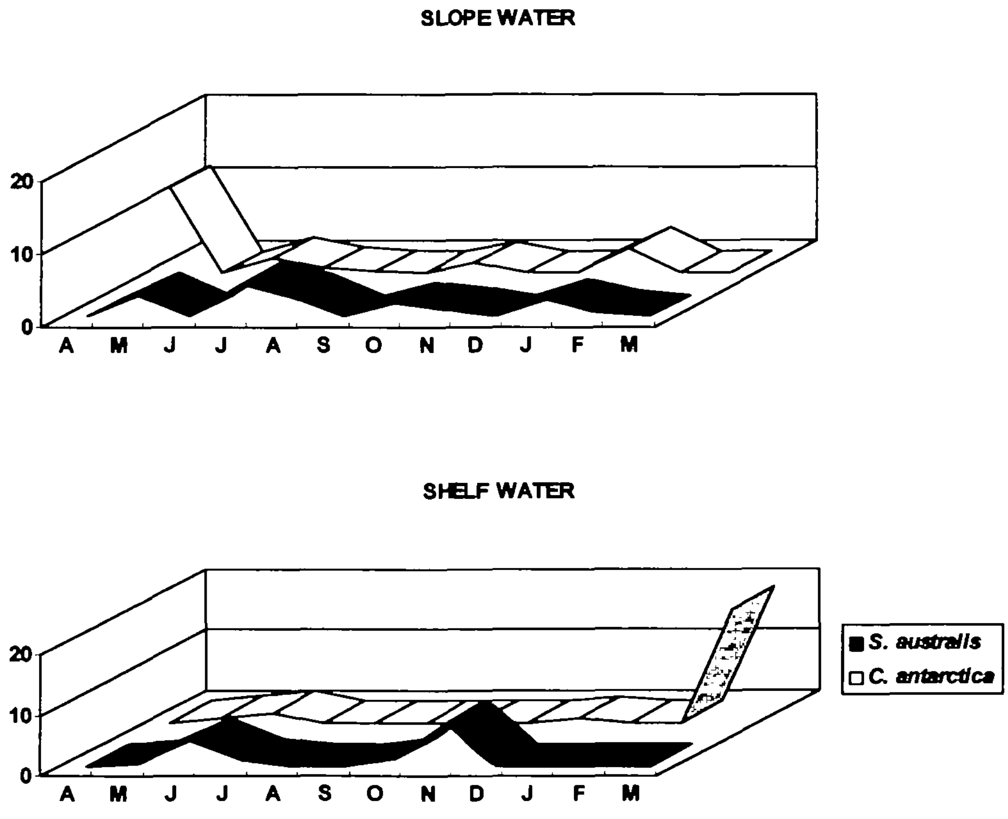

Figure 5. Mean monthly abundance (individuals/1,000 m^3) of gymnosomes in the studied area in shelf and slope water from April, 1978 to March 1979.

prey, in neritic as well as slope areas. For example, densities of *Limacina retroversa* higher than 1,000 ind./1,000 m^3 were recorded in slope water throughout the year (peaking at 67,000) and in shelf water from April to September, 1978; swarms of this species extending more than 31,000 km^2 were found (cf. Dadon, 1990, Fig. 2). Whereas swarms of *Limacina* remained for eleven months in shelf water of the same area (Dadon, op. cit.), the residence time of swarms of both gymnosomes were shorter than one month.

The abundance of the gymnosomes in the area followed neither the general cycle observed for total zooplankton nor the pattern of their prey. In addition, the abundance pattern of *Spongiobranchaea australis* differed from that *Clione antarctica* (Fig. 5).

Consequently, the abundance of *Spongiobranchaea australis* and *Clione antarctica* in the area depends on short term migration events more than on intrinsic population regulatory factors. The aggregates are rapidly repatriated northward and also penetrate the outer shelf water, but they remain there only during a short period and cannot preclude the final expatriation. A similar dynamic pattern was described for other zooplanktonic organisms in the area (i.e., Dadon, 1990).

It can be concluded that the presence of gymnosomes in the Argentine Sea depends on transport via the Malvinas Current. This current connects the basic area of the species' range (the Circumpolar Current) with the marginal areas of the range (the neritic zone and the Brazil—Malvinas Convergence), where the presence of gymnosomes cannot be maintained without a continuous input.

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