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Cnidaria from the Croker passage (Antarctic Peninsula) with a special focus on Siphonophorae

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Abstract Studies of "gelatinous" zooplankton are rather rare, and little is known about the biology and ecology of Antarctic Cnidaria, especially for siphonophores. More investigations are necessary for complementing the current information on the "gelatinous" zooplankton inhabiting this important but little know biogeographical region, especially because siphonophores very likely play a significant role in the Antarctic food chains. The species composition, abundance and vertical distribution of planktonic cnidarians in the Croker Passage were evaluated using the data obtained from three expeditions. Zooplankton were sampled with a double plankton net between 0 and 1,200 m water depth in both summer and winter seasons. In total, ten species of siphonophores and four species of medusae were identified. Siphonophore assemblages were dominated by *Dimophyes arctica*, *Pyrostephos vanhoeffeni*, and *Diphyes dispar*. *D. arctica* and *D. dispar* occurred in greatest numbers in summer, mainly in the upper mesopelagic zone. *P. vanhoeffeni*, a cryophilic species, occurred most abundantly in winter (in the lower mesopelagic zone), when they probably reproduce. Restricted circulation from the Bellingshausen Sea over the continental shelf into Croker Passage may exclude the deeper-living oceanic fauna from the area of investigation, as indicated by the low abundances of *Crystallophyes amygdalina*, *Muggiaea* sp., and *Heteropyramis* spp. Four species of medusae were identified. The highest abundance was noted for *Solmundella bitentaculata* and *Arctapodema* sp. These occurred most abundantly in the middle (January) and end (April) of summer.

Introduction

The seasonal biological processes, trophic dependencies, reproductive success, and, in effect, species abundance and biomass of plankton in the Southern Ocean, are largely under the control of powerful physical processes (Rakusa-Suszczewski 1999). The most significant of these include ice cover, low temperatures, and almost total darkness for several months annually. The Antarctic zooplankton is characterized by a relatively low number of species (Mackintosh 1934; Hardy and Gunther 1935; Voronina 1977), many of which have a circumpolar distribution (Mackintosh 1937; Baker 1954), and perform seasonal vertical migrations (Ommaney 1936; Mackintosh 1937; David 1958; Andrews 1966; Kane 1966; Timonin 1968; Voronina 1970, 1972; Voronina et al. 1978). Most publications on Antarctic zooplankton focus on Copepoda and Euphausiaceae, which are the main components of the assemblages. There is a serious lack of information on the so-called "gelatinous" zooplankton, which Pugh (1989) rightly referred to as the "forgotten fauna". It includes Hydromedusae, Siphonophorae, Scyphomedusae, Ctenophora, Heteropoda, Pteropoda, Thaliacea, Appendicularia, and rather rare meroplanktonic larvae (Hamner et al. 1975). These taxa cover two or three trophic levels (Hamner et al. 1975; Biggs 1977); however, their role in the vertical transfer of energy is still not entirely clear (Bruland and Silver 1981).

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In the Southern Ocean "gelatinous" macroplankton organisms exhibit a high level of species diversity and occur in relatively high abundances, but information on the range of occurrence and biomass mostly concerns Salpida, which are strong filter feeders that can compete with krill for food resources. Data on the number of individuals (medusae and ctenophores), the number of polygastric and eudoxid stages (for siphonophores from the suborder of Calycophorae), and the number of colonies (for siphonophores from the suborder of Physophorae) are comparatively rare (Pagès et al. 1996). Hydrozoa do not occur very abundantly in the waters of the Southern Ocean (Boysen-Ennen and Piatkowski 1988); however, Huntley and Hobson (1978), as well as Pugh (1974), reported that the predatory nature of medusae and siphonophores might result in reduced herbivore abundance, and, additionally, they might compete with fish for food resources, thus, significantly impacting zooplankton structure and dynamics (Pagès and Gili 1992). It has been also shown that many fishes feed on gelatinous zooplankton (Purcell and Arai 2001), although some fish species may depend heavily and be specialized to feed on gelatinous species, others utilize them only occasionally (Mianzan et al. 2001). There is also evidence that they affect the food web from microplankton (e.g., Colin et al. 2005) to whales (Purcell et al. in press cited in Purcell 2009) and as parts of the oceans become increasingly disturbed and overfished, energy that previously went into production of fishes may be switched over to the production of pelagic Cnidaria or Ctenophora (Mills 1995). Since jellyfish also feed on the eggs and larvae of commercially important food fish, outbreaks of jellyfish may ultimately impact on the fish biomass available to fisheries (Pauly et al. 2009). The mechanisms behind these increase in gelatinous populations are open to speculation but may include climate change (Brodeur et al. 1999; Atkinson et al. 2004; Lynam et al. 2004, 2005; Purcell and Decker 2005; Purcell 2005; Link and Ford 2006; Attrill et al. 2007), species introductions (Shiganova 1998; Mills 2001; Graham and Bayha 2007), eutrophication (Purcell et al. 1999; Arai 2001; Xian et al. 2005), removal of commercially important fish stocks (Parsons and Lalli 2002; Lynam et al. 2006), or some interaction of these factors (Purcell et al. 2007 cited in Brodeur et al. 2008).

The fauna of planktonic gelatinous carnivores of the Southern Ocean is incompletely documented (Bouillon et al. 2004), although medusae can be a conspicuous part of the Antarctic pelagic community (Larson and Harbison 1990). In the Antarctic Polar Frontal Zone in the South Georgia sector, in summer 1994, gelatinous carnivores, together with myctophid fish, were the most abundant nektonic organisms (Mills 2001). They may play an important role in the food chain of Antarctic waters (Pagès and Gili 1989) but knowledge of the ecology and physiology of these animals is still inadequate (Bidigare and Biggs 1980).

Materials and methods

Samples were collected in the vicinity of the Croker Passage (64°00′S and 61°50′W (± 50′)) during three American expeditions aboard M/S *Polar Duke* from December 1985 to February 1986, from February to April 1988, and from June to August 1989, respectively. Zooplankton organisms were collected with a prototype closed, double plankton net 27 × 35 inches in size (0.61 m^2 and 0.596 m^2 sampling surface), with a mesh size of 500 μm and 150 μm or 500 and 200 μm (or 250 μm) (Cnidaria sampled with a net of mesh size 500 μm and 250 μm were analyzed). The water flow rate through the nets was recorded with flowmeters. Two vertical sample series were collected during each sampling event, one during the day and one at night, from the following depths: 0–50 m, 50–100 m, 100–200 m, 200–400 m, 400–600 m, 600–1,000 m or 1,200 m.

The material collected was preserved immediately in a 4% solution of buffered formalin. Analysis of the resulting 68 samples was done in the laboratory and abundance of individuals expressed per 1,000 m^2 and 1,000 m^3. The temperature profile was determined with XBTs (Table 1).

Samples were analyzed for Cnidaria, with special emphasis placed on Siphonophorae. The specimens were identified following Totton (1965), Alvarino (1981), Pagès et al. (1992) and Pagès and Gili (1992). Individuals of the various species of Siphonophora were identified as polygastric (asexual), divided into upper and lower nectophore and eudoxid (sexual) stages, or the nectophores alone were taken into consideration. With eudoxid stages, whole individuals and gonophores were counted, since most of the eudoxids that occurred were incomplete (i.e., the gonophores were separated from the bracts). Because of this, during analysis the gonophores were usually taken into consideration as they were better preserved and the more characteristic element of the organism.

The material that was used for analysis was not in excellent condition, as it had also been preserved in formalin, which leads to deformations in organism shape after a certain time and 21.3% of medusa could not be identified. Additional studies conducted with much fresher biological

Table 1 Vertical temperature in different seasons in Croker Passage (after Żmijewska and Yen 1993)

Collection period	Surface water temperature [°C]	Temperature at 800 m [°C]
12. 12. 85	2	0,2
29–31. 01. 86	0,2	0,3
Mid 04.88	−0,4	−1
End 06. 89	−1,3	−1
Beginning 08. 89	−1,3	−1

material would permit identifying the animals with greater precision.

Results

Croker Passage is one of the main connections between the Gerlache and Bransfield straits (Hopkins 1985) and is delineated to the west by the Hoseason, Liege, and Brabant Islands and to the east by Christianid and Two Hummock Islands (Figure 1). At 1,200 m it is the deepest part of the western shore of the Antarctic Peninsula (Żmijewska and Yen 1993). Similar to Bransfield Strait, Croker Passage is under the influence of warmer waters with relatively low salinity from the Bellingshausen Sea and colder, more saline waters from the Weddell Sea (Gordon and Nowalin 1978). Depths not exceeding 500 m in the region of the Boyd and Bransfield Straits make it easier for mesopelagic waters from the open part of the Southern Ocean to flow into Croker Passage (Hopkins 1985). The limited circulation of the Bellingshausen Sea above the continental shelf is why there is not a well-developed zone of Circumpolar Deep Waters (Lancraft et al. 2004). The geographical location of the passage renders this area very calm, and studies can be conducted practically all year (Żmijewska and Bielecka 2000).

A specific isothermal temperature distribution occurs in this area, and was also observed by Hopkins (1985) (Fig. 2). The results obtained during sampling in 1985, 1986, and 1988 are also similar (Table 1).

The results of the studies indicated that over 90% of Cnidarians were Siphonophorae, while less than 10% were medusae, all of which belong to the order of Trachymedusae.
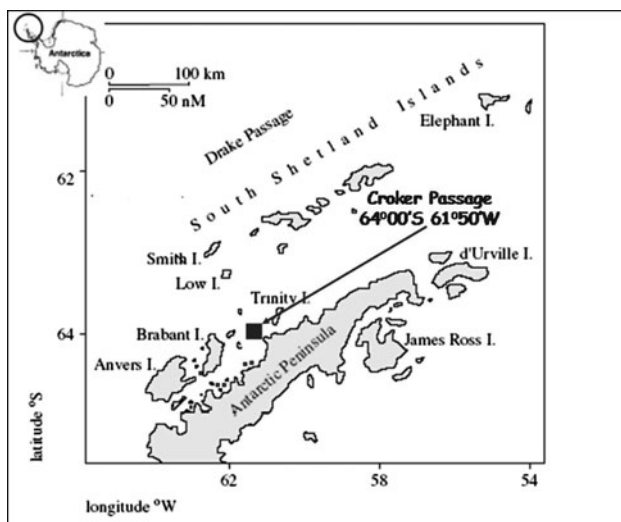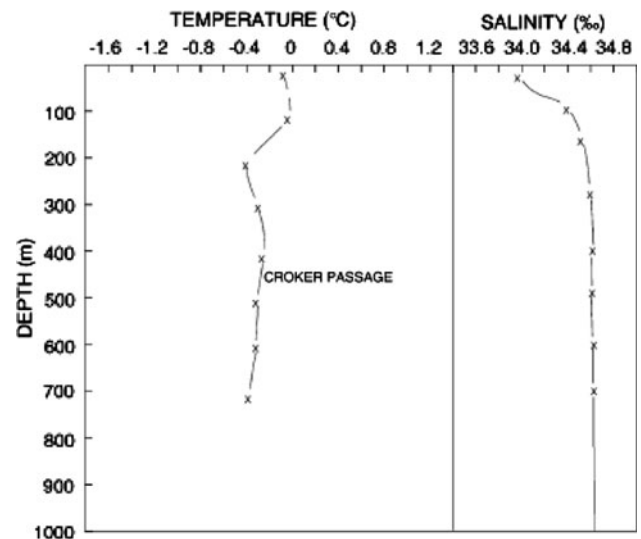

Fig. 2 Hydrographic data from the Croker Passage study area (Hopkins 1985). Note temperatures below 0°C at depths of 200 m and greater (after Lancraft et al. 2004)

Siphonophorae

Four genera and six species of siphonophores belonging to two subgenera were identified in the material: Calycophorae and Physonectae: *Halistemma* sp.*, *Pyrostephos vanhoeffeni*, *Vogtia serrata*, *Dimophyes arctica*, *Diphyes antarctica*, *D. dispar*, *Muggiaea* sp., *Clausophyes* spp., *Crystallophyes amygdalina*, *Heteropyramis* spp. (Fig. 3). Densities ranged from 0 to 6,680 indiv./1,000 m^2.

D. arctica was the dominant species throughout the study period, especially in December and January (about 1,500 indiv./1,000 m^2 in December 1985; about 1,000 indiv./1,000 m^2 in January 1985; Fig. 4, 5a). By April the abundance of this animal had decreased by over half, and by June and July it was at its minimum density (Fig. 5a). To a depth of 600 m, this species comprised in excess of 80% of all siphonophores, while in the 1,000–1,200 m zone *D. arctica* was essentially absent (Fig. 6). The highest abundance of individuals was noted at depths ranging from 100–400 m (>1,000 indiv./1,000 m^2), with the maximum density in the 200–400 m zone (about 1,300 indiv./1,000 m^2) (Fig. 7a). This value decreased systematically with increasing depth (Fig. 7a).

P. vanhoeffeni was a next (after *D. arctica*) dominant species numerically (Fig. 3). Its abundance ranged from 0 to 1,760 indiv./1,000 m^2. In summer, *P. vanhoeffeni* was practically absent, but at the end of summer the share of this taxon grew to about 30% (Fig. 4). Its maximum number was recorded in April (>200 indiv./1,000 m^2) (Fig. 5b). Maximum numbers were confirmed at depths of 800–1,000 m (mean >600 indiv./1,000 m^2) (Fig. 5b).

Fig. 1 Croker Passage—area of sample collections (*Filled square*)

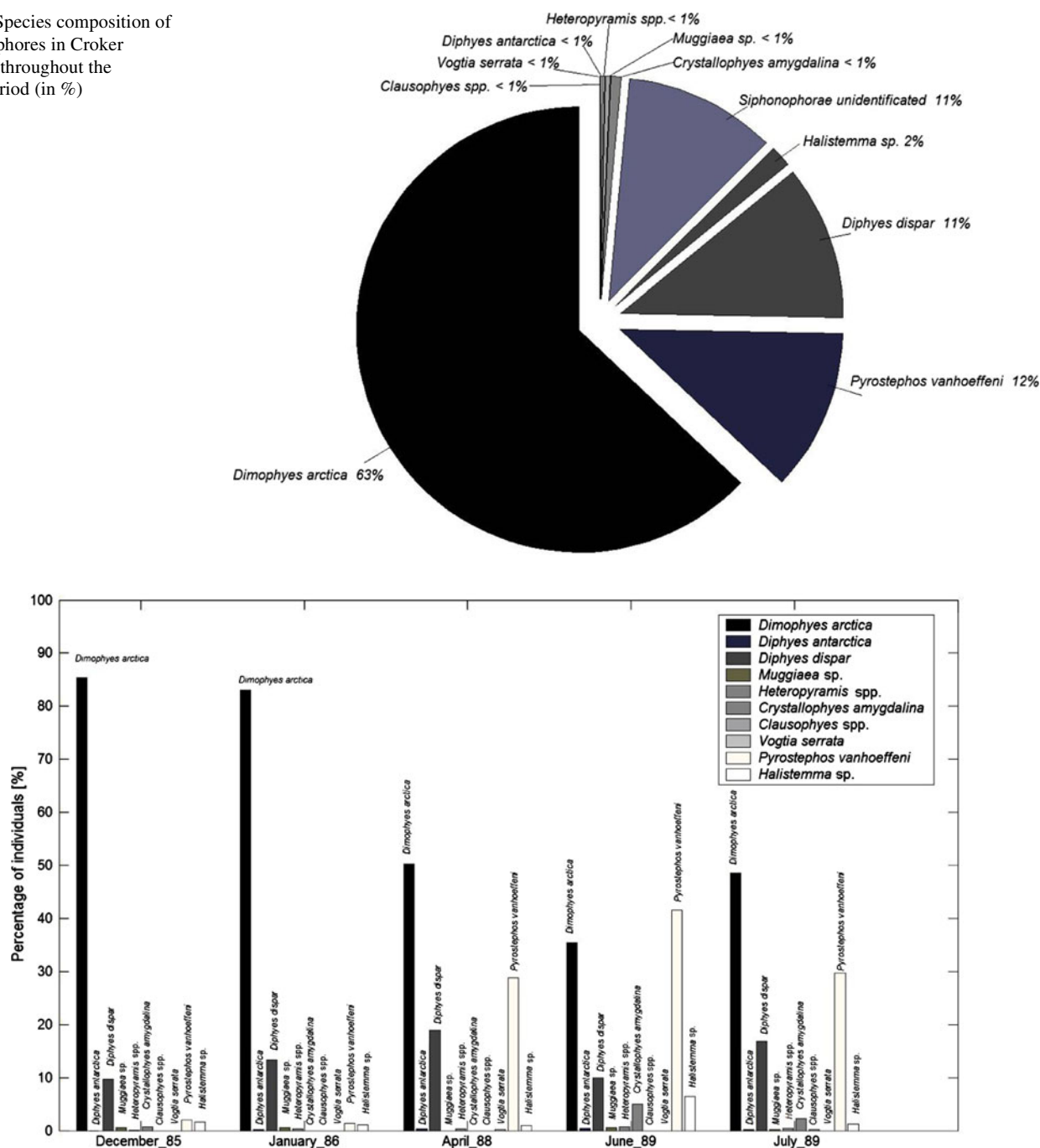**Fig. 3** Species composition of siphonophores in Croker Passage throughout the study period (in %)

Fig. 4 Seasonal variation in the share of siphonophores in Croker Passage throughout the study period (in %)

The analysis of the seasonal variation of *D. dispar* indicated that summer densities were higher (about 150 indiv./ 1,000 m²), than winter (Fig. 4). The greatest share of *D. dispar* was confirmed in the 1,000–1,200 m zone (Fig. 6).

Halistemma sp. comprised 1.58% of all the siphonophores (Fig. 3). Because of the low numbers of individuals in the samples, it was very difficult to analyze seasonal variation precisely. The analysis of the vertical distribution indicated that this taxon occurred in the 100–800 m zone

permanently, but in low numbers, while in the 800–1,000 m zone individuals from the genus *Halistemma* sp. comprised slightly less than 10% of all siphonophores (Fig. 6).

Species that accounted for less than 1% of all siphonophores included: *Heteropyramis* spp. (0.15%), *C. amygdalina* (0.63%), *Muggiaea* sp. (0.30%), *D. antarctica* (0.10%) (Fig. 3). *Clausophyes* spp. occurred only once. *C. amygdalina* was more abundant in the winter months (June, July), but this species was practically absent in the summer

Fig. 5 **a** Seasonal variation in the abundance of *Dimophyes arctica* in the Croker Passage (mean from day to night) (indiv./1,000 m²). **b** Seasonal variation in the abundance of *Pyrostephos vanhoeffeni* in the Croker Passage (mean from day to night) (indiv./1,000 m²)
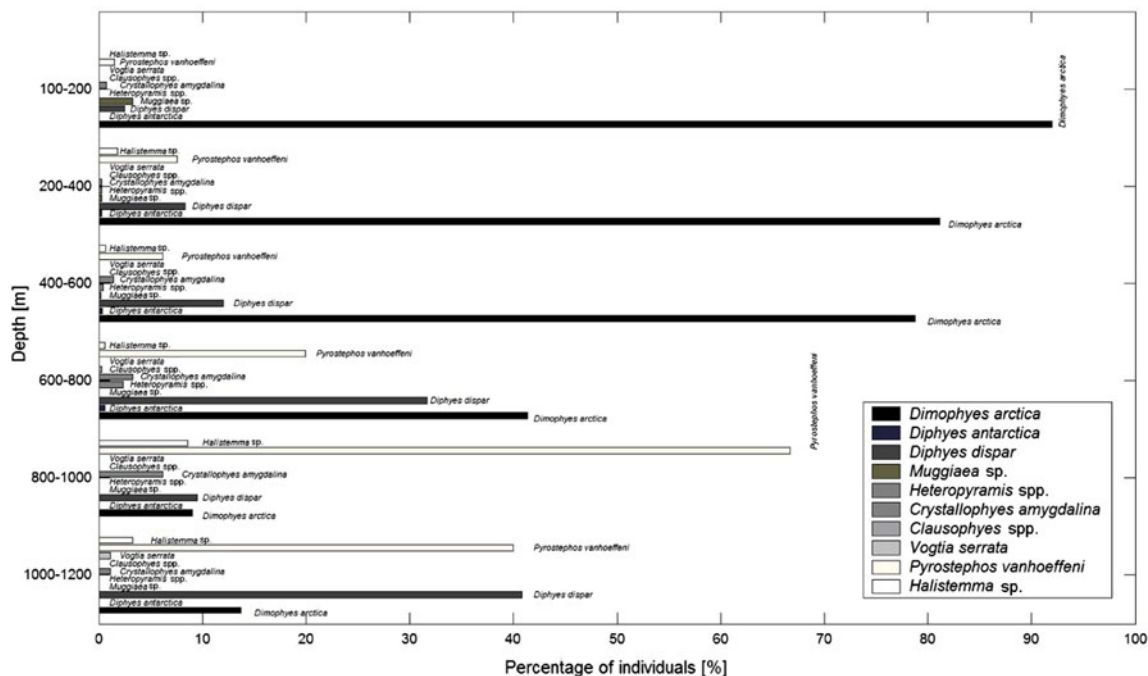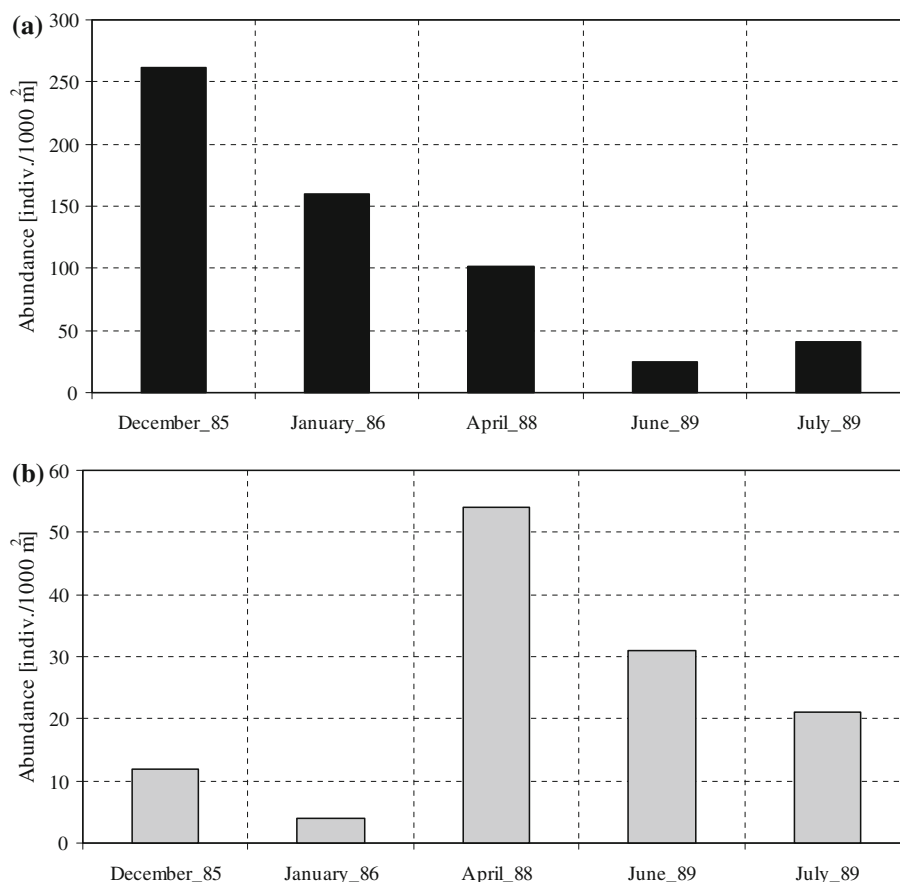

Fig. 6 Vertical distribution of siphonophores in Croker Passage throughout the study period (in %)

(Fig. 4). It occurred in the water column at depths of 400–1,200 m, with the highest share (about 5%) noted nearest the bottom (800–1,000 m) (Fig. 6). The abundance of *Heteropyramis* spp. was low throughout all of the months studied (Fig. 4). The analysis of the vertical distribution indicated a total absence of this species in the top 400 m
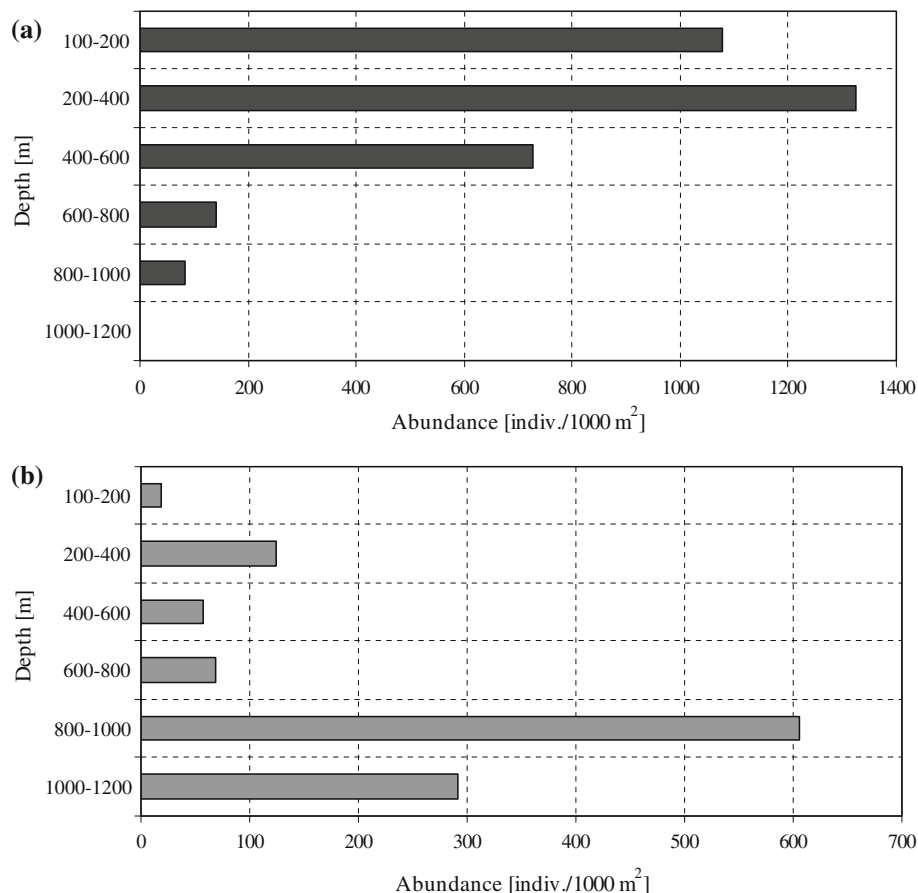
with largest share being found in the 600–800 m zone (Fig. 6). *Muggiaea* sp. was most visible in the summer months (December, January), although the numbers were insignificant (Fig. 4). The analysis of the vertical distribution indicated that this genus occurred mainly in the 100- to 200-m zone (Fig. 6).

D. antarctica and *Clausophyes* spp. occurred in such small numbers that a closer analysis (seasonal variation, depth preferences) was not possible.

Medusae

The density of medusae reached a maximum of 1,040 indiv./1,000 m². The qualitative analysis of the plankton material indicated the presence of four species, as follows: *Solmundella bitentaculata*, *Haliscera* sp., *Cunina* sp., and *Arctapodema* sp.

S. bitentaculata was the most abundant. From December through the months analyzed subsequently, the abundance of individuals increased systematically, and by April it reached the maximum (on average about 200 indiv./ 1,000 m²) (Fig. 8a). With the onset of winter in June a substantial drop in abundance was noted, and in July *S. bitentaculata* occurred very rarely. The vertical distribution was rather difficult to evaluate because small aggregations of

this species were identified in each of the zones analyzed; however, the highest quantity was noted at depths ranging from 1,000–1,200 m (mean of over 300 indiv./1,000 m²) (Fig. 9a).

Arctapodema sp. reached its highest mean density in January at over 150 indiv./1,000 m² (Fig. 8b). In the subsequent months, the number of individuals of this genus remained at a stable, but low, level (Fig. 8b). The analysis of the vertical distribution of *Arctapodema* sp. indicated that the greatest concentrations of individuals of this species (>100 indiv./1,000 m²) occurred in the 400–600 m level, while at other depths it was noted only in small quantities (Fig. 9b).

*Haliscera* sp. individuals were only noted at three stations at a maximum number near 10–20 indiv./1,000 m³.

A representative of the genus *Cunina* was confirmed just once.

Discussion

Although "Gelatinous" organisms are widely distributed in all oceans (Haeckel 1881; Totton 1965; Biggs 1977; Pagès and Kurbjeweit 1994), their taxonomic analysis still poses many problems. The fragile structure of the medusa body

Fig. 8 **a** Seasonal variation in the number of *Solmundella bitentaculata* in the Croker Passage (mean from day to night) (indiv./1,000 m^2). **b** Seasonal variation in the number of *Arctapodema sp.* in the Croker Passage (mean from day to night) (indiv./1,000 m^2)
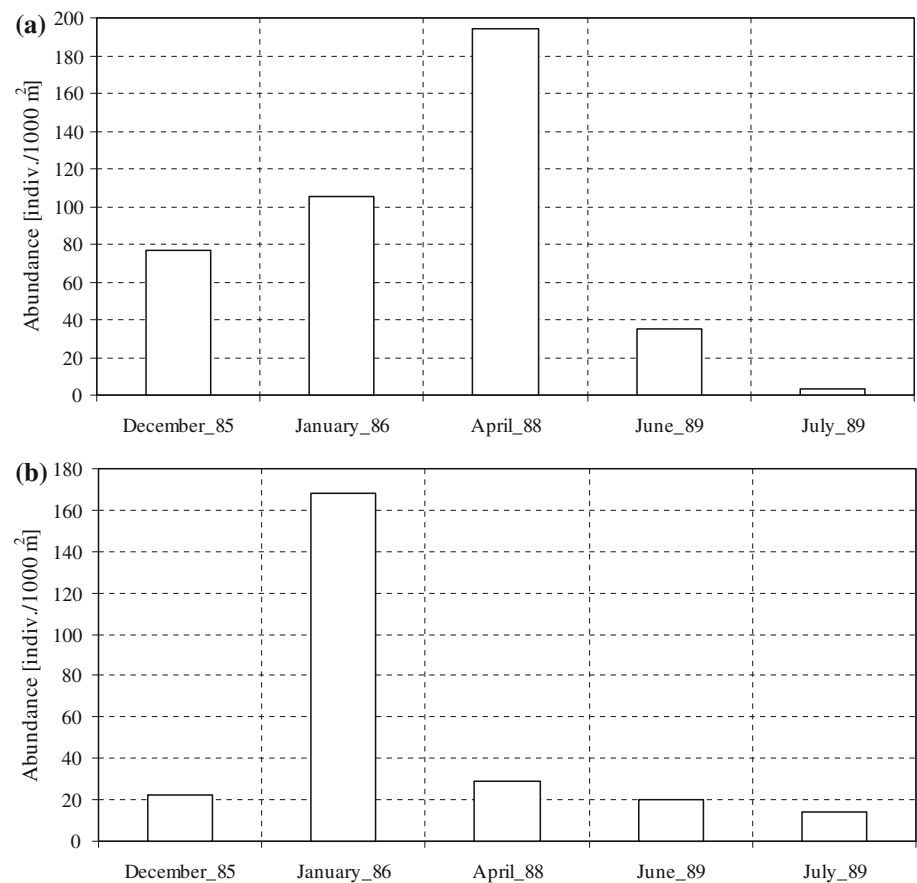
means that they frequently suffer mechanical damage in the nets, and only fragments of siphonophores are usually caught due to their typical colonial body plan and extreme fragility (Silguero and Robinson 2000). This has led to a huge deficit of information on the group as a whole including those from the Antarctic region.

Siphonophorae

Among Cnidaria, siphonophores were dominant in the Croker Passage, as Pugh et al. (1997) also reported it from the Weddell Sea. Mean abundances and depth distribution of the same siphonophoran and medusan species occurring in both the Weddell Sea (after Pagès and Kurbjeweit 1994) and the Croker Passage are shown in Table 2.

According to Haddock (2005), there are approximately 160 described species of siphonophore, but this is a biased sample that is skewed in favor of robust species found at shallow depths. Pugh (1999) suggests that currently there are about 175 known species from three orders (Cystonectae, Physonectae, and Calycophorae), while in the Antarctic in summer 46 species have been recorded (Alvarino et al. 1990). Publications that have appeared based on more precise studies refer mainly to the region of the Weddell Sea and its eastern parts (Pagès et al. 1994; Pagès and Schnack-

Schiel 1996; Pugh et al. 1997). It appears that studies conducted in other Antarctic regions, especially for the western parts, focus on species that are characteristic, those that are noted most frequently, and those that are most quantitatively significant, such as *D. arctica* and *D. antarctica* (Pagès and Gili 1992). Consequently, the current study is the first comprehensive study of siphonophores conducted in this region of the Antarctic. According to Lancraft et al. (1991, 2004), the Croker Passage species list is that of a modified open-ocean community mixed with nearshore species.

In Croker Passage, *D. arctica* was the most abundantly occurring species. According to a study by Witek et al. (1985), this was also the most abundant species in the Bransfield and Drake straits. Pagès et al. (1994) also found this species to be the most abundant in the Weddell Sea although densities in Croker Passage were high in comparison with other results from the Weddell Sea (Pagès and Kurbjeweit 1994; Pagès et al. 1994; Pugh et al. 1997; Boysen-Ennen and Piatkowski 1988).

D. arctica was dominant throughout the study period. High concentrations in the summer months were probably related to the reproduction of this organism at this time, and the success of which was certainly dependent on the quantity of food also occurring then. In the case of the suborder
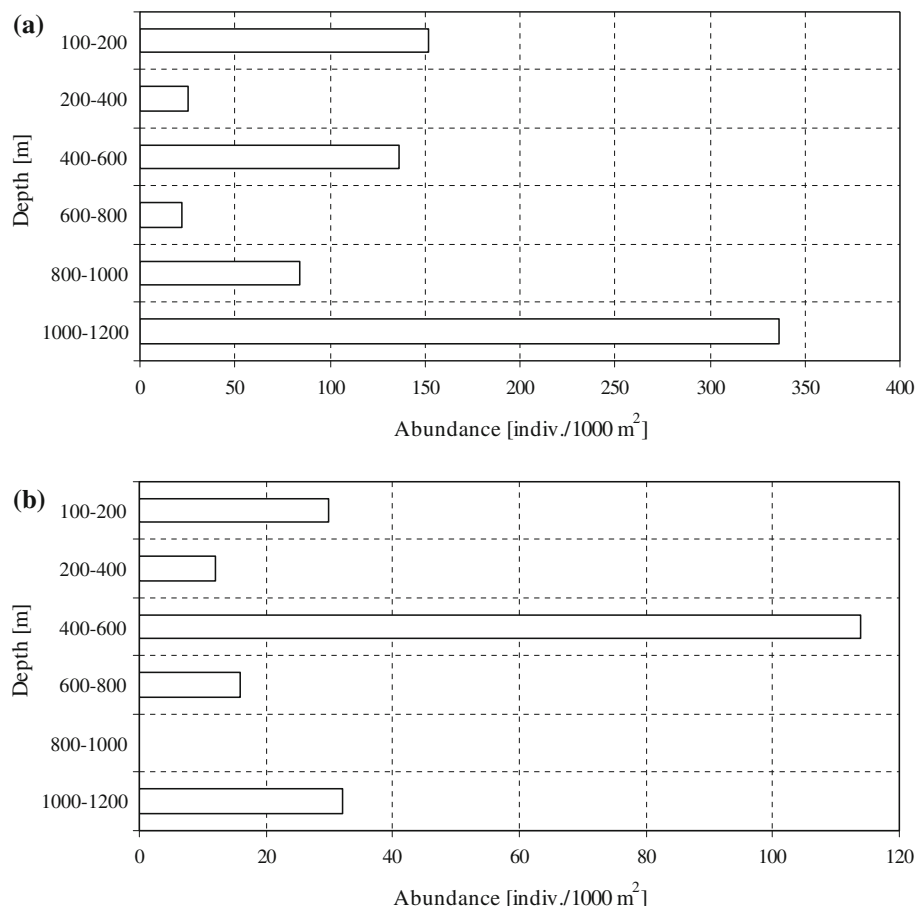
Calycophorae, to which *D. arctica* is classified, 66% of the diet is comprised of Copepoda (Purcell 1981). *D. arctica* is a cosmopolitan species with a bipolar range that occurs primarily in the epipelagic zone (Moser 1925; Leloup and Hentschel 1938; Kramp 1948; Hosia et al. 2008); however, in the Southern (Alvarino 1981) and Northern Atlantic it occurs abundantly in the meso- and bathypelagic zones (Kirkpatrick and Pugh 1984). In Croker Passage, the highest abundance of individuals occurred at depths of 100–400 m, with the maximum density in the 200–400 m zone. In the eastern Weddell Sea, *D.arctica* did not occur in the near surface cold water but was concentrated in and below the thermocline reaching highest abundance in the ASF, particularly in the vicinity of the slope (Pagès and Schnack-Schiel 1996). It can be concluded that, as in the Weddell Sea, this taxon is epi- and mesopelagic in Croker Passage.

The occurrence of *P. vanhoeffeni* in large quantities at the end of summer and the onset of winter is probably the result of two factors. Mackintosh (1934) suggested that this species is more tolerant of cold water. In the Weddell Sea, this species was mainly noted in the coastal zones (Boysen-Ennen and Piatkowski 1988). Because its highest abundance was confirmed in Croker Passage at the end of summer (April) and the beginning of winter, it can be

presumed that *P. vanhoeffeni* reproduces at the end of summer or at the beginning of winter. The highest share of *P. vanhoeffeni* was confirmed in two depth horizons: 800–1,000 m and 1,000–1,200 m. According to Pagès et al. (1994), this species has a wide range of occurrence in the water column, and individuals of it were also noted in Croker Passage throughout the depth spectrum analyzed. Boysen-Ennen and Piatkowski (1988) concluded that *P. vanhoeffeni* occurs to a depth of 300 m, with an abundance peak in the 200–300 m zone, although Pagès and Schnack-Schiel (1996) in the eastern Weddell Sea collected specimens only in the colder surface waters above the thermocline. However, Hopkins (1985) emphasized that it was also noted at depths of 1,000 m.

One species that certainly prefers higher temperatures than those prevailing in the waters of the Southern Ocean is *D. dispar*. It occurred in fairly high quantities in Croker Passage. This probably indicates that although it prefers higher temperatures, it also acclimates well to borderline low thermal conditions such as those prevailing in the waters of the Southern Ocean. According to Alvarino et al. (1990), this species is characteristic in Subantarctic waters in spring and in Antarctic waters in summer. The highest abundance noted was about 300 indiv./1,000 m², and

Table 2 Total number (*N*) of specimens and mean densities per 1,000 m³ (±SD) by depth interval in the Weddell Sea* (after Pagès and Kurbjeweit 1994) and in the Croker Passage, for each siphonophoran (*an* anterior nectophore, *b* bract, *e* eudoxid) and medusan species

Species	Weddell sea N	Croker passage N	Depth interval (m)						
			Weddell Sea 200–100 (n = 11)	Croker Passage 200–100 (n = 10)	Weddell sea 500–200 (n = 13)	Croker passage 400–200 (n = 12)	Weddell sea 1,000–500 (n = 9)	Croker passage 1,000–600 (n = 5)	1,000–800 (n = 5)
Pyrostephos vanhoeffeni (Moser 1925)	120	1,549	0	1,3 ± 2,4	0	28,5 ± 2,0	0	53,0 ± 96,8	81,2 ± 106,5
Vogtia (*Vogtia serrata** Moser 1925)	4	8	0	0	5,5 ± 12,5	0	0,7 ± 2,2	0	0
Diphyes antarctica (Moser 1925)	433	16	0 *an* / 8,1 ± 18,7 *e*	0	0,8 ± 3,1 *an* / 3,0 ± 5,7 *e*	1,0 ± 938,1 *n*	0	0	0
Dimophyes arctica (Chun 1897)	4,069	8,281	11,4 ± 154,5 *an* / 45,5 ± 58,7 *e*	68,9 ± 69,9 *n*	48,3 ± 31,3 *an* / 154,1 ± 223,2 *e*	419,2 ± 938,1 *n*	2,1 ± 6,4 *an* / 52,5 ± 23,5 *e*	202,2 ± 280,7 *n*	11,2 ± 14,8 *n*
Muggiaea (*Muggiaea bargmannae** Totton 1954)	15,420	48	515,2 ± 421,5 *n* / 9,8 ± 22,8 *e*	2,2 ± 3,2 *n*	329,9 ± 206,2 *n* / 231,5 ± 172,4 *e*	1,9 ± 2,9 *n*	58,5 ± 37,2 *n* / 184,6 ± 90,8 *e*	0	0
Heteropyramis (*Heteropyramis crystallina** Moser 1925)	1,465	24	0	0	2,5 ± 6,4 *n*	0,8 ± 5,7 *n*	65,6 ± 13,4 *n* / 93,6 ± 20,5	0	0
Crystallophyes amygdalina (Moser 1925)	439	99	0	0,7 ± 2,2 *n*	6,5 ± 11,1 *an*	0,8 ± 2,9 *n*	20,5 ± 13,3 *an*	0	8,2 ± 16,1 *n*
Solmundella bitentaculata (Quoy and Gaimard 1833)	905	931	29,5 ± 74,2	6,4 ± 16,6	19,3 ± 25,7	9,7 ± 19,6	6,58 ± 11,1	33,8 ± 38,9	81,2 ± 106,5
Arctapodema (*Arctapodema ampla** Vanhöffen 1902)	6,400	356	0	2,2 ± 6,9	244,5 ± 271,4	1,4 ± 2,8	357,6 ± 167,4	7,8 ± 14,3	0
Haliscera (*Haliscera conica** Vanhöffen 1902)	453	6	0	0	25,5 ± 39,9	0	13,2 ± 11,7	0	0

D. dispar was confirmed at depths of 1,000 to 1,200 m. Thus, it is characterized by an epipelagic range, but it can also occasionally occur in deeper zones (Pagès and Gili 1992). In the waters of the Antarctic it occurs in the epi-, mezo-, and bathypelagic zones (Alvarino et al. 1990; this study).

Halistemma sp. is another likely "resident' of Antarctic waters, but it is difficult to interpret our data since there are few results regarding this species in the literature. The species mentioned in the Antarctic is *Halistemma cupuliferum*, whose occurrence was confirmed in the mesopelagic waters off South Georgia (Alvarino et al. 1990). In the Antarctic, the species *Halistemma cupuliferum* was noted at depths from 0 to 1,000 m (Alvarino et al. 1990); however, the results obtained during the current study suggest that this species prefers the deeper parts of the water column as the highest share of this species (>10%) was noted in the 800–1,000 m zone.

Restricted circulation from the Bellingshausen Sea over the continental shelf into Croker Passage, as indicated by it's lack of a well-developed Upper Circumpolar Deep Water zone, a water mass typically in the Bellingshausen Sea and Bransfield Strait (Grelowski and Tokarczyk 1985), may exclude the deeper-living oceanic fauna from the Croker Passage (Lancraft et al. 2004) like *C. amygdalina*, *Muggiaea* sp., *Heteropyramis* spp., which were very rare in Croker Passage. *C. amygdalina* and *H. crystallina* in the eastern Weddell Sea occurred below 350 m at oceanic stations, in the warm Circumpolar Deep Water and their vertical distributions were strongly affected by the ASF near the slope where they were collected (Pagès and Schnack-Schiel 1996). Several publications (mainly Totton 1954) suggest that *C. amygdalina* is a species with a wide range of occurrence (cited in Pagès et al. 1994), but one that is, however, fairly rare. Pagès and Gili (1989) noted just five individuals during the "Magga Dan" expedition from Africa to the Antarctic, while Pagès and Schnack-Schiel (1996) reported the maximum presence of 66 indiv./1,000 m^3 in the Weddell Sea. The species *Heteropyramis* spp. comprised 0.17% of all siphonophores in the Croker Passage. In principle, there are two species, *Heteropyramis (Thalassophyes) crystallina* and *Heteropyramis maculata*, in the Southern Ocean. The first occurs the most abundantly, especially in the Weddell Sea (Pagès and Kurbjeweit 1994; Pagès et al. 1994; Pagès and Schnack-Schiel 1996; Pugh et al. 1997). The poor state of the biological material used in the current study combined with the very similar builds of these two species made it impossible to perform a precise taxonomic classification. The next species that occurs sporadically is *Muggiaea* sp. Most publications, primarily those referring to studies conducted in the Weddell Sea, mention the species *Muggiaea bargmannae*. Totton (1954) noted *Muggiaea bargmannae* in the Southern Hemisphere only as far as the Antarctic Convergence zone, while Stephanyants (1967) reported the occurrence of this species in the Northern Hemisphere in the Sea of Okhotsk and the Bering Sea. *Muggiaea bargmannae* is included to the typical oceanic fauna because, for example, in the Weddell Sea occurred at all oceanic stations and mainly in and just below the thermocline. Near the continental slope, both stages (sexual and asexual) were collected in low numbers (Pagès and Schnack-Schiel 1996).

D. antarctica made a very small contribution to the zooplankton of Croker Passage. The low abundance noted is not surprising in comparison to results obtained in Drake and Bransfield straits (Witek et al. 1985), Croker Passage (Hopkins 1985), or in the Weddell Sea (Boysen-Ennen and Piatkowski 1988), where its abundance was also low. It appears that although this species, along with *D. arctica*, is most frequently mentioned in publications, it is not of ecological significance in Croker Passage.

Vogtia serrata occurred just once. Hopkins and Torres (1988) confirmed that in the Weddell Sea this species only occurred in oceanic waters, while Pagès et al. (1994) reported that is has a wide range of occurrence that essentially includes all oceans, with the exception of that surrounding the Arctic. Other authors concluded that this is a cosmopolitan bathypelagic species (Moser 1925) that only inhabits deeper zones associated with the warm deep-water layer of the West Wind Drift (Boysen-Ennen and Piatkowski 1988). The results of studies suggest that in Croker Passage this species is a "guest" that drifts in occasionally along with moving water masses.

A similar situation was noted with regard to the genus *Clausophyes* spp. Pagès et al. (1994) and Pugh et al. (1997) identified the presence of three species, *Clausophyes moserae*, *Clausophyes galeata*, and *Clausophyes laetmata*, in the Weddell Sea. Pugh et al. (1997) determined the maximum abundance of *C. galatea* in the 1,610- to 1,800-m zone, while Pagès et al. (1994) reported that *C. moserae* usually occur at depths of 500–1,500 m in the North Atlantic. Thus, this species, similarly to *V. serrata*, might be linked to the warm deep-water layer of the West Wind Drift. This might rule out the presence of these animals in the studied region.

Medusae

The dominant medusa, *S. bitentaculata* is fairly widely distributed in Antarctic waters, as well as in tropical and boreal regions (Larson et al. 1989). High abundance was noted in the current study, while Hopkins (1985) noted lower abundance of this species in the Croker Passage, as did Pagès and Kurbjeweit (1994) in the Weddell Sea. Studies indicated that *S. bitentaculata* presumably reproduce in the second half of the summer. The share of *Arctapodema* sp. in Croker Passage was also substantial. In essence, two

species are mentioned from the Southern Ocean: *Arctapodema ampla* and *Arctapodema australis*. In quantitative terms, *Arctapodema* sp. does not occur as abundantly in Croker Passage as in the Weddell Sea, where Pagés and Kurbjeweit (1994) noted in excess of 960 indiv./1,000 m^3 of the species *A. ampla*. This species exhibited the highest mean density in the Croker Passage in January. This probably stems from the fact that this species probably reproduces in early summer. In the Croker Passage, *Arctapodema* sp. appears to be characteristic of the upper mesopelagic zone (400–600 m), which concurs to a certain extent with the results of Pagés and Kurbjeweit (1994), who reported the presence of *A. ampla* in the Weddell Sea in the 200–1,000 m zone, and also classified it as mesopelagic. The presence of *Haliscera* sp. was also noted in Croker Passage. *Haliscera conica* is one of the species that is commonly found in the Southern Ocean. Pugh et al. (1997) reported that it occurs mainly in the lower reaches of the epipelagic and upper mesopelagic zones. In Croker Passage it was noted in the lower part of the mesopelagic zone. The species *Cunina* sp. was noted just once, in one sample. It appears that *Cunina* sp. is very rare since Pagés et al. (1994) reported at most 1 indiv./10,000 m^3, and Pugh et al. (1997) noted a maximum of about 2 indiv./10,000 m^3 of *C. duplicata* in the Weddell Sea. The difference, however, is that, although noted in small quantities, this genus appeared at a fairly high frequency.

The Southern Ocean cannot be conceived of as a homogeneous ecosystem (Piatkowski 1989). Because of their position, the waters near the Antarctic Peninsula are influenced by many water masses and this impacts the composition and abundance of zooplankton. The general uniformity of important species in Croker Passage when compared with offshore regions and the notable differences in species composition support the contention that the Croker Passage area is a transition zone between oceanic mesopelagic and nearshore pelagic fauna (Lancraft et al. 2004).

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