



Vertical migration of Siphonophora (Cnidaria) and their productivity in the Croker Passage, the Antarctic

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Abstract: The population structure, seasonal and diel changes in vertical distribution of two siphonophore species, *Dimophyes arctica* and *Pyrostephos vanhoeffeni*, in Croker Passage (Antarctic Peninsula) are examined, and compared with the results obtained by other authors in various oceanic areas. Zooplankton samples were taken at discrete depth intervals between 0 and 1200 m during day and night shifts, in both summer and winter seasons. *Dimophyes arctica* was present both in polygastric and eudoxid forms, with the latter being dominant throughout the entire study period. The results obtained demonstrate that Antarctic waters clearly enhance the reproductive ability of this species when compared with specimens from other oceanic regions. Maximum densities of *Dimophyes arctica* were recorded in December in the 200–400 m depth horizon. However, high concentrations of eudoxids were also recorded at deeper parts of the water column. *Pyrostephos vanhoeffeni* was, in contrast, most abundant in autumn and winter, and both species were found to proliferate and disperse or sink further down the water column during autumn and winter. Daily vertical migration was observed only during the summer period.

Key words: Antarctic Peninsula, siphonophores, population structure, productivity.

Introduction

Studies on “gelatinous” zooplankton, particularly cnidarian siphonophores, have increased in recent years. However, our knowledge of the biology and ecology of these animals, particularly in the Antarctic region, is poor. Traditional net studies have often ignored siphonophores in favour of more robust invertebrates, like crustaceans. As a result, quantitative and qualitative data on the seasonal and daily changes in the siphonophore population abundances are quite scarce (Hosia and Bamstedt 2008).

Studies performed outside the Antarctic region show that the distribution of many siphonophore species in different horizontal layers may be related to changes

in light level (Barham 1963), temperature (Pagès and Schnack-Schiel 1996), oxygen (Robison *et al.* 1998), prey distribution (Pagès and Kurbjeweit 1994) or weather (Barham 1963). Furthermore, distribution can change seasonally (Silguero and Robison 2000) or on a diel basis (Pugh 1977, 1984). Few studies have yet been performed on the horizontal and vertical distribution of siphonophores in Antarctic waters. Knowledge of the life spans and reproductive capacity of siphonophores is also sparse, as is information on the effects of specific hydrological conditions of Antarctic waters on the life cycles of indigenous species.

Antarctic marine ecosystems are characterized by consistent low temperatures and a pronounced seasonal variation in light conditions, which is further exacerbated by winter ice cover (Clarke and Peck 1991). As a result, zooplankton is characterized by seasonality and a tendency to migrate horizontally (Żmijewska and Yen 1993). Large volumes of data on the behavior and structure of the Antarctic pelagic fauna concern mainly Copepoda and Euphausiacea. Almost nothing is known about the effects of environmental factors on the population diversity of Siphonophora and their ability to undergo vertical migration through the water column. In this study, two species of Siphonophora quite common in Antarctic waters were analysed: *Dimophyes arctica* (Chun, 1897), known to be cosmopolitan (Pagès and Orejas 1999, Stepanjants *et al.* 2006), and *Pyrostephos vanhoeffeni* (Moser, 1925), also noted to be present in the South Atlantic and in the Pacific Ocean (Pagès and Orejas 1999, Guerrero *et al.* 2013). The results obtained are compared with those found by other researchers in other parts of the world ocean.

Our study aims to describe the population structure, and seasonal and daily vertical migrations of these two siphonophores occurring in Croker Passage, as well as the probable factors influencing those elements of their biology. It is the first comprehensive research on this subject performed in Antarctic waters.

Materials and methods

Study area. — Croker Passage is one of the main connections between Gerlache and Bransfield Straits (Hopkins 1985). Its boundaries are defined to the west by Hoseason Island, Liege Island, and Brabant Island and to the east by the Christiania Islands and Two Hummock Island (Fig. 1). This area is the deepest (1200 m) basin along the western shore of the Antarctic Peninsula (Żmijewska and Yen 1993). Like Bransfield Strait, Croker Passage is under the influence of warmer and less saline waters from Bellingshausen Sea as well as colder, more saline waters from the Weddell Sea (Gordon and Nowlin 1978). Depths not exceeding 500 m in the region of 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). Circulation of Bellingshausen Sea above the continental shelf is limited, leading to a poorly developed zone of Circumpolar Deep Waters in

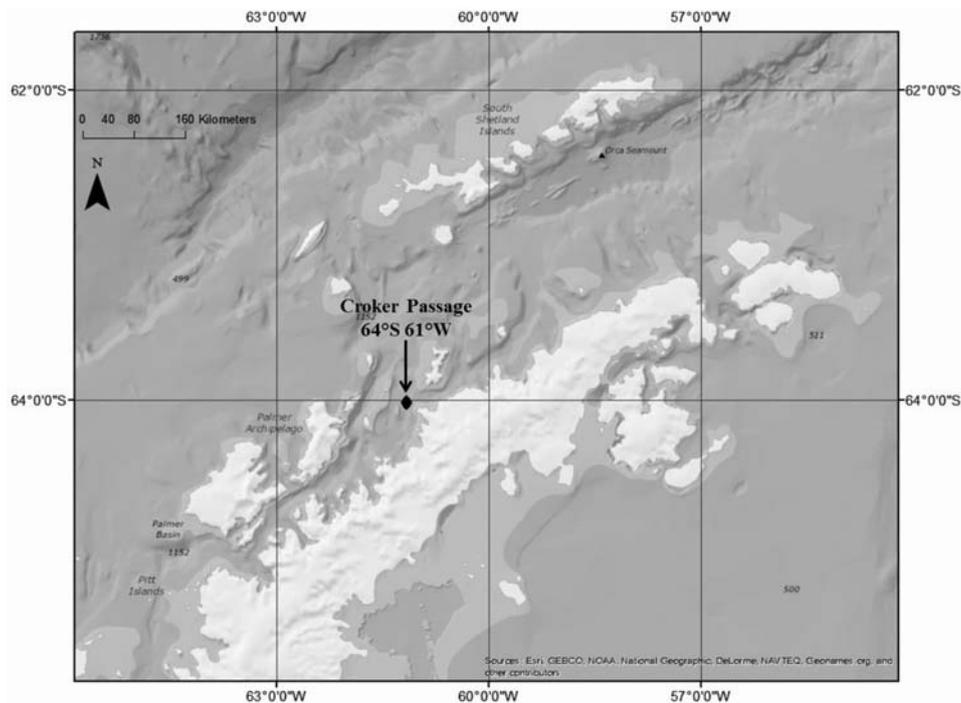


Fig. 1. Croker Passage – area of sample collections. Sources: ESRI, GEBCO, NOAA, National Geographic, DeLorme, NAVTEQ, Geonames.org, and other contributors.

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

Collection period	Surface water temperature [°C]	Temperature at 800 m [°C]
12 January 1985	2	0.2
29–31 January 1986	0.2	0.3
Mid February 1988	-0.4	-1
End of June 1989	-1.3	-1
Beginning of August 1989	-1.3	-1

this region (Lancraft *et al.* 2004). The geographical location of the passage makes this area very calm, and studies can be conducted practically all year round (Żmijewska and Yen 1993). The water column in Croker Passage is isothermal, as Hopkins (1985) also observed (Fig. 2). The temperature data obtained during sampling in 1985, 1986, and 1988 are also similar (Table 1).

Sampling methods. — Samples were collected in the Croker Passage (64°00' S and 61°50' W ($\pm 50'$)) (Fig. 1) during three American expeditions aboard the R/V *Polar Duke* from December 1985 to February 1986 and from June to August 1989.

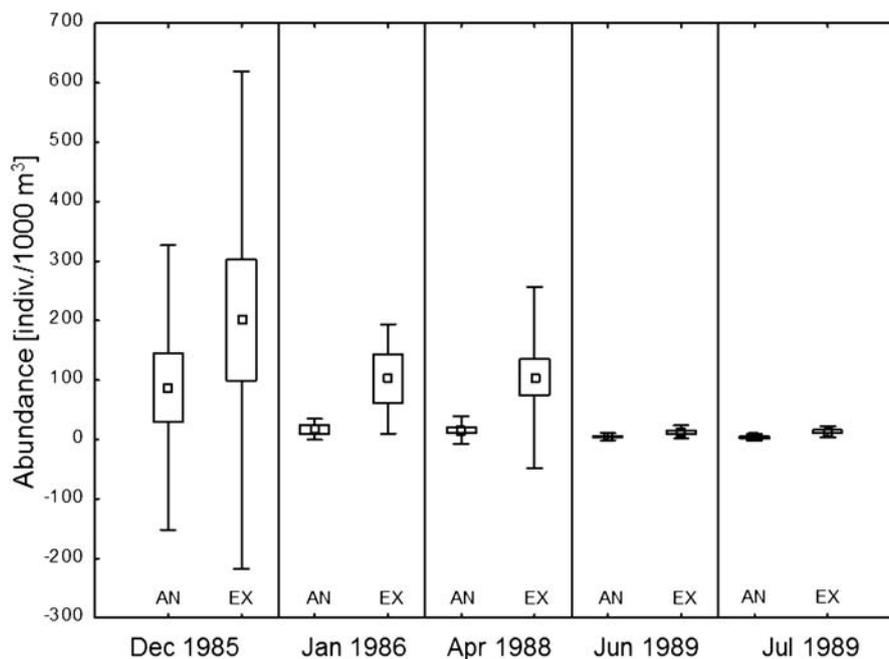


Fig. 2. Seasonal changes in the population abundance of *Dimophyes arctica* population in the Croker Passage (AN – anterior nectophores, EX – eudoxids).

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 $500 \mu\text{m}$ and $150 \mu\text{m}$ or $500 \mu\text{m}$ and $200 \mu\text{m}$. 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: 0–25 m, 25–50 m, 50–100 m, 100–200 m, 200–400 m, 400–600 m, 600–1000 m, 800–1000 m or 1200 m. The material was preserved immediately in a 4% solution of buffered formalin. Altogether, 68 samples were collected. Abundance of siphonophore individuals was expressed as mean numbers of individuals per 1000 m^3 . The temperature profile was determined with XBTs (Table 1).

Siphonophores were identified following Moser (1925) and Mapstone (2009). Individuals of various species were identified as polygastric (anterior nectophores –

Table 2
Seasonal changes in the population abundance of *Dimophyes arctica* population (mean densities with standard deviation) in the Croker Passage (AN – anterior nectophores, EX – eudoxids).

	December 1985	January 1986	April 1988	June 1989	July 1989
AN	87.41 ± 238.90	17 ± 17.78	15.46 ± 23.26	4.61 ± 5.71	3.54 ± 5.96
EX	200.82 ± 418.88	102 ± 91.93	104.71 ± 152.19	12.5 ± 10.89	13.09 ± 8.95

asexual) or eudoxid (sexual) stages, or the number of nectophores was noted. In this study, there were analysed the population structure and vertical distribution of two species which represent two suborders of siphonophores – Calycophorae and Physonectae. These are *Dimophyes arctica*, which was the dominant species, and *Pyrostephos vanhoeffeni*, a large physonect that breaks up so readily during capture with nets that the pneumatophore is almost always lost and the nectophores separated from the nectosome. Thus, nectophore numbers rather than pneumatophore numbers are used in this study, unlike in Hosia and Bamstedt (2007).

Results

Dimophyes arctica occurred during the entire study period in both polygastric (anterior nectophore) and eudoxid forms (either bracts alone, or bracts with a gonophore still attached). In the area of Croker Passage, the eudoxid was the dominant form. Quantitative analysis showed that *D. arctica* occurred most abundantly in December, with an average abundance of 87.41 indiv./1000 m³ for anterior nectophores and an average 200.82 indiv./1000 m³ for eudoxids (Fig. 2, Table 2). During Antarctic winter the population of this siphonophore was reduced to minute quantities, and the mean density of individuals did not exceed 4.61 anterior nectophores/1000 m³ and 13.09 eudoxids/1000 m³ (Fig. 2, Table 2).

The analysis of seasonal changes in the vertical distribution of this species showed that the core of the summer population occurred at depths from 200 to 1000 m (Fig. 3), with maximum densities in a layer 200–400 m deep. However, a visible difference in the preference of polygastric and eudoxid forms to occupy variable levels of the water columns was noted. Polygastric forms dominated shallow horizons of the water column in summer periods, with their maximal numbers of an average of 394 individuals per 1000 m³ at the 200–400 m horizon (a small concentration of polygastric forms were noted below this depth). Eudoxid forms, on the other hand, were noted in substantive amounts at lower depths (Fig. 3). In autumn and winter the *Dimophyes arctica* population was dispersed throughout the water column but they also displayed a tendency to occupy the deeper levels of the water columns (Fig. 3, Table 3). The maximal concentration of eudoxids (187.2 individuals per 1000 m³) was recorded at 600–1000 m in autumn. In the case of polygastrics, however, based on the present findings, one could only observe dispersed individuals along specific depth horizons (Fig. 3, Table 3). Both forms showed an increased depth of occurrence in the autumn/winter seasons, confirmed by weighted mean depth (WMD) indices, which in summer were 291.74 m for the polygastric form, and 347.35 m for the eudoxid form, while in the winter these values were 345.37 m for the polygastric form and 469.22 m for the eudoxid (Table 3).

In summer there was a marked difference in the vertical distribution of the *Dimophyes arctica* population (both anterior nectophores and eudoxids) be-

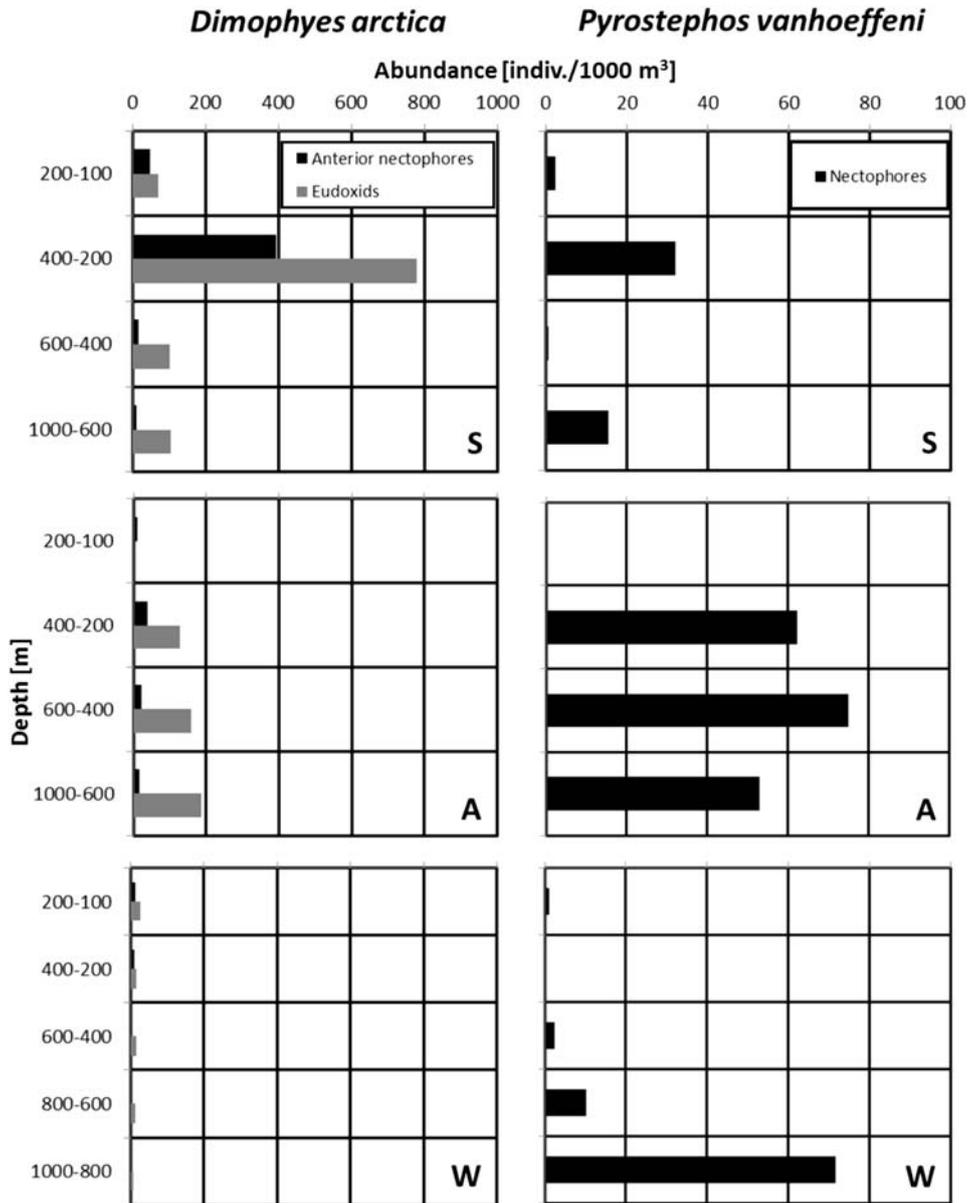


Fig. 3. Vertical distribution of *Dimophyes arctica* and *Pyrostephos vanhoeffeni* populations in the summer (S), autumn (A) and winter (W) seasons in the Croker Passage (mean densities).

tween day and night. The analysis showed that during summer days both forms appeared at depths from 25 m to 400 m, whereas at night the population dispersed to deeper layers, ranging from 100 m to 200 m, with the peak population figure at a depth of 200–400 m (Fig. 4, Table 4). During the autumn and winter

Table 3
 Seasonal changes in the distribution of *Dimophyes arctica* population in the water column (mean and standard deviation) and weighted mean depth (WMD) for its abundance (AN – anterior nectophores, EX – eudoxids).

Depth	AN	EX	Depth	AN	EX	Depth	AN	EX
[m]	[indiv./1000 m ³]		[m]	[indiv./1000 m ³]		[m]	[indiv./1000 m ³]	
Summer			Autumn			Winter		
200–100	48.50 ±38.23	71 ±43.34	200–100	10 ±14.14	0	200–100	11.33 ±8.50	27.67 ±13.58
400–200	394 ±528.28	778.33 ±843.11	400–200	37.25 ±26.25	128.25 ±96.57	400–200	10.4 ±3.85	15 ±3.74
600–400	16.5 ±21.81	102 ±88.41	600–400	21.8 ±28.93	158 ±168.62	600–400	3.5 ±0.71	16.5 ±3.54
1000–600	11.5 ±12.02	105.5 ±125.16	1000–600	14.40 ±28.40	187.2 ±253.33	800–600	0.28 ±0.76	12.43 ±8.88
–	–	–	–	–	–	1000–800	2.6 ±5.27	8.4 ±9.86
WMD [m]	291.74	347.35	WMD [m]	456.57	579.59	WMD [m]	345.37	469.22

Table 4
 Weighted mean depth (WMD) for the abundances in the water column of *Dimophyes arctica* and *Pyrostephos vanhoeffeni* populations in the summer, autumn and winter seasons (AN – anterior nectophores, EX – eudoxids, NE – nectophores).

WMD [m]	<i>Dimophyes arctica</i>				<i>Pyrostephos vanhoeffeni</i>	
	AN	EX	AN	EX	NE	
	Day		Night		Day	Night
	Summer				Summer	
	209.70	121.70	289.50	346.50	293.18	514.28
Autumn				Autumn		
	368.18	420.97	586.46	498.10	999.03	547.00
Winter				Winter		
	261.36	571.67	405.73	574.63	912.96	882.82

months this trend was not so strongly expressed (Fig. 4, Table 4), supposedly due to the fact that the population was more dispersed throughout the water column than during the summer, and displayed a tendency to inhabit deeper depths (Figs 3, 4, Table 4).

Pyrostephos vanhoeffeni occurred in small numbers during summer, and the density of nectophores did not exceed 32 nectophores in 1000 m³ (in a layer between 200 and 400 m) (Fig. 3, Table 5). This species was recorded much more frequently and in larger quantities in winter than in summer. The maximum density in winter reached 71.6 nectophores/1000 m³ between 800 and 1000 m (Fig. 3, Table 5).

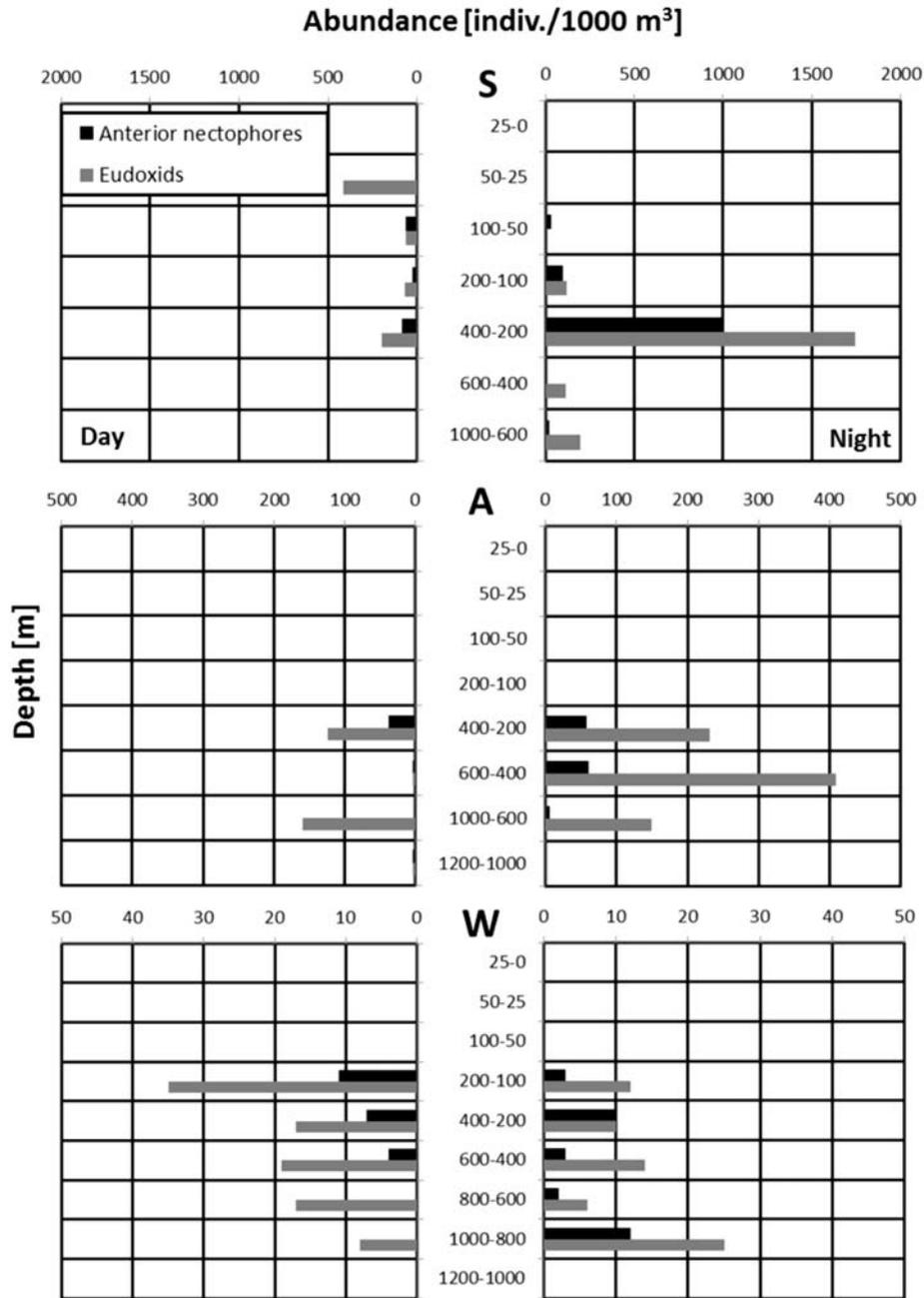


Fig. 4. Daily changes in vertical distribution of *Dimophyes arctica* in summer (S), autumn (A) and winter (W) seasons in the Croker Passage.

In Croker Passage *Pyrostephos vanhoeffeni* shows a general tendency to inhabit deeper parts of the water column. In Antarctic summer a peak abundance of

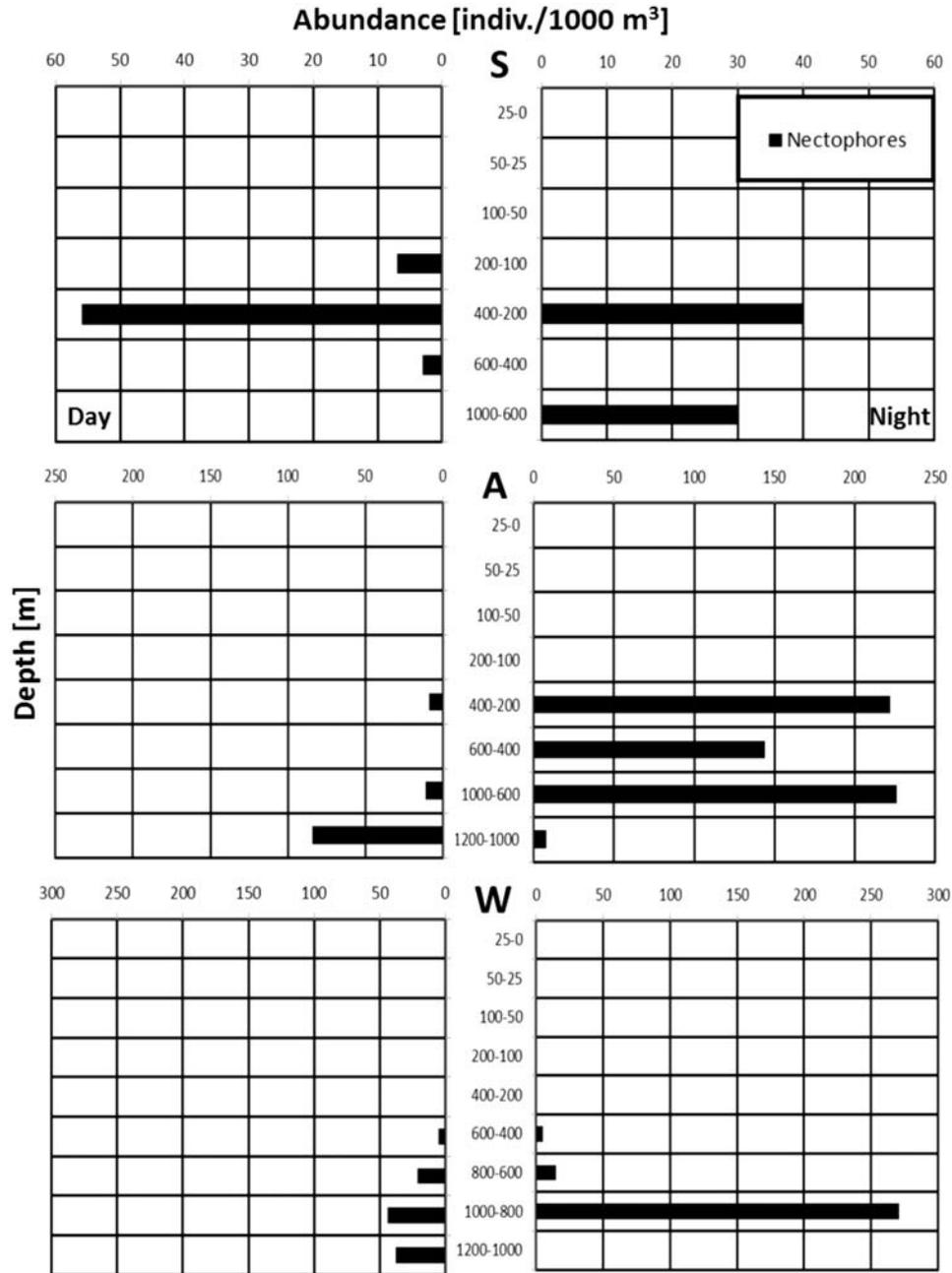


Fig. 5. Daily changes in vertical distribution of *Pyrostephos vanhoeffeni* populations in summer (S), autumn (A) and winter (W) seasons in the Croker Passage.

32 indiv./1000 m³ was recorded in the 200–400 m horizon, whereas in autumn/winter the population of this species reduced to a maximum density of 71.6

Table 5
 Seasonal changes in the distribution of *Pyrostephos vanhoeffeni* population in the water column (mean and standard deviation) and weighted mean depth (WMD) for its abundance (NE – nectophores).

Depth [m]	NE [indiv./1000 m ³]	Depth [m]	NE [indiv./1000 m ³]	Depth [m]	NE [indiv./1000 m ³]
Summer		Autumn		Winter	
200–100	2.5±3.32	200–100	0	200–100	1±1.73
400–200	32±28.84	400–200	62.25±106.75	400–200	0
600–400	0.75±1.5	600–400	75±105.60	600–400	2.5±3.54
1000–600	15.5±20.51	1000–600	53±96.80	800–600	10.14±8.07
–	–	–	–	1000–800	71.6±112.67
WMD [m]	401.39	WMD [m]	533.41	WMD [m]	857.78

indiv./1000 m³ between 800 and 1000 m (Fig. 3, Table 5). This is confirmed by the increase in WMD index from 401.39 m in summer to 533.41 m in autumn and 857.78 m in winter (Table 4). During the study this species was never observed migrating vertically on a daily basis (Fig. 5).

Discussion

Siphonophores have long been recognized as widespread inhabitants of the world's oceans (Pagès and Kurbjeweit 1994), but they are difficult to study as a group because of their great fragility and frequent damage during capture, particularly with plankton nets. Thus, quantitative data on seasonal siphonophore abundance in the literature are scarce (Hosia and Bamstedt 2008), particularly from the Antarctic region.

There are also few studies of diel vertical migration in siphonophores, due to various associated problems inherent in such studies. These have been well summarized by Mackie *et al.* (1987), and include depth intervals of samples too far apart to capture the small sinusoidal patterns exhibited by some species, among other difficulties. Thus, no diel migration has been reliably identified for the small calycofhoran *Dimophyes arctica* in any previously published studies, nor for the larger physonect *Pyrostephos vanhoeffeni*.

Siphonophores are predators, with a feeding ecology that varies depending on both mobility and body size (Purcell 1997). Most calycofhoran species feed on small copepods, while physonects prefer larger prey, including bigger crustaceans, such as krill (Purcell 1981). The size of the colony greatly influences the mobility of the siphonophores, and consequently its feeding strategy. Most large siphonophores are lie-and-wait predators (Silguero and Robison 2000).

Antarctica is a highly seasonal environment because of a pronounced annual cycle of solar radiation, and consequently heat and light penetrating into the sea

water (Murphy *et al.* 1936). This seasonal cycle controls the intensity of primary production and is probably the most significant biological factor affecting the heterotrophic pelagic community. In addition, seasonal and daily migration can play an important role for most zooplankton species, but for siphonophores such analyses are very rare and fragmentary. As a result, the present study is the first to include an analysis of seasonal and daily changes in vertical distribution for two species in the Antarctic region.

Dimophyes arctica strongly dominated the siphonophore assemblages in Croker Passage during all periods of the study, with highest densities recorded in the middle of the summer season. Predator abundance depends on prey resources, so the population of predators (like siphonophores) feeding primarily on herbivores would increase in the summer period accordingly (Clarke and Peck 1991). Production and maturation times of *Muggiaea atlantica* (Cunningham, 1893) eudoxids in the Mediterranean Sea were correlated with prey availability (Purcell 1982). Silguero and Robison (2000) speculated that in Monterey Bay the peak in the abundance of the polygastric stage of *Lensia conoidea* (Keferstein *et Ehlert*, 1860) and *Chuniphyes multidentata* (Lens *et van Riemsdijk*, 1908) recorded 6 weeks after the phytoplankton bloom, could be due to the increased food availability leading to liberation and maturation of eudoxids and the subsequent production of polygastric colonies. Favourable temperature and prey concentrations probably also contributed to the higher densities of *L. conoidea* and *D. arctica* eudoxid and polygastric forms observed during summer and autumn in Korsfjord (Hosia and Bamstedt 2008).

Results of our study and a literature survey of the population structure of *Dimophyes arctica* from different parts of the world's oceans exhibited few notable differences. Mapstone and Arai (1992) in the central Strait of Georgia (British Columbia) recorded 4810 anterior nectophores in 1000 m³, but only 40 eudoxids in 1000 m³. Hosia *et al.* (2008) in the Mid-Atlantic Ridge recorded a maximum of 212 polygastric and 259 eudoxid stage individuals in 1000 m³ over the period of one year (Table 6). Different results were also obtained by Palma *et al.* (2007) in the southern channels of Chile, by Hosia and Bamstedt (2008) in western Norwegian fjords, and by Boysen-Ennen and Piatkowski (1988), Alvarino *et al.* (1990), Pagès and Kurbjeweit (1994) and Toda *et al.* (2010) in the Southern Ocean (Table 6).

This difference in structure of the population of species under variable oceanic habitats (mainly in spring and summer periods) are initially the result of the water area's productivity followed by the difference in water temperature. For example, the average temperature in the Strait of Georgia oscillates between 7.5 and 12.5°C (Johannessen and McCarter 2010). Palma *et al.* (2007) and Hosia *et al.* (2008) also noted a temperature of above 10°C during summer in their research area. It would appear then, that a higher temperature meaningfully enhances growth in the overall population of *Dimophyes arctica*. Interestingly, the high productivity of Antarctic waters makes the production of eudoxids during Antarctic summer periods more effective than in other water regions. It also seems that Croker Passage may

Table 6
Abundances of *Dimophyes arctica* in different oceanic areas (AN – anterior nectophores, EX – eudoxids).

Study area	Study period	AN [indiv./1000 m ³]			EX [indiv./1000 m ³]			Reference
		Max. density	Mean max. density ± SD	Mean density ± SD	Max. density	Mean max. density ± SD	Mean density ± SD	
Arctic's Canada Basin	August–September 2003	Rare						Hopcroft <i>et al.</i> (2005)
Lancaster Sound and Western Baffin Bay (Arctic)	July–October 1978	Rare						Buchanan and Sekerak (1982)
Korsfjord (Western Norway)	2003	–	–	265.44	–	–	–	Hosia and Bamstedt (2007)
Fanafjord (Western Norway)		–	–	4.51	–	–	–	
Western Norwegian fjords	2003	–	~200 (May)	–	–	~700 (Sep.)	–	Hosia and Bamstedt (2008)
Mid-Atlantic Ridge (North Atlantic)	June–July 2004	212	–	15.42 ± 42.13	259	–	25.33 ± 53.38	Hosia <i>et al.</i> (2008)
Lützow-Holm Bay (Indian sector of the Southern Ocean)	January 2005	11.92	–	2.63 ± 3.64	–	–	–	Toda <i>et al.</i> (2010)
Lützow-Holm Bay (Indian sector of the Southern Ocean)	January 2006	2.25	–	0.29 ± 0.53	–	–	–	
Weddell Sea (Atlantic sector of the Southern Ocean)	November–December 1990	–	48.3 ± 31.3	–	–	154.1 ± 223.2	–	Pagès and Kurbjeweit (1994)
Weddell Sea (Atlantic sector of the Southern Ocean)	February–March 1983	–	–	85 ± 108	–	–	–	Boysen-Ennen and Piatkowski (1988)
Southern Ocean	December 1962–1969	~10000	–	–	–	–	–	Alvarino <i>et al.</i> (1990)
Southern channels of Chile	November 2003	–	–	13 ± 49	–	–	15 ± 44	Palma <i>et al.</i> (2007)

be a very productive region even for the Antarctic. Toda *et al.* (2010) in Lützow-Holm Bay found maximally 11.92 nectophores per 1000 m³ (Table 6). Boysen-Ennen and Piatkowski (1988) and Pagès and Kurbjeweit (1994) also recorded smaller abundances of individuals (both anterior nectophores and eudoxids) of *D. arctica* in the Weddell Sea (Table 6).

One can therefore duly assert that the most important factor limiting proliferation of *Dimophyes arctica* is not temperature but the availability of food. Copepods

constitute 66% of the Calycothorae diet (e.g. *D. arctica*) (Purcell 1981). As a result, at the beginning of the summer, *D. arctica* had enough food to carry out effective reproductive processes, which was confirmed in the high number of eudoxids observed at this time. The higher number of eudoxids may be also due to the fact that this developmental stage can probably live for a long time in the water column, if the food is available in large quantities.

Based on this result one can also suggest, that, though the species is considered typical of cold areas, its proliferation in warm water areas is in fact distinctively higher. Thus, it might be worth assuming that its evolution is not of polar origin. We could say that it is a cold-water siphonophore, because it occurs in much deeper water layers in the tropical and equatorial regions of all seas, unless it is brought up in upwelling as noted by Daniel (1985). More so, since *Dimophyes arctica* concentrations in the Arctic are not known to be high. Hopcroft *et al.* (2005) classified the species as extremely rare, and so did Buchanan and Sekerak (1982) (Table 6). A higher concentration of the species is more frequently observed in the Antarctic, which might be the direct result of an abundance of food in the ecosystem of this region which stimulates reproduction.

Dimophyes arctica probably migrates seasonally, because the summer peak of the population was in the 200–400 m layer, while in winter this species dispersed or moved to higher parts of the water column. This tendency was more obvious for eudoxid forms and may be somehow related to the so-called interzonal migrating copepods, which also move to deeper waters during the winter time. In the Weddell Sea, in the summer season, Pugh *et al.* (1997) noted that nectophores of *D. arctica* were most abundant in the 250–400 m depth range, whereas eudoxids predominated in the 100–400 m range. Toda *et al.* (2010) found a maximal abundance of nectophores in the 50–100 m depth range in Lützow-Holm Bay.

Daily changes in the vertical distribution of *Dimophyes arctica* were also quite evident but only in the summer time. Part of the population moves to the higher water layers during the night giving the impression of a reverse diel migration. This type of migration was observed by Pugh (1984) in the region off Fuerteventura (Canary Islands) for the *Vogtia serrata* (Moser, 1925). There was no note on daily migration of *D. arctica*, but Pugh (1984) did not observe this species in the cold waters.

Pyrostephos vanhoeffeni was the second most abundant siphonophore species in Croker Passage, with the largest number of records for this species in the same area in an earlier study (Panasiuk-Chodnicka and Żmijewska 2010). The highest abundance of nectophores was noted in the 800–1000 m horizon, at approximately 81.2 nectophores per 1000 m³ (Panasiuk-Chodnicka and Żmijewska 2010). This number is relatively low. Palma *et al.* (2007) noted an average of 547 nectophores/1000 m³ in the southern channels of Chile, whilst Guerrero *et al.* (2013) noted 310 nectophores/1000 m³ in San Matias Gulf (Patagonia). *P. vanhoeffeni* has been described as endemic to Antarctic and sub-Antarctic waters (Alvarino *et al.* 1990). In the opinion of Guerrero *et al.* (2013) this species may have a prefer-

ence for colder water with a high food availability. In San Matias Gulf maximum densities of this species were found during spring, when it occupied the main spawning area for hake (González *et al.* 2010). This siphonophore could be entering the Gulf with the colder and more nutrient rich sub-Antarctic water masses of the Patagonian Coastal Current (Gagliardini and Rivas 2004).

The highest abundance of *P. vanhoeffeni* occurred in winter. Compared with *Dimophyes arctica*, this species prefers rather deeper water, since a high concentration of nectophores in Croker Passage was noted at the depth of 1000 m. The WMD index rate rose to 857.78 m in winter periods (it was 401.39 m in summer), which suggests that the species undergoes seasonal migration. A lack of published data cannot support this observation. In the Strait of Georgia in the NE Pacific *Pyrostephos vanhoeffeni* is replaced by *Nanomia bijuga* (Delle Chiaje, 1844). In the central Strait of Georgia Mapstone and Arai (1992) recorded a maximum abundance of *Nanomia bijuga* in May, at 200 and 155 m, deeper than *D. arctica*. However, in spring individuals of *N. bijuga* were dispersed in the water column (Mapstone and Arai 1992). Studies conducted so far in western Norwegian fjords also confirm a relatively deep distribution of another physonect siphonophores such as colonies of *Nanomia cara* (Agassiz, 1865) (Gorsky *et al.* 2000, Hosia and Bamstedt 2008).

Antarctic physical properties are not comparable to other parts of the world ocean. Extremely low temperature is noted in the region but high primary production during the Antarctic summer may instigate a rise in the population of some species (e.g. *Dimophyes arctica*). On the other hand, hydrological conditions and distribution of specific water masses, including those connected with the West Wind Drift, may hamper the abundance and proliferation of other species (e.g. *Pyrostephos vanhoeffeni*).

Hopkins (1985) generally observed no changes of temperature with depth gradient in our study area. Similar results were obtained in our study. As the result of a lack of the distinct thermocline, certain species that show no migration tendency in other oceans, may undergo it in Antarctic waters. Moreover, in our research region vertical distribution of both siphonophore species may be more closely linked to the vertical migrations of their potential prey – copepods and krill. Studies which were carried out at the same time in the same area, in the aspect of seasonal and daily changes in vertical distribution of dominant Antarctic copepods by Żmijewska and Yen (1993) showed that in summer copepods concentrated mainly in the upper layers and at the end of July were absent from the surface water and occurred in the mesopelagic water layer. Krill larvae also migrate into deep water from late January to March (Huntley *et al.* 1989). Quetin *et al.* (1996) reported that during summer juvenile stages of krill are usually concentrated in a layer 0–100 m deep, while in winter juvenile stages of krill are observed as deep as 700 m. The lipid analysis of the *P. vanhoeffeni* colony revealed that 70% was formed by struc-

tural lipids, the main fraction of krill lipid reserves (Hagen 1988), which indicates that this siphonophore had preyed upon krill.

The result of analysis as presented in these studies show beyond doubt that the effectiveness of reproduction of the same species in different parts of the world oceans may vary meaningfully. It was also shown that distinct seasonality characterising the research region along with biological and hydrological specifics may induce horizontal migration of siphonophores which is largely correlated with the behaviour of their potential prey.

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