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Trophic importance of the chaetognaths *Eukrohnia hamata* and *Sagitta gazellae* in the pelagic system of the Prince Edward Islands (Southern Ocean)

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Abstract Trophodynamics and predation impact of the 2 dominant chaetognaths *Eukrohnia hamata* and *Sagitta gazellae* were investigated at 19 stations in the vicinity of the Prince Edward Islands and at a 24-h station occupied at the sub-Antarctic Front in late summer (April/May) 1996. During the entire investigation, the zooplankton assemblages were numerically dominated by copepods with densities ranging from 21 to 170 ind. m^{-3}. Amongst the copepods, *Clausocalanus brevipes*, *Metridia gerlachei* and *M. lucens* dominated accounting for $>90\%$ of the total. Generally, chaetognaths were identified as the second most important group composing at times up to 30% (mean $=$ 14.7%) of total zooplankton abundance. Of the two chaetognath species, *E. hamata* was generally numerically dominant. Gut content analysis showed that both chaetognath species are opportunistic predators generally feeding on the most abundant prey, copepods. No feeding patterns were evident during the 24-h station, suggesting that both species feed continuously. The feeding rates of *E. hamata* ranged from 0 to 0.50 prey ind. day^{-1} and between 0 and 0.90 prey ind. day^{-1} for *S. gazellae*. The maximum total predation impact of *E. hamata* was equivalent to 5.2% of the copepod standing stock or up to 103% of copepod production per day. For *S. gazellae* the predation impact was lower, reaching a level of 3.2% of the copepod standing stock or 63% of the daily copepod production. Chaetognaths can, therefore, be regarded as an important pelagic predator of the Prince Edward Islands subsystem.

Introduction

The Prince Edward Islands (47°S; 38°E) are situated in the sub-Antarctic waters of the West Wind Drift between the sub-Antarctic Front (SAF) and the Antarctic Polar Front (APF) (Deacon 1983; Lutjeharms 1985). Meanders in the APF and SAF result in the interchange of Antarctic and sub-Antarctic waters in the region of the islands, which is reflected in changes in the phyto- and zooplankton assemblages species composition (Boden and Parker 1986). Indeed, according to Perissinotto and Boden (1989), zooplankton assemblages in the region of the Prince Edward Islands exhibit a high degree of variation with frequent changes in dominance.

The trophic relationships between the macrozooplankton and land-based predators, including birds (mainly penguins) and seals in the vicinity of the islands, are relatively well understood (Brown et al. 1990; Cooper and Brown 1990; Perissinotto and McQuaid 1992). Gut content analyses have shown that both the swimming prawn, *Nauticaris marionis*, and myctophid fish feed on copepods (Perissinotto and McQuaid 1990; Pakhomov et al. 1996). However, little is known of the relationships that exist between pelagic predators and mesozooplankton in the waters surrounding the islands.

Chaetognaths compose a significant proportion of total zooplankton stock in the Southern Ocean and are considered as important predators of copepods (Piatkowski 1985, 1989; Oresland 1990; Hosie 1994; Tarling et al. 1995). In the high Antarctic, chaetognaths have been shown to consume up to 4% of the mesozooplankton stock (Oresland 1995). Studies in the waters surrounding the Prince Edward Islands have shown that after copepods, chaetognaths are the most important contributors to total zooplankton stock (Grindley and Lane 1979; Allanson et al. 1985; Boden and Parker 1986). The contribution of chaetognaths to total zooplankton varies dramatically during different years (Allanson et al. 1985), which suggests that there may be

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very great shifts in the impact of these organisms on mesozooplankton standing stock.

The trophodynamics and predation impact of the two most abundant chaetognath species during a year of their scarcity were recently studied at two 24-h stations occupied in the in-shore and off-shore region of the islands (Froneman et al. in press). The results of this investigation showed that the combined predation impact of the two chaetognath species was equivalent to up to 1.5% of the copepod standing stock or 16% of the daily copepod production (Froneman et al. in press). The aim of this study is to present further data on feeding studies of the two dominant chaetognath species, *Eukrohnia hamata* and *Sagitta gazellae*, in the waters surrounding the Prince Edward Islands during late summer 1996 when these predators were abundant.

Materials and methods

The feeding and predation impact of the two dominant chaetognath species, *Eukrohnia hamata* and *Sagitta gazellae*, as well as the community structure of the zooplankton assemblages in the waters surrounding the Prince Edward Islands, were investigated at 18 stations along a transect conducted upstream and in the vicinity of the archipelago aboard the MV S.A. *Agulhas* (voyage 81) during late austral summer (April/May) 1996 (Fig. 1). In addition a 24-h station was occupied in the vicinity of the sub-Antarctic Front (SAF).

Zooplankton samples were collected using a bongo net with a mesh size of 300 µm. The net was fitted with a Universal Underwater Unit (U^3) that continuously measured depth and seawater temperature. The volume filtered by the net was calculated using electronic flowmeter data. Towing speed varied from 1.5 to 3.0 knots and the net was towed obliquely between 0 and 300 m or 0 m to bottom within the inter-island region. At the 24-h station occupied in the vicinity of the SAF, sampling was undertaken at ≈4-h intervals. The samples were fixed with 4–6% buffered formalin and examined in the laboratory in a 1/10 subsample for taxonomic identification. The chaetognaths were identified using the work of O'Sullivan (1982) while the remaining components of the zooplankton and the prey items of the chaetognaths were identified using the keys of Boltovskoy (1981) and Razouls (1994).

The predation impact of the two chaetognath species was estimated from gut content analysis (Oresland 1987, 1995). Individuals were dissected so that the gut content could be examined under a Wild Heerbrug dissecting microscope at between × 120 and × 250 magnification. Where possible a minimum of 100 stomachs of each chaetognath species were examined at each station, although at stations where less than 100 animals were caught the entire sample was examined. In order to account for cod end feeding, prey found in the foregut (upper quarter of the gut) were omitted from the counts (Feigenbaum and Maris 1984). When unidentifiable copepod fragments were found in the stomachs, it was assumed that these represented the remains of a single prey item only.

The feeding rates (Fr, prey day^{-1}) of each chaetognath species were calculated using the equation of Oresland (1995):

$$\mathrm{Fr} = (\text{mean NPC}/\mathrm{Dt}) \times 24 \qquad (1)$$

where NPC is the mean number of prey per chaetognath and Dt is the digestive time.

For *S. gazellae*, the Dt value was estimated from the empirical equation, $\mathrm{Dt} = 10.96e^{-0.086T}$ derived for *Sagitta* spp. by Stuart and Verheye (1991), where T is temperature (°C). For *E. hamata*, a Dt value of 10 h was assumed (Oresland 1995). As a result of the gut content analysis showing that copepods account for > 80% of the total number of prey in the stomachs of the two chaetognath species, only the predation impact on copepods was examined in this study. The predation impact of the chaetognaths on copepods was calculated by combining daily feeding rate with their densities. The results were expressed as a percentage of the copepod standing stock consumed per day. To estimate the predation impact of the chaetognaths on the daily copepod production, a daily production rate of 5% for the entire community was assumed (Voronina 1984; Vinogradov and Shushkina 1987).

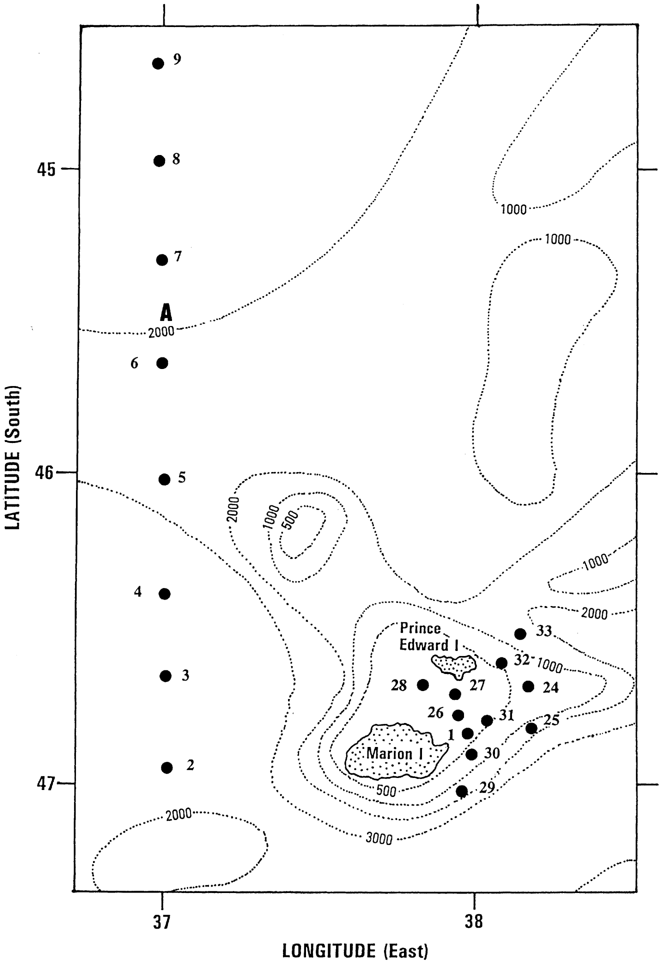

Fig. 1 Sampling area and position of stations occupied in late austral summer (May) 1996. Station A designating position of 24-h station occupied in the vicinity of the sub-Antarctic Front is shown by *A*

To identify possible relationships between predation impact, zooplankton abundance and physico-chemical parameters Pearson correlation analyses were performed using the computer package, Statgraphics, Version 6 (Statistical Graphics, Rockville, U.S.A.).

Results

Zooplankton community structure and distribution

The eight most abundant zooplankton species constituting >95% of total zooplankton abundance and the abundances of the two chaetognath species are shown in Table 1. No clear patterns in the distribution of zooplankton were evident. Although densities at off-shore

Table 1 Mean abundances of the most abundant mesozooplankton and chaetognath species along a transect conducted in the waters surrounding the Prince Edward Islands during late austral summer (April/May) 1996. Results expressed are ind. m^{-3} (+ present but in low abundances; – absent)

Species	MS1	MS2	MS3	MS4	MS5	MS6	MS7	MS8	MS9	MS24	MS25	MS26	MS27	MS28	MS29	MS30	MS31	MS32	MS33
Copepoda																			
Aetideus armatus	0.1	0.4	1.5	+	0.1	+	0.5	0.9	0.5	+	1.2	+	+	+	+	3.0	1.7	0.7	1.4
Calanus simillimus	0.1	+	+	+	+	+	0.1	+	+	0.1	+	3.4	1.5	+	+	1.6	+	+	+
Clausocalanus brevipes	111.1	17.9	15.1	17.1	44.3	29.4	22.4	16.7	23.7	3.8	12.7	13.5	111.5	36.8	45.4	3.2	13.2	4.1	15.2
C. laticeps	+	+	+	+	+	+	+	0.5	+	+	+	2.3	+	+	+	1.6	1.7	+	1.4
Metridia gerlachei	3.5	+	+	+	+	1.3	+	+	–	5.6	–	–	–	–	–	–	+	–	–
M. lucens	+	9.9	3.4	3.6	10.1	13.4	+	5.0	8.5	8.5	7.7	6.5	40.3	35.4	+	6.3	18.2	38.5	23.9
Oithona antarctica	+	+	+	1.5	+	+	+	+	+	+	+	–	–	1.5	+	+	–	+	–
O. frigida	+	7.6	3.6	3.3	3.1	9.2	5.2	3.4	2.5	+	1.3	1.3	7.4	4.9	9.8	5.4	31.1	7.9	25.3
O. similis	1.3	0.7	1.6	3.0	0.3	0.8	0.5	1.9	+	1.4	1.2	1.7	3.7	1.4	2.4				
Pleuromamma spp.	–	4.5	4.7	4.2	2.8	5.4	+	+	19.9	+	2.9	+	5.2.	18.7	2.0	+	+	19.9	1.4
Rhincalanus gigas	+	–	3.3	1.9	–	+	0.9	1.2	–	1.4	+	–	–	–	2.9	+	2.9	–	5.6
Total	117.8	41.0	33.2	34.6	60.7	59.5	29.6	29.6	55.1	20.8	27.0	28.7	169.6	98.7	62.5	21.1	69.0	71.7	86.8
Ostracoda	2.1	+	+	+	4.7	+	+	5.5	1.8	2.1	6.4	3.4	7.4	+	5.4	3.0	5.6	9.1	5.1
Pteropoda																			
Limacina spp.	2.1	4.5	10.4	4.2	6.6	4.8	4.7	5.3	5.5	4.6	3.4	+	1.5	6.2	5.4	1.9	14.9	2.9	3.5
Chaetognatha																			
Eukrohnia hamata	0.8	3.9	8.5	8.1	2.1	5.4	12.2	4.2	2.6	5.3	5.7	5.9	2.4	1.2	4.9	3.2	13.2	4.1	15.2
Sagitta gazellae	1.3	1.0	1.9	1.4	2.6	2.2	1.4	7.8	0.4	1.2	1.4	4.0	2.8	3.9	3.7	2.0	3.7	1.4	0.3

stations did not differ significantly from those at shelf stations ($P > 0.05$), slightly elevated densities were found within the inter-island region. During the entire investigation, mesozooplankton comprising copepods were the most numerous component of the zooplankton. Densities of copepods ranged between 21 and 170 ind. m^{-3} (Table 1). Among the copepods, *Clausocalanus brevipes* was identified as the single most abundant species, constituting between 26 and 87% of total zooplankton. Exceptions were stations MS 17 and MS 29 where *Metridia gerlachei* dominated numerically (Table 1). *Metridia lucens* was identified as being the second most abundant copepod species. At times this species constituted up to 43% of total zooplankton although its contribution was generally < 20% of the total. Also well represented among the copepods were *Oithona* spp. (mainly *Oithona similis* and *O. frigida*), *Pleuromamma* spp. and *Rhincalanus gigas* (Table 1). Densities of these species were, however, always < 10% of the total.

Generally, chaetognaths represented by *Eukrohnia hamata* and *Sagitta gazellae* were the second most abundant component of the zooplankton assemblages. Exceptions were stn. MS1 where the pteropod *Limacina* spp. represented the second most important component and stns. MS 27 and MS 32 where ostracods were more abundant (Table 1). At times the two chaetognath species accounted for up to 30% of all zooplankton counted, although generally they contributed ≈15% of the total. Throughout the survey pteropods, mainly *Limacina* spp., and ostracods were generally the third and fourth most abundant groups. Their contribution to total zooplankton abundances was, however, < 5% at all stations (Table 1).

Chaetognath standing stock and distribution

Generally, highest abundances of chaetognaths were recorded within the inter-island regions. *Eukrohnia hamata* generally dominated chaetognath standing stock composing at times up to 98% of the total. Exceptions were stations MS 1, 5, 8 and 17 where *Sagitta gazellae* dominated numerically. Densities of *E. hamata* ranged from 0.8 to 18.7 ind. m^{-3} while *S. gazellae* densities ranged between 0.2 and 7.8 ind. m^{-3} with the highest abundances generally found at the off-shore stations (Table 1). Throughout the 24-h station occupied in the vicinity of the SAF, no diurnal vertical migration patterns for either chaetognath species were observed (Fig. 2).

Gut content analysis and predation impact

A total of 2,206 stomachs of *E. hamata* and 1,479 of *S. gazellae* (including the 24-h station occupied in the vicinity of the SAF) were examined for the presence and identification of food in their guts. Prey items were found in the guts of 169 *E. hamata* and 46 *S. gazellae*. Of

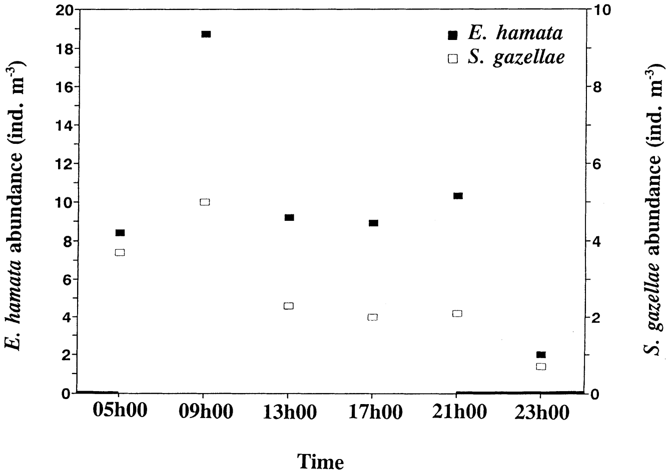

Fig. 2 Diurnal vertical migration patterns of *Eukrohnia hamata* and *Sagitta gazellae* at the 24-h station occupied in the vicinity of the sub-Antarctic Front (SAF). Period of darkness is indicated by thickening of the horizontal axis

the total number of prey found in the guts of *S. gazellae*, six were found in the foregut and were, therefore, omitted from the analysis. Thus, of the total number of chaetognaths examined, 94% of *E. hamata* and 97% of *S. gazellae* contained no food items in their guts. While both species' main prey items were copepods (Table 2), *S. gazellae* appeared to consume a wider variety of prey. These included large copepods (*Eucalanus longiceps*) and eggs. No mandibular structures of any prey were found in the guts of either species. Multiple prey were found in the guts of seven *S. gazellae* while only single prey were recorded in the stomachs of *Eukrohnia hamata*. Unfortunately, due to the advanced state of digestion generally found in *Eukrohnia hamata*, we were unable to identify what copepod species were being consumed or determine whether multiple prey were in their guts. Cannibalism was observed in both species (Table 2). The contribution of chaetognaths to the total number of prey items identified in the guts of the two chaetognaths was highest in *S. gazellae* (≈8%) compared to <1% for *Eukrohnia hamata*.

Table 2 Gut contents (% contribution) of *Eukrohnia hamata* and *Sagitta gazellae* in the waters surrounding the Prince Edward Islands during late austral summer (April/May) 1996

Food item	*Eukrohnia hamata* (n = 169)	*Sagitta gazellae* (n = 46)
Copepoda		
Calanus spp.	0.5	–
Eucalanus longiceps	–	5
Paraeuchaeta spp.	–	2.5
Pleuromamma spp.	–	5
Scolecithricella spp.	–	2.5
Oncaea spp.	–	2.5
Copepod fragments	26	62.5
Chaetognatha		
Sagitta gazellae	0.5	15
Eukrohnia hamata	–	2.5
Other		
Crustacean eggs	–	2.5
Oil droplets	73	–

Predation impact

The mean number of prey (NPC), daily feeding rate (Fr) and predation impact of *Eukrohnia hamata* and *S. gazellae* on copepod standing stock and daily copepod production are shown in Tables 3 and 4. Analysis of

Table 3 Mean number of prey (*NPC*), daily feeding rate (*Fr*) and predation impact of the two chaetognath species on copepod standing stock during the survey conducted in the waters surrounding the Prince Edward Islands in late austral summer (April/May) 1996

Station	*Eukrohnia hamata*				*Sagitta gazellae*			
	NPC	Fr	% copepod st. consumed day^{-1}	% copepod prod. consumed day^{-1}	NPC	Fr	% copepod st. consumed day^{-1}	% copepod prod. consumed day^{-1}
MS1	0.10	0.24	0.1	2.8	0.10	0.40	0.4	8.2
MS2	0.21	0.50	4.6	91.7	0.05	0.20	0.5	9.6
MS3	0.01	0.02	0.5	10.1	0.01	0.05	0.2	4.7
MS4	0.05	0.12	2.6	51.2	0.11	0.45	1.7	33.1
MS5	0.04	0.10	0.3	5.5	0.04	0.14	0.5	10.2
MS6	0.01	0.02	0.2	3.6	0.09	0.36	1.1	22.5
MS7	0.07	0.17	4.5	89.4	0.04	0.16	0.5	9.9
MS8	0.05	0.12	1.5	29.1	0.08	0.32	0.7	12.1
MS9	0.03	0.07	0.3	5.9	0	0	0	0
MS24	0	0	0	0	0	0	0	0
MS25	0	0	0	0	0.06	0.26	1.0	20.0
MS26	0.06	0.14	2.7	50.1	0.01	0.06	0.7	13.9
MS27	0.08	0.19	1.3	27.9	0.08	0.32	2.7	54.4
MS28	0	0	0	0	0	0	0	0
MS29	0.08	0.19	0.7	14.3	0	0	0	0
MS30	0.06	0.14	1.4	27.5	0.03	0.11	0.6	12.8
MS31	0.03	0.07	1.1	22.2	0.02	0.06	0.3	5.2
MS32	0.11	0.25	0.7	12.9	0.10	0.41	0.4	7.1
MS33	0.09	0.22	2.8	55.4	0.05	0.20	0.6	1.2

Table 4 Mean number of prey (*NPC*), daily feeding rate (*Fr*) and predation impact of two chaetognath species on copepods during the 24-h station occupied in the vicinity of the sub-Antarctic Front in late austral summer (April/May) 1996

Time (hours)	*Eukrohnia hamata*				*Sagitta gazellae*			
	NPC	Fr	% copepod st. consumed day^{-1}	% copepod prod. consumed day^{-1}	NPC	Fr	% copepod st. consumed day^{-1}	% copepod prod. consumed day^{-1}
0500	0.04	0.10	1.3	25.6	0	0	0.7	13.1
0900	0.09	0.22	5.2	103.0	0.07	0.27	0.6	11.4
1300	0.03	0.07	1.2	24.4	0.23	0.90	2.2	44.1
1700	0.01	0.02	0.4	8.3	0.19	0.74	3.2	63.3
2100	0.06	0.14	2.3	45.3	0.06	0.24	1.0	19.3
2300	0	0	0	0	0	0	0	0

variance (ANOVA) indicated that the NPC and Fr values for both species were not significantly different between the day and night samples during the 24-h station occupied in the vicinity of the SAF ($F = 0.112$ and $F = 0.497$; $P > 0.05$ in both cases).

The NPC rates observed in *Eukrohnia hamata* ranged from 0 to 0.21 prey ind.$^{-1}$, corresponding to a feeding rate of up to 0.5 prey day^{-1} (Table 3). These rates are equal to a daily loss of up to 5.2% of the copepod standing stock or between 0 and 103% of the daily copepod production during the investigation (Tables 3, 4).

Generally, both the NPC and Fr rates observed in *S. gazellae* were higher than those of *Eukrohnia hamata* (Tables 3, 4). The mean number of prey items observed in *S. gazellae* varied from 0 to 0.23 (Tables 3, 4). These rates are equal to a daily feeding rate of between 0 and 0.90 prey, which corresponds to a daily impact equivalent to between 0 and 3.2% of the copepod standing stock or up to 63.3% of the daily copepod production (Tables 3, 4).

Discussion

The waters surrounding the Prince Edward Islands are generally characterised by elevated phytoplankton production rates (Boden 1988; Perissinotto 1989; Perissinotto et al. 1992) and zooplankton biomass (Allanson et al. 1985; Perissinotto & Boden 1989). Although data on the ecological role of carnivorous zooplankton/micronekton in the vicinity of other oceanic islands, in particular South Georgia, are available (Oresland and Ward 1993; Pakhomov and Perissinotto 1996), little is known of the importance of these organisms in the waters surrounding the Prince Edward Islands. This is despite the large number of studies that have investigated the predation impact of the land-based predators on the zooplankton assemblages in the waters surrounding the islands (Brown et al. 1990; Wilkinson and Bester 1990; Perissinotto and McQuaid 1992). The results of this study show that chaetognaths are important predators of copepods in the waters surrounding the Prince Edward Islands and can therefore be regarded as a key component of the pelagic subsystem of the Prince Edward Islands.

The numerical dominance of copepods and chaetognaths among the zooplankton assemblages during this investigation agrees well with previous studies conducted in the vicinity of the islands (Grindley and Lane 1979; Allanson et al. 1985; Perissinotto 1989; Perissinotto and Boden 1989). The estimates of copepod abundance during this investigation, particularly the small *Oithona* spp. are, however, likely to be underestimated due to the net mesh size employed during this study (Oresland 1990). Although the dominant species during this investigation differ from previous studies, shifts in the dominants are a characteristic of the zooplankton assemblages in the water surrounding the island (Perissinotto and Boden 1989). The contribution of the larger zooplankton and micronekton to total zooplankton is, however, likely to be underestimated due to net avoidance. The predominance of the oceanic species throughout the investigation can be related to the general circulation patterns in the region of the islands, which advect zooplankton from the off-shore region upstream of the island to the vicinity of the islands (Perissinotto 1989). The high abundances of mesozooplankton generally found within the inter-island region suggest a concentrating mechanism. Possibly this may result from shallow water depth between the islands (<200 m), which prevents the wide distribution of zooplankton within the water column. Also, the elevated zooplankton biomass within the inter-island region may have been associated with the high chlorophyll concentrations recorded there. Indeed, a study conducted in parallel with this study showed that total zooplankton abundance in the inter-island region was significantly correlated to total chlorophyll concentration ($r^2 = 0.48$; $P < 0.05$) (unpublished data).

During the 24-h station occupied in the vicinity of the SAF, chaetognath abundances did not differ significantly over the diurnal period (Fig. 2). The absence of diurnal migration patterns for these species has been documented in the Southern Ocean (Hagen 1985; Oresland 1990; Pakhomov 1994) and suggests that competition between the two chaetognath species may be high due to trophic overlap. Segregation of feeding intensity has been suggested as a possible mechanism to reduce intra-specific competition among co-existing chaetognath species (Stuart and Verheye 1991).

However, both the mean number of prey (NPC) and daily feeding rate (Fr) did not differ significantly over the diurnal period ($P < 0.05$) suggesting that the two chaetognath species did not employ this behaviourial mechanism to reduce competition during this investigation. The ability of the chaetognaths to feed continuously can be related to the method of prey detection, i.e., sensing vibrations via sensory hairs (Feigenbaum and Maris 1984). Dietary overlap between the two chaetognath species may possibly have been reduced by selective feeding. Gut content analysis showed that *S. gazellae* appeared to feed on a wider variety of prey (Table 2). It should, however, be pointed out that due to the advanced state of digestion generally found in *Eukrohnia hamata*, we were unable to identify the prey species consumed by this species.

Gut content analysis of *Eukrohnia hamata* showed that large oil droplets formed up to 73% of the total items identified in their stomachs (Table 2). The presence of large droplets in the guts of *Eukrohnia hamata* has been documented in previous studies in the Southern Ocean (Oresland 1990; Froneman et al. in press) and elsewhere (Samemoto 1989). Lipids accumulated from consumed prey have been shown to occur in guts of polar ctenophores and medusae and are thought to represent an important energy reserve during winter (Larson 1990). The function of lipid droplets in the guts of *Eukrohnia hamata* is unknown although it has been suggested that they act as a buoyancy mechanism or represent an energy reserve (Oresland 1990). Bamstedt (1978) showed that the highest lipid concentrations in *Eukrohnia hamata* were found during winter. It is possible that the presence of oil lipid droplets in the guts of *Eukrohnia hamata* may represent an adaptive strategy in response to the variability in food supply generally recorded in polar regions. The absence of the oil droplets in the guts of *S. gazellae* suggests that other adaptive mechanisms are employed by this species. Larger *S. gazellae* are able to consume a wider variety of prey (Table 2) and are, therefore, not subject to food shortages. For example, high rates of cannibalism were documented among *S. gazellae*, but were almost absent among the smaller *Eukrohnia hamata*.

The combined predation impact of the two chaetognath species during this study was equivalent to up to 6% of the copepod standing stock or up to 130% of the daily copepod production (Tables 3, 4). It should be pointed out that the estimates of chaetognath predation on copepod daily production should be regarded as crude as we have employed an average daily production rate of 5% for the entire copepod production. The estimates of copepod standing stock removed are higher than those of similar studies conducted in the high Antarctic (Oresland 1990, 1995). The high predation impact during this study can be related to the high abundances of chaetognaths, which at times corresponded to up to ≈30% of the total zooplankton (Table 1). The estimates of predation impact by the chaetognaths should, however, be regarded as conservative for the following reasons. Firstly, we have assumed that the unidentifiable remains of prey in the stomachs of *Eukrohnia hamata* were remains of a single prey. Multiple prey in the guts of this species have been documented in the Southern Ocean (Oresland 1990). Secondly, the possibility that prey are egested during capture cannot be excluded (Feigenbaum and Maris 1984). This is partially supported by gut content analysis results which showed that >90% of all chaetognaths examined had no prey in their guts. Finally, Oresland (1987) showed that the digestion times (Dt) of chaetognaths varied considerably with prey size. Our average Dt values employed during this study do not, therefore, take into account differences in prey size. In the absence of carnivore/prey studies in the waters surrounding the islands, we are unable to compare our results with other components of the carnivore assemblage. However, a recent study conducted in the waters surrounding South Georgia showed that the predation impact of the hyperiid amphipod, *Themisto gaudichaudi*, never exceeded 3% of the mesozooplankton standing stock or 70% of the secondary production (Pakhomov and Perissinotto 1996). These facts suggest that chaetognaths are a key component of the pelagic subsystem of the Prince Edward Islands.

The benthic community in the waters surrounding the Prince Edward Islands has a high species diversity and large biomass (Parker 1984). According to Perissinotto et al. (1990), the presence of such a community implies a high rate of food supply in the water column, probably of phytoplankton origin. The faecal pellets produced by zooplankton may theoretically further contribute to the supply of food. However, copepods, the dominant component of the zooplankton assemblages during this investigation, contribute little to carbon flux due to coprophagy and coprohexy, which serve to retain the carbon in the surface waters (Fortier et al. 1994). As a consequence, copepods appear to contribute little to the supply of food to the benthic community within the inter-island region. Studies conducted in the coastal waters of California have shown that chaetognaths may contribute significantly to vertical carbon flux through the production of carbon-rich faecal pellets with high sinking rates (Nagasawa 1985; Dilling and Alldredge 1993). The contribution of chaetognaths to carbon flux during this study can be estimated by employing the equation of Dilling and Alldredge (1993): faecal carbon production rate (mg C m^{-2} day^{-1}) = mg C pellet × no. pellets $ind.^{-1}$ day^{-1} × no. ind. m^{-3} × height of zone (m). A carbon content of 0.9 μg per pellet and two pellets produced daily was assumed (Dilling and Alldredge 1993). The euphotic zone was assumed to be 100 m. Based on these assumptions, in the vicinity of the Prince Edward Islands chaetognaths contributed between 0.4 and 2.9 mg C m^{-2} day^{-1} during this investigation, suggesting that these organisms represent an important mechanism coupling the pelagic subsystem with the benthic community within the inter-island region.

In a previous study, Perissinotto (1989) suggested that zooplankton in the waters around the island were derived from allochthonous zooplankton advected to the island through Ekman drift resulting from the prevailing westerly winds. During this investigation, we have shown that chaetognaths were able to consume the entire daily mesozooplankton production in the upstream region of the island. This suggests that chaetognaths may dramatically affect the energy dynamics of the island through their impact on the allochthonous zooplankton that is subsequently advected to the island. Conversely, chaetognaths may act as an important coupling mechanism between the pelagic and benthic subsystems. In order to understand the significance of these organisms within the whole food web of the Prince Edward Islands, further studies, in particular on their importance as food source for the top predators and their role in transferring secondary production to the benthic community, require attention.

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