

New data on *Martialia hyadesi* feeding in the Scotia Sea during winter; with emphasis on seasonal and annual variability

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The diet of the seven star flying squid, *Martialia hyadesi*, from the South Georgia sector of the Scotia Sea was described from stomach contents collected in winter (June) 2001. Diet was dominated by the hyperiid amphipod, *Themisto gaudichaudii*, fish (nine species, mainly myctophids) and cephalopods (mainly cannibalism). The absence of krill, *Euphausia superba*, and the presence of larger myctophids in the diet are discussed in terms of seasonal and annual prey availability.

INTRODUCTION

The ommastrephid squid *Martialia hyadesi* (Rochebrune & Mabile, 1889) has a circumpolar distribution in association with the Antarctic Polar Frontal Zone (APFZ). Juveniles have been found near the Falklands, suggesting that spawning takes place on the Southern Patagonian Shelf edge. *Martialia hyadesi* then migrate southwards during the austral winter to feeding grounds around the APFZ (Cairistiona et al., 2001).

South Georgia waters lie within the Southern Ocean, to the south of the Polar Front, and are characterized by seasonal high growth rates and high-energy transfer between trophic levels. The role of cephalopods in the South Georgia ecosystem is reflected by their importance in the diet of apex predators (Rodhouse & Nigmatullin, 1996).

Exploratory fisheries have been conducted in February 1989, June 1996, January 1997 and June/July 1997 to assess the potential for commercial exploitation of *Martialia hyadesi* (Agnew & Miney, 2001). Samples caught from the shelf break to the north of Shag Rocks and in the area north-west of South Georgia show that *M. hyadesi* occupies an important niche in the Southern Ocean trophic web as an opportunistic predator feeding on mesopelagic fish, crustaceans and other cephalopods (Rodhouse et al., 1992). However, due to the opportunistic nature of *M. hyadesi* feeding, coupled with the geographical range of their feeding grounds, studies investigating annual, seasonal and regional variation are required to fully describe the diet of *M. hyadesi*. This study analyses variability in the diet of *M. hyadesi* by comparing new data from the June 2001 exploratory fishery with previous trophic studies.

MATERIALS AND METHODS

'In Sung 707', a squid jigger from the Republic of Korea, conducted exploratory fishing for *Martialia hyadesi*, between 10 and 30 June 2001 (Agnew & Miney, 2001). A

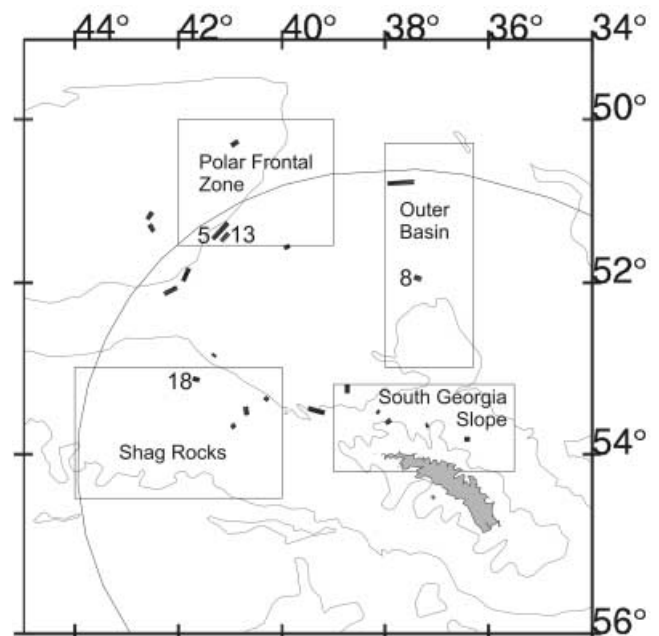


Figure 1. The positions fished by the 'In Sung 707' during the *Martialia hyadesi* jigger survey in CCAMLR Sub-area 48.3, June 2001. Samples came from labelled Drifts 5, 8, 13 and 18. The four regions defined for the exploratory fishery, South Georgia slope, Shag Rocks, Outer Basin and Polar Frontal Zone, are indicated. The island of South Georgia (filled), the 200 m and 3000 m contour lines and the 200 mile economic exclusion zone are shown.

CCAMLR (Commission for the Conservation of Antarctic Marine Living Resources) observer collected two samples from the Polar Frontal Zone (Drifts 5 and 13), one from the outer basin (Drift 8), and one from Shag Rocks area (Drift 18) (Figure 1). No *M. hyadesi* were caught from the South Georgia slope region. Squid were frozen whole and transported to the British Antarctic Survey (BAS) Applied Fisheries Laboratory at King Edward Point for analysis.

Table 1. Sex ratio and size range of *Martialia hyadesi* for each drift.

Drift	♂	♀	% Mantle length (mm)		Mantle length (mm)	
			♂	♀	Mean $2 \pm SE$	Range
5	29	11	72.5	27.5	267 \pm 6	228–312
8	21	19	52.5	47.5	253 \pm 5	227–298
13	12	8	60	40	256 \pm 6	230–280
18	12	8	60	40	257 \pm 7	225–291

SE, standard error.

Meristic measurements, sex, maturity (Rodhouse et al., 1992) and wet weight of stomach contents were recorded for all specimens. Empty stomachs were discarded before random sub samples were selected for dietary analysis. Twenty stomachs from Drifts 13 and 18, and 40 stomachs (to allow for a more detailed analysis of prey fish species) from Drifts 5 and 8 were selected. Prey species were identified to the lowest possible taxonomic grouping, counted and dry weights measured.

Crustacean fragments were identified from the residual eyes and appendages and the pteropod, *Limacina*, was identified from its shell (Boltovskoy, 1999). Cephalopods were identified from sucker rings, or beaks following the methods of Gonzalez & Rodhouse (1998). Mantle lengths of *M. hyadesi* in the diet were calculated from the lower rostral lengths of beaks. For Drifts 5 and 8 sagittal otoliths were identified to species and fish total lengths back calculated from otolith length (Reid, 1996). Only one prey item was counted when the similarity of size and shape indicated that both the left and right otolith of a fish were present.

Sex ratio was compared using a χ^2 analysis. Mantle lengths from all four drifts were normally distributed and differences were tested with one-way analysis of variance (ANOVA) followed by a *post hoc* Tukey multiple comparison test. To compare diets between drifts, prey were classified into six taxonomic groupings: *Themisto gaudichaudii*, cephalopod, fish, unidentified crustacean, molluscs and unidentified. Regional differences in occurrence were tested using a χ^2 -test. Dry weights were converted into proportions to prevent unequal ration size biasing comparisons. Mollusc shells were too small to weigh accurately. A Kruskal–Wallis test was used to test for differences between dietary proportions.

RESULTS

As there was no significant sex bias in the number of each sex examined (all drifts combined; $\chi^2=3.46$, $P=0.33$, $df=3$; Table 1), this factor did not have to be controlled during the following analyses. All females were at an early stage of maturation (all Stage II) and the males were mature (Stages IV and V).

Mantle length (ML) ranged from 225–312 mm with one small but significant difference between drifts (ANOVA $F=5.48$, $P<0.01$, $df=3$) (Table 1). *Martialia hyadesi* from Drift 5 were larger than squid from Drift 8 (Tukey test: critical value $q_{0.05,115,4}=3.69$, $q=5.51$, $P<0.01$).

The hyperiid amphipod, *Themisto gaudichaudii*, was the dominant prey species occurring in 79% of *M. hyadesi* stomachs (Table 2). Cephalopods, mainly cannibalism, (39% of stomachs) and fish (39% of stomachs) were the other main dietary components. Mollusc shells, identified as the pteropod *Limacina*, were found in 18% of stomachs but were too small to weigh. *Martialia hyadesi* caught in Drift 5 had significantly different numbers of each prey

Table 2. Prey items found in *Martialia hyadesi* stomachs from four drifts.

Drifts	5				8				13				18			
	N	%f	Wp	%Wp	N	%f	Wp	%Wp	N	%f	Wp	%Wp	N	%f	Wp	%Wp
Amphipod																
<i>Themisto gaudichaudii</i>	38	95	0.56 \pm 0.28	43.55	33	82.5	0.25 \pm 0.11	45.90	13	65	0.14 \pm 0.12	26.24	15	75	0.10 \pm 0.10	17.43
Cephalopod																
<i>Martialia hyadesi</i>	15	37.5	0.26 \pm 0.27	11.46	21	52.5	0.14 \pm 0.11	2.29	7	35	0.17 \pm 0.15	23.97	6	30	0.16 \pm 0.14	23.82
<i>Gonatus antarcticus</i>	1	2.5	0.001 \pm 0.002	0.04	1	2.5	0.003 \pm 0.006	0.49	1	5	0.04 \pm 0.09	4.76	0	0	0	0
Fish																
unidentified/mixed	6	15	0.32 \pm 0.31	13.63	3	7.5	0.11 \pm 0.14	8.91	8	40	0.63 \pm 0.56	35.14	6	30	0.25 \pm 0.22	24.85
<i>G. fraseri</i>	3	7.5	0.03 \pm 0.05*	1.87	0	0	0	0	—	—	—	—	—	—	—	—
<i>G. nicholsi</i>	2	5	0.09 \pm 0.18*	2.49	0	0	0	0	—	—	—	—	—	—	—	—
<i>K. anderssoni</i>	3	7.5	0.01 \pm 0.02	2.26	3	7.5	0.06 \pm 0.08*	4.69	—	—	—	—	—	—	—	—
<i>P. choriodon</i>	6	15	0.05 \pm 0.06*	3.44	1	2.5	0.03 \pm 0.07	2.47	—	—	—	—	—	—	—	—
<i>P. tensoni</i>	0	0	0	0	1	2.5	0.02 \pm 0.04	2.47	—	—	—	—	—	—	—	—
<i>N. coatsi</i>	0	0	0	0	1	2.5	*	—	—	—	—	—	—	—	—	—
<i>P. gracilis</i>	2	5	0.03 \pm 0.07*	2.10	0	0	0	0	—	—	—	—	—	—	—	—
<i>S. nordenskjoldii</i>	0	0	0	0	1	2.5	0.01 \pm 0.02	2.47	—	—	—	—	—	—	—	—
<i>Notothenia</i> spp.	2	5	0.002 \pm 0.003*	0.11	0	0	0	0	—	—	—	—	—	—	—	—
Mollusc																
<i>Limacina</i>	20	50	0	0	1	2.5	0	0	1	5	0	0	3	15	0	0
Crustacean	0	0	0	0	0	0	0	0	1	5	0.03 \pm 0.06	4.94	1	5	0.04 \pm 0.09	4.85
Unidentified	12	30	0.19 \pm 0.21	19.03	6	15	0.02 \pm 0.02	9.66	1	5	0.01 \pm 0.02	4.93	6	30	0.12 \pm 0.09	29.06

N, number of stomachs in which prey species was found; %f, per cent frequency of occurrence; Wp, average dry weight of prey species found in stomach contents (± 2 standard errors); %Wp, average per cent of weight of prey species. *, not complete weight as some of this species inseparable from other species.

taxa in the diet to those caught in Drift 8 ($\chi^2=18.17$, $P<0.01$, $df=4$). The numbers of fish ($\chi^2=10.01$, $P<0.01$, $df=1$) and molluscs ($\chi^2=23.31$, $P<0.01$, $df=1$) accounted for this difference (Table 2).

Themisto gaudichaudii was the main dietary component by weight for Drifts 5 (43%) and 8 (46%) but accounted for a significantly smaller proportion of stomach content weight for Drifts 13 (26%) and 18 (17%) (Kruskal–Wallis test: $H=9.80$, $df=3$, $P=0.02$). Fish were the main component by weight for Drifts 13 (35%) and 18 (25%).

Thirty-eight fish, nine species, mainly myctophids, were identified from 25 otoliths pairs and only 13 single otoliths. *Krefflichthys anderssoni* was the most abundant fish prey species (12 fish in Drift 5 and 7 fish in Drift 8), although the greatest number of squid preyed upon *Protomyctophum choriodon*. Single species from the families Paralepididae, Gempylidae, Melamphaidae, and Nototheniidae were also found in stomach contents (Table 2).

The total length of fish in the diet, ranged from 39.9–175 mm but did not correlate with squid ML. The Nototheniidae could not be identified to species and the length of this specimen could therefore not be calculated.

Over 30% of squid consumed cephalopods in their diet. Three *Gonatus antarcticus* (one from each of Drifts 5, 8 and 13) and four *M. hyadesi* (Drifts 5 and 8) were identified from beaks. The remaining cephalopods were identified as *M. hyadesi* from sucker rings. Dietary *M. hyadesi* ranged from 111–181 ML.

DISCUSSION

The hyperiid amphipod, *Themisto gaudichaudii* and fish, mainly myctophids, dominated the diet of *Martialia hyadesi* caught during June 2001. There were only small differences in ML of *M. hyadesi* (4%) between drifts and therefore differences in diet are most likely due to environmental variability of prey rather than ontogenetic changes in feeding. The squid caught in 2001 (mean ML 253–267 mm) were a similar size to those caught in 1989 (mean ML 244–260 mm). There was also no relationship between diet and squid size for the squid caught in 1989 (Rodhouse et al., 1992). There was, however, a larger size-range of fish in *M. hyadesi* diet in this study (40–175 mm) than in the 1989 study (15–80 mm; Rodhouse et al., 1992). This is probably due to seasonal differences in the availability of smaller, juvenile myctophids.

Themisto gaudichaudii is the most abundant pelagic amphipod in the Scotia Sea (Rodhouse et al., 1992) and was the main dietary component of *M. hyadesi* in this study with 79% of stomachs containing amphipod remains. This compares with 16.4% *T. gaudichaudii* in stomach contents from the *M. hyadesi* in the 1989 study (Rodhouse et al., 1992). In years of poor krill availability many species, including the commercially important mackerel icefish, *Champsocephalus gunnari*, (Murphy et al., 1998) and macaroni penguins (Croxall et al., 1999) will switch to feeding on *T. gaudichaudii*. In some subantarctic areas *T. gaudichaudii* therefore has a central trophic role similar to *Euphausia superba*.

Twenty-three per cent of *M. hyadesi* stomachs contained krill, *Euphausia superba*, in February 1989 (Rodhouse et al., 1992); 11% of stomachs contained krill in the 1996 study (Gonzalez & Rodhouse, 1998), however, no krill were

recorded in 2001. *Euphausia superba* populations in the Scotia Sea are known to fluctuate markedly from year to year, however, all years for which we have dietary information were classified as years when krill were abundant in the Scotia Sea (Murphy et al., 1998; K. Reid, BAS personal communication). The structure of krill populations varies considerably between summer and winter, which may lead to reduction in krill in *M. hyadesi* diet during winter. Krill abundance recorded during 2001 showed that krill biomass had dropped markedly from a peak of 34.7 g m⁻² in summer to 7.8 g m⁻² in March, the start of winter (Brierly et al., 2002). The variation in krill in *M. hyadesi* diet between winter 1996 and 2001 cannot be explained by annual krill availability and might therefore be due to differential encounter rates or prey selection.

Gonzalez & Rodhouse (1998) studied the *Martialia hyadesi* diet at South Georgia in winter 1996 and also found a high proportion (54%) of squid (mainly *Gonatus antarcticus* as well as 9% cannibalism). *Martialia hyadesi* had a high proportion of cephalopod in the diet in winter 2001 (30–53%) compared with summer 1989 (5%, Rodhouse et al., 1992). *Gonatus antarcticus* was taken in small numbers in 2001 but the major cephalopod component was due to cannibalism of *M. hyadesi*. Ommastrephid squid are thought to exhibit cannibalistic behaviour en route to spawning grounds if feeding is poor; this ensures survival of at least part of the school (Rodhouse & Nigmatullin, 1996). The lights of fishing vessels, whilst jigging, have been a suggested cause of cannibalism in some species e.g. *Illex illecebrosus* and *Nototodarous gouldi* (Rodhouse et al., 1992). It is unlikely that such a substantial squid component in the diet could be due to fishing related cannibalism alone and is more likely to be linked with the low abundance of krill in winter and the change in diet composition.

In 2001 there were differences between the species of fish consumed in the Polar Frontal Zone and the Outer Basin. There were also fewer myctophid species in *M. hyadesi* diet at both these locations in 2001 (25–60%) than in 1989 (77%, Rodhouse et al., 1992). This could be due to variation in myctophid abundance or differences in methodology. The majority of otoliths (66%) in this study were visually paired as left and right otoliths from the same fish. The presence of pairs of lenses also often confirmed this. Counting pairs of otoliths as one fish, as opposed to assuming each otolith is from a different fish, will partly explain the lower occurrence of fish in the diet compared with Rodhouse et al. (1992).

The interpretation of stomach content analysis is influenced by several factors. The digestion time of different prey species in the gut will affect the likelihood of finding species in stomach contents. The pteropod *Limacina*, was found in greatest numbers in *M. hyadesi* from Drift 5 Polar Frontal Zone. It was not possible to identify and separate out the soft pteropod flesh, possibly leading to underestimation of the importance of this prey species. It is also possible that the *Limacina* were actually dietary components of the myctophids or cephalopods within the diet of *M. hyadesi*. Hard structures, such as shells, carapaces and otoliths are relatively indigestible and will tend to be over-represented in the diet, however, rejection of hard structures e.g. otoliths from larger fish might occur as squid use their beaks to take bites out of larger prey species.

There were significant differences in *Martialia hyadesi* diet both within and between regions in 2001. More samples would be required to confirm such small-scale regional differences but larger scale seasonal and annual differences were detected. *Martialia hyadesi* clearly has the ability to alter its diet, switching from feeding on *Euphausia superba* to *Themisto gaudichaudii* and preying on larger myctophids, in response to prey availability. A time series of diet studies could therefore provide an index of variability in feeding conditions in this region of the Southern Ocean.

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