Vol. 108: 43-57, 1994 | MARINE ECOLOGY PROGRESS SERIES Mar. Ecol. Prog. Ser. | Published May 12

Variations in the diet composition and feeding intensity of mackerel icefish *Champsocephalus gunnari* at South Georgia (Antarctic)

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ABSTRACT: The diet composition and feeding intensity of mackerel icefish *Champsocephalus gunnari* around Shag Rocks and the mainland of South Georgia was analyzed from ca 8700 stomachs collected in January/February 1985, January/February 1991 and January 1992. Main prey items were krill *Euphausia superba*, the amphipod hyperiid *Themisto gaudichaudii*, mysids (primarily *Antarctomysis maxima*), and in 1985 also *Thysanoessa* species. The proportion of krill and *T. gaudichaudii* in the diet varied considerably among the 3 years, whereas the proportion of mysids in the diet remained fairly constant. Krill appears to be the preferred food. In years of krill shortage, such as in 1991, krill was replaced by *T. gaudichaudii*. The occurrence of krill in the diet in 1991 was among the lowest within a 28 yr period of investigation. Variation in food composition among sampling sites was high. This high variation appears to be primarily associated with differences in prey availability, but much less with prey size selectivity. Feeding intensity varied considerably among seasons. It was highest in 1992. The proportion of empty stomachs was uncommonly high and stomach content weight was uncommonly low in January 1991, a period when energy-rich food was needed for the final maturation of gonads. At the same time, an unusually high proportion of sexually mature fish showed no signs of the gonad development necessary for spawning in that season. It was hypothesized that as in some other non-Antarctic fish species the shortage of suitable food may have forced the fish to sacrifice gonad maturation in order to maintain body size.

KEY WORDS: Food · Feeding · Reproduction · Southern Ocean · Notothenioides

INTRODUCTION

Mackerel icefish *Champsocephalus gunnari* has been the target species of the fishery around South Georgia from 1975/76 to 1989/90. Stock size fluctuated considerably for 2 reasons: large variations in recruitment and a high intermittent fishing mortality (Kock 1991). Stock size in the early 1990s was low compared with the mid-1970s and the early and mid-1980s (SC-CAMLR 1992).

Several qualitative studies of the dietary composition of mackerel icefish around South Georgia and its seasonal and interannual variation have been made (reviews in Kock 1981, Kozlov et al. 1988). Mackerel icefish have a limited prey spectrum. The main prey items are krill *Euphausia superba*, the amphipod hyperiid *Themisto gaudichaudii*, mysids (mostly *Antarctomysis maxima*) and in some years euphausiids of the genus *Thysanoessa*. Stomach content analyses conducted on mackerel icefish since 1965 by various authors suggest considerable interannual variation in the occurrence of the main prey items, in particular of krill (Fig. 1a).

Mackerel icefish at South Georgia spawn annually from February to May (Lisovenko & Silyanova 1980). A proportion of the adult population, varying from year to year, show no signs of the gonad development necessary for spawning in the current season. The proportion of sexually mature fish found in this non-reproductive state prior to spawning is commonly 10 to

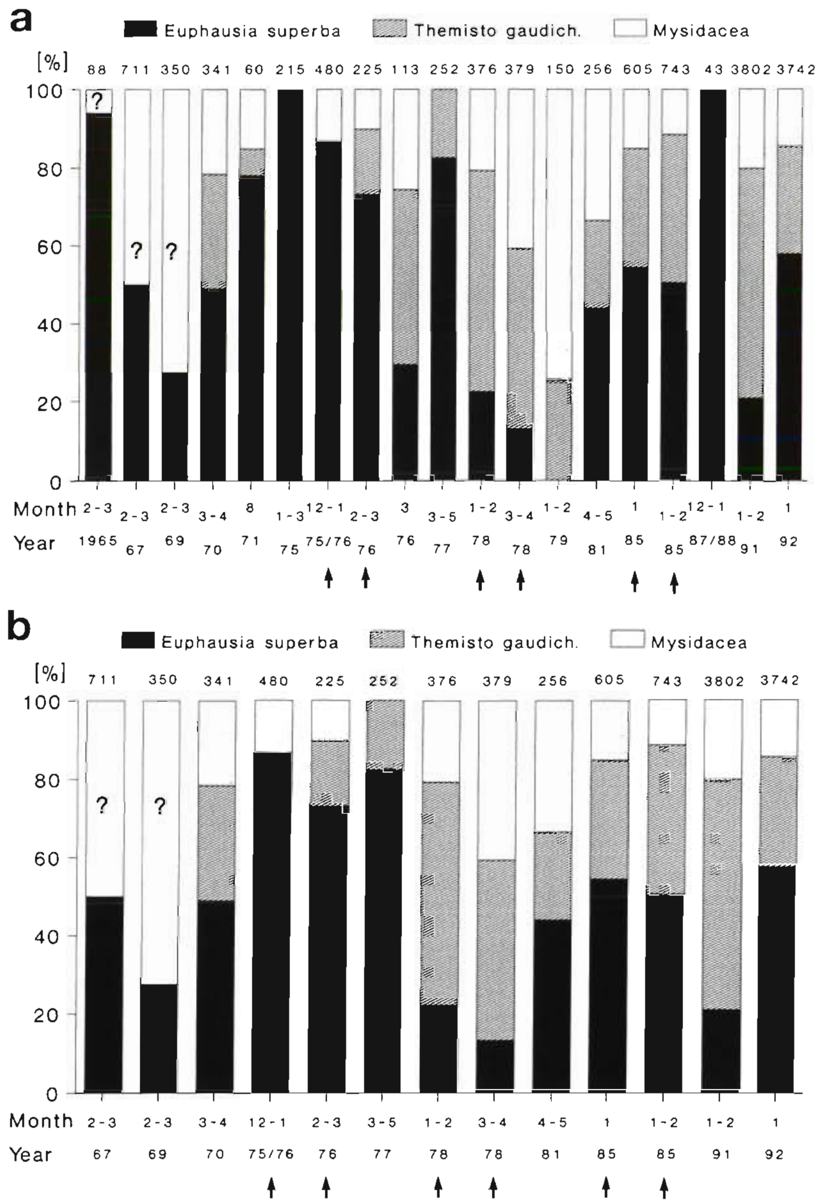


Fig. 1. *Champsocephalus gunnari.* Frequency of occurrence (in %) of the main prey items *Euphausia superba, Themisto gaudichaudii* and Mysidacea in the diet of mackerel icefish at South Georgia from 1965 to 1992. (a) All sample sizes included. (b) Sample sizes ≤215 excluded. Numbers above columns denote sample size. Frequencies have been scaled down to 100%. Arrows denote investigations in the same season.
Data sources:
2-3, 1965-69: Permitin & Tarverdiyeva (1972), data not provided for prey items other than krill
3-4, 1970; 8, 1971; 1-3, 1975; 2-3, 1976; 3-4, 1978; 1-2, 1979; 1-2, 1985: Kozlov et al. (1988)
12-1, 1975/76: Kock (1981)
1-2, 1978: Kock (unpubl.)
3, 1976: Linkowski & Rembiszewski (1978)
3-5, 1977: Kompowski (1980)
4-5, 1981: Tarverdiyeva (1982)
12-1, 1987/88: McKenna (1991)
1-2, 1985; 1-2, 1991; 1, 1992: this study

20% (Kock 1990), but may reach ca 60% as in January/February 1991 (Everson et al. 1991). We have hypothesized that limited food availability and/or shortage of suitable food, such as krill, may be one of the causes inducing non-reproductive state, as has been demonstrated in other iteroparous marine fish species (Fedorov 1971, Tyler & Dunn 1976, Burton & Idler 1987, Burton 1991).

In 1991, we established a programme to monitor food composition and feeding intensity of mackerel icefish around South Georgia. The objective was to assess the extent and likely causes of its interannual variation. This information could then be related to that on the abundance of prey species, such as krill, and to features of the reproductive cycle of mackerel icefish which are monitored concomitantly.

We report here on our observations in January/February 1991 (Kock et al. 1992) and January 1992 and compare them to earlier investigations by 2 of the authors in January/February 1985 (Wilhelms & Kock unpubl.).

MATERIAL AND METHODS

The fish were obtained during the Demersal Fish Surveys of the Federal Republic of Germany in 1985 and the United Kingdom in 1991 and 1992 around South Georgia and Shag Rocks (Kock 1986, Everson et al. 1992a, b). Sampling stations for qualitative stomach content analyses were randomly selected from the entire set of stations. Sampling for quantitative stom-

Table 1 Numbers of stations trawled, sampled and numbers of fish investigated around Shag Rocks and the mainland of South Georgia

Year	Area	Qualitative investigations: No. of stns: Trawled	Sampled	No. of stomachs: Investigated	With food	Quantitative investigations: No. of stns sampled	No. of stomachs: Investigated	With food	Length range (cm)
1985	Shag Rocks	7	3	89	79 (88.8%)	3	79	69 (87.3%)	22–42
	South Georgia	77	25	743	650 (87.5%)	25	728	635 (87.4%)	13–56
1991	Shag Rocks	12	1	68	27 (39.7%)	2	61	50 (82.0%)	19–37
	South Georgia	66	43	3802	2547 (67.0%)	6	211	131 (62.1%)	12–51
1992	Shag Rocks	12	4	287	276 (96.1%)	2	117	104 (88.9%)	17–38
	South Georgia	75	40	3742	2781 (74.3%)	7	450	364 (80.9%)	12–60

ach content analyses was carried out randomly from a subset of these stations.

Qualitative stomach content analyses were undertaken at sea on freshly caught fish randomly collected from the catch. Quantitative investigations were conducted on fish that were frozen within 60 min of capture. These analyses were undertaken in a laboratory ashore. Summary information on the material studied is provided in Table 1. Sampling on all 3 surveys was confined to daylight hours, i.e. 5:00 to 20:00 h. Length of fish ranged from 12 to 60 cm total length, but was mostly 20 to 36 cm (Fig. 2) which included the predominant size classes in the stock (Kock 1986, Everson et al. 1992a, b). Typical sample size in 1991 and 1992 was 100 stomachs per station. In 1985, sampling intensity was less and typical sample size was 30 fish per haul.

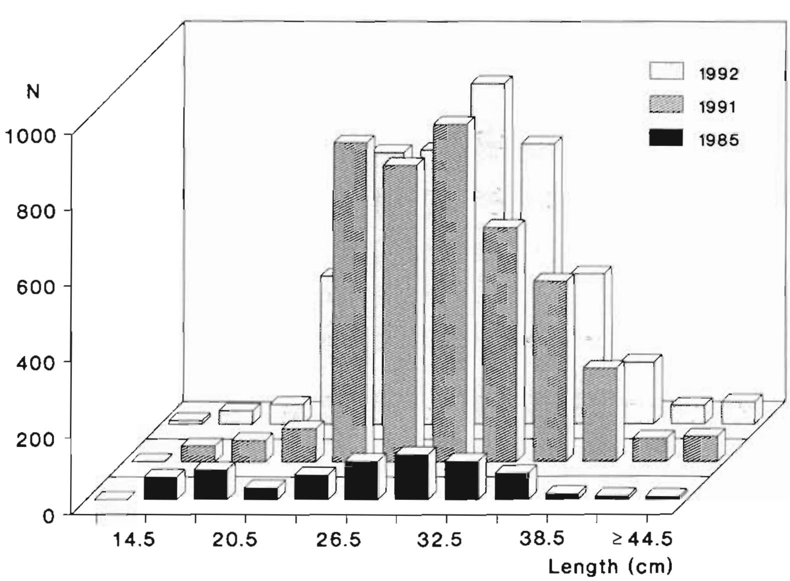


Fig. 2. *Champsocephalus gunnari*. Length compositions of fish investigated in 1985, 1991 and 1991 (grouped in 3 cm intervals)

Prey availability (= geographic location of sampling) and prey size selectivity (= fish length) are the variables most likely to influence variation in diet composition between sampling stations. The following relationship was investigated using the data from qualitative stomach content analyses:

Frequency of occurrence of a given food item = *f*(Sampling station, Fish length)

This relationship was used in order to evaluate whether the 2 variables were the main sources of variation and to what extent each of the 2 variables contributed to the variance. An analysis of covariance was performed using fish length as metric covariable and sampling station as categorical variable (Fahrmeier & Hamerle 1984). The prey items were grouped into the following categories: Krill; *Themisto gaudichaudii*; Mysidacea; *Thysanoessa* spp.; and Others. Fish lengths were grouped into 3 cm intervals. The GLM routine of the SAS package was used for the analysis (SAS 1987). By comparing minimum and maximum variance (Schuchard-Ficher et al. 1988) the variance of the frequencies of occurrence between stations was found to be very heterogeneous both with respect to sampling station and to fish length. In order to obtain homoscedasticity (a requirement to apply an analysis of covariance) the data were transformed according to the formula

$$fo_{ij} / STD_j$$

where fo_{ij} is the ith observation of the frequency of occurrence on sampling station j; and STD_j is the standard deviation of the observations fo_{ij} on the jth sampling station. This transformation leads to observations fo_{ij} with unit variance per sampling station.

Stomach fullness was estimated according to the following 5-point scale: 0, empty; 1, ¼ full; 2, ½ full; 3, ¾ full; 4, 4/4 full with stomach wall extended. Prey items were identified to the lowest taxon possible; in general this was to species or genus. The occurrence of each taxon was recorded and augmented by information on its prevalence. Occurrence was expressed as a percentage of all stomachs investigated containing food. Despite its shortcomings (Pillay 1952) the 'frequency of occurrence' method gives reasonable results in species with a limited food spectrum (Kock 1981). In 1985, for example, the frequency of occurrence of krill was 64.5% and this corresponded to a proportion of 53.0% by weight. The advantage of the method is that it is quick, requires a minimum of apparatus and time, and results from a number of similar studies from previous seasons can be used for comparison.

Length of freshly ingested krill was measured from the anterior margin of the eye to the tip of the telson (Siegel 1982). For *Themisto gaudichaudii*, length was measured from the anterior margin of the eye to the tip of the uropods. In the case of *Antarctomysis maxima* and *Thysanoessa* spp., length was measured from the tip of the rostrum to the tip of the telson (Mauchline 1980). Eye diameter (ED) of broken and half-digested krill was converted to krill length by the following equation:

$$\text{Length (mm)} = 12.84 + 14.92\,\text{ED}$$

(V. Siegel pers. comm.)

Stomach content wet weights were obtained from fish that were thawed quickly in the laboratory ashore, blotted with absorbant paper and the food bolus was then weighed to an accuracy of 0.1 g.

RESULTS

Diet composition

Stomach contents composition of mackerel icefish in the vicinity of South Georgia and Shag Rocks for the 3 seasons examined is set out in Tables 2 & 4 respectively. Krill, *Themisto gaudichaudii* and mysids formed the overwhelming part of the diet around South Georgia in all seasons studied (Table 2). The importance of krill as a prey item is shown in Table 3. The occurrence of mysids in the diet remained fairly constant over all 3 seasons (Table 2). *Thysanoessa* spp. formed a substantial portion of the diet in 1985, outnumbering even mysids. Other prey species or groups did not account for more than ca 7% of the diet except in 1985 (Table 2). There was little correlation in the co-occur-

Table 2. *Champsocephalus gunnari*. Frequency of occurrence (%) of prey items in the diet of mackerel icefish around South Georgia

Prey item	1985	1991	1992
Euphausia superba	64.5	22.3	65.3
E. frigida	1.7	–	0.1
E. triacantha	0.3	0.4	<0.1
Thysanoessa spp.[a]	25.2	3.1	5.1
Themisto gaudichaudii	50.5	63.1	31.3
Mysidacea[b]	13.9	21.8	16.5
Notocrangon antarcticus	0.2	<0.1	0.1
Chorismus antarcticus	–	–	<0.1
Pisces	2.3	3.3	1.1
Myctophidae[c]	0.3	1.9	0.2
Early life stages[d]	–	1.1	0.4
C. gunnari	–	0.2	0.3
Other species[e]	2.0	0.1	0.2
Others[f]	3.1	0.1	0.3

[a] *Thysanoessa macrura* and *T. vicina* are almost impossible to distinguish even when only slightly digested
[b] Primarily *Antarctomysis maxima*
[c] *Electrona* species, *Gymnoscopelus* species
[d] Predominantly *C. gunnari* age class 0
[e] *Pseudochaenichthys georgianus*, *Chaenocephalus aceratus*, *Muraenolepis microps*
[f] Porifera, Echinodermata, Copepoda, Crustacea unidentified, Hydrozoa, Hyperiidae species

Table 3. *Euphausia superba*. Frequency of occurrence (in %) of krill in 1985, 1991 and 1992

	1985	1991	1992
Total	64.5	22.3	65.3
Sole prey	22.9	15.2	48.6
Dominant prey	28.2	3.8	15.3

Table 4. *Champsocephalus gunnari*. Frequency of occurrence (%) of prey items in the diet of mackerel icefish in the Shag Rocks area

Prey item	1985	1991	1992
Euphausia superba	26.5	25.0	89.2
E. triacantha	–	11.1	–
Thysanoessa spp.[a]	86.8	3.7	20.9
Themisto gaudichaudii	17.1	85.2	27.8
Pisces	11.6	–	
Myctophidae	1.3	–	–
C. gunnari	–	3.7	–
Unidentified	10.3	–	–
Others	3.8	–	–

[a] See Table 2

rence of prey items (r ≤ ± 0.3, Pearson's correlation coefficient).

At Shag Rocks, the dietary composition was more limited. Mysids were absent while the dominant prey was *Thysanoessa* spp. in 1985, *Themisto gaudichaudii* in 1991, and krill in 1992 (Table 4).

Length compositions of the prey organisms were very similar in all 3 seasons. The bulk of *Themisto gaudichaudii* and *Thysanoessa* spp. were 10 to 20 mm long whereas mysids and krill were mostly in the size range of 28 to 38 and 25 to 55 mm respectively (Fig. 3). Fish in the diet were 40 to 100 mm long.

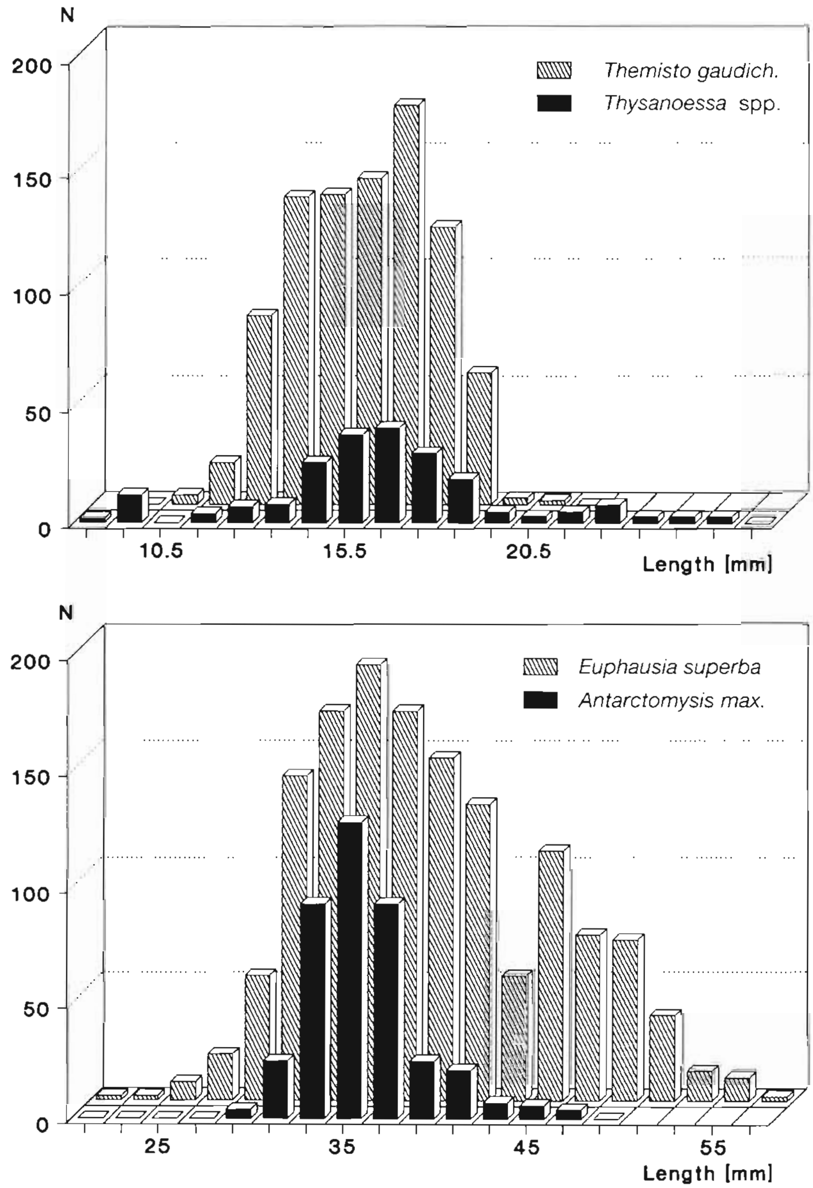


Fig. 3. *Champsocephalus gunnari*. Length composition of *Euphausia superba*, *Antarctomysis maxima*, *Thysanoessa* spp. and *Themisto gaudichaudii* in the diet of mackerel icefish around South Georgia in 1985

Variation in diet composition

Considerable variation in diet composition existed among stations or localities (i.e. groups of stations): the occurrence of mysids was highest in fish in the west and southeast of South Georgia in 1991 and 1992 and probably also in 1985 (Fig. 4). No clear year-to-year pattern was obvious in krill and *Themisto gaudichaudii*. Krill formed a substantial portion of the diet at most stations in 1985 and 1992 (Fig. 4a, c). In 1991, krill occurred frequently only in fish from stations on the eastern and northeastern portion of the shelf (Fig. 4b). *T. gaudichaudii* was ubiquitous in the diet during all 3 surveys with the exception of the southeast region of the shelf in 1992 (Fig. 4a to c). It formed the staple food only in 1991, in particular in the area west of 37° W (Fig. 4b). *Thysanoessa* spp. made up a noticeable portion of the diet only in 1985, especially in the Shag Rocks area (Fig. 4a, 'Others'). Fish formed a significant share of the diet only in 1991 on some stations in the southeastern (early life stages; Fig. 4b, 'Others') and the western region of the shelf (*Gymnoscopelus* spp., *Electrona* spp.; Fig. 4b, 'Others').

Length composition of mackerel icefish varied considerably among stations. A relationship of the occurrence of prey organisms to fish length was only apparent in *Thysanoessa* spp. in that the occurrence of *Thysanoessa* spp. declined with increasing fish length. However, no such trend was obvious for the similar-sized *Themisto gaudichaudii* suggesting little size selectivity during feeding. The occurrence of mysids was most frequent in the smallest and largest size classes in 1991 and 1992. The occurrence of krill was positively correlated to fish length only in 1992 (Fig. 5).

Results of the analysis of covariance confirmed that geographical location and fish length explained most of the variance observed in the occurrence of the various food items, in particular in 1991 and 1992. The poorer fit of the 1985 data (Table 5) may be due to the much smaller sample sizes investigated in that season. The results of the analysis of covariance also demon-

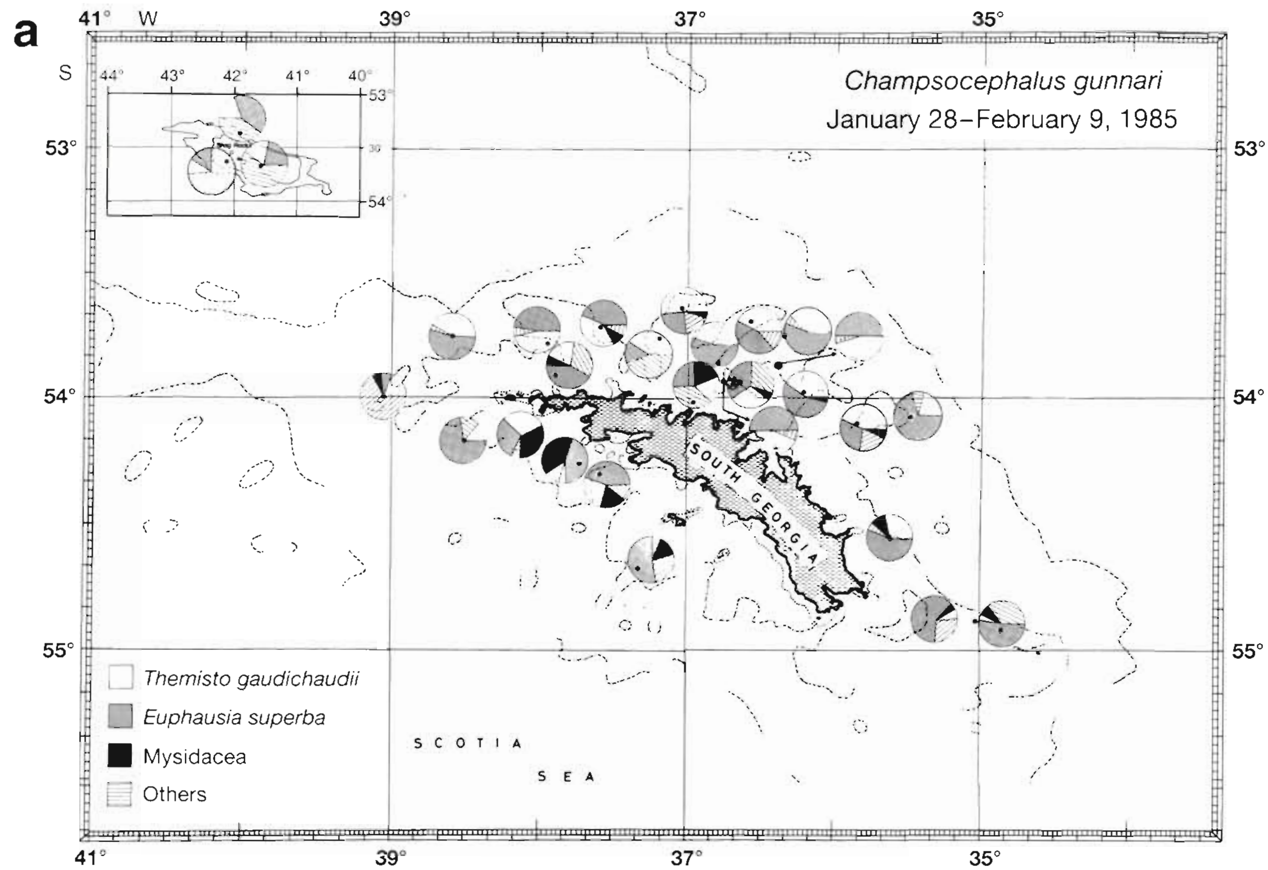


Fig. 4. *Champsocephalus gunnari*. Spatial variation in the frequency of occurrence of the main prey items in mackerel icefish around South Georgia. This page: (a) 1985; facing page: (b) 1991 and (c) 1992

strated that location of station was the variable contributing primarily to the variance. Fish length contribution to the variance was only 0.4 to 17.6% in 1985, 0.4 to 18.7% in 1991 and 2.7 to 53.0% in 1992. Fish length always contributed less than 7% with respect to the 3 main prey items krill, *Themisto gaudichaudii* and mysids (Table 5). Fish length contributed significantly only to the variance with respect to the occurrence of *Thysanoessa* spp. in all 3 seasons and to krill and *T. gaudichaudii* in 1992 (Table 5).

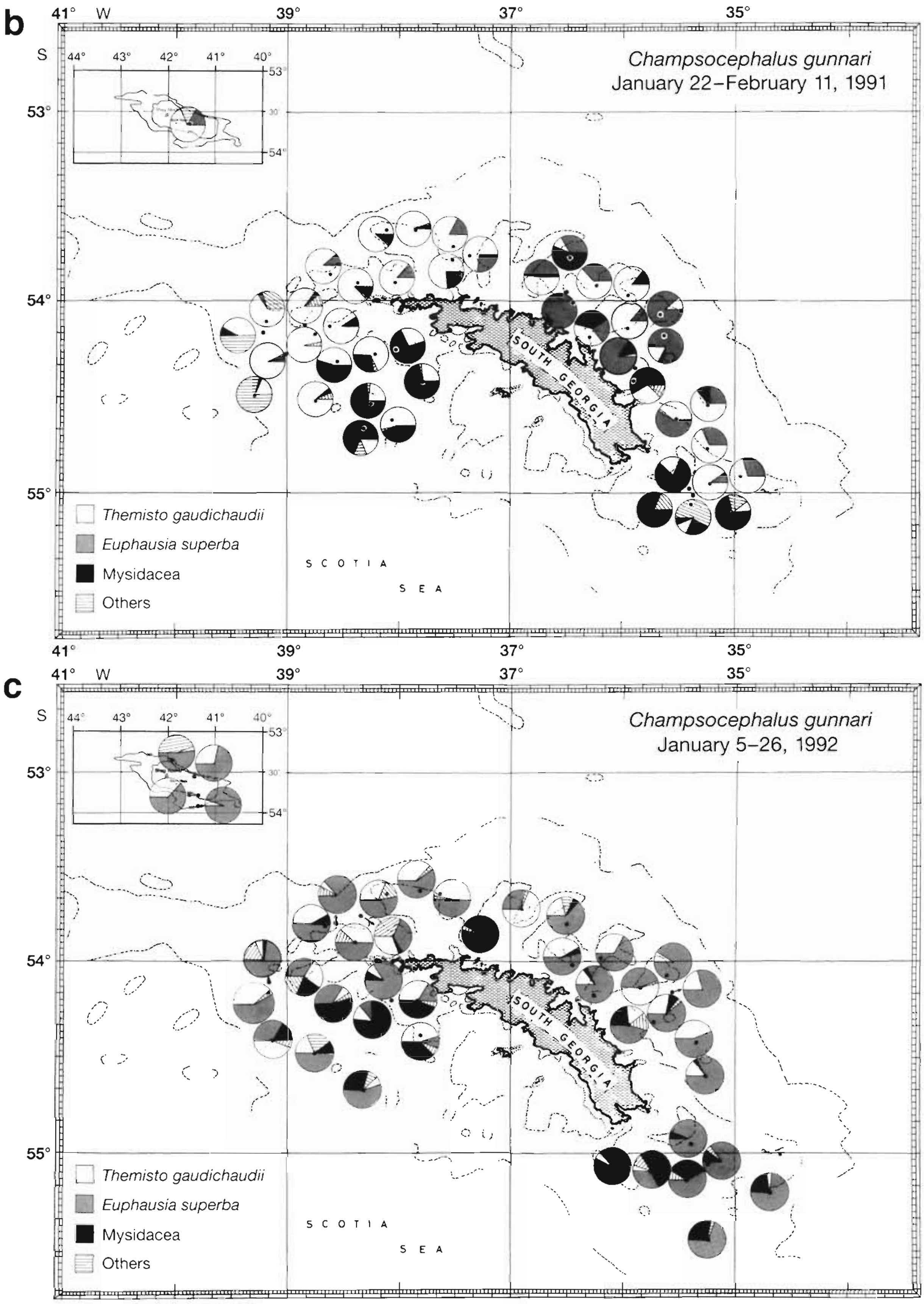
Feeding intensity

Feeding intensity varied considerably among the 3 seasons. This is clearly reflected both in the (somewhat subjective) estimate of stomach fullness (Fig. 6) and the quantitative estimate expressed as the percentage of stomach content wet weight to total fish weight (Fig. 7).

The proportion of empty stomachs was highest in 1991 and lowest in 1992. It varied considerably among stations (Fig. 8). In 1991, the proportion of empty stomachs often exceeded 40% per station, particularly in sampling sites west of 37° W (Fig. 8b). Low proportions of empty stomachs (< 20%) were only found in some stations east of Cumberland Bay (54° to 54° 20' S) and west and northwest of Clerke Rocks (54° 40' to 55° 10' S). In 1985, proportions of empty stomachs exceeded 20% only in a few sites northeast and in one station west of the island (Fig. 8a). Sampling sites with high proportions of empty stomachs in 1992 were concentrated in the east and southeast portions of the shelf and in an area south of the northern tip of the island (Fig. 8c). Stations on the eastern shelf (54° 10' to 54° 30' S) consisted to a large extent of fish of > 30 cm which were in pre-spawning or even spawning condition. Those may have reduced or ceased feeding prior to spawning (Kock 1981). No such pre-spawning or spawning aggregations were encountered in this area or in other areas of the shelf in 1985 and 1991.

The proportions of empty stomachs in the Shag Rocks area were less than 10% in 1985 and 1992 (Fig. 8a, c). In 1991, only 1 site was sampled in that region. The proportion of empty stomachs then exceeded 50% (Fig. 8b).

Feeding intensity based on stomach content wet weight in relation to fish weight rarely exceeded 4% in


b
41° W
39°
37°
35°
S
53°
54°
55°
Champsocephalus gunnari
January 22–February 11, 1991
SOUTH GEORGIA
Themisto gaudichaudii
Euphausia superba
Mysidacea
Others
SCOTIA
SEA
c
Champsocephalus gunnari
January 5–26, 1992
SOUTH GEORGIA
Themisto gaudichaudii
Euphausia superba
Mysidacea
Others
SCOTIA
SEA

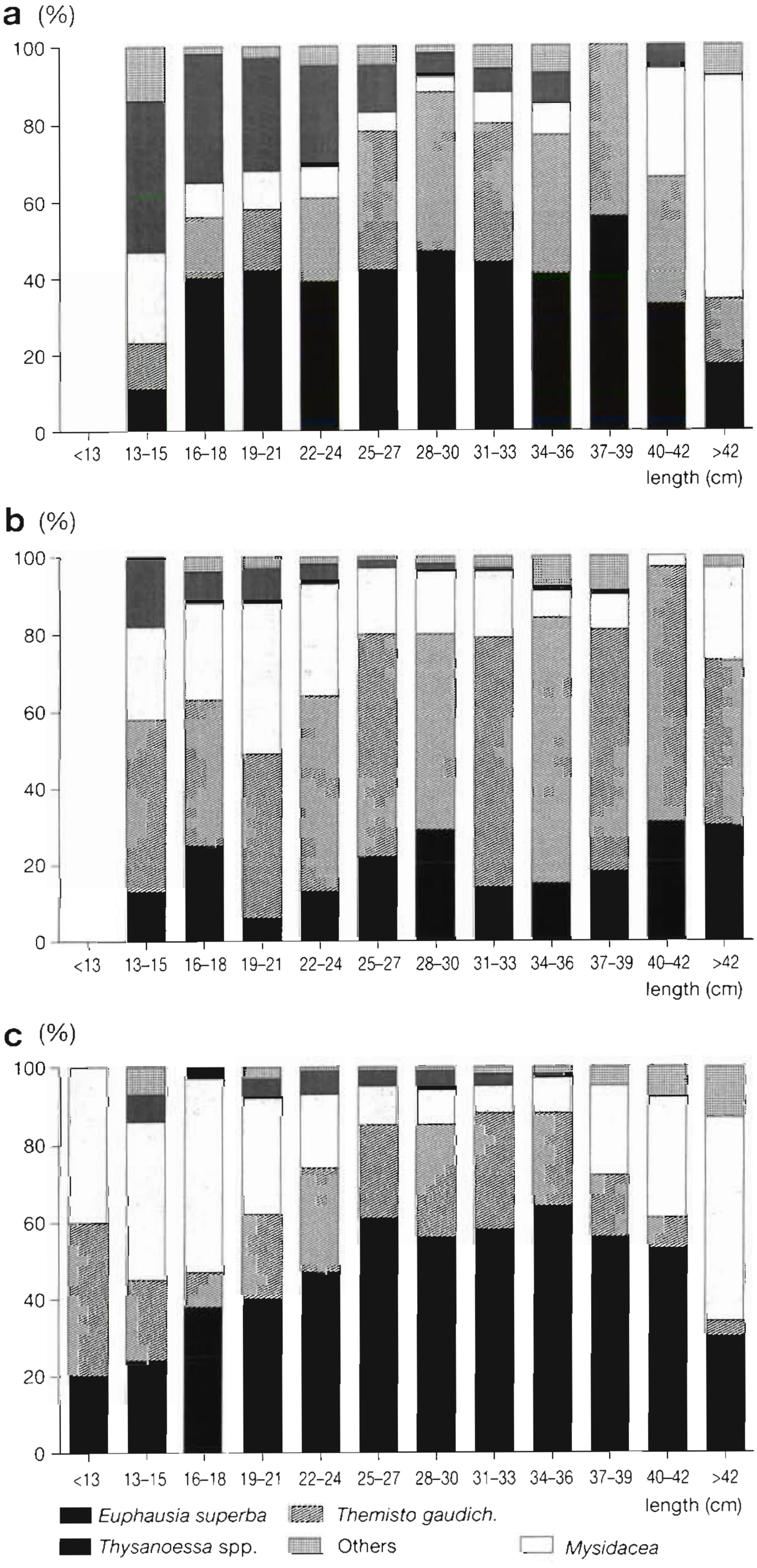


Fig. 5. *Champsocephalus gunnari*. Frequency of occurrence of the main prey items per 3 cm length class in mackerel icefish around South Georgia in (a) 1985, (b) 1991 and (c) 1992

1985 and 2% in 1991. In 1992, however, feeding intensities up to 6% were common (Fig. 7). Average feeding intensity (median, and 25% and 75% percentiles) was 1.07% (0.31 to 2.40%) in 1985, 0.27% (0.0 to 1.21%) in 1991 and 2.19% (0.63 to 4.43%) in 1992.

DISCUSSION

As could be envisaged from earlier investigations, krill, *Themisto gaudichaudii*, mysids and *Thysanoessa* sp. formed the staple food of mackerel icefish in 1985, 1991 and 1992. However, even in years of high krill abundance around the island, such as 1992, the proportion of krill in the diet around South Georgia was much lower than in the southern Scotia Arc (South Orkney Islands, South Shetland Islands) where krill commonly constitutes more than 90% of the diet (Kozlov et al. 1988, Gröhsler 1992). *T. gaudichaudii* forms an important proportion of the diet also around the Kerguelen Islands while krill is replaced by the smaller *Euphausia vallentini*, *E. similis* and by myctophids (Chechun 1984, Duhamel 1987).

With the exception of the smallest length groups the occurrence of the main food items around South Georgia varied little with length of fish suggesting little positive size selectivity. This indicates that availability was the main factor influencing diet composition and that the difference in size composition of fish between stations contributed little to the variation observed in prey composition between stations.

Estimates of median feeding intensity, at least in 1985 and 1992, fell within the ranges of values observed in other populations of the species and in other notothenioids (Gröhsler 1992, Kock 1992, Pakhomov & Tseitlin 1992). Our estimates are likely to be biased in 2 ways. Firstly, feeding of mackerel icefish probably takes place mainly during the night when fish leave the bottom and disperse in the water column (Duhamel & Hureau 1985, Frolkina & Shlibanov 1992). Secondly, decay times and gastric evacuation rates, which are dependent on prey type and

Table 5. Results of analysis of covariance (data standardized to SD = 1). *Statistically significant at $p \leq 0.05$

Y variable	*X* variable	*F* Partial	*F* Total	Marginal significance level Partial *F*	Marginal significance level Total *F*	R^2
1985 data						
Euphausia superba	Location	12.71	12.20	0.0001	0.0001	0.72
	Fish length	1.00		0.3183		
Themisto gaudichaudii	Location	8.95	8.57	0.0001	0.0001	0.65
	Fish length	0.04		0.8354		
Mysidacea	Location	6.69	6.46	0.0001	0.0001	0.58
	Fish length	1.43		0.2351		
Thysanoessa spp.	Location	23.29	22.57	0.0001	0.0001	0.83
	Fish length	4.41		0.0381		
Others	Location	1.15	1.10	0.3125	0.3616	0.19
	Fish length	0.00		0.9943		
1991 data						
Euphausia superba	Location	112.79	110.08	0.0001*	0.0001*	0.95
	Fish length	1.37		0.2433		
Themisto gaudichaudii	Location	159.50	155.65	0.0001*	0.0001*	0.96
	Fish length	1.91		0.1682		
Mysidacea	Location	124.16	121.15	0.0001*	0.0001*	0.95
	Fish length	0.77		0.3802		
Thysanoessa spp.	Location	20.47	20.08	0.0001*	0.0001*	0.76
	Fish length	4.70		0.0312		
Others	Location	20.36	19.93	0.0001*	0.0001*	0.76
	Fish length	2.79		0.0959		
1992 data						
Euphausia superba	Location	162.01	158.43	0.0001*	0.0001*	0.97
	Fish length	4.48		0.0353		
Themisto gaudichaudii	Location	98.23	96.16	0.0001*	0.0001*	0.95
	Fish length	7.06		0.0084		
Mysidacea	Location	45.57	44.57	0.0001*	0.0001*	0.89
	Fish length	1.42		0.2350		
Thysanoessa spp.	Location	66.43	65.18	0.0001*	0.0001*	0.92
	Fish length	11.51		0.0008		
Others	Location	1.85	1.86	0.0021*	0.0019*	0.26
	Fish length	2.09		0.1500		

prey size, are little known (Kock 1992). They are likely to be in the order of 48 to 72 h for krill and hyperiids (Kock 1992). Sampling in the course of the surveys was only carried out during daylight hours and stomach contents in various stages of decay were found. Hence, weight loss due to digestion should have led to an unknown downward bias in our estimates of feeding intensity. An unknown, but small proportion of fish do not empty their stomachs completely before they commence feeding again. This would positively bias estimates of feeding intensity. Feeding intensity of captive juvenile *Notothenia neglecta* (= *N. coriiceps*) fed to satiation on brown shrimp *Crangon crangon* after starva-

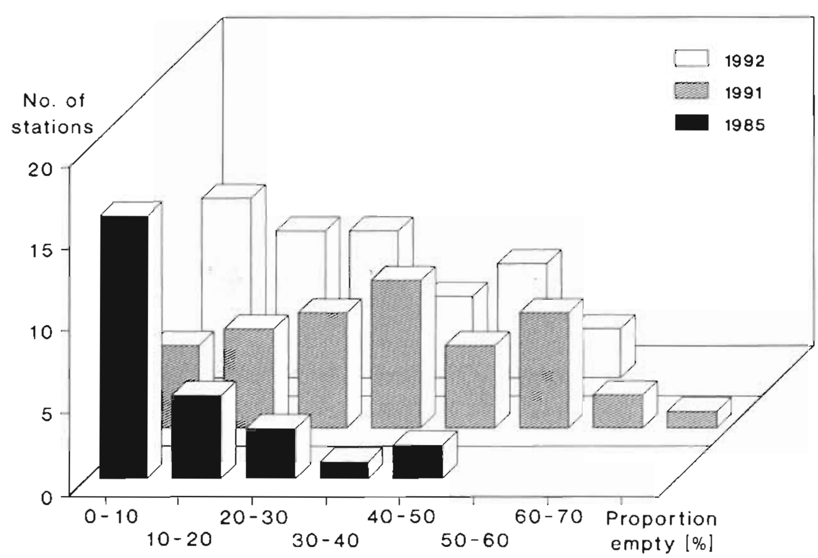


Fig. 6. *Champsocephalus gunnari*. Proportions of empty stomachs in mackerel icefish around South Georgia in 1985, 1991 and 1992

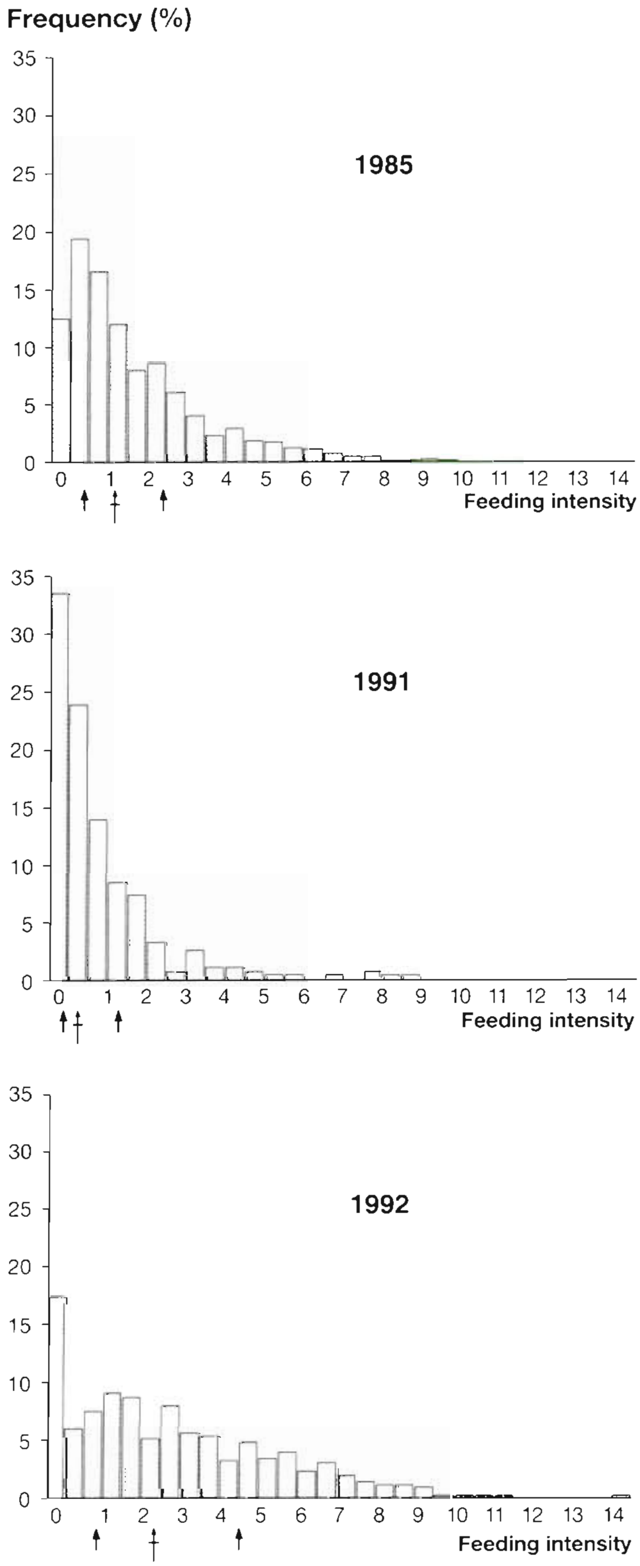


Fig. 7 *Champsocephalus gunnari*. Feeding intensity (expressed as the percentage of the stomach content wet weight to total weight of the fish) in mackerel icefish around South Georgia in 1985, 1991 and 1992. Arrows denote the median value and the 25 % and 75 % percentiles

tion was 7 to 9% (Johnston & Battram 1993), i.e. towards the upper bound of the range observed in mackerel icefish in 1992.

Our study and earlier investigations revealed considerable interannual variation in the importance of krill and *Themisto gaudichaudii* as prey items around South Georgia (Fig. 1a). Krill appears to be the preferred diet, replaced by the ubiquitous, but much smaller, *T. gaudichaudii* and sometimes *Thysanoessa* spp. in years of krill scarcity. Both species are known to form aggregations (Rustad 1930, Kane 1966) which vary with seasons and years (Hardy & Gunther 1935, Atkinson & Peck 1988). It is unlikely, however, that their aggregations are comparable in size and density with those of krill.

Lipid contents and thus energy values of *Themisto gaudichaudii* and *Thysanoessa* spp. do not appear to differ substantially from the lipid content of krill (Clarke 1984, Reinhardt & Van Vleet 1986, Hagen 1988). However, wet weights of medium-sized *T. gaudichaudii* (15 mm) and *Thysanoessa* spp. (16 mm) account for only ca 12 and 6% respectively of a medium-sized (40 mm) krill (Hagen 1988, Morris et al. 1988). Foraging on *T. gaudichaudii* and *Thysanoessa* spp. may therefore be less advantageous in energetic terms than preying on krill.

The proportion of (engibenthic) mysids in the diet remained fairly constant with the exception of a few years (1975, 1979, 1987/88) (Fig. 1a). However, sample sizes in those years were very low (Kozlov et al. 1988, McKenna 1991) and given the regular geographical pattern of occurrence in our analyses are unlikely to reflect the proportion of mysids in the diet representatively.

Considerable interannual variation exists in the distribution and abundance of krill in the vicinity of South Georgia (Everson 1992). In January/February 1985, small krill aggregations were scattered over most of the east side of South Georgia with dense concentrations only forming north of the Fortuna Bay/Stromness Bay area (ca 54° S), east of Cumberland Bay, off Gold Harbour and west of Clerke Rocks (Kock unpubl.). In January/February 1991, hardly any krill aggregations were detected on the shelf with the exception of a limited area on the east side of the island from 53° 40' to 54° 20' S (J. Watkins pers. comm.). Krill were again abundant in January 1992 with numerous dense concentrations present over most of the shelf (I. Everson & C. Goss unpubl.). This interannual variation in distribution and abundance of krill was clearly reflected in the spatial variation of the diet of mackerel icefish during the 3 years of our study.

However, one must be very cautious not to relate all year-to-year variation apparent from the various investigations on the diet of mackerel icefish since 1965

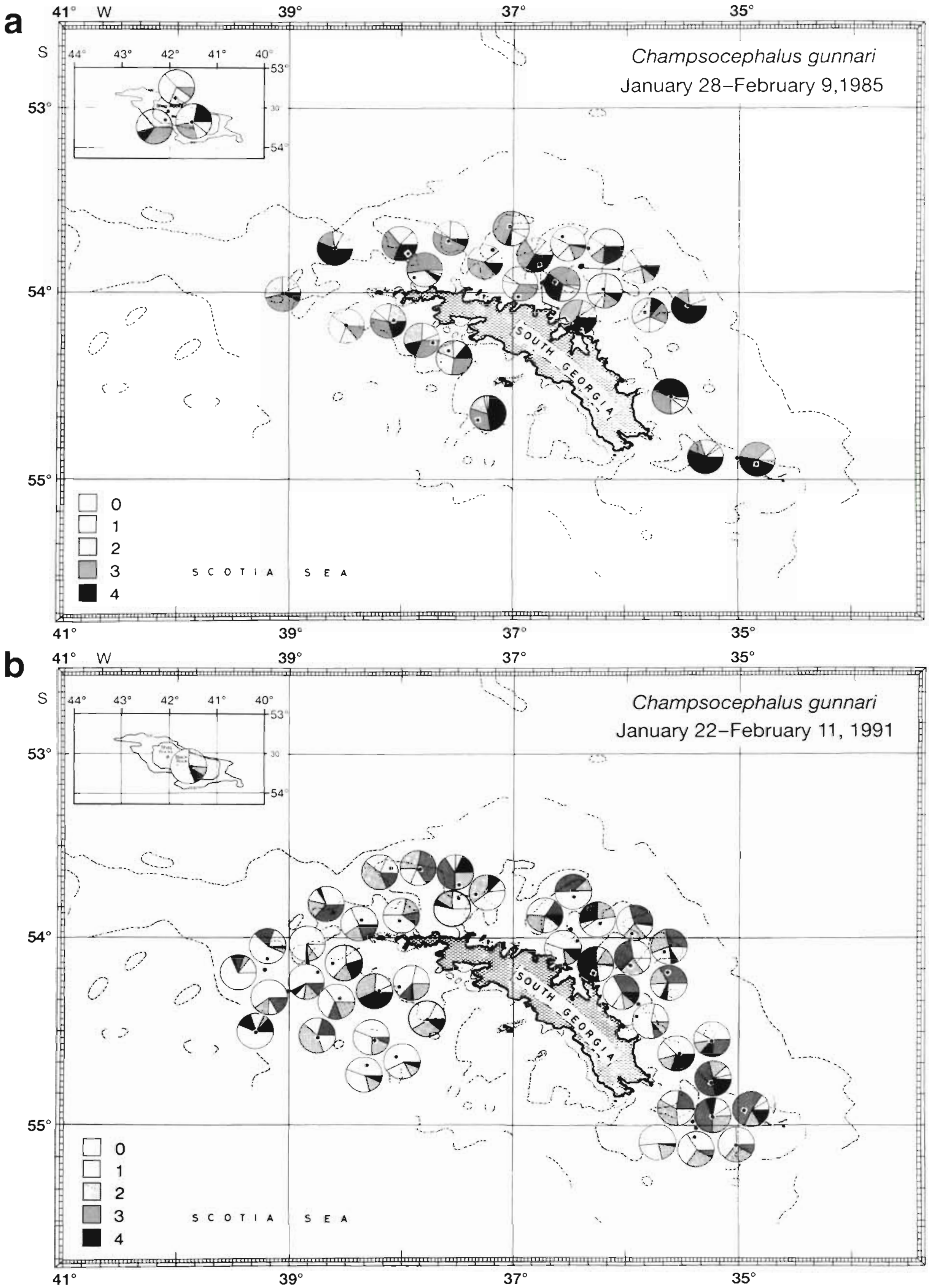


Fig. 8. *Champsocephalus gunnari.* Spatial variation in the degree of stomach fullness in mackerel icefish around South Georgia. (a) 1985, (b) 1991 and (c, overleaf) 1992

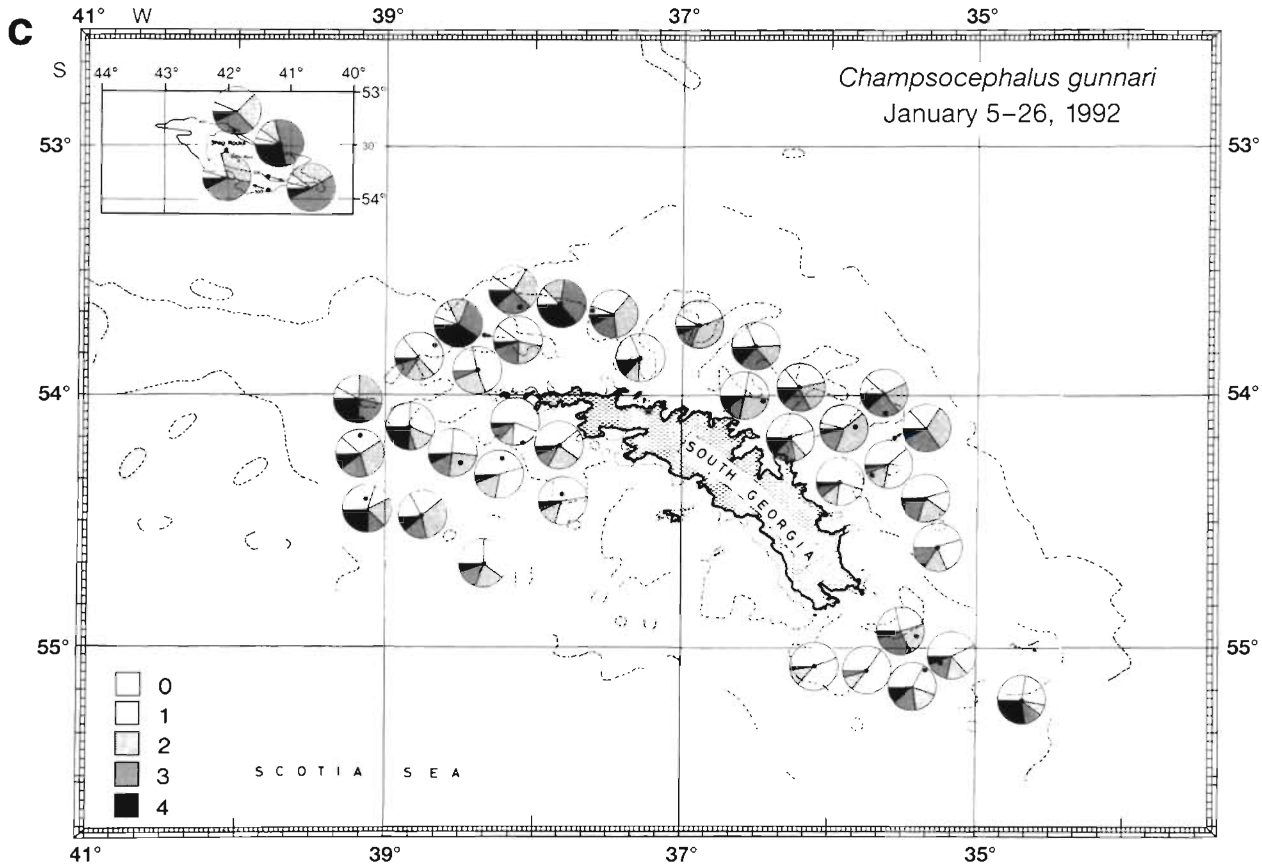


Fig. 8c (see previous page)

indiscriminately to interannual variation in the availability of krill around South Georgia. This could only be done with information on seasonal variation in the occurrence of krill around the island and the extent of sampling during each of these studies. Seasonal variation, at least over a relatively short period of several months, may be less important given the relatively slow rate of exchange of water between the Antarctic Circumpolar Current and the shelf of South Georgia (Atkinson & Peck 1988). This hypothesis is supported by observations in 1975/76 and 1977/78: net sampling and echo surveys of krill from November/December 1975 to April 1976 (Fischer 1978, Kock 1978, Pommeranz 1978) and November 1977 to March 1978 (Bonner et al. 1978, Fischer 1979, Wörner 1979) revealed a high abundance of krill in 1975/76 and a low abundance of krill in 1977/78 over the whole period of investigation. This low intra-seasonal but large inter-seasonal difference in krill abundance around the island is clearly reflected in the variation of its occurrence in the diet of mackerel icefish in 2 pairs of investigations in 1976 and 1978 (Fig. 1a, b; arrows).

Representativeness of sampling, i.e. sample size and even coverage of the distributional range of mackerel icefish, appears to be a much more crucial factor: large variations in sample size (41 to 3802) among authors (Fig. 1a) suggest non-representative sampling in some years. Excluding sample sizes ≤215 (chosen on an arbitrary basis) reduced the variation between years to some extent but not substantially (Fig. 1b). In years when sample sizes were larger (i.e. several hundred stomachs) and probably covered the range of mackerel icefish more evenly, investigations by 2 different authors in the same season or months led to essentially very similar results, such as in 1976, in 1978 and in 1985 (Fig. 1a, b; arrows). However, representativeness of sampling is difficult to assess from sample size alone when no information on the number and location of stations is given.

Despite large spatial and seasonal variations in stomach fullness the proportion of empty stomachs of mackerel icefish around South Georgia in December to February was commonly of the order of 10 to 20% (Kozlov et al. 1988). The slightly higher proportion of empty stomachs in 1992 may have been caused by the sampling of fish in prespawning and spawning condition which had already ceased feeding (Kock 1981). Feeding intensity in 1991 was substantially less than in 1985 and 1992 (Fig. 7). The high proportion of stomachs containing no or little food and the low feeding intensity in 1991 reflected a situation uncommon in most other seasons.

Despite these reservations, our results suggest that extensive food studies in mackerel icefish could serve as an indicator of krill availability over the shelf of South Georgia. They suggest that krill availability in January/February 1991 was one of lowest within the 28 yr period of observation. Krill abundance was comparable to 1977/78 (Fig. 1b), a season when krill biomass around the island was found to be very low (Bonner et al. 1978, Wörner 1979). The scarcity of krill in both seasons led to detrimental effects on the reproductive performance of krill-eating high-level predators, such as black-browed albatross *Diomedea melanophris*, gentoo and macaroni penguins *Pygoscelis papua* and *Eudyptes chrysolophus*, and Antarctic fur seals *Arctocephalus gazella* (Croxall et al. 1988, Lunn & Boyd 1993, Lunn et al. 1993, Croxall & Rothery 1994, Prince et al. 1994, Boyd et al. in press).

Part of the population of mackerel icefish around South Georgia does not spawn each year although spawning takes place annually (Lisovenko & Silyanova 1980, Sosinski 1985, Kock 1990). Such an intermission of spawning is also not uncommon in another population of the species on the Kerguelen shelf (Duhamel 1987), in Antarctic silverfish (*Pleuragramma antarcticum*) (Faleeva & Gerasimchook 1990) and in fish species outside the Southern Ocean, such as Atlantic cod *Gadus morhua*, Greenland halibut *Reinhardtius hippoglossoides* and winter flounder *Pseudopleuronectes americanus* (Thurow 1970, Fedorov 1971, Burton & Idler 1987). The proportion of mackerel icefish around South Georgia intermitting spawning varies from year to year. In January/February 1985, ca 10% of the sexually mature females were observed with gonads in resting stage (Kock 1990). However, in January/February 1978 ca 30% and in January/February 1991, ca 60% of the adult females around the mainland of South Georgia were found in non-reproductive state (Kock 1990, Everson et al. 1991). In both years, krill availability was poor (Bonner et al. 1978, Wörner 1979, J. Watkins pers. comm.).

Prior to spawning, the mass of the ovaries of mackerel icefish constitutes 20 to 30% of the total body weight (Lisovenko & Silyanova 1980, Kock & Kellermann 1991). Hence, the energy demands associated with reproduction are substantial and may temporarily exceed the energy supplied by the available food. In such cases fish have to utilize reserves accumulated when food supply is in excess of the energy demand. We do not know if prey (in particular krill) availability was as low earlier in the 1990/91 season as during the 3 wk of the survey. However, a number of observations provided evidence that this seemed to have been the case: (1) the intra-seasonal variation in the abundance of krill around the island observed in other seasons was low; (2) the condition factor of mackerel icefish in 1991 was significantly lower compared to 1992 (Everson et al. 1992c); and (3) fur seals on Bird Island arrived late, were in poorer condition, gave birth to lighter pups and had shorter perinatal periods (Lunn & Boyd 1993).

In winter flounder, low food levels reduced the recruitment of vitellogenic oocytes (Tyler & Dunn 1976). Limiting food experimentally induced the non-reproductive state in winter flounder (Burton & Idler 1987) and a reversal of the non-reproductive state by improved feeding (Burton 1991). Under these circumstances, a prolonged period of food shortage would not only have affected the condition of fish, but could have had severe consequences on the final development of the gonads and could have led to the abnormal gonad maturation processes and the high proportion of sexually mature fish in non-reproductive state observed in 1991 (Everson et al. 1991). It may be hypothesized that this is an adaptive strategy: in the face of a shortage of suitable food, if fish have been unable to refuel their energy stores sufficiently after the last spawning, gonad maturation is sacrificed for the maintenance of somatic tissue (Tyler & Dunn 1976). Omission of a spawning cycle would furthermore promote over-winter survival. However, we do not at present know if a prolonged period of food shortage alone has led to the high proportion of sexuallly mature fish in non-reproductive stage.

Acknowledgements. We are very much indebted to S. Campbell, Dr G. Parkes, J. Szlakowski, Z. Cielniaszek and C. Goss for their extensive support during the field work. We are very grateful to Drs J. P. Croxall and L. Peck, and the 3 unknown reviewers for their constructive comments on the manuscript. We are indebted to Ms Urte Harm for the preparation of some of the graphs and Dr P. Ward for the determination of the mysids collected in 1985. We gratefully acknowledge the assistance of the masters and the crews of FRV 'Walther Herwig' and MV 'Falklands Protector' The surveys were funded by the German Federal Ministries of Food, Agriculture and Forestry and of Research and Technology (1985) and by the South Georgia Commission (1991, 1992).

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This article was submitted to the editor

Manuscript first received: October 11, 1993
Revised version accepted: February 25, 1994