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ANALYSIS OF THE DIET OF *CHAMPSOCEPHALUS GUNNARI* AT SOUTH GEORGIA IN LATE SUMMER FROM 1994 TO 1997, *DR EDUARDO L. HOLMBERG* SURVEYS

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Abstract

The diet composition of the mackerel icefish (*Champsocephalus gunnari*) caught in CCAMLR Subarea 48.3 in late summer from 1994 to 1997 was analysed using frequency of occurrence (F%) and dietary coefficient (Q%) methods. Krill (*Euphausia superba*), followed by the amphipod hyperiid *Themisto gaudichaudii*, was the main food item around South Georgia and Shag Rocks in the period investigated, except in 1994, when the order of importance of these two species in the diet of *C. gunnari* was reversed. The consumption of other prey items such as mysids and *Thysanoessa* sp., which are known to be important alternative food in years of krill scarcity, as well as fish, was only occasional or negligible and varied from year to year. The spatial distribution of the main prey items in the diet of *C. gunnari*, as well as of the proportions of stomachs with/without food in Subarea 48.3, did not show a consistent pattern from year to year. Likewise, in the four surveys by the *Dr Eduardo L. Holmberg* from 1994 to 1997, high proportions of fish had empty stomachs, a phenomenon which could be caused by several concurrent factors. The variation of the diet according to the length of *C. gunnari* did not reveal any selectivity pattern for any of the prey items. The availability of krill in Subarea 48.3 during the period investigated can be defined as low in 1994 (equivalent to years of krill scarcity), intermediate in 1995 (below years of historically high abundance), and high in 1996 and 1997 (in line with years of high krill abundance). This information is well in accord with independent information from acoustic surveys and krill-dependent species monitored under the CCAMLR Ecosystem Monitoring Program (CEMP).

Résumé

Dans le présent document, les auteurs analysent la composition du régime alimentaire du poisson des glaces (*Champsocephalus gunnari*) capturé dans la sous-zone 48.3 de la CCAMLR à la fin de l'été, de 1994 à 1997, à partir de méthodes de fréquence d'observation (F%) et de coefficient alimentaire (Q%). Le krill (*Euphausia superba*) était la principale source d'alimentation autour de la Géorgie du Sud et des îlots Shag pendant la période étudiée, suivi de l'amphipode hyperiid *Themisto gaudichaudii*, sauf en 1994 où l'ordre d'importance de ces deux espèces était inversé dans le régime alimentaire de *C. gunnari*. La consommation d'autres proies telles que des mysides et *Thysanoessa* sp., alimentation de remplacement les années où le krill est rare, ainsi que de poissons, n'était qu'occasionnelle ou négligeable et variait d'une année à une autre. Aucune tendance régulière d'année en année dans la sous-zone 48.3 ne découle de la distribution spatiale des principales proies dans le régime alimentaire de *C. gunnari*, ni de la proportion d'estomacs vides/remplis. De plus, dans les quatre campagnes d'évaluation effectuées par le *Dr Eduardo L. Holmberg* de 1994 à 1997, une proportion élevée de poissons avaient l'estomac vide, phénomène qui pourrait résulter de plusieurs facteurs simultanés. La variation du régime alimentaire en fonction de la longueur de *C. gunnari* ne révèle pas de tendance de sélectivité de l'une des proies. La disponibilité du krill dans la sous-zone 48.3 pendant la période étudiée peut être définie comme étant faible en 1994 (équivalente aux années où le krill est rare), moyenne en 1995 (inférieure aux années connues pour leur grande abondance) et élevée en 1996 et 1997 (allant de pair avec les années de grande abondance). Ces informations confortent les informations indépendantes fournies par les campagnes d'évaluation acoustique et les suivis des espèces dépendant du krill effectués dans le cadre du Programme de contrôle de l'écosystème de la CCAMLR (CEMP).

Резюме

Состав рациона ледяной рыбы (*Champsocephalus gunnari*), выловленной в Подрайоне 48.3 АНТКОМа в конце каждого лета с 1994 по 1997 г., исследовался

с помощью методов, основанных на частоте встречаемости (F%) и коэффициенте рациона питания (Q%). В районах Южной Георгии и скал Шаг первое и второе места в рационе питания заняли криль (*Euphausia superba*) и амфипод *Themisto gaudichaudii* соответственно во все годы исследования за исключением 1994 г., когда по важности в рационе *C. gunnari* эти виды поменялись местами. Потребление других объектов питания, таких как мизид и видов рода *Thysanoessa*, являющихся важной альтернативной пищей в годы дефицита криля, а также рыбы, было случайным или ничтожным и носило изменчивый характер из года в год. В Подрайоне 48.3 не наблюдалось четко выраженной межгодовой закономерности пространственного распространения ни основных объектов питания в рационе *C. gunnari*, ни долей желудков с пищей/без пищи. Четыре съемки, выполненные с судна *Dr Eduardo L. Holmberg* с 1994 по 1997 г., выявили большие доли рыб с пустыми желудками, что может объясниться рядом совпадающих факторов. Состав рациона *C. gunnari* в зависимости от длины не указал на существование какой-либо селективности при выборе различных объектов питания. Наличие криля в Подрайоне 48.3 было низким в 1994 г. (эквивалентно уровню в годы дефицита криля), средним в 1995 г. (ниже уровня в годы исторически высокой численности) и высоким в 1996 и 1997 гг. (приблизительно на том же уровне, что и в годы высокой численности криля). Эта информация хорошо согласуется с информацией, полученной в результате акустических съемок и мониторинга питающихся крилем видов в рамках Программы АНТКОМа по мониторингу экосистемы (CEMP).

Resumen

Se analizó la composición de la dieta del draco rayado (*Champsocephalus gunnari*), capturado en la Subárea 48.3 de la CCRVMA al final de los veranos de 1994 a 1997, mediante los métodos de frecuencia de ocurrencia (F%) y coeficiente alimentario (Q%). El kril (*Euphausia superba*), seguido por el anfípodo hipérido *Themisto gaudichaudii*, fue el componente principal de la dieta de *C. gunnari* alrededor de Georgia del Sur y de las Rocas Cormorán durante el período de investigación, excepto en el año 1994, cuando se invirtió el orden de importancia de estas dos especies. La ingestión de otras presas tales como misidáceos y *Thysanoessa* sp., que se sabe representan una fuente de alimento alternativa en años de escasez de kril, como así también el consumo de peces, fue ocasional o insignificante, y varió de un año a otro. La distribución espacial de los componentes principales de la dieta de *C. gunnari*, y la proporción de estómagos con alimento y vacíos en la Subárea 48.3 no mostraron un patrón definido de un año a otro. Asimismo, en los cuatro estudios efectuados por el *Dr Eduardo L. Holmberg* desde 1994 hasta 1997, se observó que una alta proporción de peces tenían estómagos vacíos, fenómeno que puede atribuirse a una serie de factores que actúan en forma simultánea. La variación de la dieta en función de la talla de *C. gunnari* no reveló un patrón de selectividad para ninguno de los componentes de la dieta. La disponibilidad de kril en la Subárea 48.3 durante el período de estudio puede definirse como: baja en 1994 (equivalente a años de escasez de kril), intermedia en 1995 (menor que en años de gran abundancia histórica), y alta en 1996 y 1997 (equivalente a años de gran abundancia de kril). Esta información está de acuerdo con datos independientes provenientes de prospecciones acústicas y de estudios de seguimiento de especies dependientes de kril realizados en el marco del Programa de Seguimiento del Ecosistema de la CCRVMA (CEMP).

Keywords: icefish, diet, feeding, krill, South Georgia, CCAMLR

INTRODUCTION

The mackerel icefish (*Champsocephalus gunnari*) is one of the commercially important species of interest to CCAMLR. The fishery for this species started in the Atlantic and the Indian sectors of the Antarctic in the early 1970s (CCAMLR, 1990a). In the Atlantic sector, *C. gunnari* has been caught mainly around South Georgia and Shag Rocks – intensively up to the end of the 1980s and at lower levels up to the early 1990s (CCAMLR, 1990b, 1997).

Several studies have focused on the diet composition of *C. gunnari* (reviewed in Kozlov et al., 1988; Kock et al., 1994a). Together with other

Table 1: Details of fish samples examined.

Year/Month	Area	Number of Stations Sampled	Processed	Number of Stomachs Examined	Empty	Length Range (TL in cm)
1994 (Feb–Mar)	Shag Rocks	7	7	163	73 (45%)	18–29
	South Georgia	54	37	473	156 (33%)	12–56
1995 (Feb)	Shag Rocks	6	5	249	99 (40%)	22–36
	South Georgia	43	32	1 070	302 (38%)	11–54
1996 (Mar–Apr)	Shag Rocks	7	6	372	211 (57%)	21–38
	South Georgia	30	27	826	458 (56%)	12–54
1997 (Mar–Apr)	Shag Rocks	7	7	320	291 (91%)	18–41
	South Georgia	36	31	972	397 (41%)	10–55

biological and oceanographic information (e.g. reproductive aspects, physical-chemical parameters), knowledge of the seasonal and interannual variation in the feeding patterns of *C. gunnari* may be useful for the interpretation of the interannual variability in stock size. In addition, the diet composition of *C. gunnari* can be used as an indicator of variability in the abundance of krill, which is its main food source (Kock et al., 1994a).

We present here an analysis of the stomach contents together with relevant observations on the reproductive condition of *C. gunnari* from South Georgia (CCAMLR Subarea 48.3), using samples collected during cruises of the RV *Dr Eduardo L. Holmberg* in late summer from 1994 to 1997*. Earlier studies on this matter carried out in Subarea 48.3 are summarised in Kock et al. (1994b).

MATERIALS AND METHODS

Materials for this study were collected during four consecutive surveys of the RV *Dr Eduardo L. Holmberg* in Subarea 48.3 in late summer from 1994 to 1997. The surveys were organised and sponsored by the 'Instituto Antártico Argentino' in conjunction with the 'Instituto Nacional de Investigación y Desarrollo Pesquero'. Since the ship was not available for the same periods each year, there was a maximum difference in starting time of 38 days (discussed below). The stomach contents of 4 445 specimens of *C. gunnari* were analysed. In addition, gonad maturation stages were determined according to a five-point scale (Kock and Kellermann, 1991). In larger catches, the fish were subsampled to cover all the sizes present in the samples; in smaller catches, the whole catch was analysed. In order to facilitate comparisons, information for South Georgia (SG) and Shag Rocks (SR) is presented separately and in formats compatible with previous studies submitted to the CCAMLR Working Group on Fish Stock Assessment (WG-FSA). Details of fish samples examined are given in Table 1.

Minimum and maximum sample sizes taken for each haul were determined using the expression $s = \sqrt{n\ p\ q}$, where p is the proportion to be estimated, $q = 1 - p$, s is the estimated standard error of the proportion and n is the sample size. A sample size of 6 provides estimates with CVs (coefficient of variation) of about 20% or smaller, while a sample size of 25 ensures CVs of at least 10%. We established a maximum n of 50, which yields CVs better than 7%.

In the 1994 survey, a set of sampling sites was selected along random tracks with the aim of obtaining even areal coverages in three depth and four geographical strata (see Marschoff et al., 1994 – Table 2). In the subsequent surveys, this set of sampling sites was maintained and enlarged on the same basis. Only those samples with $n > 6$ specimens were included in the analysis. At least in 60% of the stations in 1995 (60%), 1996 (61%) and 1997 (61%) n was ≥25. In 1994, n in 40% of the stations was ≥20, mainly due to the low abundance of *C. gunnari* in that year (see below).

Except on a few occasions (four 24-hour stations in 1994), catches were obtained during daylight, from 0700 to 1900 hours (see details in Marschoff et al. 1994, 1995, 1996, 1997). During the first leg (February) of the 1994 survey, stomach contents were analysed qualitatively on board immediately after the catch was taken. On the second leg of the 1994 survey and during the

* Data from the 1994 survey have been partially presented in Barrera-Oro et al. (1997).

next three surveys, stomachs were frozen at -30°C and later examined at the Instituto Antártico Argentino. For the aim of this study, the main food items were identified and grouped into the following categories: krill (*Euphausia superba*), *Themisto gaudichaudii*, mysids (mostly *Antarctomysis maxima*), *Thysanoessa* sp. and fish (Channichthyidae, Myctophidae). The presence of other taxa (e.g. other *Euphausia* spp.) was negligible (F% < 0.5) and therefore the category 'others' is not described in detail in this work.

The diet of *C. gunnari* was analysed by the frequency of occurrence of each prey item, expressed as a percentage of all stomachs containing food (F%). Except for those stomachs with highly digested contents, all stomachs collected in the 1994, 1996 and 1997 surveys were also analysed using the Hureau method (Hureau, 1970). According to this method, dietary data are expressed in terms of the dietary coefficient 'Q', which is the product of the percentage by number and the percentage by weight of each prey type. Overall, in 6% of the stomachs the material was too digested to be identifiable.

Although the frequency-of-occurrence method presents shortcomings and advantages, in general this procedure is used because it allows quick comparison among the results of similar dietary studies (see Kock et al., 1994a). However, this method does not discriminate between the number or weight of organisms of single prey items, indicating only 'presence' or 'absence' and therefore is very sensitive to small amounts of prey. The coefficient 'Q' gives a more consistent measure of the importance of each prey type in the diet because it combines numeric and weight data. The difficulty with the first method is evident in our analysis of data from the 1994 survey, in which the importance of krill in the diet is overestimated by the frequency-of-occurrence method, when compared with the dietary coefficient 'Q' (Hureau, 1970).

The index of stomach fullness was evaluated according to a five-point scale: 0 (empty), 1 (25% full), 2 (50% full), 3 (75% full), 4 (100% full).

During the four surveys, *C. gunnari* was caught in all the trawls but one around SR. Around SG, its frequency of occurrence at the stations increased from 72% in 1994 to 84% in 1995, 95% in 1996 and 94% in 1997. In order to estimate the relative weight of each size class, all results were recalculated for the whole population of *C. gunnari* in the area (Marschoff et al., 1996).

The length compositions (total length = TL) of fish are expressed in 1-cm intervals. For the analysis of prey in relation to the size of *C. gunnari*, fish were grouped into 3-cm size classes.

RESULTS

Size Composition

The length compositions of *C. gunnari* sampled during each of the surveys are represented in Figure 1. The size range was from 7 to 62 cm. Around SG in 1994 and 1995, there were two peaks, 14–18/21–25 cm and 13–15/25–28 cm respectively, which, according to age/length keys elaborated with material from the 1994 and 1995 surveys, correspond to age groups 1 to 3 years (Barrera-Oro et al., 1994, 1995). In 1996 and 1997 fish between 16 and 20 cm predominated; in 1997 a peak between 25 and 30 cm was also evident. At SR, the range of predominant sizes was narrower. It should be noted that in this area at depths deeper than 250 m we were unable to find suitable grounds for trawling.

Diet Composition

The frequency of occurrence (%) of the main prey items found in the stomachs of *C. gunnari* is represented in Figure 2, where values are weighted to give a total of 100%. Data for SR in 1997 were not included due to the limited number of stomachs containing food. Krill, followed by *T. gaudichaudii*, was the main prey item in all four years. Mysids were eaten occasionally in 1995 around SG (4%) and SR (8%) and in 1996 around SR (11%); they occurred in small quantities in the rest of the samples (only 1% around SG in 1994). Fish were more frequently found in stomachs around SG in 1994 (7%) and 1997 (6%). *Thysanoessa* sp. were eaten around SG occasionally (6% in 1997) or in negligible amounts (0.7% in 1995, 0.5% in 1996). They were frequent prey items around SR only in 1995 (35%).

Occurrence of Krill in the Diet

For the purpose of interpreting the availability of krill in the area based on a dietary analysis of *C. gunnari* by frequency of occurrence, we have compared our data to the series of historical data (Kock et al., 1994b) (Figure 3). In the 1994 survey by RV *Dr Eduardo L. Holmberg* krill was eaten with

frequencies of 66% (43% as the sole prey of *C. gunnari*) at SG and 81% (77% as sole prey) at SR, values which fall within the range of krill abundance (Figure 2). In 1995 an intermediate presence of krill was observed around SG (38% as sole prey) and very low levels around SR (13% as sole prey). In 1996 and 1997 a high occurrence of krill as sole prey was noted in Subarea 48.3 (72% and 88% at SG and 81% and 75% at SR respectively); this is in line with the years of high krill abundance 1975 to 1977, 1985 and 1992 (65–83%) (Figure 3).

In order to test the reliability of the results of dietary analysis from the RV *Dr Eduardo L. Holmberg* surveys obtained using the frequency-of-occurrence method, many stomach samples (except in 1995) were also analysed by using the Hureau method (Hureau, 1970) (Figure 4). For the dataset of 1994, this analysis gave different results to those obtained by the first method: the dietary coefficient (Q%) showed a greater importance of *T. gaudichaudii* (75–80%) than krill (20–25%) in both the SG and SR areas. For the datasets of 1996 and 1997, the Hureau method (Hureau, 1970) confirmed the results obtained by the frequency-of-occurrence method: it highlighted the importance of krill in the diet (99%) compared to other prey items (e.g. at SG, *T. gaudichaudii* ≤1%, others negligible).

Spatial Distribution of the Main Food Items in the Diet

The spatial distribution of the main prey items in the diet of *C. gunnari* in the area of investigation is shown in Figure 5. Only stations with $n > 6$ stomachs with food are represented. In the four RV *Dr Eduardo L. Holmberg* surveys, the main prey krill and *T. gaudichaudii* occurred in stomachs at most of the stations without a definite spatial pattern, except for an apparent higher concentration of krill in the southeastern part of the SG shelf (south of 54°55'S) in February 1995 and in March/April 1997. At one station in this zone in the 1995 survey, a large number of *Notothenia rossii* specimens were caught, most of which had preyed intensively on *C. gunnari* (TL = 12–20 cm) and, secondarily, on krill. *C. gunnari* of the same length range were taken in the same catch. Their stomachs exhibited a high frequency of occurrence of krill (73%), similar to that observed in the stomachs of those specimens ingested by *N. rossii*. This fact might also indicate that the presence of krill was higher in that particular zone.

Considering the four sampling periods around SG, krill and *T. gaudichaudii* were seldom found as sole prey items (1–3 and 1–2 stations respectively). As expected, there was interannual spatial variation in the occurrence of other less-important food items: e.g. the fairly uniform distribution of mysids around SG only in February 1995 and the higher occurrence of *Thysanoessa* sp. in the northeastern and eastern portions of the shelf in March/April 1997 (Figure 5).

Feeding Intensity

Evaluation of stomach fullness showed high proportions of empty stomachs in the four RV *Dr Eduardo L. Holmberg* surveys from 1994 to 1997 (Figure 6). In 1996 and 1997, these proportions were the highest of the series (41–56% at SG; 57–91% at SR). The association of sampling time and fish size with the proportion of empty stomachs in these two surveys was tested using the Spearman rank coefficient. Sampling times covered the period from 0700 to 1900 hours and the association was studied on a haul-by-haul basis. Fish lengths were grouped in 3-cm intervals, and the proportion of empty stomachs was calculated for each length, taking into account the weighting system used to calculate length distributions. These two association coefficients were not significant in both years (Table 2).

Table 2: Spearman association coefficients (r) between sampling time/fish size and the proportion of empty stomachs in 1996 and 1997.

Year	Sampling Time	Fish Size
1996	$r = -0.11$ $P > 0.05$	$r = -0.44$ $P > 0.2$
1997	$R = -0.13$ $P > 0.4$	$R = -0.11$ $P > 0.5$

In general, this study shows more food available around SG (fewer empty stomachs, higher degrees of stomach fullness: 2–4), except in 1996 (Figure 6). In that year, food availability may have been homogeneous in the whole area, since the profiles of the proportions of degrees 0–4 were parallel around SG and SR.

The spatial distribution of the proportions of stomachs with/without food in the area of investigation did not show a consistent pattern from year to year (Figure 7). In February/March 1994, a sequence of six stations with lower

proportions of empty stomachs (<22%) compared to the average value (33%) was observed in the northern shelf of SG (around 37°00'S, 54°00'W). In February 1995, the distribution of empty stomachs around SG did not show a definite pattern, with values about average (except in isolated cases). In March/April of 1996 and 1997 empty stomachs predominated in the north-western region of the SG shelf (around 54°05'S, 38°30'W in 1996 and 54°10'S, 39°00'W in 1997). In March/April 1997 empty stomachs were also predominant in the south of the region (around 55°00'S, 37°00'W) and highly so at SR (91% on average) (Figure 7).

Variation of Diet with Fish Length

In general, variation in the diet with respect to the length of *C. gunnari* around SG did not show a pattern for any of the prey items (Figure 8). In March/April of 1996 and 1997, which according to this study were years of high krill abundance, the preference for this item by all fish length groups was evident (Figure 8).

Reproductive Condition

The reproductive condition of *C. gunnari* was analysed for the 1994 (Macchi and Barrera-Oro, 1995, discussed below) and 1996 RV *Dr Eduardo L. Holmberg* surveys. In 1996, the survey was carried out in March/April, well within the spawning months of *C. gunnari* (March to May), when the greatest availability of food is necessary for final ovarian maturation. The proportion of 1996 spawners, represented by fish with ovaries in advanced, total and post-spawning maturity stages, was high, representing 56% of the total number of fish sampled and 79% of mature fish. In the same year, no significant association was found between the proportion of empty stomachs (56%) and ovarian maturation stages ($r = 0.82$, $P = 0.09$). About 60% of the fish in total spawning or spent condition (stages IV and V) exhibited empty stomachs.

DISCUSSION

Analysis of the length compositions of *C. gunnari* shows that, in comparison to data from the 1991 and 1992 surveys (no data available for 1993) (Kock et al., 1994a), a higher proportion of small fish (ranges 12–20 cm/1–2 years) was found in the catches during the RV *Dr Eduardo L. Holmberg* surveys over the whole sampling period from 1994 to 1997 (Figure 1).

Although other methods of diet analysis have been recently proposed in the literature (i.e. logistic regression, Stefansson and Palsson (1997)), we preferred to use a methodological approach which enabled us to compare our data with historical datasets.

Our results of diet composition analysis of *C. gunnari* using the frequency-of-occurrence method are compared with analogous data from previous surveys in the region (1967–1994), reported and compiled by Kock et al. (1994b) (Figure 3). As in the historical data series, krill and *T. gaudichaudii* constituted the main food items in all four years, showing interannual variation in their importance in the diet (Figure 2). Mysids were eaten only occasionally in 1995 and 1996, whereas they were virtually absent in the stomachs in the rest of the samples. Likewise, an unusually 'high' proportion of fish was found to be a food item around SG in 1994 and 1997. Euphausiids of the genus *Thysanoessa*, known to be an important alternative food in years of krill scarcity, were found in the stomachs of *C. gunnari* around SG in small (1997) or negligible quantities (1995, 1996) and were a frequent prey item only around SR in 1995.

The results of dietary analysis (by F%) of the 1994 RV *Dr Eduardo L. Holmberg* survey are in contrast to those obtained approximately one month earlier (January/February 1994) in the same area during the RV *Cordella* survey (Kock et al., 1994b), where krill was very scarce in the stomachs (6–8% at SG and SR), being virtually replaced by *T. gaudichaudii* (69% at SG, 56% at SR), mysids (24% at SG) and *Thysanoessa* sp. (40% at SR). Furthermore, according to those data the occurrence of krill in the diet of *C. gunnari* was the lowest registered for cruises carried out over the last 30 years, even lower than in 1977/78 and 1991, years of krill 'shortage' (Figures 2 and 3) (Kock et al., 1994b; this study).

During the RV *Cordella* survey, the sample size ($n \geq 30$) and sampling density were larger than during the RV *Dr Eduardo L. Holmberg* 1994 survey. However, it is unlikely that the discrepancies regarding the occurrence of krill and other prey (e.g. mysids at SG) between the two surveys are due only to methodological differences (Kock et al., 1994b).

The difference found between the two 1994 cruises concerning the frequency of occurrence of krill in the diet of *C. gunnari* may be related to a slight increase in dispersed krill, which might have occurred in the four-week period between

surveys. During the 1994 RV *Dr Eduardo L. Holmberg* survey, a change was detected in surface temperature around South Georgia of about -0.5 to -1.0°C over a period of 20 days. Such a change can only be explained by water movements, and not by cooling of local water masses which could have favoured the entrance of krill into the region investigated.

The occurrence of the main prey items around SG did not show a variation pattern associated with the length of *C. gunnari* (Figure 8). This agrees with the results of Kock et al. (1994a) for 1985, 1991 and 1992. The clear preference for krill by all the fish length groups in 1996 and 1997, years of high krill abundance, supports earlier findings by Kock et al. (1994a) that variation in diet composition is mainly influenced by prey availability and is not due to size selectivity.

High proportions of empty stomachs were found in the four RV *Dr Eduardo L. Holmberg* surveys from 1994 to 1997 (Figure 6). The historical range for the period December to February is 10 to 20% (Kozlov et al., 1988). Moreover, our values for empty stomachs for 1996 and 1997 (41–56% at SG; 57–91% at SR) are in line with or even higher than those reported for 1991 (40–50%, Kock et al., 1994a) and 1994 (40–60%, Kock et al., 1994b; 33–45%, this study) when krill was scarce. This seems to be in disagreement with our results of dietary analysis for 1996 and 1997, which indicate that a lot of krill was available for *C. gunnari*. This could be related to the fact that when krill are abundant they form dense but spatially separated aggregations, resulting in non-uniform krill availability.

It was also observed that in 1996 and 1997, the association of sampling time and fish size with the proportion of empty stomachs was not significant (Table 2). The possibility that a fraction of the fish caught regurgitates due to abrupt pressure changes during net hauling operations was considered, but this effect should also have been observed in previous surveys.

The reproductive success of *C. gunnari* off South Georgia could be closely related to the availability of krill, its main food source (Kock et al., 1994a). This suggestion is based on the high proportion of sexually mature fish (up to 60%, in comparison to historical values of 15–20%) that did not spawn at South Georgia in the 1991 summer season, in concurrence with a low density of krill in the area (Everson et al., 1991). A similar situation was observed in 1994: a histological analysis of the gonadal development in *C. gunnari* from specimens collected during the RV *Dr Eduardo L. Holmberg* survey in 1994 showed that 41% of the mature females exhibited ovaries in a pre-reproductive regression stage and it was consequently suggested that a high proportion of the sampled population did not spawn in that season (Macchi and Barrera-Oro, 1995). The regression stage is also called 'atresia' and has been previously reported by Everson et al. (1991), who indicated the macroscopical resemblance of this condition to a normal stage 2. The apparent reproductive failure of *C. gunnari* in the area agrees well with the results obtained from the dietary analysis, indicating a low abundance of krill around South Georgia during the 1994 summer season.

The high proportion of 1996 spawners (nearly 80% of mature fish) is in the range known for years of high food availability (75–85%), in contrast to the low values reported for 1991 and 1994 when there was a shortage of krill (40% and 59% respectively, see Everson et al., 1991; Macchi and Barrera-Oro, 1995). These facts support the hypothesis that krill was abundant in the area in the 1996 summer season, and the high proportion of empty stomachs found (56%) might be also related to factors other than seasonal food availability, such as the reproductive stage (Kock, 1981, fide Kock et al., 1994a). We found no statistically significant association at the 5% level between the proportion of empty stomachs and the ovarian maturation stages. However, the low value of the test probability ($r = 0.82$, $P = 0.09$) suggests the existence of an underlying biological relationship. The assumption that *C. gunnari* stop feeding during spawning (as does, for example, *Dissostichus eleginoides*) was also considered: 63% of the fish in total spawning or spent condition had not eaten, but these represented only 19% of all the empty stomachs found.

Around the SG shelf, aggregations of krill have usually been found in years of high krill abundance (e.g. 1985 and 1992); this phenomenon is reflected in the spatial variation of the diet of *C. gunnari* (Kock et al., 1994a). During the 1994 RV *Dr Eduardo L. Holmberg* survey no such aggregations were detected by acoustic methods (120 kHz), a result in agreement with density estimates for the area in the same season (Brierley and Watkins, 1995). Likewise, the information derived from krill-dependent species such as gentoo penguins (*Pygoscelis papua*) and fur seals (*Arctocephalus gazella*) under the CCAMLR Ecosystem Monitoring Program (CEMP), also

indicated that in the 1993/94 season krill availability around SG was very low (SC-CAMLR, 1995). A similar situation is reported in Kock et al. (1994a) for the 1977/78 and 1991 seasons, when the occurrence of krill in the diet of *C. gunnari* was very low. These years have been reported as krill scarce, which had a detrimental effect on krill-eating predators such as the black-browed albatross (*Diomedea melanophris*), macaroni penguin (*Eudyptes chrysolophus*), gentoo penguin and fur seal (Kock et al.,1994a).

Fairly large numbers of krill aggregations were observed by hydroacoustic means during the RV *Dr Eduardo L. Holmberg* surveys from 1995 to 1997, which is in agreement with other information available on krill abundance, obtained using hydroacoustics, as well as predator data (SC-CAMLR, 1995, 1996, 1997). In 1994/95 the indices of reproductive success in gentoo penguins and fur seals indicated normal krill availability, contrasting with the previous season. In 1995/96 krill density estimates were much higher than those obtained in 1994 and are reflected in the improved breeding success of predators. In 1996/97 predator reproductive success was the best in the last four years, while krill biomass densities were comparable with those in the previous year and were relatively high for the region.

The results of the study of *C. gunnari* diet and the evidence obtained from the analysis of the ovarian maturation stages provide an insight into the interannual variation of krill availability in Subarea 48.3 over the period investigated. In February/March 1994 krill abundance was low, equivalent to those years of krill scarcity. In February 1995 krill availability was somewhat below the years of high abundance, but certainly above the 1994 level. In March/April of 1996 and 1997 krill was available in large quantities, in line with the years of high krill abundance, but a large proportion of fish exhibited empty stomachs at levels even higher than those reported for years of krill shortage. This last finding might be caused by several concurrent factors. The interannual variation in the consumption of other less-important prey such as *T. gaudichaudii*, *Thysanoessa* sp., mysids and fish is related to the abundance of krill in the area. During the period studied, information on krill availability derived from the stomach contents of *C. gunnari* is well in accord with independent information from acoustic surveys and krill-dependent species monitored under CEMP.

While food availability studies are probably not able to predict the strength of any particular fish species year class, they are a valuable tool for understanding the biological phenomena underlying the highly variable dynamics of the *C. gunnari* population.

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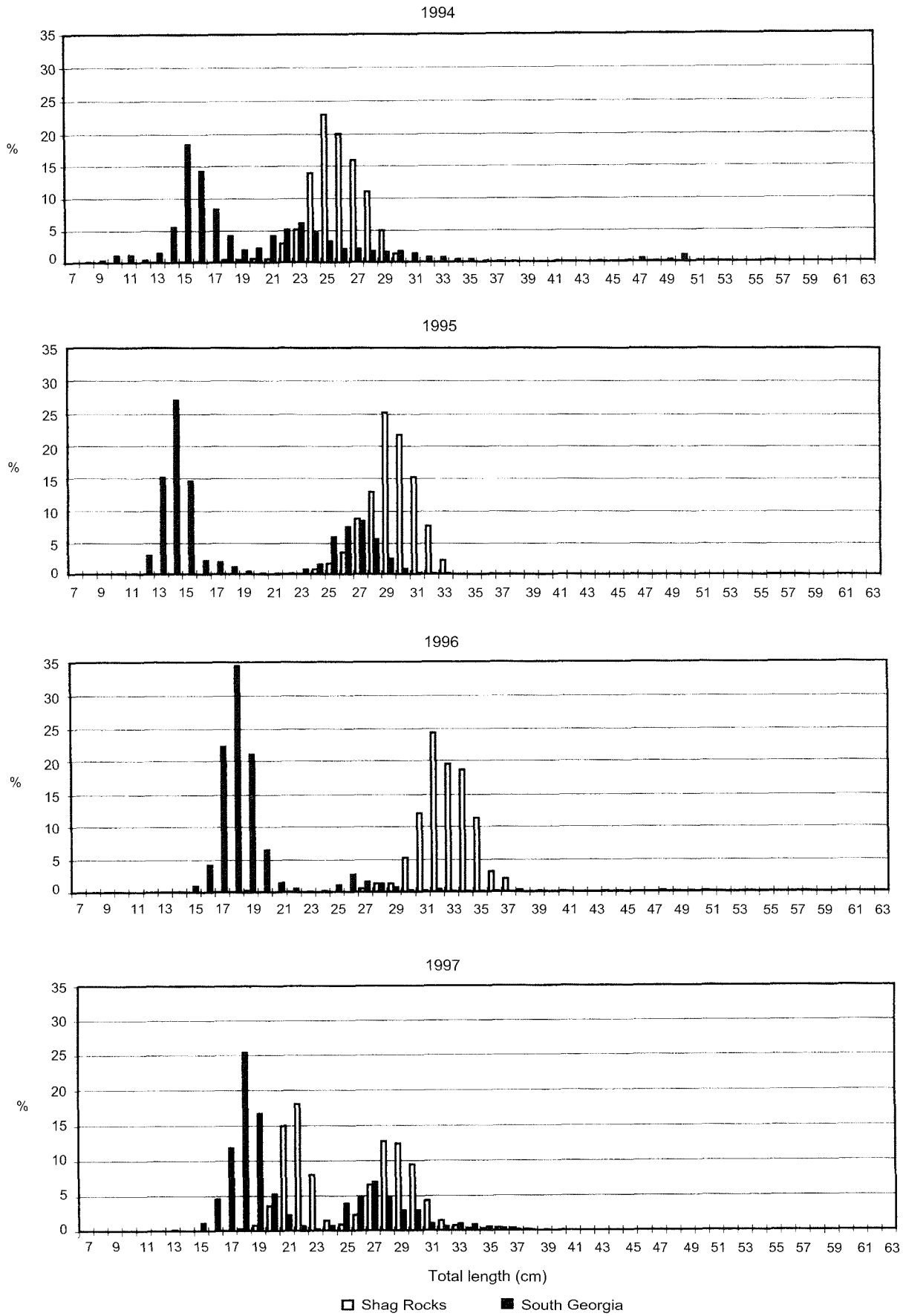


Figure 1: Length-frequency distribution of *Champsocephalus gunnari* around South Georgia and Shag Rocks, 1994 to 1997.

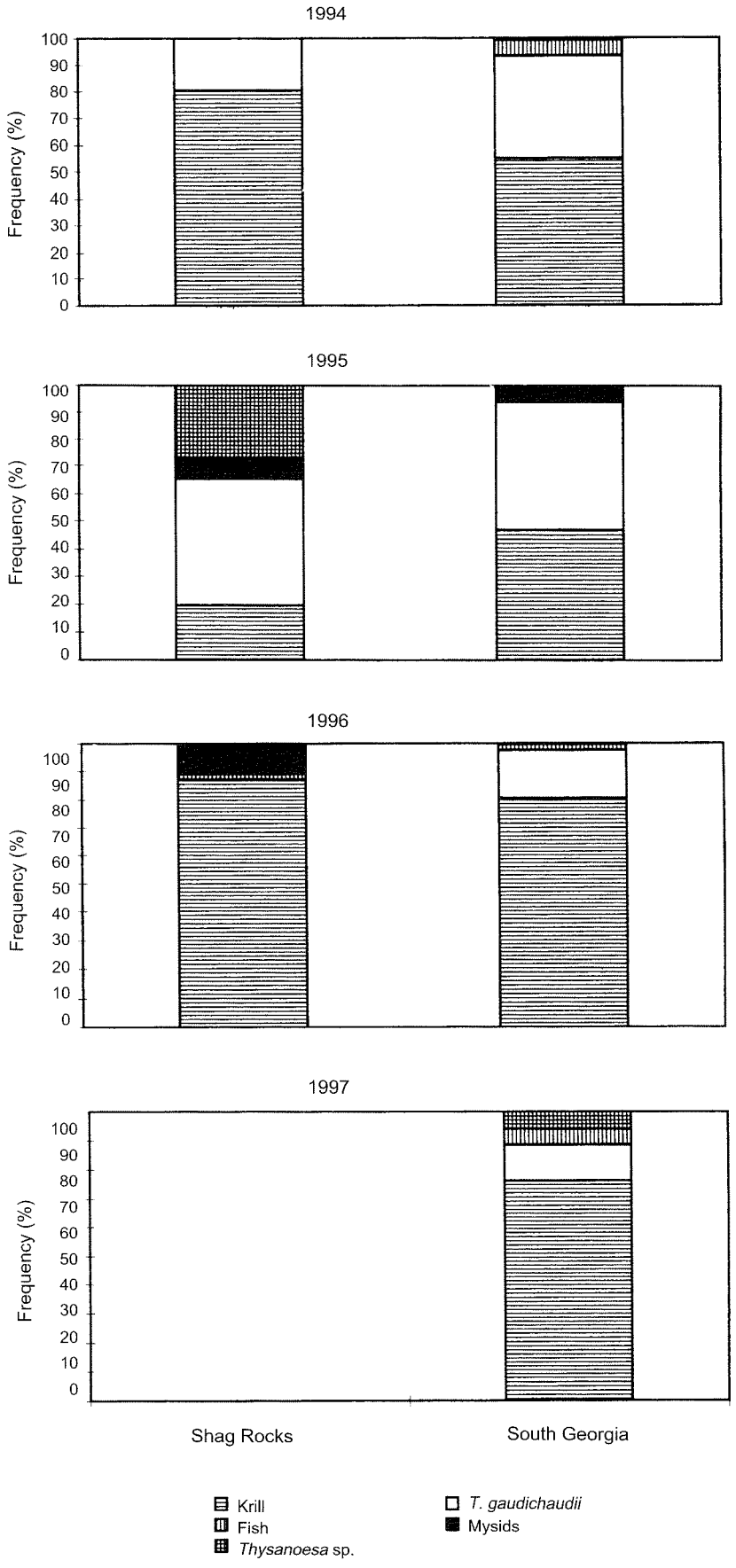


Figure 2: Frequency of occurrence (F%) of prey items in the diet of *Champsocephalus gunnari* around South Georgia and Shag Rocks from 1994 to 1997.

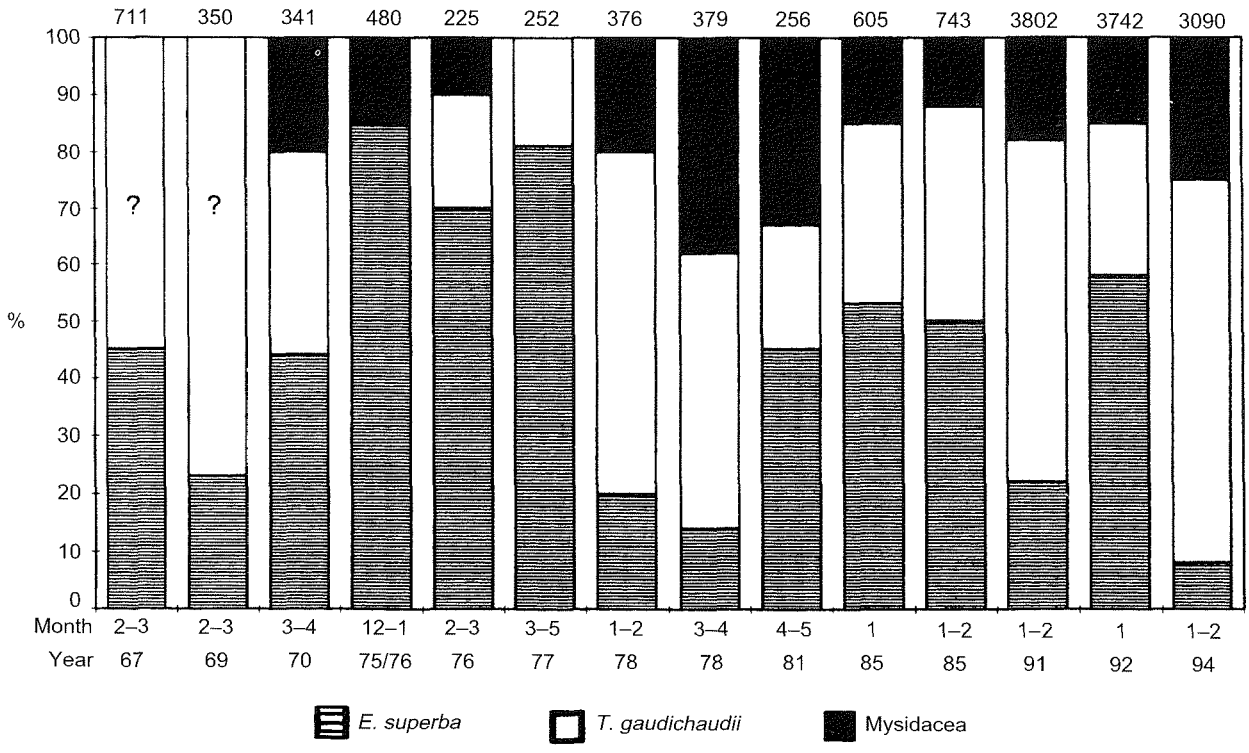


Figure 3: Frequency of occurrence (F%) of the main prey items (krill, *Themisto gaudichaudii* and mysids) in the diet of *Champsocephalus gunnari* around South Georgia from 1965 to 1994. Reproduced from Kock et al. (1994b – Figure 7); source in Kock et al. (1994a – Figure 1b). The number of stomachs analysed is given above each histogram.

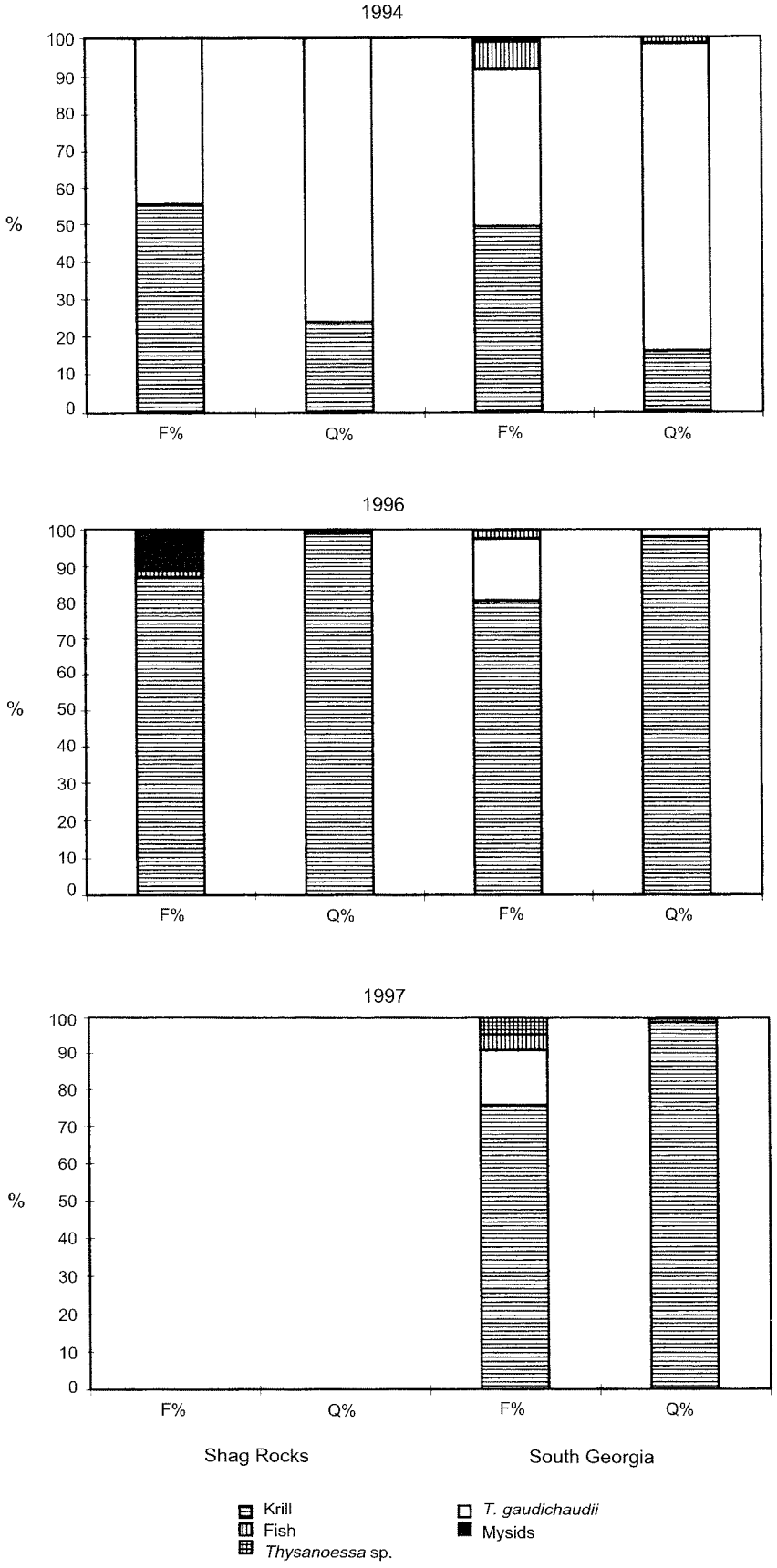


Figure 4: Comparative analysis of the diet of *Champsocephalus gunnari* by frequency of occurrence (F%) and dietary coefficient (Q%) in 1994, 1996 and 1997.

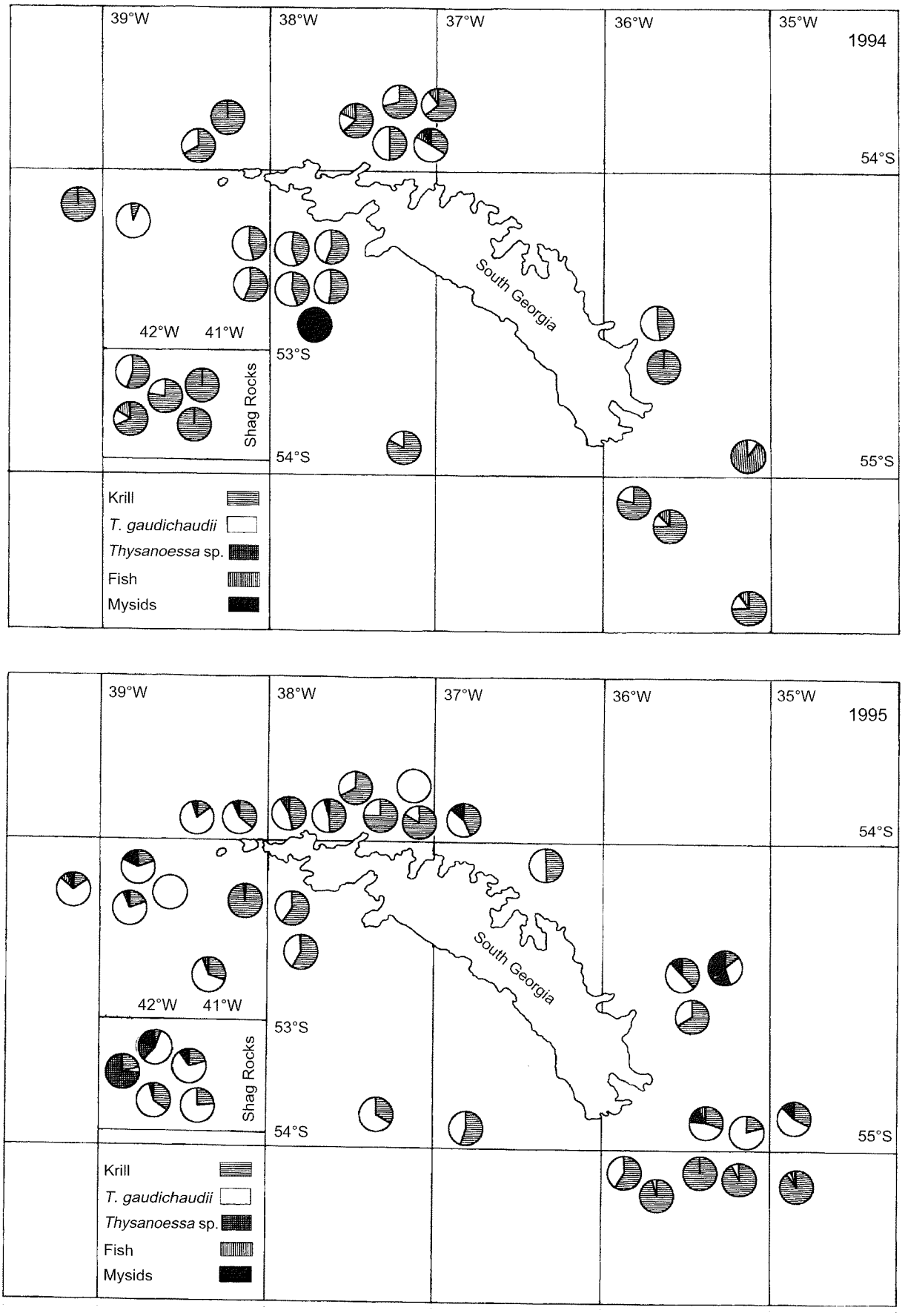


Figure 5: Spatial distribution of the diet composition (in F%) of *Champsocephalus gunnari* around South Georgia and Shag Rocks from 1994 to 1997.

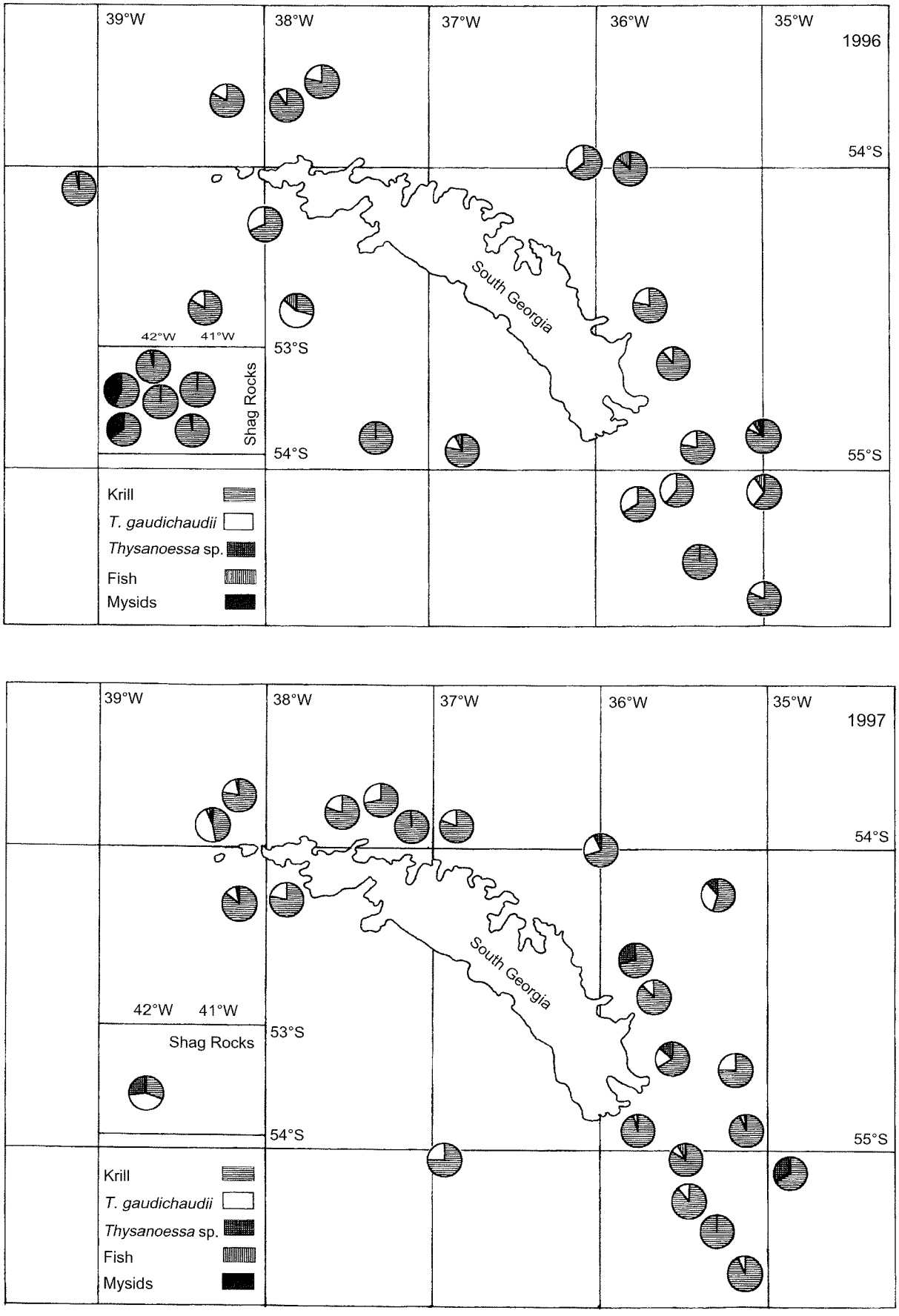


Figure 5 (continued)

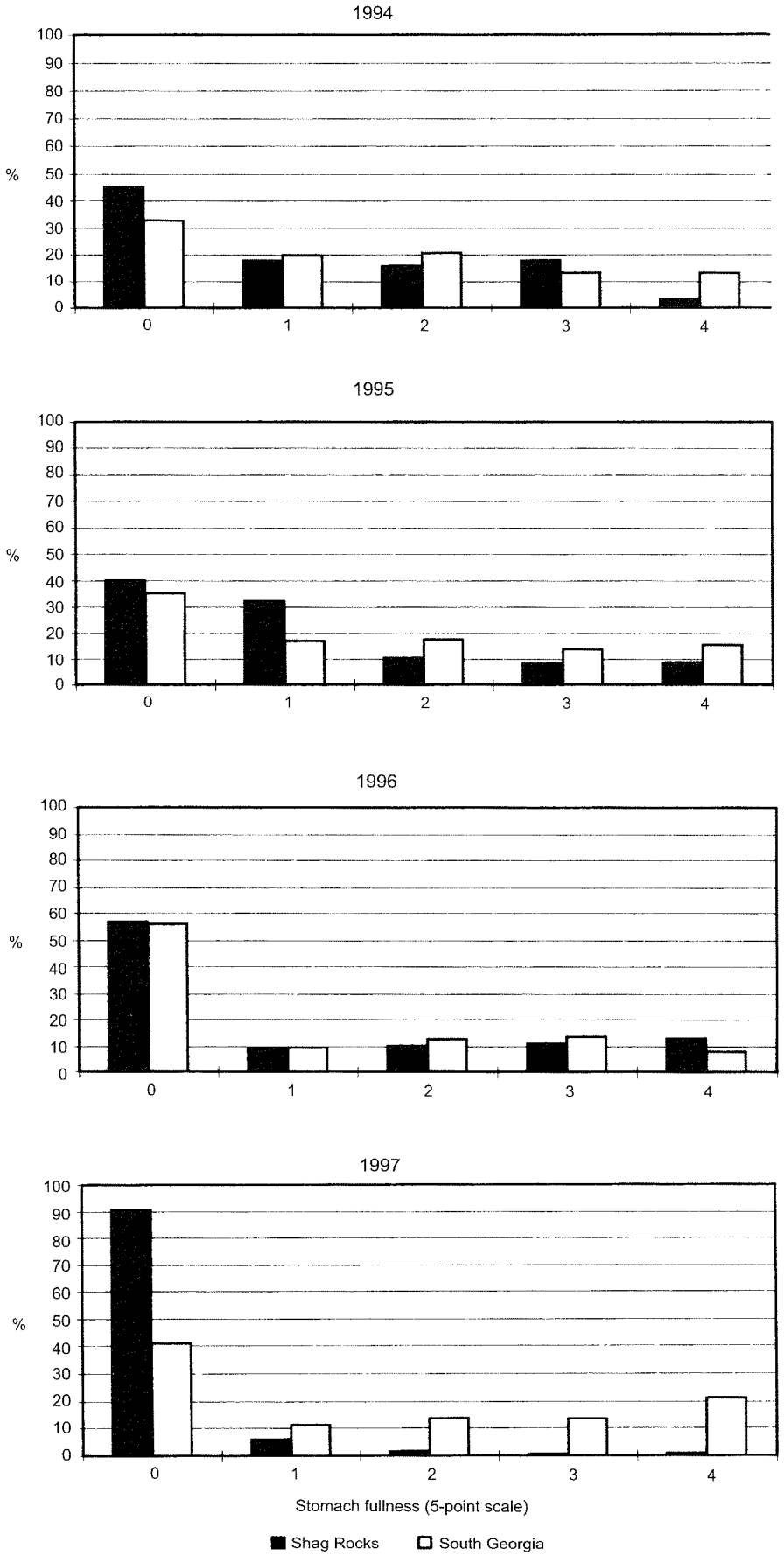


Figure 6: Index of stomach fullness in *Champsocephalus gunnari* around South Georgia and Shag Rocks from 1994 to 1997.

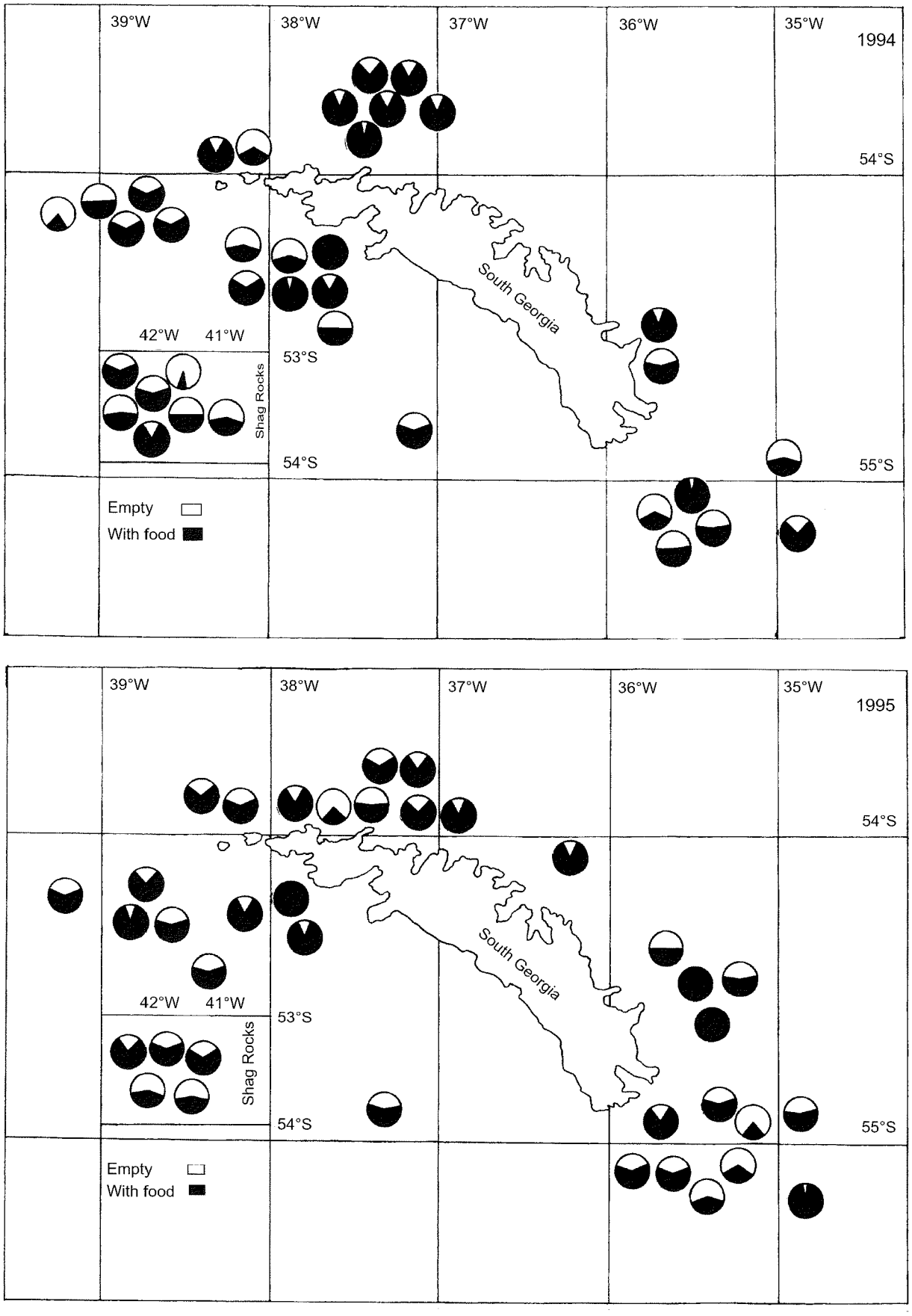
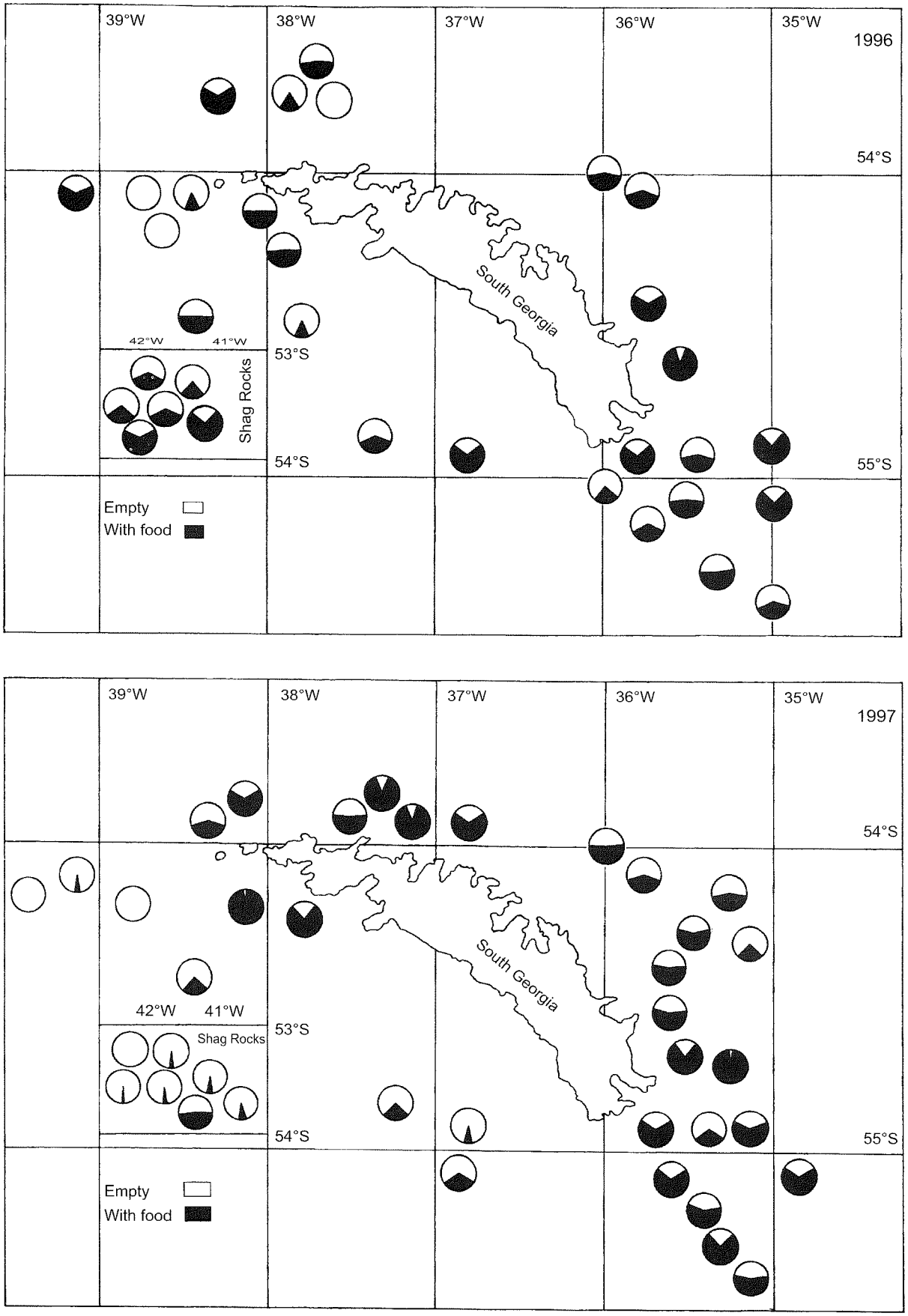


Figure 7: Spatial distribution of the stations from 1994 to 1997, showing proportions of stomachs with and without food.



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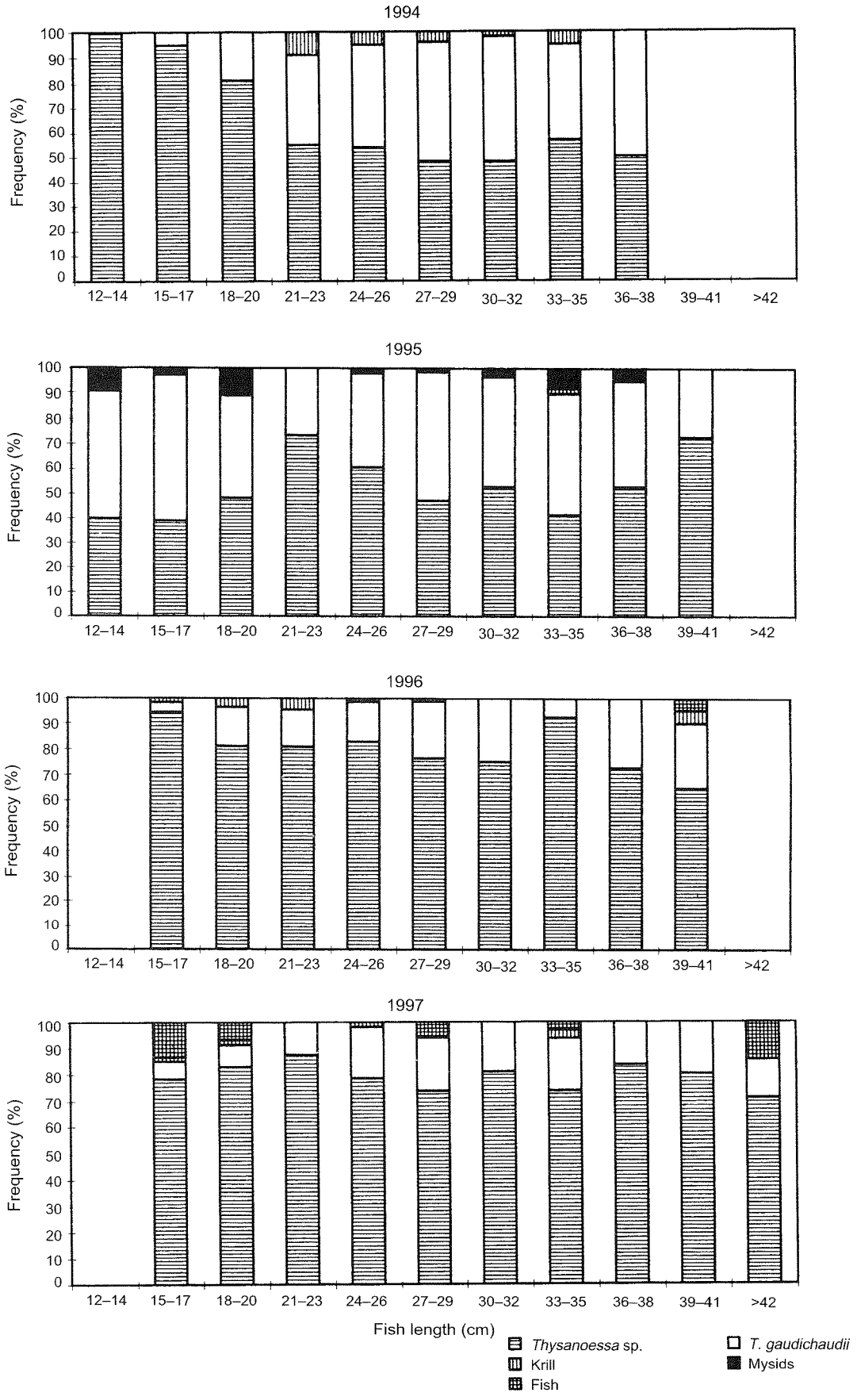

Figure 8: Variation in the diet in relation to the length of *Champsocephalus gunnari* around South Georgia from 1994 to 1997.

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