DISTRIBUTION OF MACKEREL ICEFISH (*CHAMPSOCEPHALUS GUNNARI*) (CHANNICHTHYIDAE) AROUND SOUTH GEORGIA AT VARIOUS STAGES OF ITS LIFE CYCLE

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Abstract

The distribution of mackerel icefish (*Champsocephalus gunnari*) around South Georgia (FAO Statistical Subarea 48.3) at various stages of its life cycle was studied using material collected by AtlantNIRO from 1970 to 1991. This study took into account the spatial–temporal variability of *C. gunnari*. Young fish of the first age group (<15 cm in length) were mainly found in the southern part of the study area, immature fish (15–25 cm) in the east and southwest, and adults (25–39 cm) in the north. The distribution of *C. gunnari* changes during its life cycle. Fish larvae inhabit the upper 100 m layer of pelagic waters. Young fish (<6 cm) were mainly observed near the bottom and at depths of up to 75 m from the bottom. Young fish undertake vertical migrations into the water column during the day and return to the bottom layers at night. Immature fish were found to be distributed throughout the water column at all times of the day, but they also undertake vertical diurnal migrations similar to those of mature fish. Mature fish were found near the bottom during the day and in the water column at night. Larger fish (>40 cm) did not undertake vertical migrations. Variations found in the depth distribution of *C. gunnari* relate both to fish length and season.

Résumé

La répartition du poisson des glaces (*Champsocephalus gunnari*) autour de la Géorgie du Sud (sous-zone statistique 48.3 de la FAO) à divers stades de son cycle vital est étudiée à partir de matériel recueilli par AtlantNIRO de 1970 à 1991. Cette étude tient compte de la variabilité spatio-temporelle de *C. gunnari*. Les jeunes poissons de la première classe d'âge (<15 cm de longueur) étaient, le plus souvent, rencontrés dans la partie sud de la région étudiée, les immatures (15–25 cm) à l'est et au sud-ouest et les adultes (25–39 cm) au nord. La répartition de *C. gunnari* change au cours de son cycle vital. Les larves de poisson fréquentent la couche des 100 m supérieurs des eaux pélagiques. Les jeunes poissons (<6 cm) étaient observés près du fond et à des profondeurs allant jusqu'à 75 m du fond. Ils effectuent une migration verticale dans la colonne d'eau le jour et retournent aux couches du fond la nuit. Les poissons immatures étaient présents dans toute la colonne d'eau toute la journée, mais eux aussi effectuent une migration verticale de jour, comme les poissons matures. Ces derniers se trouvaient près du fond de jour et dans la colonne d'eau de nuit. Les poissons les plus grands (>40 cm) n'effectuaient pas de migrations verticales. Les variations de la distribution des longueurs de *C. gunnari* sont fonction tant de la longueur des poissons que de la saison.

Резюме

Распределение щуковидной белокровки (*Champsocephalus gunnari*) в районе Южной Георгии (Статистический подрайон ФАО 48.3) на различных стадиях жизненного цикла исследовалось по материалам, собранным АтлантНИРО в период с 1970 по 1991 гг. При исследовании учитывалась пространственно-временная изменчивость *C. gunnari*. Молодь первой возрастной группы (длиной <15 см) в основном была обнаружена в южной части исследуемого района, неполовозрелая рыба (15–25 см) – на востоке и юго-западе, а половозрелая рыба (25–39 см) – на севере. Распределение *C. gunnari* изменяется в течение ее жизненного цикла. Личинки обитают в верхнем 100-метровом слое пелагиали. Молодь (<6 см) в основном наблюдается около дна и в толще воды в пределах 75 м от дна. Молодь совершает вертикальные миграции в толщу воды в дневное время и возвращается в придонный слой к ночи. Было обнаружено, что неполовозрелая рыба распределяется по всей толще воды в течение дня, но вместе с тем она уже осуществляет суточные вертикальные

перемещения подобно половозрелой рыбе. Половозрелая рыба в дневное время находится около дна, а ночью – в толще воды. Крупная рыба (>40 см) не совершает вертикальных миграций. Различия, обнаруженные в распределении *C. gunnari* по глубине, связаны как с размерами рыбы, так и со временем года.

Resumen

El material recolectado por AtlantNIRO desde 1970 hasta 1991 fue utilizado para estudiar la distribución del draco rayado (*Champsocephalus gunnari*) en las distintas etapas de su ciclo de vida alrededor de Georgia del Sur (Subárea estadística 48.3 de la FAO). Este estudio tomó en cuenta la variabilidad espacial y temporal de *C. gunnari*. Se encontró que los peces jóvenes del primer grupo de edad (<15 cm de largo) predominaron en el sector sur de la zona de estudio, los peces inmaduros (15–25 cm) en los sectores este y suroeste, y los adultos (25–39 cm) en el norte. La distribución de *C. gunnari* cambia durante su ciclo de vida. Las larvas se encuentran en la capa superior de las aguas pelágicas hasta los 100 m de profundidad. Los peces jóvenes (<6 cm) se concentraron cerca del fondo y hasta 75 m del fondo. Estos peces realizan migraciones diurnas en sentido vertical en la columna de agua durante el día, retornando a las capas más profundas por la noche. Si bien se encontró que los peces inmaduros estaban distribuidos a lo largo de la columna de agua durante el día, también realizaron migraciones diurnas en sentido vertical similares a las de los peces adultos. Los peces adultos se concentraron cerca del fondo durante el día y en la columna de agua por la noche. Los peces más grandes (>40 cm) no realizaron migraciones verticales. Las variaciones en la distribución batimétrica de *C. gunnari* se relacionan tanto con la talla del pez como con la temporada.

Keywords: mackerel icefish, *Champsocephalus gunnari*, Subarea 48.3, South Georgia, life cycle, diurnal vertical migration, distribution, functional structure of distribution area, CCAMLR

INTRODUCTION

Mackerel icefish (*Champsocephalus gunnari*) is one of the main commercial species in the South Georgia area (FAO Statistical Subarea 48.3). The biology and distribution of *C. gunnari* have been the subject of many publications (e.g. Permitin, 1973, 1982, 1987; Efremenko, 1979, 1982, 1983; Lisovenko, 1982; Lubimova, 1980, 1987; Shust, 1987, 1998; Olsen, 1955; Kock, 1979, 1981, 1989; North, 1987; Parkes, 2000; Sosinski, 1981, 1985; Sosinski and Skora, 1985; White, 1998). In these publications, however, analysis of the distribution of *C. gunnari* is limited to the description of locations where the species has been found. Similarly, a description of the vertical distribution of the species is limited mostly to records of depths at which fish have been observed. Variability of the distribution of *C. gunnari* by depth stratum and season at various stages of its life cycle has not been considered, and studies conducted on vertical diurnal migrations of the species only considered larvae. The limited data on the seasonal migration of *C. gunnari* which have been published have generally been confined to the description of spawning migrations of *C. gunnari* from the northern and northeastern shelf areas of South Georgia towards fjords or into the open sea below a depth of 100 m.

The study presented here considers the ecology of *C. gunnari* at different stages of its life cycle, taking into account the spatial–temporal variability of this species' distribution over the South Georgia area. All data collected in the past on the horizontal and vertical distribution of *C. gunnari* at different temporal (diurnal, season, year) and spatial scales for each developmental stage were analysed.

MATERIAL AND METHODS

The data used in this study were collected by AtlantNIRO scientists during 50 research and commercial cruises carried out from 1970 to 1991, and six pelagic and seven bottom trawl surveys undertaken from 1984 to 1991 in the South Georgia area.

The material analysed consists of about 400 000 length measurements, and more than 90 000 biological records (maturity stages, fat and stomach content and stomach fullness).

Methods for pelagic juvenile fish surveys are described by Frolkina et al. (1998). Bottom trawl surveys were carried out using the same survey design as pelagic surveys. Survey designs were randomly stratified and trawling stations were selected using a table of random numbers.

Bottom trawl surveys were carried out using a 'Hake-4 m' trawl net, which had a small-mesh

panel inserted in the codend (mesh opening of 10 mm) and was modified to reduce damage in operations on hard ground. In order to reduce the impact of catches on diurnal migrations of fish, trawls were carried out only during the day and were confined to the following depth ranges: 100–200, 201–300 and 301–500 m. The duration of each trawl was 30 min at a speed of 3–3.5 knots.

For reference purposes, the entire shelf area around South Georgia and Shag Rocks was subdivided into five study areas: to the east, west, north and south of South Georgia, and around Shag Rocks (Figure 1).

The length composition of *C. gunnari* in catches was taken into account when studying its distribution in relation to growth. The following length groups were defined:

Young fish: up to 15 cm total length and one year old. The ecological niche occupied by young fish is distinctly different from that of older fish. Young fish were caught only in pelagic trawls.

Immature fish: from 15 to 25 cm total length and generally at maturity stage II (Lisovenko and Silyanova, 1980). The ecology of this group could be described as 'transitional' between younger and older groups. Immature fish were caught by both bottom and pelagic trawls.

Mature fish: mature fish from 25 to 40 cm total length. A negligible quantity of immature fish was also recorded in this length group.

Large mature fish: over 40 cm total length. Classified by Lubimova (1980) as a special group not only in terms of distribution, but also because of the range of maturity stages observed in these fish.

Fish distribution was considered between the depth ranges of 100–150 and 151–200 m, and thereafter at 50 m intervals to a depth of 500 m (see Figure 2). The relative frequency of occurrence of fish at each depth was calculated as the percentage of the total number of fish (100%) in all samples collected for each month.

Similarly, in order to map spatial distribution of the different length groups, the relative frequency of occurrence of fish of each group was calculated as the percentage of the total number of fish (100%) in all samples collected for each month.

Special surveys were conducted in order to study vertical diurnal migrations of young and immature fish (Trunov et al., 1999, 2000). The surveys included 24-hour sampling stations.

Vertical diurnal migrations of larger fish were studied using data collected by fisheries scouting and research vessels during years of high fish abundance (i.e. 1982/83, 1983/84 and 1986/87). Samples of catches per hour of trawling were taken during the day using both bottom and midwater trawls (Frolkina and Shlibanov, 1991). In addition, data from 24-hour hydroacoustic and biological sampling stations were used.

RESULTS

The spatial distribution of the young fish group was studied using the results from trawl surveys of juvenile fish. The largest catches were taken mainly in the south, whereas the lowest catches were taken to the north of the shelf (Frolkina et al., 1998) (Table 1). In the Shag Rocks area no fish smaller than 12 cm were found in catches taken by pelagic and bottom trawls. During the entire observation period fish of this size were found in this region only once, in November–December 1986 (Frolkina et al., 1998). The vertical distribution of young fish was studied using data from 24-hour stations conducted in June–July. In the upper 50 m layer only single specimens of young fish were recorded (Trunov et al., 2000). Young fish of 9–15 cm formed dense aggregations at dawn and during daylight hours at a bottom depth of 125–140 m, and less dense aggregations at 75–125 m. At night fish moved deeper into the near-bottom layer (5–15 m from the bottom). Data from midwater trawls by fishing vessels showed that 1-year-old fish (<15 cm) were mainly distributed in pelagic waters. The distribution of young fish by depth was analysed only for the autumn–winter period when pelagic surveys were carried out. In autumn, young fish of about 6 cm were caught at depths of 100–150 m (RV *Evrika*, 1988). In winter, catches of more than 100 individuals per 30 min trawl (8–15 cm) were taken at a bottom depth of 150–200 m, with less fish taken at 200–300 m. Only a few individuals were caught below the 300 m isobath.

Immature fish were caught over the entire shelf area and off Shag Rocks. They were predominant in catches taken to the east of South Georgia (15–76% of the total catch) (Table 2). In the northern and southern shelf areas the proportion of immature fish varied significantly between years from 2 to 49% in the north shelf area and from 4 to 50% in the south area. In the western shelf area fish were

Table 1: Length composition of *Champsocephalus gunnari* less than 15 cm in length on the shelf of South Georgia (based on pelagic survey results).

Vessel Name, Cruise Dates	Parameters	East	North	South	West
Evrika	Mean length (mm)	62	58	61	55
30/3–7/4/1988	Length range (mm)	30–90	40–70	30–90	30–70
	Modal length,	50 mm 33%	50 mm 62%	50 mm 38%	50 mm 77%
	% of fish of dominant length	60 mm 48%	60 mm 28%	60 mm 45%	
	Number of individuals	563	240	410	94
Gizhiga	Mean length (mm)	91	100	96	95
25/5–8/6/1984	Length range (mm)	70–130	80–130	70–130	70–130
	Modal length,	80 mm 46%	90 mm 30.5%	80 mm 31%	80 mm 21%
	% of fish of dominant length	90 mm 29%	100 mm 33%	90 mm 18%	90 mm 49%
				100 mm 26%	
	Number of individuals	370	85	458	587
Anchar	Mean length (mm)	80	81	78	76
29/5–7/6/1990	Length range (mm)	60–120	60–100	60–110	60–100
	Modal length,	70 mm 46%	70 mm 36%	70 mm 56%	70 mm 66%
	% of fish of dominant length	80 mm 34%	80 mm 54%	80 mm 25%	80 mm 18%
	Number of individuals	2 267	1 400	2 113	2 001
Gizhiga	Mean length (mm)	108	108	108	99
30/5–29/6/1986	Length range (mm)	60–130	80–130	60–140	70–120
	Modal length,	100 mm 46%	100 mm 26%	100 mm 39%	90 mm 55%
	% of fish of dominant length	110 mm 25%	110 mm 38%	110 mm 21%	100 mm 34%
	Number of individuals	110	53	567	334
P. Latvii	Mean length (mm)	113	100	116	101
8–24/7/1989	Length range (mm)	90–150	80–140	80–150	70–150
	Modal length,	100 mm 29%	90 mm 34%	100 mm 28%	90 mm 44%
	% of fish of dominant length	110 mm 43%	100 mm 59%	120 mm 20%	100 mm 47%
	Number of individuals	585	259	451	696
Gizhiga	Mean length (mm)	103	101	108	100
7/7–8/8/1987	Length range (mm)	80–130	80–130	70–150	80–140
	Modal length,	90 mm 28%	90 mm 41%	90 mm 24%	90 mm 45%
	% of fish of dominant length	100 mm 56%	100 mm 41%	100 mm 45%	100 mm 38%
	Number of individuals	506	895	2 459	1 678

Table 2: Length composition of *Champsocephalus gunnari* over 15 cm in length on the shelf of South Georgia (based on pelagic survey results).

Vessel Name, Cruise Dates	Parameters	East	North	South	West	Shag Rocks
Anchar	Mean length (cm)	26.1	34.9	28.9	32.5	
7–30/4/1990	Length range (cm)	15–55	15–52	15–45	16–52	no
	L = 15–25 cm (%)	66.75	6.70	31.87	9.16	data
	L = 26–39 cm (%)	24.42	85.77	64.63	86.62	
	L = >40 cm (%)	8.84	7.53	3.49	4.22	
	Number of individuals	1 245	3 520	2 262	4 192	
Atlantida	Mean length (cm)	26.8	31.8	29.6	31.5	32.3
1/4–27/5/1991	Length range (cm)	14–52	14–54	15–47	17–47	14–43
	L = 15–25 cm (%)	45.10	16.71	23.48	13.10	2.23
	L = 26–39 cm (%)	51.82	64.03	72.56	82.83	95.88
	L = >40 cm (%)	2.99	15.03	3.96	4.08	1.87
	Number of individuals	3 140	3 260	1 465	7 140	4 331
Gizhiga	Mean length (cm)	26.7	27.1	32.5	31.7	
24/4–23/5/1984	Length range (cm)	15–43	10–51	20–54	13–50	no
	L = 15–25 cm (%)	51.55	44.24	8.0	16.12	data
	L = 26–39 cm (%)	46.80	52.05	88.12	81.03	
	L = >40 cm (%)	1.66	2.19	3.96	2.79	
	Number of individuals	906	1 510	303	1 861	
Gizhiga	Mean length (cm)	33.6	36.8	37.1	31.4	
10–31/8/ 1987	Length range (cm)	19–54	22–58	22–53	19–56	no
	L = 15–25 cm (%)	15.59	1.71	3.73	0.85	data
	L = 26–39 cm (%)	76.31	76.15	79.05	97.34	
	L = >40 cm (%)	8.10	22.13	17.22	1.81	
	Number of individuals	667	348	482	827	
Gizhiga	Mean length (cm)	26.8	28.8	26.9	29.9	28.8
16/9–21/10/1986	Length range (cm)	12–53	11–55	11–52	11–49	17–43
	L = 15–25 cm (%)	39.97	13.41	41.31	22.14	38.16
	L = 26–39 cm (%)	58.01	82.87	42.27	76.88	60.56
	L = >40 cm (%)	1.57	0.18	4.13	0.74	1.28
	Number of individuals	4 837	6 837	2 181	4 079	3 527
P. Latvii	Mean length (cm)	27.6	27.8	27.0	29.1	26.5
10/12/1988–3/1/1989	Length range (cm)	13–56	12–57	12–56	12–51	15–43
	L = 15–25 cm (%)	41.31	49.75	50.4	33.63	40.60
	L = 26–39 cm (%)	43.38	44.69	45.4	58.81	58.92
	L = >40 cm (%)	8.72	4.92	2.56	2.63	0.49
	Number of individuals	1 513	1 403	1 055	4 457	10 493

less abundant when compared to other locations (1–33%). The peak of abundance of immature fish was observed in October. Immature fish comprised 21–22% of catches taken near the bottom during the day and at night. A similar proportion of immature fish was observed in catches taken in the water column during the night (23%). During the day the proportion of immature fish in the water column increased to 34% (Figure 3). Immature fish were usually caught within the entire depth range surveyed, and most often at locations with a depth range of 100–350 m. Fish distribution by depth varied according to the time of year. From November to June the largest quantity of immature fish was observed at a bottom depth of 100–250 m, and from July to October at 200–300 m.

Mature fish were distributed over the entire area of the South Georgia and Shag Rocks shelves. The proportion of mature fish in catches varied from 70 to 90%. During most of the year the highest density aggregations of mature fish were observed in the north. During the day fish were observed near the bottom. Peak catches were obtained in the middle of the day. At dusk fish aggregations ascended into the upper layers of the water column and bottom trawl catches decreased sharply. At dawn fish migrated to the bottom and catches increased again (Frolkina and Shlibanov, 1991). During trawl surveys, mature fish occurred within the entire depth range from 100 to 500 m, and up to 400 m in commercial catches. Fish distribution by depth varied throughout the year (Figure 3). In spring–summer, mature fish were caught at bottom depths ranging from 100 to 450 m. In March, they occurred at bottom depths of 100–150 m, however high numbers of fish were observed at locations with bottom depths of 250–300 m. In April, all mature fish were distributed in depths of up to 200 m, with the bulk of fish observed at depths of 150–200 m. From May, mature fish gradually moved to the 250–350 m depth range where they remained until October.

Large mature fish of more than 40 cm were caught over the entire South Georgia area and in shallow waters off Shag Rocks. It should be noted that only on the eastern shelf were fish of this group caught near the coast at depths of less than 200 m. In all other areas they occurred only in deeper water. There were insignificant proportions of large fish in catches during the year. Only in March and April did the proportion of large fish in catches increase significantly, from 6.4 to 10.4% respectively (Figure 2). Fish of this length group were always found near the bottom. At night, individuals of up to 42–43 cm were caught in pelagic trawls and fish of up to 54–56 cm in bottom trawls (Figure 3). These fish occurred in variable numbers at depths of 100–500 m and in commercial quantities at depths of 100–350 m (Figure 2). Aggregation densities at various depths varied throughout the year. From October to March these fish were mainly caught at depths of 100–300 m, in April and May they were most abundant at depths of 100–250 m (the highest catches were obtained at 150–200 m), in winter (June–October) at depths of 250–350 m (Figure 2).

Over the year, variations in the physiological condition of *C. gunnari*, maturity stage, stomach fullness and intestinal fat, were observed (Figure 4). Fish at maturity stages II and III were found in catches throughout the year (Figure 4a). Females with gonads at maturity stage IV were caught from November to July, with maximum catches between March and July. The highest numbers of females with gonads at maturity stage V were observed in April–May; however, the proportion of such fish in catches was insignificant. Seasonal differences were also observed in indices of stomach fullness and intestinal fat (Figure 4b–e). Analysis of all fish at maturity stage II showed the highest index of stomach fullness was in December–January, the lowest in June–October, the highest index of intestinal fat was observed in July and the lowest in October. The index of stomach fullness for fish at maturity stage III was at its maximum in March, and gradually reduced during the transition to maturity stage IV. For fish at maturity stage III, throughout the year, indices of stomach fullness and intestinal fat were similar to fish at stage II. For *C. gunnari* at maturity stage IV, the highest index of stomach fullness was observed in April. The index decreased gradually in the following months. By April–May, when the fish stopped feeding, the index of intestinal fat was the highest.

Analysis of food composition was carried out on samples of *C. gunnari* taken during the bottom and pelagic surveys in 1990. Food items included krill (*Euphausia superba*) (50–70%), amphipods (15–20%) and fish including young *C. gunnari*, *Notothenia larseni* and myctophids. The highest content of krill was observed in samples taken in the southern shelf area (about 70%). In addition, a significant proportion of food comprised young fish of the same species (about 15%), and *N. larseni* and amphipods amounted to 2% each. In the northeast, the proportions were krill 60%, amphipods about 15%, myctophids and young *C. gunnari* about 2% each. In the northwest, krill constituted about 50%, other euphausiids and myctophids 5% each, and amphipods a significant proportion of about 40%. Differences in food composition by area are related to the distribution of food species. For example,

while krill represented the main food item in the diet of fish in near-bottom and bottom layers, it was not the only food item. In contrast, the diet of fish in pelagic layers consisted of krill in excess of 95%. Differences in food composition were also found between fish of different lengths. The food of fish of 25–29 cm comprised krill (about 60%) and amphipods (35%), while fish of 33–35 cm consumed mainly krill (90%).

Previous studies (Shnar and Shlibanov, 1989) showed that *C. gunnari* inhabited waters with a temperature range of 0.6 to 1.8ºC. Within this range, the densest aggregations fished were at locations where the water temperature was between 1.0 and 1.4ºC. The formation of fish aggregations is limited by these minimum and maximum temperatures. In spring–summer, temperatures outside the optimal range for *C. gunnari* were observed initially in the layer from 200 m depth to the bottom, and at the end of the season, in the 50–75 m bottom layer. During this period *C. gunnari* undertakes diurnal vertical migrations into pelagic waters, being found within 60 m from the bottom (Frolkina and Shlibanov, 1991).

According to publications such as Kock (1981), the minimum length of mature *C. gunnari* is 16 cm for females and 17 cm for males. In the data presented in this paper, the smallest mature female was 18 cm. Females of less than 25 cm were an insignificant proportion of the mature fish, while 50% of fish reached maturity at a length of 26–27 cm, and 80% at 30 cm. According to Kock (1981) all fish larger than 27 cm were mature.

The distribution of females at maturity stages IV and V was analysed for March–May. In March all pre-spawning fish were concentrated mainly in the northeast area of the shelf at bottom depths of 200–300 m (Figure 5). At other locations, only individual specimens at maturity stage IV were found. In April, pre-spawning fish in the northeast were distributed closer to the coast, while small fish were caught at depths of less than 200 m, and middle-sized and large fish at depths of more than 200 m. At the same time, pre-spawning fish were observed in large numbers in the northern and western shelf areas. The pre-spawning fish began to move gradually westward to depths greater than 200 m. During May, only pre-spawning females of 30–39 cm were caught in the northern and eastern areas of the shelf. Fish outside this length range were not observed in these areas because they had migrated to spawning grounds in areas not suitable for the fishery. At the same time, pre-spawning and spawning fish were caught at depths of 300–350 m in the western and southwestern areas of the shelf.

During the bottom trawl survey in 1984, the maturation rate of gonads of *C. gunnari* caught in the western shelf area was studied. It was found that the number of pre-spawning females increased from 20–31% to 90–93% during the period from 2 to 23 May (Table 3). In the southern and western shelf areas at depths of 200–340 m, pre-spawning fish predominated in catches. On 19 and 20 May, they were predominant in catches over the entire shelf. In the northern and western areas, pre-spawning fish were caught at depths of 300–340 m. Catches of spawning fish during that time were insignificant. In the northern and eastern areas of the shelf at depths of 160 to 170 m, the proportion of spawning females was about 10%. In the southern and eastern areas, only individual fish were found with mature gonads, while in the Shag Rocks and Black Rocks areas no pre-spawning and spawning fish were observed. This implies that spawning in 1984 occurred in late May–June, mainly in the southwest shelf area. At all locations, excluding the north and east areas, spawning was observed at depths of 300–350 m.

DISCUSSION

Our studies revealed that the ecology of *C. gunnari* varied both within and between years and with respect to stages of its life cycle. Variations observed relate both to spatial and vertical distribution of the species during the year. A general picture of *C. gunnari* is distributed was obtained and its functional structure described. The South Georgia population of *C. gunnari* is distributed over the entire shelf and slope area up to 500 m depth (Lisovenko, 1982; Lubimova, 1980, 1987; Shust, 1987, 1998; Olsen, 1955; Kock, 1979, 1981, 1989; North, 1987; Sosinski, 1981, 1985; Sosinski and Skora, 1985). Fish of all age groups have been observed in the area.

Larvae at various stages of development and 1-year-old fish (<10 cm) are found in the upper layers of coastal and shelf zones in the Fortuna and Cumberland Gulf fjords in the northwestern shelf area and Royal Fjord in the northeast (Efremenko, 1979, 1983; Kock, 1981, 1989; North, 1987). Young fish older than one year inhabit pelagic waters and the shelf area, mainly in the north. Aggregations of fish of these two age groups were observed in the northeastern and eastern areas of the shelf, close to spawning grounds (Shust, 1998).

According to the results of pelagic surveys conducted by AtlantNIRO, permanent concentrations of *C. gunnari* were observed not only in the eastern and southeastern areas of the shelf but

Table 3: Maturity stages of *Champsocephalus gunnari* on the South Georgia shelf (30 April to 3 May 1984), Shag Rocks and Black Rock (11–15 June 1984) (%).

Area	Young Fish			Maturity Stage										Immature	Mature	*N*
	Larvae	M	F	II		III		IV		V		VI–III				
				M	F	M	F	M	F	M	F	M	F			
Northeast	26.0	28.5	45.5	61.4	29.6	8.8	27.5	28.1	33.0	1.7	9.9	-	-	57.0	43.0	200
Northwest	1.5	35.1	63.4	3.9	3.4	56.2	62.5	39.5	31.1	0.4	1.0	-	-	5.0	95.0	800
Southwest	18.4	33.9	47.7	7.9	15.7	10.7	7.2	75.7	72.3	0.6	4.0	5.1	0.8	28.5	71.5	522
Shag Rocks, Black Rock	72.0	9.0	19.0	88.9	94.7	1.1	-	-	-	-	-	-	5.3	98.0	2.0	100

also in the southwestern area. It seems likely that anticyclonic water circulations are responsible for transportation of *C. gunnari* larvae into the area, from spawning grounds located in the fjords. In addition, it was found that young fish concentrated also in the southwest area of the shelf (catches exceeded 10 000 fish per 30 min trawl). This area is close to spawning grounds. Young fish were caught in the vicinity of dense krill aggregations. However, the by-catch of young fish in krill aggregations was very small or zero (Frolkina et al., 1992). Young fish of up to 15 cm in length were distributed in two groups: one length group was located in the southern and southwestern areas of the shelf and another was distributed in the southern and eastern areas. The results of trawl surveys of juvenile fish show that the length composition of young fish in these groups differs significantly. Larger fish were found in the eastern shelf area, while smaller fish were from the west of the shelf. This relates to the earlier hatching of young fish in the fjords, and to the availability of food, such as small krill, in the eastern area of the shelf during September and October. As they grow, fish of both length groups move progressively to the north of the shelf; one group to the east and northeast and another group to the west and northwest. Until they reach three years of age (at a length of about 25 cm) these groups remain distributed mainly in the western and eastern areas of the shelf. At the same time, part of the western group also migrates into shallow waters near Shag Rocks. This conclusion is proved by similarities in age–length distribution and mean length of 2- to 4-year-old fish in the western and Shag Rocks areas, as well as by the absence of young *C. gunnari* in catches taken during juvenile surveys in the Shag Rocks area (Frolkina, 2001). The eastern group differs significantly from the western group. Because some fish of the western group migrate into the Shag Rocks area, the proportion of immature fish in this group is much less than in the eastern group. The mean fish length in the eastern and northeastern areas of the shelf is therefore lower than in the western and northwestern areas. It should be noted that the bottom in the eastern and western areas of the shelf is rather soft and the area of depths of less than 200 m is rather large. In addition, permanent water circulations observed there concentrate food items and create favourable conditions for feeding of immature fish. On reaching maturity (i.e. by 3 years old) most *C. gunnari* migrate northwards, where they remain for most of the year (excluding the spawning period). At that time the two groups mix. In general, the largest fish concentrate in the northwestern area of the shelf.

Only *C. gunnari* over 11 cm in length were caught near Shag Rocks. As a rule, this species is not fished commercially until it reaches three years of age; rarely at the age of 2 years. The age–length distribution for all years of observation showed that from time to time an entire year class may be absent from catches taken over several years (Frolkina, 2001). For reasons as yet unknown, this could be linked to an absence of fish migration from the western area of the South Georgia shelf. It was noted previously that the age–length structure of the western and Shag Rocks groups is similar for 2- to 4-year-old fish. Subsequently the number of larger fish off Shag Rocks decreased sharply, while on the South Georgia shelf, catches of 5- to 7-year-old fish continued to be significant. The maximum length of *C. gunnari* in research catches taken off South Georgia is 69 cm, while in commercial catches in that area fish of 53 cm are found. However, in the Shag Rocks area these values are 47 and 41 cm respectively. In our opinion, fish which migrate to the Shag Rocks area most probably die after reaching two years of age. The abovementioned discussion supports our theory that the Shag Rocks area represents feeding grounds or an area of extended habitat for *C. gunnari*.

A comparison of the distribution of immature and adult fish revealed the spatial segregation of these groups. This seems to be a mechanism which protects immatures from cannibalism by adult fish (immatures constitute about 20% of the diet of adult fish).

The annual life cycle of mature fish comprised three periods: feeding, spawning and over-wintering, while that of immatures comprises only two periods: feeding and over-wintering.

The feeding period of pre-spawning fish starts in October (in September in anomalous warm years and in November in anomalous cool years) and finishes in March–April. Immatures and fish that failed to spawn continue feeding until June–July. Young fish up to 15 cm in length are found in areas close to spawning grounds in the south-eastern and southwestern areas of the shelf at depths of 100–200 m, the area where large concentrations of small crustaceans are available during the austral spring–summer. Immature fish up to 20–25 cm in length are distributed during this period in the eastern and western areas of the shelf at depths of 100–300 m, i.e. in areas where krill concentrations are also found. Mature fish, i.e fish older than the first year of maturity, also form concentrations on the shelf at the beginning of the feeding season. In October–November, fish which reach maturity stage I move northeastwards and form dense feeding aggregations. Fish which

spawned repeatedly in the same area at the beginning of the feeding period also concentrated. By December–February *C. gunnari* occupy the entire north area of the shelf (Bunato, 1991). As the feeding of fish is intense, indices of stomach fullness and intestinal fat increase significantly. The migration of large *C. gunnari* takes place in the spring–summer period, mainly northwards into areas with a wide range of depths (100–450 m). Fish distribution during that time relates to krill distribution and not to water depth. At the beginning of the feeding season when krill aggregations have generally been observed in the eastern and northeastern areas of the shelf, mature fish concentrated only in the northeastern area. When krill was distributed over the whole northern area, *C. gunnari* migration followed krill concentrations. When krill concentrations were available over the entire shelf, fish aggregations were stable and no long migrations were undertaken. When krill were absent or rare near South Georgia (e.g. in 1984) fish were scattered over the shelf. Aggregations formed temporarily, the intensity of feeding migrations increased and catch per unit effort decreased sharply. Our data on the vertical diurnal distribution of *C. gunnari* (Frolkina and Shlibanov, 1991) as well as published data (Kock, 1981) demonstrate that in the absence of krill, *C. gunnari* changes its diet to other pelagic crustaceans which do not form aggregations as dense as krill. Therefore, when searching for food at such times, *C. gunnari* is distributed in pelagic waters for most of the 24-hour period (even during the day). During such periods two peaks (day and night) were observed in the diurnal feeding cycle. Fish aggregation densities during the feeding period were related not only to year-class strength and krill availability in the area, but also to light intensity. During cloudy days fish were distributed in the water column for most of the day. In such cases fish aggregations were only short-lived. At night, *C. gunnari* occupies the 15–100 m layer from the bottom. The smaller the fish, the closer to the surface they moved in their search for food. Because water temperature in the layer 60 m from the bottom was within 0.6–1.8ºC, the temperature could not be a limiting factor for fish distribution. Therefore, during that period fish aggregations were short-lived and related to food availability, especially krill, and not to other environmental factors. Differences in the depth distribution of immature and mature fish during the feeding period were related to the depths of areas of distribution, i.e. immature fish were distributed in the eastern and western areas of the shelf where depth was mainly about 200 m, while mature fish were distributed in the northern area with depths from 100 to 500 m.

It is known from other publications that spawning grounds of *C. gunnari* are located in the northern coastal zone, bays and fjords of South Georgia, as well as in its shelf zone (Kock, 1981; Lisovenko, 1982). It was found that there are more than one, i.e. at least two, main spawning grounds of *C. gunnari*: one is located in fjords on the northern and northeastern coast and is a traditional area of reproduction for many species of notothenioids; the second is located to the southwest of South Georgia at depths of 300–350 m.

The duration of the spawning period varied at each spawning ground. At the first location, spawning begins in March (Kock, 1981), and at the second, in late May. Spawning finishes in June–July in both locations. Fish at first maturity and large fish approach the spawning area and begin spawning earlier than fish which spawn repeatedly. The highest number of females was observed among fish at first maturity, and the lowest number observed among large fish. In spite of the fact that in different spawning grounds, spawning occurred at different depths, the near-bottom temperature during spawning was similar and varied insignificantly from 1.55 to 1.65ºC. As a rule, peak spawning was observed in late May–June. The time of spawning relates to the temperature regime of the year, i.e. in warmer years fish spawned earlier, while in cooler years spawning occurred later. Thus, in 1987, which was anomalously cool, spawning was observed as late as June–July. With the transition to pre-spawning condition fish gradually cease feeding: the index of intestinal fat at that time is the highest (Figure 4). Fish then gradually move into deep water, closer to spawning grounds (Figure 5). It should be noted that during the entire pre-spawning period, more than 40% of fish in catches were at maturity stages II and III. However, their numbers decreased when fish gonads developed from maturity stage III to IV, and increased when spawning fish migrated into areas inaccessible to the fishery. The presence of such fish in all length groups confirmed the conclusion of AtlantNIRO scientists (Alekseeva and Alekseev, 1997) that some *C. gunnari* do not spawn annually. In our opinion, this is one of the important mechanisms of the species abundance regulation.

The spawning migration starts in March–April. In March all pre-spawning fish concentrate in the northeastern area at depths of 200–300 m. In April they are distributed in that area close to the coast. Smaller fish were observed at a depth of less than 200 m and larger fish at a depth of more than 200 m. In May, only females of 30–39 cm were caught in the northeast area. There were no fish smaller or

larger than that because all others had already migrated to the coast, i.e. into areas inaccessible to the fishery. Spawning of fish at maturity stage I (25–30 cm) and of large fish (>40 cm) takes less time than it does for fish which had spawned repeatedly which begins simultaneously with other fish but finishes much later. These conclusions were confirmed by Kock (1981), who found that fish at maturity stage I and large fish began spawning in bays and fjords. Therefore, spawning of fish which had spawned repeatedly to the east of South Georgia is prolonged. It starts in March–April and finishes in June, and in cool years as late as July. In the northwestern area pre-spawning aggregations appear in April. By May these aggregations gradually move westwards and then southwestwards and southwards. Spawning in these areas begins in May at depths of more than 300–350 m. However, it is possible that in the southern areas fish also spawn near the coast.

The over-wintering period of *C. gunnari* begins in June–July and continues until September–October. Post-spawning and over-wintering migrations of fish occur simultaneously. After spawning, fish return to the north of the shelf and gradually migrate to depths of 250–300 m, i.e. to the warm deep-water layers. Fish that did not spawn during the season and continued to feed, do eventually migrate to the same areas. Feeding intensity in winter is low, the index of stomach fullness varies from 0.5 to 1, and the index of intestinal fat reduces from 2.5 in July to 1.5 in October.

The vertical distribution of *C. gunnari* varied with growth and increasing body weight. After hatching in August–September to January–February, larvae are distributed in the upper 100 m layer (Efremenko, 1979; North, 1987). The development and growth of larvae took place in the spring–summer period when the upper water layers are becoming warmer. Subsequently fish gradually migrate into deeper waters. At the age of one year, young fish continue to be distributed in the water column and to form large aggregations even at depths of up to 50–100 from the bottom depending on the time of day. As a rule, vertical diurnal migrations of young fish take place within 75 m from the bottom, the fish being closer to the bottom at night and distributed throughout the entire layer during the day. Comparative analysis of trawl catches taken during the day and at night showed that during the day young fish were more aggregated than at night. Daytime catches significantly exceeded nocturnal ones, while nocturnal catches, in terms of their absolute values, were less variable than daytime catches (Trunov et al., 2000).

Therefore, on the basis of the data collected, it is possible to conclude that young fish are distributed at greater depths than have been described in earlier publications (Shust, 1998).

Immature fish at age 2 to 3 already form aggregations at near-bottom levels. The fish are still distributed in the water column both by day and at night. Nevertheless, it is highly likely that immature fish undertake diurnal migrations, moving from the bottom layer into the water column and back, while a high proportion of them continue to stay in the water column during the day and the frequency of occurrence of immature fish increases due to a reduction in the ratio of mature fish.

Mature fish form concentrations during the day near the bottom, i.e. in the area in which they are fished by bottom trawls. At night these fish ascend in the water column and disperse. The densest concentrations at night were observed at depths of 5–30 m from the bottom.

Mature fish of more than 40 cm are distributed near the bottom throughout the day.

It should be noted that vertical diurnal migrations of young fish are the reverse of those of adult fish. This could be considered as an ecological adaptation of the species in order to protect the offspring. It is related to the fact that cannibalism is widespread in *C. gunnari* populations and fish larger than 25 cm in length feed upon young fish of the same species.

The longer and heavier fish become, the less time they spend in the water column. This may be explained by the absence of a swim-bladder in *C. gunnari* and the subsequent increase in energy losses for buoyancy control.

CONCLUSIONS

(i) *C. gunnari* is characterised by a temporal and spatial segregation of distribution areas at different stages of its life cycle (Figure 6):

- the highest number of young fish are distributed in the southern shelf area;
- as fish grow, they move to the north of the shelf along the eastern and western

shelf areas, while the bulk of small fish migrate to the northeast along the eastern shelf areas;

- the highest number of immature fish was found in the eastern shelf area; and
- mature and large fish are distributed during the feeding and over-wintering periods mainly in the northern shelf area of South Georgia and around Shag Rocks.

(ii) The Shag Rocks is an extension zone of the *C. gunnari* feeding grounds.

(iii) During its life cycle, *C. gunnari* changes from a pelagic species in its early developmental stages to a near-bottom pelagic species at a length of 20 cm and then becomes a bottom species at a length of more than 40 cm:

- larvae inhabit the upper pelagic 100 m layer;
- young fish of more than 60 mm are distributed in the 75 m off-bottom layer and undertake vertical diurnal migrations into the water column during the day and return closer to the bottom at night;
- immature fish are distributed in the water column for most of the day, however they already undertake vertical diurnal migrations typical of mature fish;
- mature fish undertake vertical diurnal migrations, being distributing near the bottom during the day and in the water column at night; and
- large mature fish do not migrate vertically.

(iv) Variations in the depth distribution of *C. gunnari* relate to fish length, season and biological condition.

(v) The annual cycle of mature fish is subdivided into three periods (feeding, spawning and over-wintering), while that of immature fish is divided into two periods (feeding and over-wintering):

- feeding migrations (October–February) relate to migrations of the basic food item (krill), and are observed mainly in the northern shelf area;
- the direction of spawning migrations is from the northeast to the east and north, to the coast, and from the northwest to the west and south to areas with depths of 300–350 m; and
- the direction of post-spawning migrations is to the northeast and northwest.

(vi) The lack of 1-year-old fish in the Shag Rocks area is most probably explained by water currents transporting such fish to areas outside the shelf.

(vii) The abundance of *C. gunnari* recruits is maintained by the segregation of distribution areas of young and adult fish and their different vertical distribution during the day.

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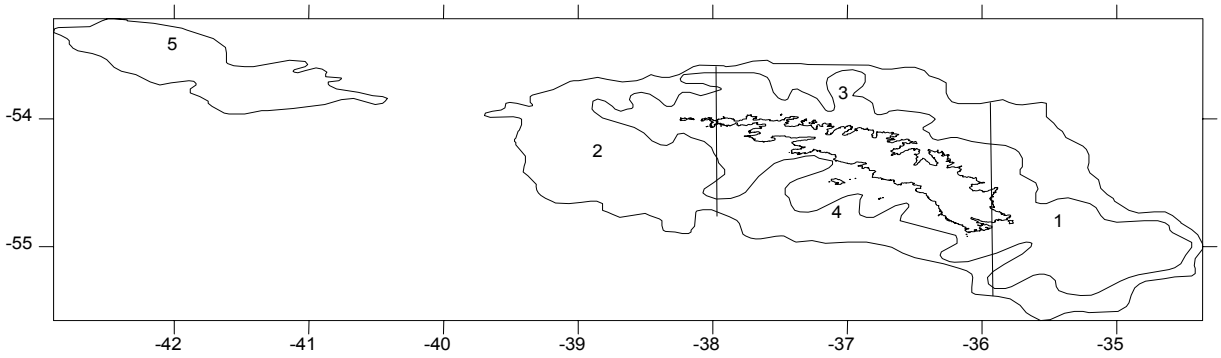

Figure 1: Location of study areas: 1 – east, 2 – west, 3 – north, 4 – south, 5 – Shag Rocks.

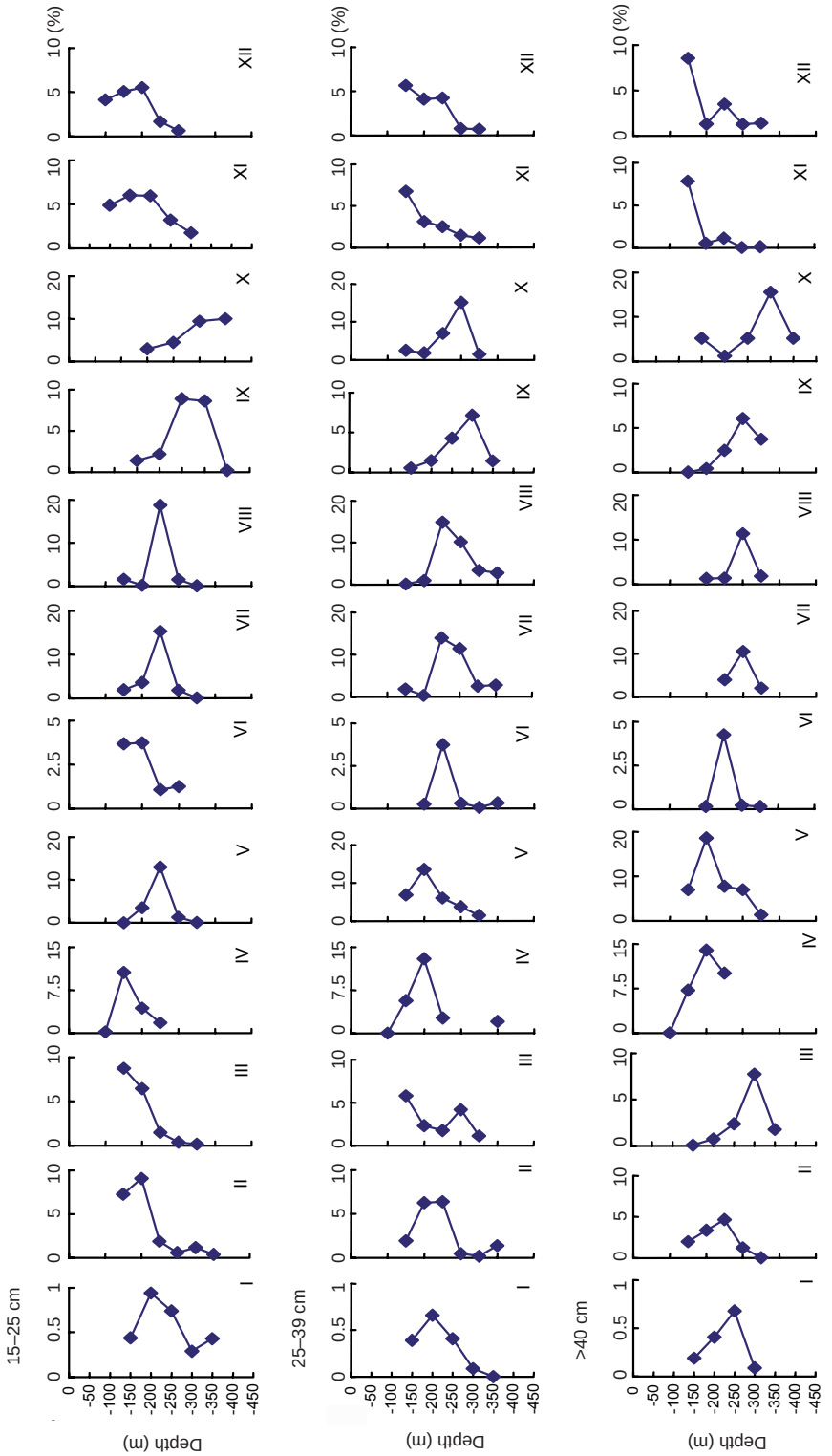

Figure 2: Distribution of various length groups by depth calculated as the percentage of the total number of fish in all samples collected for each month.

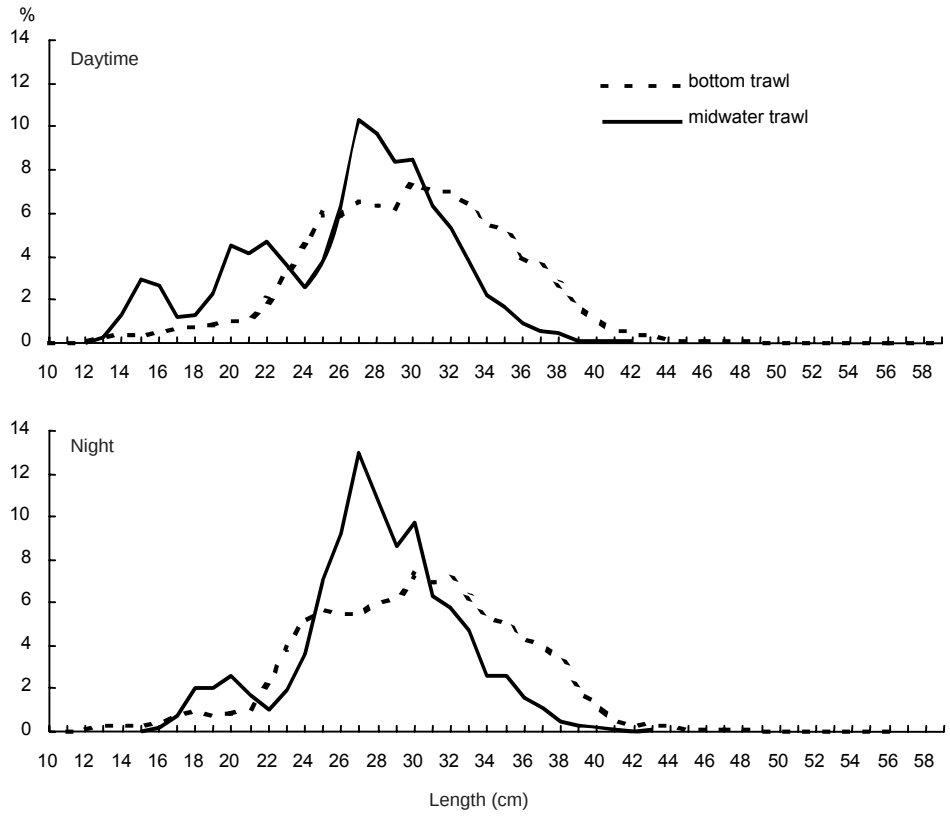

Figure 3: Length composition of *Champsocephalus gunnari* in catches of bottom and midwater trawls.

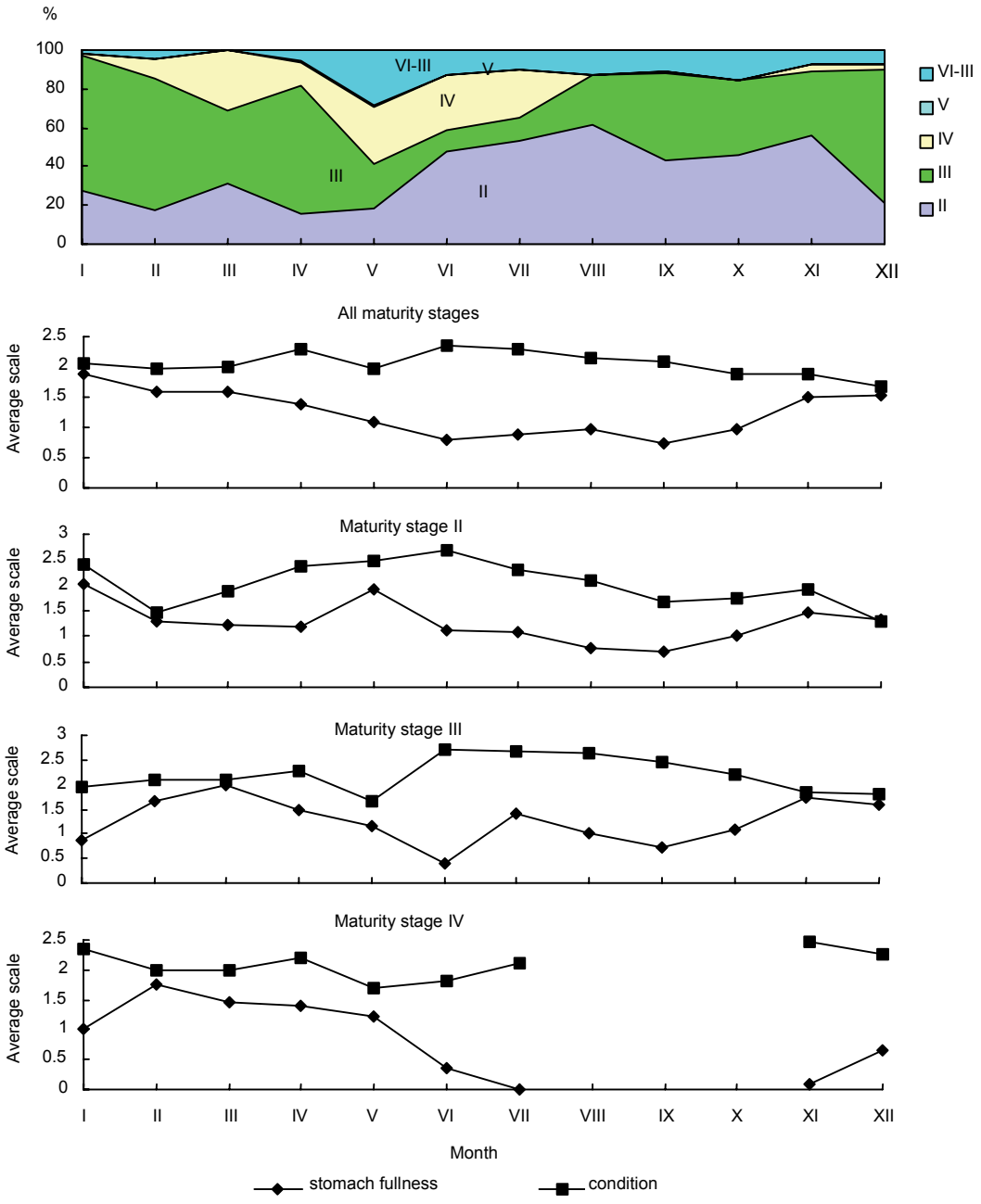

Figure 4: Dynamics of indices of maturity, stomach fullness and intestinal fat of *Champsocephalus gunnari* by month (females only): (a) proportion of fish at various stages of maturity; (b) all maturity stages; (c) maturity stage II; (d) maturity stage III; and (e) maturity stage IV.

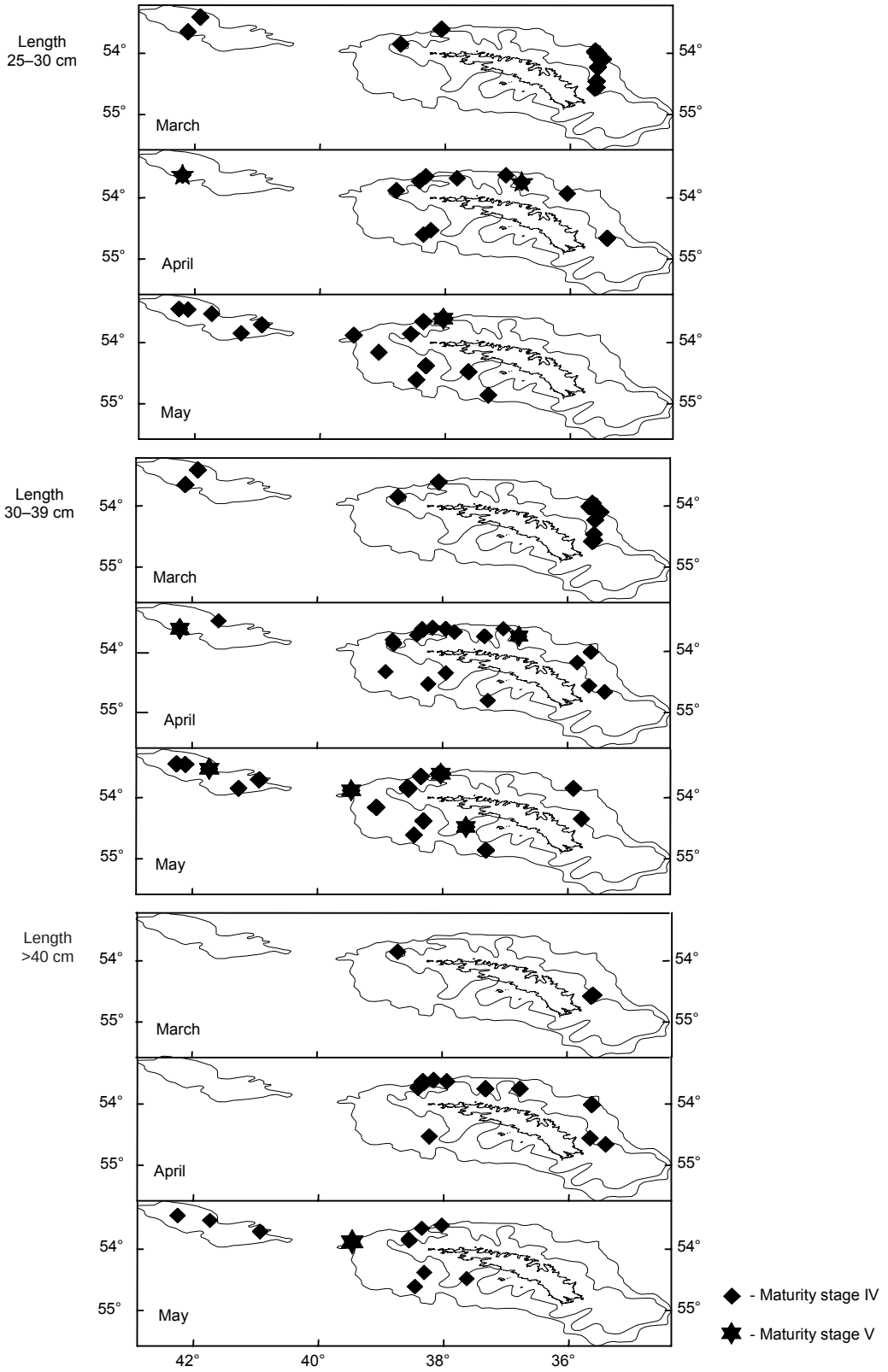

Figure 5: Distribution of *Champsocephalus gunnari* females (maturity stages IV–V) from March to May.

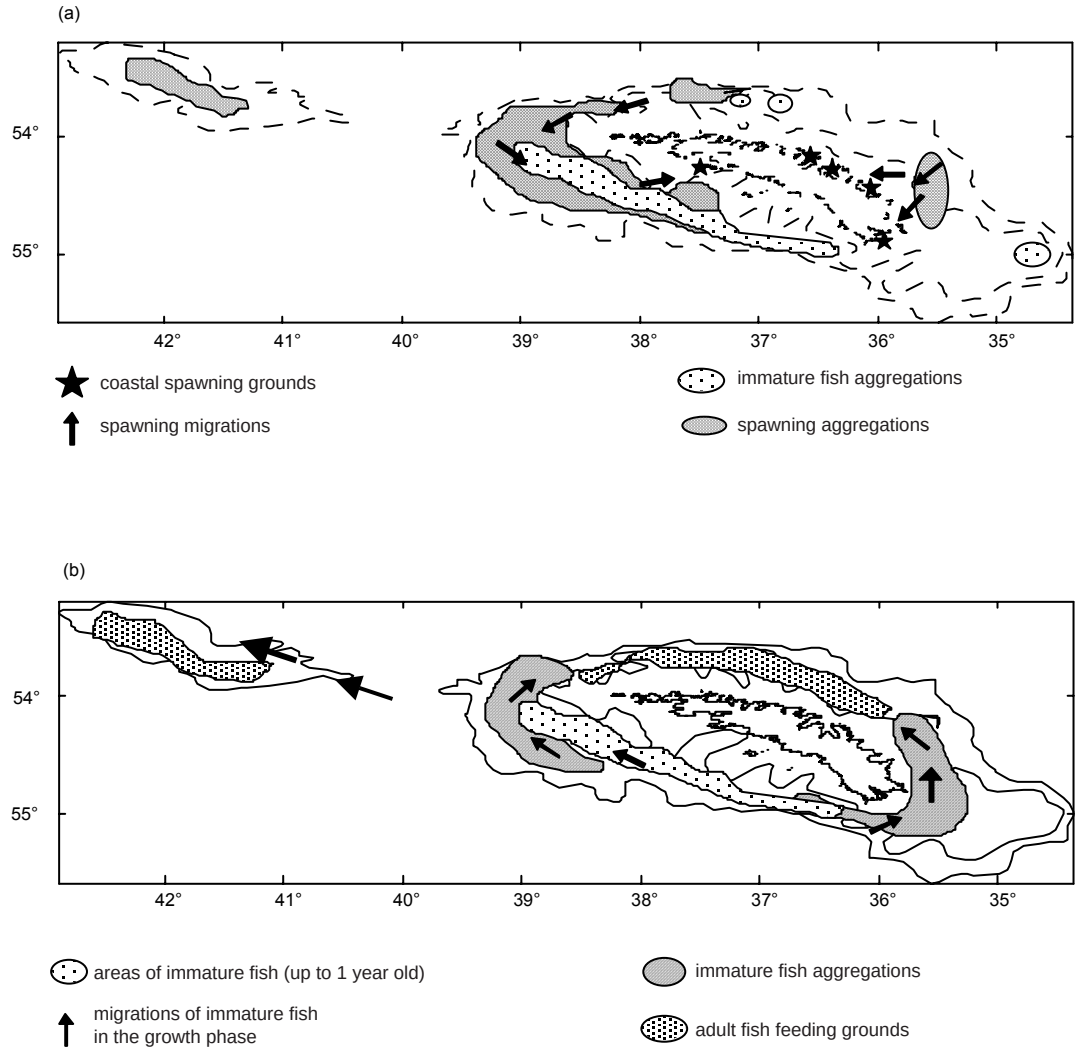

Figure 6: (a) Spawning grounds, main aggregations of immature *Champsocephalus gunnari* and pre-spawning migrations, (b) distribution of *C. gunnari* and migration routes at various life cycle stages.

Liste des tableaux

Liste des figures

Список таблиц

Список рисунков

Рис. 6: (a) Места нереста, основные скопления неполовозрелой *Champsocephalus gunnari* и преднерестовые миграции, (b) распределение *C. gunnari* и маршруты миграции на разных стадиях жизненного цикла.

Lista de las tablas

Lista de las figuras