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The influence of seasonal environmental changes on ontogenetic migrations of the squid *Loligo gahi* on the Falkland shelf

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Running title: Seasonal environmental influence on squid migrations

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ABSTRACT

The Patagonian longfin squid *Loligo gahi* undertakes spatial ontogenetic migrations on the Falkland shelf: juveniles move from spawning grounds located in shallow, inshore waters (20-50 m depths) to feeding grounds near the shelf edge (200-350 m depths). Immature squid feed and grow in these offshore feeding grounds and, upon maturation, migrate back to inshore waters to spawn. To investigate the possible influence of environmental factors on *L. gahi* migrations oceanographic transects, crossing the region of *L. gahi* occurrence, were made from the inshore waters of East Falkland eastwards to depths of 1250 m on a monthly basis from 1999 to 2001. Four main water types were found in the region: shelf, subantarctic superficial and antarctic intermediate water masses, and transient zone waters. The inshore spawning grounds fall in the shelf water mass, whereas the feeding squid (medium-sized immature and maturing individuals) were associated with the transient zone. The isotherm of 5.5°C marked the limit of squid penetration into deeper waters in all seasons. Seasonal changes in water mass characteristics and location, and corresponding seasonal changes in *L. gahi* migrations, were also studied.

Key words: environment, migrations, squid, *Loligo gahi*, Southwest Atlantic

INTRODUCTION

Migratory behavior is a characteristic feature of squid (Hanlon & Messenger, 1996). During their ontogenesis, squid undertake spatial and vertical migrations, seeking optimal environmental conditions for spawning, egg development, and juvenile and adult growth (Nesis, 1985). Nesis (1985) distinguished five types of ontogenetic vertical migrations in pelagic squid on the basis of the location of different ontogenetic stages within the water column. Demersal and near-bottom squid make their ontogenetic feeding and spawning migrations over the bottom in offshore-onshore directions (Mangold-Wirtz, 1963).

The southwest Atlantic loliginid squid *Loligo gahi* is not an exception to the rule. This relatively small squid (adults attain usually 13-17 cm mantle length, ML) is abundant in near-bottom water layers on the Falkland shelf. It has been shown that small juvenile *L. gahi* move from nursery grounds located in shallow inshore waters to offshore feeding grounds on the shelf edge at depths of 200-300 m (Hatfield & Rodhouse, 1994). Upon maturation, adults are thought to return to shallow waters to spawn (Hatfield et al., 1990). Dense aggregations of *L. gahi* are encountered, mainly during the offshore feeding period when they are targeted by the commercial trawling fleet (Hatfield and des Clers, 1998). The reason for such dense feeding concentrations of *L. gahi* is not known at present. Environmental effects on their distribution may be postulated; such effects have been found in oceanic ommastrephid squid where a hydrological front can create an effective environmental barrier for migrating schools (O'Dor & Coelho, 1993; Murata & Nakamura, 1998).

L. gahi is the coldest water loliginid species and consists of two cohorts spawning in different seasons; the first, autumn-spawning, cohort and the second, spring-spawning, cohort (Patterson, 1988). Its life cycle is closely associated with waters of subantarctic origin (Rodhouse et al., 1995). The highest concentrations of *L. gahi* are observed to the south and east of the Falkland Islands (in the so-called '*Loligo* box'; Hatfield & des Clers, 1998). The '*Loligo* box' is occupied mainly by waters associated with the northward flowing Falkland Current, consisting of Subantarctic Superficial water (SASW), Antarctic Intermediate water (AAIW) and its derivative Shelf waters which result from mixing with inshore waters (Bianchi et al., 1982). Calculation of integral circulation showed the presence of an anticyclonic (counter-clockwise) current around the Falklands (Zyryjanov & Severov, 1979) with inflows of the eastern branch of the Falkland Current to the northern part of the shelf (Maslennikov & Parfenovich, 1979). Very little is known about seasonal and inter-annual variability of oceanographic parameters around the Falkland Islands except sea-surface temperatures (SST) for which satellite derived data are available from the National Center for Atmospheric Research (U.S.A.).

SST data (together with spawning stock size estimates) were used to model the recruitment strength of the spring-spawning cohort of *L. gahi*, explaining 77% of the variance (Agnew et al., 2000). A good correlation was found between squid mantle length at a certain age (200-210 days) and SST at their hatching time: *L. gahi* of the same age which had hatched in the summer were significantly larger than their counterparts which had hatched in the winter (Hatfield, 2000). However, as the SST data are only an indirect indicator of the hydrological and dynamic processes occurring in the superficial water layers, they cannot provide a direct explanation of the bathymetric patterns of *L. gahi* distribution and its movements near the bottom.

The main aim of this work is to describe the intra-annual variability in hydrological parameters within the whole water column of the *L. gahi* habitat near the

Falkland Islands, with an attempt to reveal any environmental effects on its seasonal bathymetric distribution.

MATERIAL AND METHODS

Oceanographic data

Oceanographic data were collected every month along one latitudinal transect carried out onboard the Falkland Islands Fishery Patrol and Research vessel *Dorada*. A total of 14 monthly transects were made and analysed between November 1999 and February 2001. The transect was situated to the east of Port William (East Falkland), crossing the northern part of the '*Loligo* box'at 51°45'S, and consisted of seven hydrological stations. The westernmost station was situated above the 20-30 m depth contour at the entrance to Port William and the easternmost station was situated over 1150 m depth at approximately 55°36'W (Figure 1). Other stations were made above the 100, 200, 300, 500, and 1000 m depth contours. The distance between stations varied from 13 to 41 km and the total transect length was 154 km. Each transect took 10-11 hours to complete.

The transects were carried out around the middle of every month, subject to availability of the vessel and weather conditions. The interval between transects varied from 21 to 40 days (mean 30.5 days). Due to unforeseen circumstances transects were not performed in March and June 2000.

A CTDO sealogger SBE-25 (Sea-Bird Electronics Inc., Bellevue, USA) was deployed from the surface to 5-10 m above the bottom to obtain depth profiles of temperature (°C), salinity (PSU), and dissolved oxygen (ml l^{-1}). Temperature was measured directly whereas the other parameters were calculated using Seasoft v. 4.326 software (Sea-Bird Electronics Inc.) from the following measured parameters:

pressure (db), conductivity (S/m), oxygen current (μA) and oxygen temperature (°C). All sensors of the CTDO were calibrated once a year by Sea-Bird Electronics Inc.

Vertical profiles of temperature, salinity, dissolved oxygen and water density were interpolated along each transect using Surfer v. 7.02 software, and the data were smoothed by kriging. Temperature-salinity (T-S) diagrams on the isopicnic surface were made for each monthly transect. To analyse the temporal and spatial variability of water mass distribution along the transect a complex method (Miller, 1950) was used based on the T-S analyses and spatial and temporal variability in vertical and horizontal gradients of temperature and salinity, respectively. The T-S method was not used at the shallow water (30-m) station. The literature on temperature and salinity of water masses in the Southwest Atlantic was also used to identify the main water masses and their derivatives, as well as the borders between them (Bianchi et al., 1982).

Biological data

All vessels licensed to fish for *L. gahi* in Falkland's waters have to report their catch, duration of trawling, mean fishing depth and position on a daily basis. Catch reports for vessels fishing in the region from 50°S to 52°S and 56.7°W to 58.62°W (the northern part of the *Loligo* box, Fig. 1) were selected for the same period as oceanographic sampling, i.e. between 1 November 1999 and 28 February 2001. Commercial bottom trawl hauls commonly last several hours, during which the trawling depth can be varied (however, generally by not more than 30-50 m). The mean daily CPUE (mt/hr) was, therefore, calculated for 25m depth classes and 10 day overlapping periods for comparison with water mass distribution.

Biological data for *L. gahi* were collected by Fisheries Department observers in the same area and period. As there is no restriction on mesh size for the trawl codend in the *L. gahi* fishery (Hatfield and des Clers, 1998) it was assumed that all size groups with mantle length (ML) > 70-80 mm were fished equally. Each observer processed two random samples of 200 specimens (taken from two different trawls) a day. The biological analysis included measurement of the mantle length (5 mm length intervals) and assignment of sex and maturity stage (after Lipinski, 1979). These data were used to construct length frequency distributions for males and females, again using 10-day overlapping time periods.

RESULTS

Distribution and seasonal variability of water masses

A scheme of the main water masses encountered along the transect is presented in Figure 2. **Shelf waters** (SW) occurred from the coast to depths of 40-150 m throughout the year. They were characterised by a temperature range of 4-11°C and salinity range of 33.60-33.85‰. Concentration of dissolved oxygen was 6.25-7.75 ml/l. The vertical distribution of temperature was rather uniform with the exception of the first spring warming when a seasonal thermocline appeared above depths of 80-100 m.

The greatest offshore penetration of shelf waters in the near-bottom layers was observed in November-December (150-160 m). In May their distribution was bounded by the 40-45 m depth contour. The maximum volume and offshore penetration of the shelf waters were generally observed in spring and summer, whereas minimum volumes were recorded in autumn and winter.

Seasonal variability of the shelf water temperature was mainly attributable to solar radiation and convection, with maximum temperatures being observed in December 1999- February 2000 (9-11°C) and minimum temperatures in August-September (4.2-4.3°). The surface temperature in summer 2000/2001 was lower than in summer 1999/2000 by 0.5-0.8°C. Seasonal variability in salinity was low. During the observed period, a slight negative trend was observed leading to an overall decrease of 0.15‰. A freshening of the surface layer in June and September 2000 was probably caused by precipitation.

Transient zone waters (TZ) represented the western periphery of the Falkland Current, and were observed as a zone of steep gradients on the shelf edge. Their salinity was 33.85-34.10‰. Seasonal variability in temperature was higher in the upper layers, and lower near bottom. The maximum surface temperatures were observed in February 2000 and January 2001, and the minimum temperature in September 2000.

In contrast to shelf waters the seasonal amplitude of temperature variations was different in different layers, with a magnitude of about 5°C on the surface and 2°C near bottom. Near-bottom water attained its maximum temperature about two months later than on the surface. Periods of maximum seasonal warming (December 1999-March 2000 and December 2000-March 2001) were characterised by a great temperature range within the transient zone, 3.5 and 4°C respectively, whereas in cold season (August-October 2000) it was only about 0.7°C. A seasonal thermocline appeared in November 1999 and disappeared in April 2000, attaining its greatest development in January-February 2000. Near the bottom the position of both upper and lower limits of the transient zone varied throughout the year, being deeper in summer and shallower in winter (Figure 3).

The **Subantarctic Superficial water mass (SASW)** is situated from the surface to depths of 100-300 m, depending on station position, and represents the upper layer of the Falkland Current. Salinity of this water mass was rather stable throughout the year (34.10-34.15‰). Seasonal variability in temperature was observed only in the upper 200-m water layer, with the maxima being in February 2000 (8.5°C) and February 2001 (7.5°C), and minimum in July-September 2000 (4.5-5°C).

The **Atlantic Antarctic Intermediate water mass (AAIW)** represented the bulk of the water flow of the Falkland Current. It was situated under the SASW to the maximum depths investigated. Its main feature was the presence of an intermediate salinity minimum at its core. During the period observed this core was situated between 500 and 750 m depth (mean 630 m). Upwelling of the AAIW was observed during increases of Falkland Current intensity (April and September 2000). AAIW salinity ranged from 34.12 to 34.45‰ with the mean salinity in the core of 34.17‰. Temperature varied from 2.5 to 4.5°C (mean 3.38°C).

Temperature variability on the shelf and shelf edge

Temperature patterns on the surface and near the bottom showed different trends throughout the year (Figure 4). Above the 100-m and 200-m depth contours SST were greatest (9.2-10.8°C) in summer 2000 (January-February). SST decreased quite rapidly due to the autumn cooling and were at their minimum level (slightly more than 5°C) between July and October. Spring warming induced a rapid increase of SST in November-December up to peak levels in January 2001 of ~9.2°C. Therefore, SST in summer 2000 were much higher than those in summer 2001.

Near-bottom temperatures at the 30-m and 100-m depth contours were quite similar to those at the surface over the 100-m and 200-m contours, achieving their greatest levels in summer (January-February). However, the period of minimum temperature was shorter (about a month) than those of SST (four months). Temperatures at 100-m depth attained their minimum (4.7°C) in September and at 30-m depth in August (4.33°C), the latter being even lower than the temperature at 400-m depth during the same period.

Near-bottom temperatures at the 200-m depth contour behaved differently. They were at their lowest in November 1999 (4.9°C) and then gradually increased, attaining their highest values only in May (6.4°C). After this they dropped to 5.0°C in September and then increased through to January 2001. Near-bottom temperatures at 300-m depths showed a similar trend but with a lower amplitude than at 200-m. At 400-m depth temperatures were quite stable throughout the year (4.2-4.8°C).

Thus, one of the important features of the eastern part of the Falkland Shelf was a delay, relative to the surface and near-shore shallow waters, in reaching the maximum temperatures in the near-bottom layers. These differences were most pronounced at the 200-300-m depth contours resulting in a 3-4 months difference in seasonal timing.

Generally the period of the spring-summer warming, with a well-resolved thermocline, was followed by autumn cooling when (in May) the temperatures became almost equal through the entire water column from the coast to 200-m depth (6.4-7°C). The winter cooling (June-July) first started near the coast where the temperatures in shallow waters dropped faster than at 100-200-m depths. August and September were the coldest months inshore with the warmest water layer being situated at the depth of 200 m. The spring warming started in October with similar equality in temperatures developing as in May, but at lower level (5.1-5.4°C), followed by a sharp warming of both surface layers and shallow waters in November (Figure 4).

Seasonal variations in depth distribution of L. gahi

License conditions permit commercial trawlers fishing for *L. gahi* in Falkland waters to fish everywhere but within the 3-mile coastal zone of the '*Loligo* box'. The number of licenses issued varied from 15 to 18 per fishing season (FIG, 2000). Trawlers target *L. gahi* in every part of the *Loligo* box where it forms commercially exploitable aggregations during a given period. This provides sufficient coverage of the whole fishing area and we therefore assume that the CPUE distribution of the trawling fleet reflects the bathymetric patterns in distribution of *L. gahi* concentrations during the fishing season.

The bathymetric distribution of *L. gahi* varied in the northern part of the '*Loligo* box' throughout the year. In February-March squid occurred mainly in shallow waters at 50-125- m depths with near maximum water temperatures (9-10°C). In April-May they were concentrated deeper (at 125-175 m) in colder waters (7-8°C). Generally the depth range was quite narrow in the first half of the year, not exceeding 75 m in any given week (Figure 5). In the second half of the year the depth range was much wider (150-175 m). Most squid concentrated at 150-250 m depths in August and even deeper (175-275 m) in September-October in the warmest water layer in this period (~5°C). At the end of October *L. gahi* concentrations occurred shallower than previously (125-225 m), possibly following the start of spring warming of shallow waters, and by the end of October, when the commercial fishery closes, they had completely vanished from the fishing grounds (Figure 5). Sizes of squid in the first half of the year were generally smaller than in the second half of the year (Figure 6).

Comparing the distribution of squid with that of the different water masses present in the northern part of the '*Loligo* box' shows that in the beginning of the year *L. gahi* were concentrated in the Shelf Water Mass. In autumn squid occurred in the inshore part of the Transient Zone. In winter-spring they were encountered throughout the entire Transient Zone, leaving it and moving to the Shelf Water Mass again by November. It is notable that *L. gahi* was never encountered in the Falkland Current waters themselves - neither in the SASW nor in the AAIW.

DISCUSSION

The water mass structure, and its seasonal dynamics, to the east of the Falkland Islands are quite typical for the southern region of the Patagonian Platform with the surface layers warming, and subsequent formation of a strong thermocline at depths 50-70 m, in summer and cooling of the entire shelf water column in winter (Bianchi et al., 1982). It is notable, however, that the formation of the warm intermediate near-bottom water layer at 200-m depths on the shelf, and a shift of maximal temperatures at these depths to late autumn (Figure 7), has not been described before. This feature appeared to be very important for the depth distribution of *L. gahi* during the cold autumn and winter seasons.

The results of this study makes it possible to shed some light on the differences in depth distribution and migration of both major cohorts of *L. gahi* around the Falkland Islands. Currently it is a widely accepted hypothesis that the autumn (ASC) and spring spawning (SSC) cohorts occur on the same feeding grounds in different seasons (Patterson, 1988; Agnew et al., 1998b). The changeover between two cohorts has been indicated by a decline in the overall maturity status of squid and usually occurs in April/May (Agnew et al., 1998a). Several questions, however, remain unanswered about the life cycles of these cohorts. The results of this paper show that in summer-autumn there is only a slight change in the size of squid on their feeding grounds, whereas in winter-spring there is a continuous increase in the modal length of squid (Figure 6). Very few maturing and mature females have been caught in summer-autumn, whereas later in the year a constant maturation is evident with almost all females being mature at the end of winter/start of spring (Patterson, 1988, Hatfield et al., 1990). If the hypothesis of two cohorts changing over rather rapidly on the feeding grounds is true (Hatfield and Des Clers, 1998), why does the autumn-spawning cohort seem to have erratic growth rates and where are its mature squid?

The simultaneous analysis of intra-annual distributions of water masses, and their different hydrological parameters, with the depth distribution of *L. gahi* showed that squid of different cohorts chose the warmest available near-bottom water layers of the transient zone between shelf waters and Falkland Current as their feeding grounds on the Falkland Shelf (Figure 8). In summer, immature squid of the ASC prefer to stay in the warmer waters of the inshore boundary of the transient zone, moving to shallow shelf waters as soon as they started to mature. We suggest that continuous inshore emigration of larger maturing squid from the feeding grounds, and offshore immigration of smaller, immature squid to the feeding grounds masks growth trends, and also results in the absence of mature ASC squid in catches at this time of the year. In autumn emigration of the ASC from their feeding grounds finishes and these squid are replaced by immature squid of the SSC, which are just arriving on the shared feeding grounds. Late autumn equality in temperatures from inshore to 200-m depths enables them to penetrate deeper into the Transient Zone. Winter cooling of the Shelf Waters and formation of the warm water layer between 150 and 250 m depths in the Transient Zone restricts squid almost exclusively to this zone, their movement limited by colder waters situated both shallower and deeper. Thus, the whole SSC cohort stays in the deepwater feeding grounds in winter, and continuous growth and maturation is therefore evident in biological sampling. At this time there is no suitable route for mature squid to go to spawn, and there is not usually any influx of the autumn-spawned recruits as they still have not hatched from their egg masses (Hatfield, 2000). However, as soon as the spring warming starts at the end of October squid begin to move to shallow water to spawn, disappearing first from the deeper parts of the Transient Zone.

Loliginid squid are generally warm-water animals having their highest species diversity on the tropical and subtropical shelves of the world's oceans (Nesis, 1985). In temperate waters loliginids are much less diverse and they commonly penetrate to the polarward peripheries of their species ranges with warm water currents, an example being *L. vulgaris* and *L. forbesi* in United Kingdom waters (Waluda and Pierce, 1998). Populations of both these squid species, in the English Channel (Robin and Denis, 1999) and North Sea (Waluda and Pierce, 1998), were apparently more abundant in warmer than average water conditions. A preference for warm water masses within their habitats has been also shown for *L. vulgaris reynaudii* near the South African coast (Roberts and Sauer, 1994) and *L. pealei* in the Northwest Atlantic (Brodziak and Hendrickson, 1998). Our results show that the coldest water loliginid *L. gahi* also follows the common practice of loliginids and, therefore, tends to choose the warmest possible water layers for its distribution on the feeding grounds in a given season.

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Figure captions

Figure 1. Positions of oceanographic stations (crosses) on the monthly transect and within the *Loligo* box) off Stanley (Falkland Islands).

Figure 2. Scheme of the water mass distribution across the shelf and continental slope to the east of the Falkland Islands

Figure 3. Seasonal changes in depth distribution of *L. gahi* catches and the positions of the transient zone (upper and lower boundaries in dash lines, medium layer in solid line)

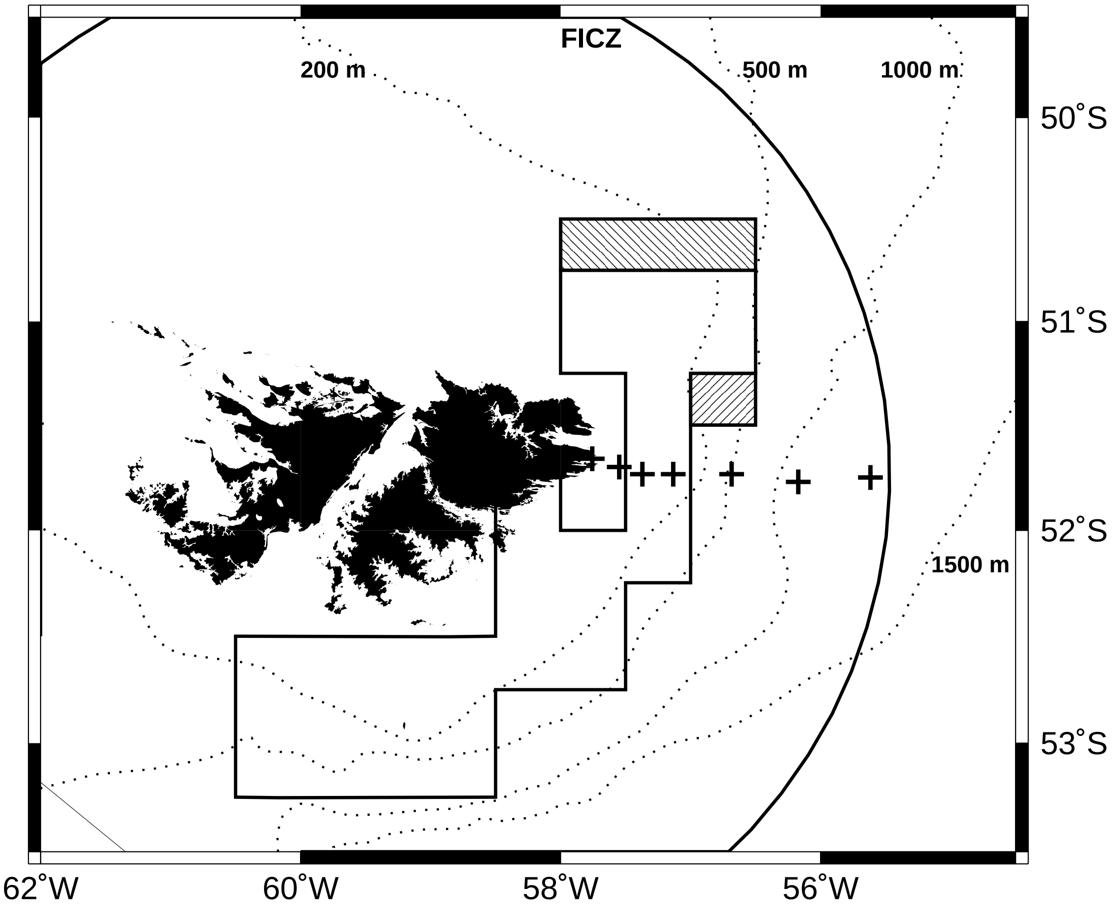
Figure 4. Seasonal temperature changes in the surface layer (SURF) over the 100- m depth contour and near the bottom (BOTT) at various depths on the Falkland islands shelf and slope

Figure 5. Seasonal changes in depth distribution of *L. gahi* catches and near-bottom temperatures

Figure 6. Seasonal changes in length frequencies of males and females of *L. gahi* in the eastern part of the Falkland shelf

Figure 7. Spatial and temporal variability of temperature [°C] in the near-bottom layer to the east of Falkland Islands in November 1999 – February 2001

Figure 8. Scheme of the ontogenetic migrations of the first (in blue) and the second (in black) cohort of *L. gahi*. Faded regions showed depths and times of commercial fishery.


FICZ
200 m
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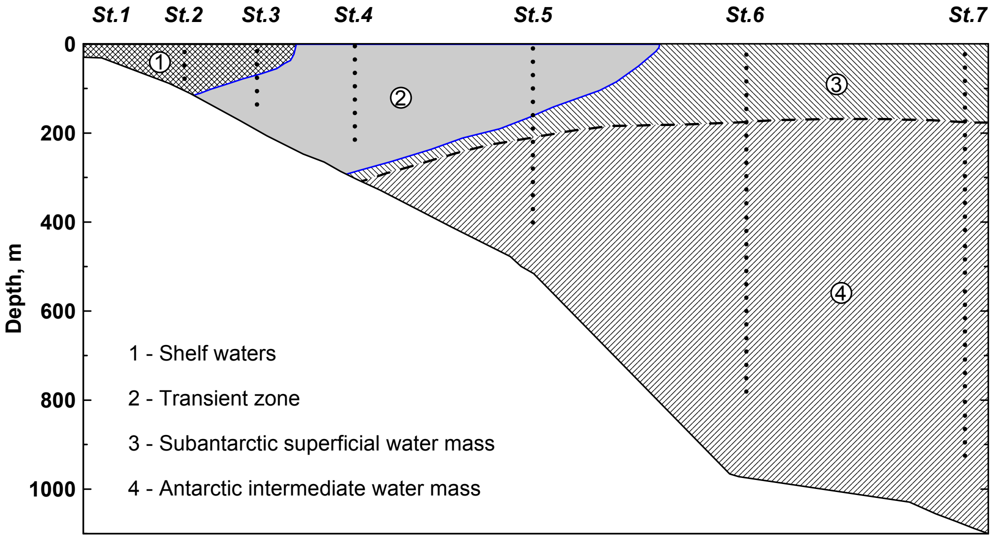
52°S
53°S
62°W
60°W
58°W
56°W

Fig. 1.


St.1
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St.7
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400
600
800
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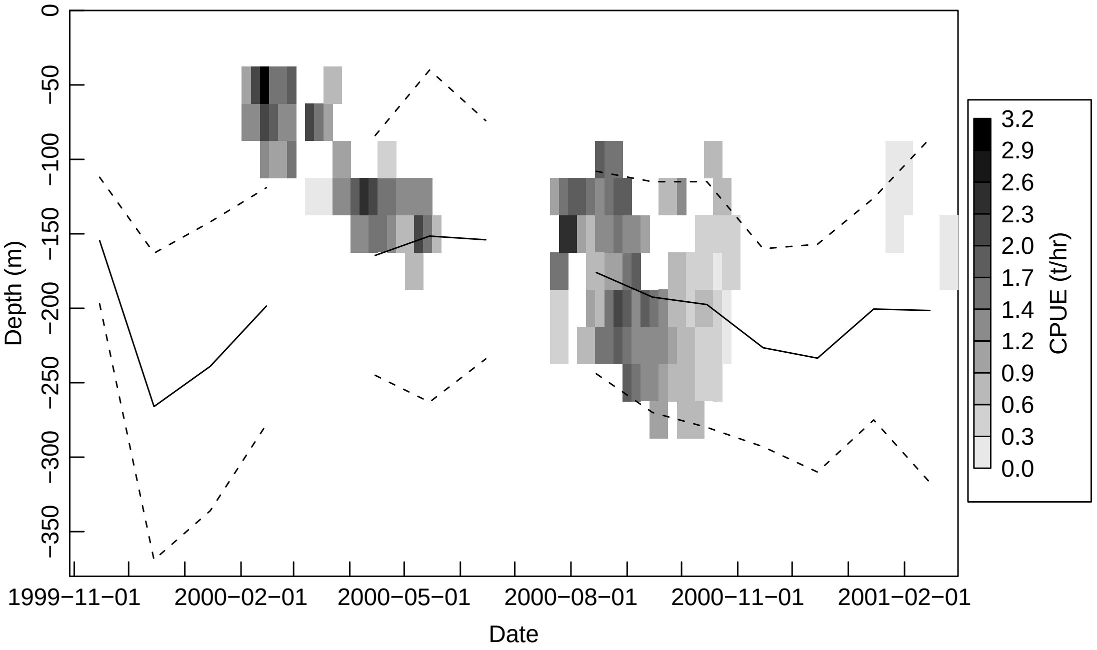
Depth, m
①
②
③
④
1 - Shelf waters
2 - Transient zone
3 - Subantarctic superficial water mass
4 - Antarctic intermediate water mass

Fig.2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Depth (m)
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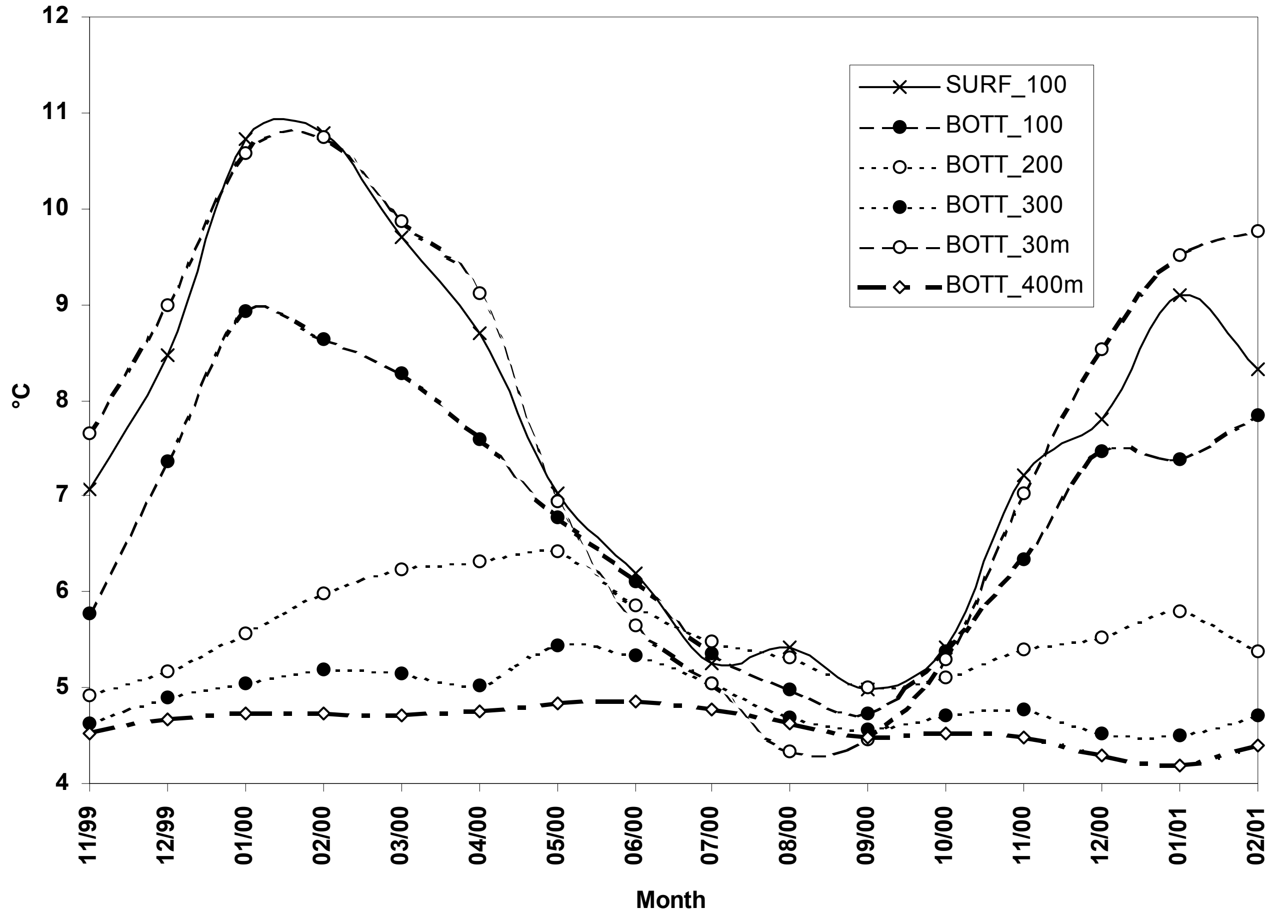
2000−08−01
2000−11−01
2001−02−01
Date
3.2
2.9
2.6
2.3
2.0
1.7
1.4
1.2
0.9
0.6
0.3
0.0
CPUE (t/hr)

Fig. 3



12
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°C
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12/99
01/00
02/00
03/00
04/00
05/00
06/00
07/00
08/00
09/00
10/00
11/00
12/00
01/01
02/01
Month
SURF_100
BOTT_100
BOTT_200
BOTT_300
BOTT_30m
BOTT_400m

Fig. 4.

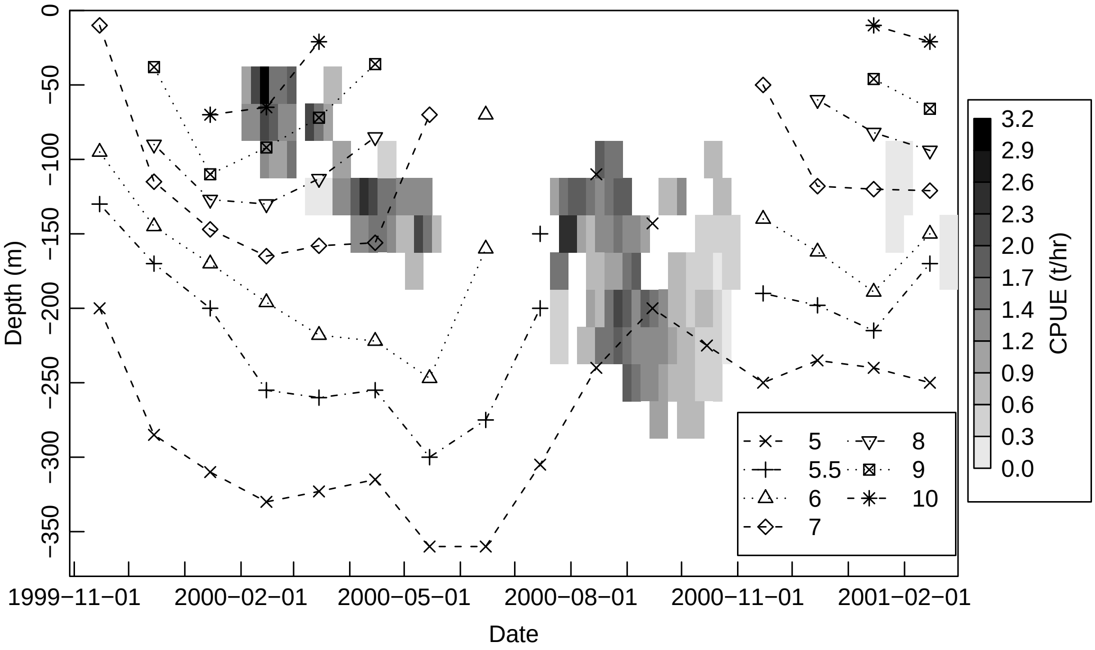
0
−50
−100
−150
−200
−250
−300
−350
Depth (m)
1999−11−01
2000−02−01
2000−05−01
2000−08−01
2000−11−01
2001−02−01
Date
5
5.5
6
7
8
9
10
3.2
2.9
2.6
2.3
2.0
1.7
1.4
1.2
0.9
0.6
0.3
0.0
CPUE (t/hr)

Fig. 5.

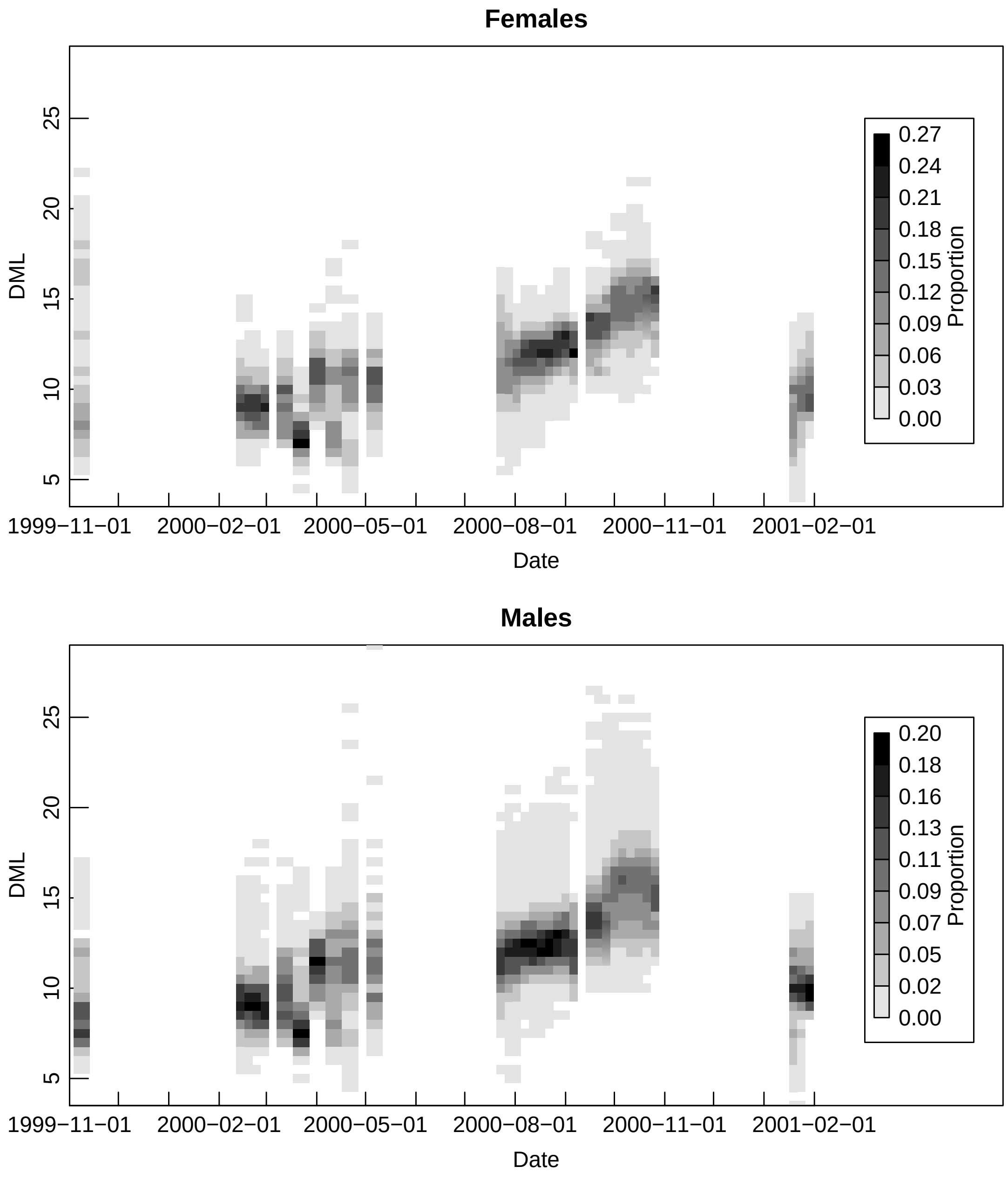
Females
DML
25
20
15
10
5
0.27
0.24
0.21
0.18
0.15
0.12
0.09
0.06
0.03
0.00
Proportion
1999−11−01
2000−02−01
2000−05−01
2000−08−01
2000−11−01
2001−02−01
Date
Males
DML
25
20
15
10
5
0.20
0.18
0.16
0.13
0.11
0.09
0.07
0.05
0.02
0.00
Proportion
1999−11−01
2000−02−01
2000−05−01
2000−08−01
2000−11−01
2001−02−01
Date

Fig. 6

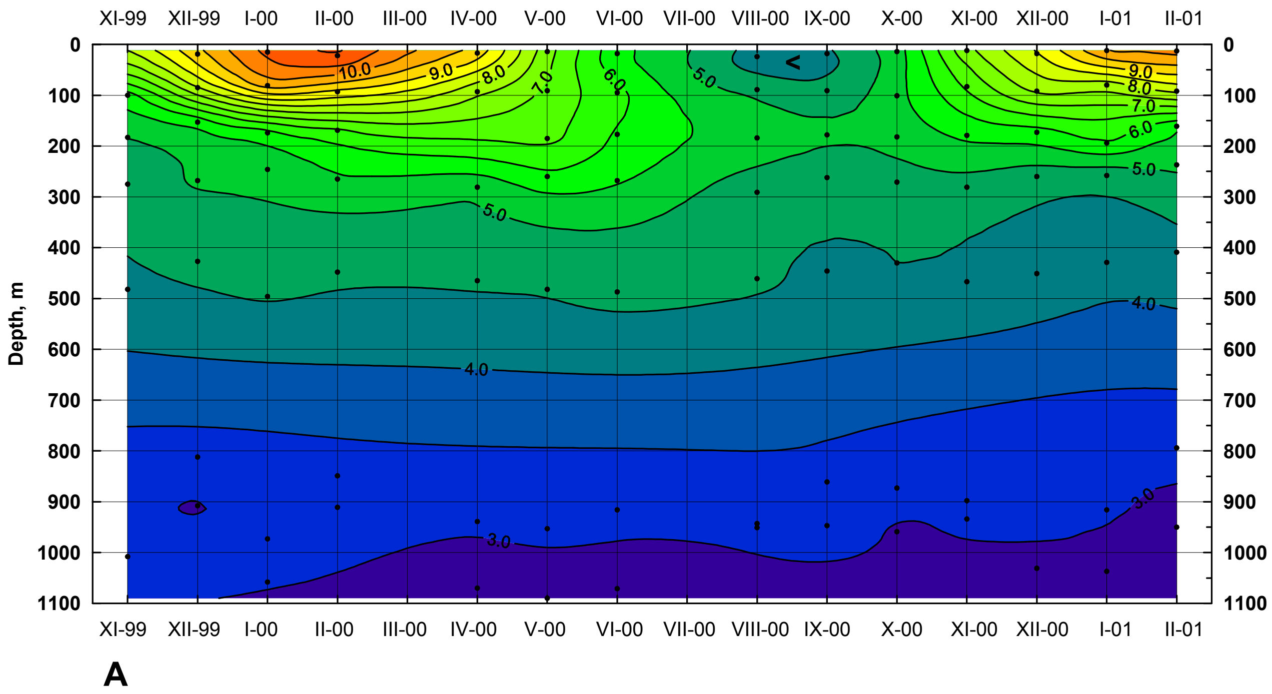
XI-99
XII-99
I-00
II-00
III-00
IV-00
V-00
VI-00
VII-00
VIII-00
IX-00
X-00
XI-00
XII-00
I-01
II-01
Depth, m
0
100
200
300
400
500
600
700
800
900
1000
1100
10.0
9.0
8.0
7.0
6.0
5.0
4.0
3.0
A

Fig. 7.

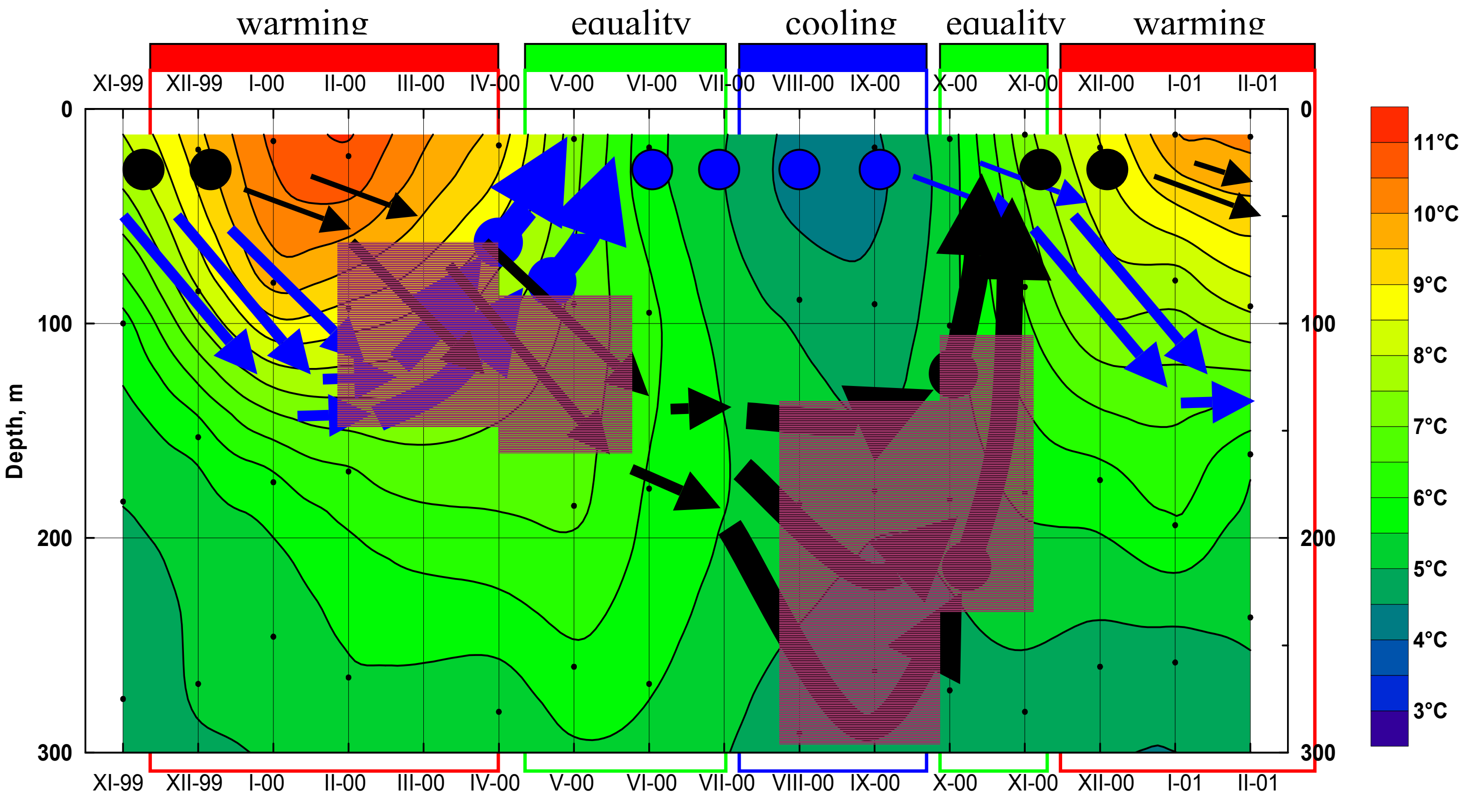
warming
equality
cooling
equality
warming
XI-99
XII-99
I-00
II-00
III-00
IV-00
V-00
VI-00
VII-00
VIII-00
IX-00
X-00
XI-00
XII-00
I-01
II-01
Depth, m
0
100
200
300
11°C
10°C
9°C
8°C
7°C
6°C
5°C
4°C
3°C

Fig. 8