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Interactions between oceanography, ecology and fishery biology of the ommastrephid squid *Martialia hyadesi* in the South Atlantic

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ABSTRACT: The seven star flying squid *Martialia hyadesi* is an oceanic slope ommastrephid with a circumpolar distribution associated with the Antarctic Polar Frontal Zone (APFZ) and is a minor, variable catch in the South Atlantic *Illex argentinus* fishery. There have been occasional unusually large catches of *M. hyadesi*, the latest being in 1995. Because of the importance of understanding the influence of the physical environment on fisheries for oceanic squid, and interest in developing a new fishery for *M. hyadesi* in the CCAMLR area, we examined specimens and data from the 1995 season and analysed 10 yr fisheries and remotely sensed oceanographic data sets from the area. The 1995 data show that *M. hyadesi* remains in the cool APFZ waters of the Falkland Current where it preys on oceanic fish and crustaceans and its distribution rarely extends over the Patagonian Shelf. The squid exploited by the fishery in 1995 were 6 to 12 mo old; females were immature but some males were fully mature. A remotely sensed sea surface temperature (SST) image revealed mesoscale features at the shelf break front between Patagonian Shelf water and APFZ water where the squid were caught. The appearance of *M. hyadesi* in the fishery over the last decade, including 1995, has been related to SST anomalies. Teleconnections probably exist between these anomalies, El Niño/Southern Oscillation (ENSO) events in the Pacific and sub-decadal oceanographic instability in the Antarctic. Squid are short-lived and populations are likely to be able to respond rapidly to environmental change. However, it is not clear at what stage in the life cycle of *M. hyadesi* these oceanographic events exert their effect. We propose 2 alternative, but not mutually exclusive, hypotheses. Warm events prior to the appearance of *M. hyadesi* may favour reproductive success of the parent generation giving rise to a strong recruitment, or alternatively this cool water species may extend its range to the edge of the Patagonian Shelf early in the development of cold oceanographic events. In either case oceanographic effects are probably mediated via the squid's prey.

KEY WORDS: *Martialia hyadesi* · Oceanography · Ecology · Fishery biology · South Atlantic

INTRODUCTION

The squid fishery in the southwest Atlantic is dominated by the Argentine shortfin squid *Illex argentinus* which is widely distributed over the Patagonian Shelf. There is also a relatively minor and variable fishery for the seven star flying squid *Martialia hyadesi*, an oceanic shelf species whose distribution extends from the open ocean in the Antarctic Polar Frontal Zone (APFZ) to the Patagonian Shelf edge (Rodhouse 1991). The *M. hyadesi* catch is small relative to the total stock (Rodhouse et al. 1993, Rodhouse in press) and small in comparison with the size of the *I. argentinus* catch. It is caught by vessels primarily targeting *I. argentinus*. *M. hyadesi* catch rate probably reflects environmentally driven variability in the stock more accurately than the catch rate of *I. argentinus* which is fully exploited, or overexploited. The *I. argentinus* stock is heavily influ-

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enced by differences in fishing effort, and catches are therefore subject to the effects of economic, social and political factors.

Martialia hyadesi occupies an important position in the trophic web of the Southern Ocean ecosystem (Rodhouse & White 1995) and it has been estimated that consumption by higher predators in the Scotia Sea amounts to at least 326 000 t yr^{-1} (Rodhouse et al. 1993). Dietary analysis of *M. hyadesi* from samples obtained in the APFZ in the Scotia Sea showed that *M. hyadesi* is an opportunist predator feeding on a range of prey including mesopelagic fish, crustaceans and cephalopods (Rodhouse et al. 1992b). Feeding concentrations have been located in mesoscale oceanographic features at the Antarctic Polar Front (APF) (Rodhouse et al. 1996). The lifespan of *M. hyadesi* is short, although it may be more than 1 yr (Rodhouse et al. 1994), and in common with other squid *M. hyadesi* is almost certainly semelparous.

Only relatively small quantities of *Martialia hyadesi* have been caught in the Falkland Islands Conservation Zone since 1987, when it was established. However, a catch of about 26 000 t of *M. hyadesi* was reported from the area in 1986 (Rodhouse 1991). There were no other records of high catch rates until 1995 when this study was initiated, although there was a small catch in 1990. The appearance of *M. hyadesi* in the area in 1986 was apparently associated with a change in the Falkland Current (Rodhouse 1991), which is a part of the Sub-Antarctic Front (SAF) (Peterson & Whitworth 1989).

During the 1995 fishing season, on which this study is based, the majority of the *Martialia hyadesi* catch was taken in a restricted region to the north of the Falkland Islands, in an area close to the shelf edge. Oceanography around the Falklands Plateau is complex and different assemblages of cephalopod species are associated with the different water masses (Rodhouse et al. 1992a). In 1995 catches were taken close to the main flow of the Falkland Current which is highly dynamic (Legeckis & Gordon 1982, Davis et al. 1996) with temporally variable eddies and fronts. Variability in the Falkland Current is related to variability in the Brazil Current (Legeckis & Gordon 1982) and is complicated by interannual variability in the proximity of both currents to the Patagonian Shelf (Olson et al. 1988, Garzoli & Garrafo 1989). Further complexity in the region also arises from interannual variability in the positions of the APF and the SAF south of the Falkland Islands; for example Ikeda et al. (1989) reported that both fronts were in different positions in each of the 4 years that they studied the area, with both positions varying by as much as 160 km.

Given the importance of understanding the influence of the physical environment on variability in squid fisheries, and the wider interest in developing a new fishery for *Martialia hyadesi* in the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) area (Rodhouse in press), we have examined the biology of *M. hyadesi* on the Patagonian shelf edge following the large catch in 1995. The objectives of this paper are to characterise the demography and trophic ecology of the *M. hyadesi* population on the Patagonian Shelf edge in 1995 when there were large numbers in the fishery, to describe the distribution of the population in relation to mesoscale oceanographic processes in the area at the time, to contrast this with the distribution of the *Illex argentinus* stock on the southern Patagonian Shelf, and to present a causal hypothesis for the variability in catch rate of *M. hyadesi* in a fishery driven by variability in the physical environment.

MATERIAL AND METHODS

Sampling methods. Twelve samples of *Martialia hyadesi* were collected aboard 6 Korean registered squid jiggers operating in the Falklands Interim Conservation and Management Zone (FICZ) and Falklands Outer Conservation Zone (FOCZ) between 10 and 23 May 1995. The vessels were of similar size (average total length 55 m; 650 GRT). Fishing was at night with lights between 80 and 120 m depth targeting marks on fish-finding echosounders. Samples were deep-frozen (−20°C) and shipped to the British Antarctic Survey in Cambridge, UK.

Data on sea surface temperature (SST), water depth, total catch per drift and catch per unit effort (CPUE) were also recorded by Falkland Islands Government (FIG) observers aboard squid jiggers in the same fleet between 24 April and 23 May 1995.

A small sample of *Martialia hyadesi* (n = 48) was also taken from a by-catch in the trawled *Loligo gahi* fishery near the 200 m isobath (50° 55' S, 56° 51' W) on the edge of the shelf to the northeast of the Falkland Islands in August 1995.

Data on ommastrephid squid catches in the Falkland Islands Conservation Zones (FOCZ and FICZ) for the last 10 yr were provided by the FIG, Japanese catches of *Martialia hyadesi* were provided by the National Research Institute for Far Seas Fisheries (NRIFSF), Shimizu, Japan, and total catches of *M. hyadesi* reported to the UN Fisheries and Agriculture Organisation (FAO) were obtained from the current yearbook (FAO 1994). Prior to 1987 the Japanese data were compiled by commercial operators and subsequently they have been prepared by NRIFSF.

Treatment of samples. A total of 336 specimens (232 females and 104 males) was analysed. Data were collected on sex and maturity stage according to Lipiński (1979). Mantle length (ML) of all squid was measured to

1 mm and body mass (BM) determined to 0.1 g. Frequency distributions of size and maturity stage were calculated as a percentage of the total number of specimens, treating male and female data separately.

Treatment of statoliths. A sample of 110 pairs of statoliths (35 males and 75 females) were dissected from the heads according to Dawe & Natsukari (1991) and stored in ethanol (96%). The right statolith of each pair, when possible, was mounted in Crystal Bond Resin®. Both sides of the statolith were ground to reveal daily growth rings using 30 µm carborundum paper for grinding and 3 µm for polishing. An optical microscope (×400) with an image analysis system was used for counting the number of growth rings. Image analysis was used for both counting and estimating increment numbers in regions of the statolith where the growth rings were obliterated or difficult to read. Where more than 15% of the rings were obliterated the statolith was rejected.

Frequency distribution of back-calculated hatch date was calculated as a percentage of the total number of specimens with male and female data pooled.

Diet analysis. Stomach contents were weighed and separated into fish, crustaceans and cephalopods. Otoliths, cephalopod beaks and crustacean integument were identified to the lowest possible taxonomic level and measured. Fish were identified from otoliths by reference to Hecht (1987), Williams & McEldowney (1990) and Reid (1996). Crustacean identification followed Brinton & Antezana (1981) and Kane (1966). Cephalopods were identified from beaks (Clarke 1986) and suckers (Rodhouse & Yeatman 1990). Prey were also identified by comparison with the reference collection of fish, crustaceans and cephalopods held at the British Antarctic Survey. Size of fish and cephalopod prey was back-calculated using equations relating body size to otolith and beak size respectively (Rodhouse & Yeatman 1990, Reid 1996). Where no recognisable parts were found, remains were removed and classified as unidentified crustacean or fish on the basis of scales, bones, fragments of integument, etc. The indices used for diet description are as follows:

(1) Occurrence index:

$$CI = 100 \times \frac{\text{no. of stomachs with prey type}}{\text{total no. of stomachs containing prey}}$$

Using this index each stomach is counted as many times as the number of prey types it contained.

(2) Frequency of occurrence:

$$F = 100 \times \frac{\text{no. of stomachs with prey type}}{\text{total no. of stomachs}}$$

Oceanographic data. A remotely sensed, infrared image of the Patagonian Shelf and oceanic region around the Falklands Islands, at 09:30 h Z on 21 April 1995, was selected from the ARIES (Antarctic Reception of Imagery for Environmental Studies) database to illustrate the surface features of mesoscale oceanographic processes in the region of the fishery.

One of the objectives of the study was to explore whether teleconnections existed between the oceanographic and biological variability observed in the *Martialia hyadesi* fishery in the South Atlantic, and variability elsewhere in the southern hemisphere. For example it has been suggested that there may be associations between El Niño/Southern Oscillation (ENSO) events in the Pacific and historical variability in the whale fishery and krill abundance (Croxall et al. 1988, Priddle et al. 1988) at South Georgia.

Thus a large-scale SST data set (Reynolds & Smith 1994) was used to integrate mesoscale variability and identify anomalous periods. The data cover the period November 1981 to July 1996, which includes the period during which the Falkland Islands squid fishery has been formally managed (1987 to 1996) and the preceding period during which the fishery was unlicensed but for which some fishery data are available (1985 to 1987). Reynolds & Smith (1994) described the National Oceanic and Atmospheric Administration (NOAA) operational global SST analyses. Seven day *in situ* ship and buoy SST data and satellite SST data were used to produce daily, weekly and monthly grids by optimum interpolation (OI) at a resolution of 1° latitude by 1° longitude. The monthly grids from the SST OI covering the period November 1981 to July 1996 have been loaded into a marine Geographical Information System (GIS) (Trathan et al. 1993). The GIS, using Arc/Info 7.0.4 (ESRI), was used to select SST OI data around the Falkland Islands.

In order to select grid cells that integrate the local mesoscale variability (but which are located away from land areas and away from areas where the bathymetry changes), the historical SST OI data set was examined in Arc/Plot, a component of Arc/Info. A single grid cell (49° 30' S, 59° 30' W), where water depth was approximately 200 m and SST relatively homogeneous, was taken as representative of the shelf north of the Falkland Islands (position arrowed in Fig. 9b).

RESULTS

Historical catch data for *Martialia hyadesi* in the southwest Atlantic

Reported catches for *Martialia hyadesi* are shown in Fig. 1b. These clearly indicate that in some years substantial quantities were caught outside the Falkland

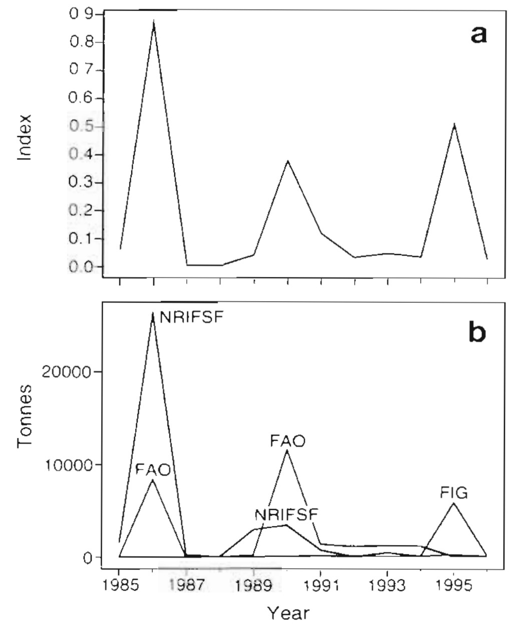


Fig. 1. *Martialia hyadesi*. (a) Average index of catches (see text for details). (b) Annual catch between 1985 and 1996 as reported to the Falkland Islands Government (FIG) Fisheries Department, Stanley, National Research Institute for Far Seas Fisheries (NRIFSF), Shimizu, Japan and the UN Fisheries and Agriculture Organisation (FAO), Rome

Islands Conservation Zones and also that FAO statistics do not include all catches. Taken together, the data provide the best available description of the fishery. Fig. 1a shows the total catch for each year expressed as a mean index in which the maximum catch in a series is given as unity and the catch for other years expressed as a proportion of the maximum. It indicates, despite the vagaries of the data, that '*Martialia hyadesi* events' occurred in 1986 (before FIG records began), 1990 and 1995.

Distribution of *Martialia hyadesi* and *Illex argentinus* in 1995: depth/temperature relations

Spatial distribution of the *Martialia hyadesi* fishery between 4 and 19 May 1995 in the FICZ/FOCZ is shown in Fig. 2 together with the distribution of the *Illex argentinus* fishery between the start of the season and 19 May. *M. hyadesi* catches were made towards the end of the *I. argentinus* season. Highest densities of *M. hyadesi* were found in the FOCZ outside the 200 m isobath to the north of the Falkland Islands (Fig. 2a). Highest densities of *I. argentinus* during the same period were in the FICZ on the shelf to the northwest of the Falkland Islands (Fig. 2b).

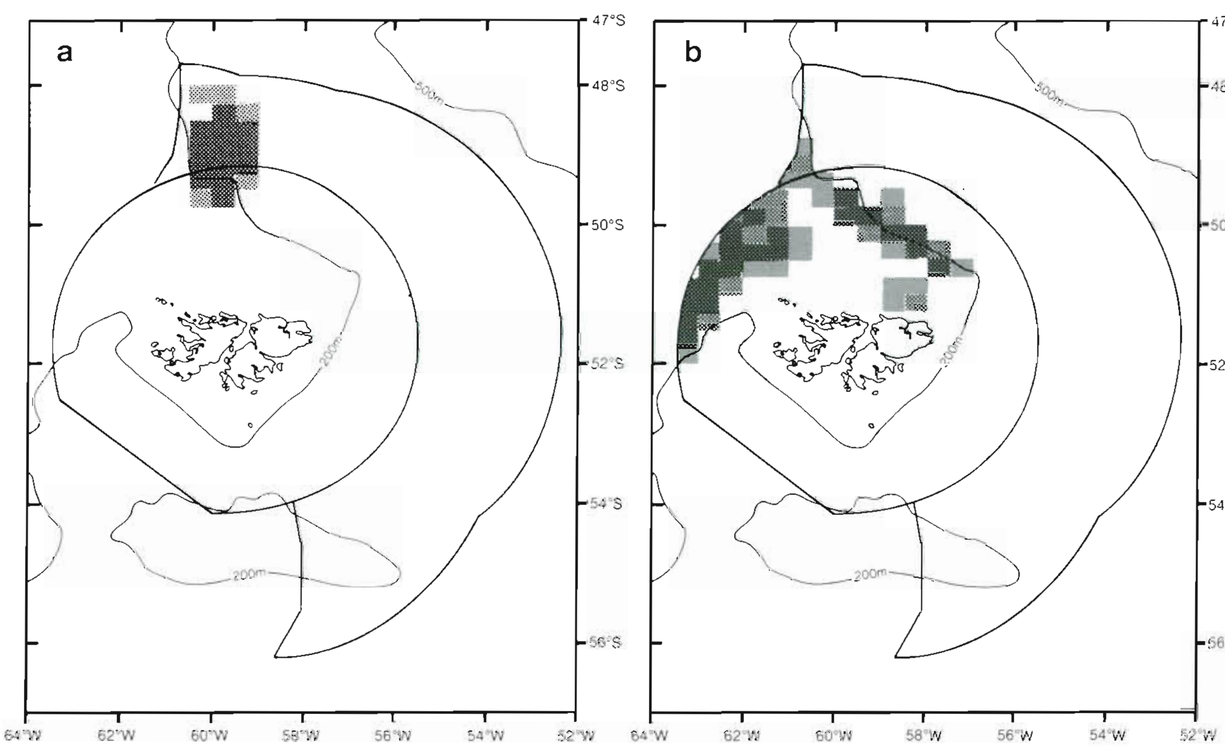


Fig. 2. Distribution of catches of (a) *Martialia hyadesi* (4 to 19 May 1995) and (b) *Illex argentinus* (1 February to 19 May 1995) in the Falklands Interim Conservation and Management Zone (FICZ) and Falklands Outer Conservation Zone (FOCZ). Isobaths for 200 and 500 m are shown; FICZ and FOCZ indicated by thick lines; density of shading indicates catch density

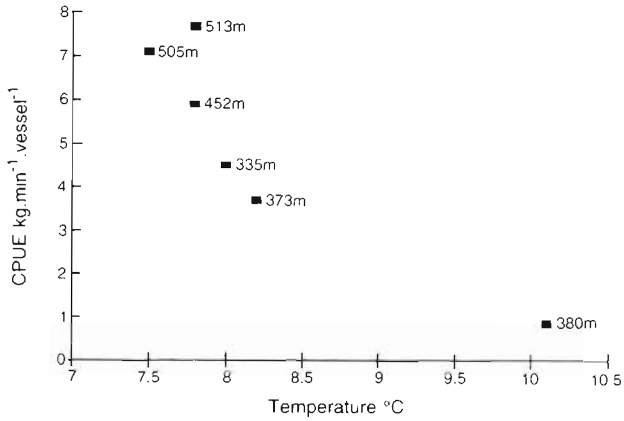


Fig. 4. *Martialia hyadesi*. Relationship between catch per unit effort (CPUE), sea surface temperature and depth recorded on 6 different squid jiggers between 12 and 19 May

The relationship between seabed depth and catch per unit of effort (CPUE) for *Illex argentinus* and *Martialia hyadesi* caught by a jigger near the Patagonian Shelf during the period 24 April to 4 May 1995 (FIG observer R. Coggan) is shown in Fig. 3. This clearly illustrates a separation in distribution between the 2 ommastrephid species, although very small numbers of each species overlap. *I. argentinus* was mostly caught over depths of about 250 m, on the Patagonian shelf edge. The maximum CPUE for *I. argentinus* was 29.3 kg min^{-1} $vessel^{-1}$ over a depth of 260 m. No substantial catches of *I. argentinus* were taken over depths >260 m. In contrast very few *M. hyadesi* were caught over depths <230 m. Highest values for CPUE recorded for *M. hyadesi* were over depths >270 m, off the edge of the continental shelf. The maximum CPUE for *M. hyadesi* was 49.6 kg min^{-1} $vessel^{-1}$ over a depth of 410 m.

The relationship between SST, depth and CPUE for *Martialia hyadesi* determined over 6 d between 12 and 19 May, on 6 different jiggers (FIG observer C. Yau) is shown in Fig. 4. CPUE was inversely related to SST, with maximum catch rates in areas where SST was 7.5 to 8.0°C (over water depths >500 m).

Population structure in 1995

Size

Size frequency distributions for males and females are shown in Fig. 5. Both sexes had unimodal distributions; mean mantle lengths (ML) for males and females were 285 ± 31 (SD) mm and 302 ± 31 (SD) mm respectively. The male and female modes were 290 and 310 mm ML respectively. Male mantle lengths were 187 to 334 mm, with a total body mass (BM) of 92 to 754 g. Females were larger, ranging from 185 to 358 mm ML with a total BM of 358 to 817 g.

Regression equations for the relationship between ML in mm and BM in g for males and females were as follows:

Males: $\ln BM = 3.408 \ln ML - 13.294$ ($r^2 = 0.97$; n = 104)
Females: $\ln BM = 3.280 \ln ML - 12.609$ ($r^2 = 0.96$; n = 232)

Both sexes of *Martialia hyadesi* showed significant ($p < 0.005$) positive allometry (i.e. slope, b > 3). Males had higher BM than females for a given ML. Body mass of *M. hyadesi* is substantially less than in *Illex argentinus* of equivalent mantle length (Rodhouse & Hatfield 1990). From the equations, male and female *M. hyadesi* of ML 300 mm have a body mass of 486 and 445 g respectively whereas male and female *I. argentinus* of the same ML have a body mass of 804 and 598 g respectively. This is because *M. hyadesi* mature at a

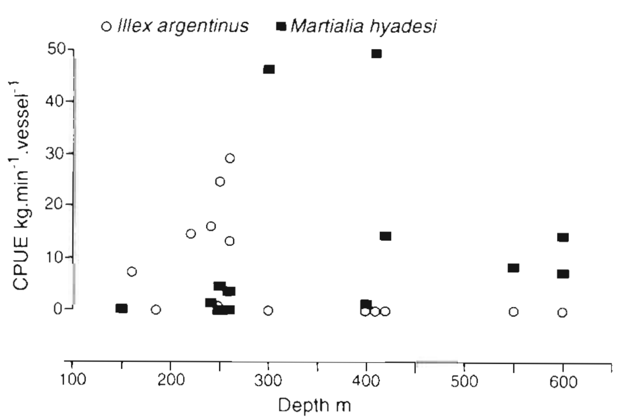


Fig. 3. *Martialia hyadesi* and *Illex argentinus*. Relationship between catch per unit effort (CPUE) and depth recorded on a single squid jigger between 24 April and 4 May

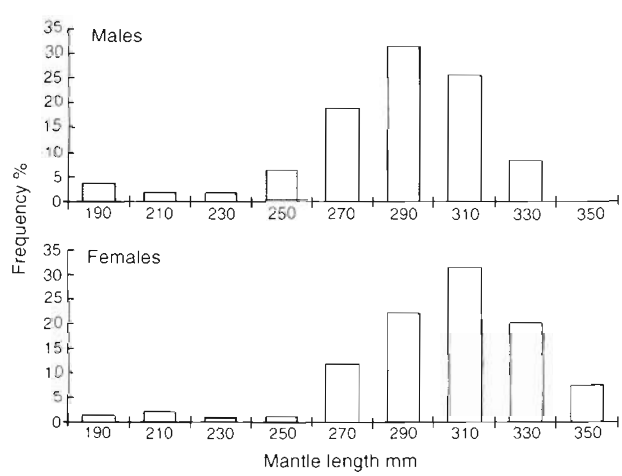


Fig. 5. *Martialia hyadesi*. Mantle length frequency distributions of males and females from the 1995 fishery

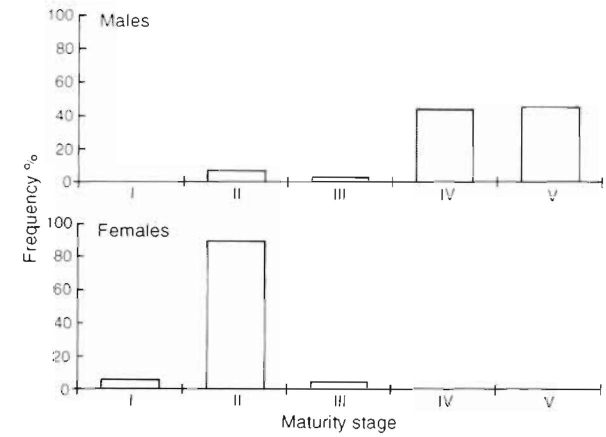


Fig. 6. *Martialia hyadesi*. Proportion of each maturity stage of males and females from the 1995 fishery

larger size (and age) so they are less mature, and hence have lower mass, at a given ML.

Sex ratio and maturity stages

Females were approximately twice as abundant in the catch as males (M:F = 0.48:1). A large proportion (>97%) of males were maturing or mature (stages IV or V) while females were mostly immature. A few females were at the preparatory stage but there were no mature females in any of the samples (Fig. 6).

Earlier observations (M. George pers. comm.) suggest the sporadic presence of mature female *Martialia hyadesi* in the vicinity of the Falkland Islands between 1991 and 1994. These records were made during summer and early autumn. ML of these mature females ranged between 280 and 415 mm ML. Two large specimens were 405 and 415 mm ML and weighed 1390 and 1360 g respectively.

Age and time of hatching

In 1995 males and females appeared in the fishery at an age of about 6 mo. The maximum age of squid examined from the catch was 330 and 357 d for males and females respectively (Fig. 7). Linear, exponential and power models were fitted to the data and the following equations obtained:

Linear:	Males	$ML = 134.13 + 0.57NI$ ($r^2 = 0.448$; $n = 45$)
	Females	$ML = 59.86 + 0.86NI$ ($r^2 = 0.799$; $n = 65$)
Exponential:	Males	$ML = 159.88e^{0.0022NI}$ ($r^2 = 0.449$; $n = 45$)
	Females	$ML = 124.65e^{0.0031NI}$ ($r^2 = 0.763$; $n = 65$)
Power:	Males	$ML = 14.04NI^{0.54}$ ($r^2 = 0.500$; $n = 45$)
	Females	$ML = 2.47NI^{0.85}$ ($r^2 = 0.805$; $n = 65$)

where NI is the number of increments (or age in days).

Goodness of fit was similar for all 3 models indicating that growth at the time of the fishery was approximately linear. Depending on the model, predicted ML at age 1 yr ranged between 338 and 352 mm for males and 372 to 386 mm for females. Using the models to extrapolate ML at 2 yr the predictions ranged between 460 and 492 mm for males and between 670 and 1198 mm for females. The maximum ML recorded for *Martialia hyadesi* is about 500 mm (Nesis 1987) and the observations of large females in the Falklands fishery recorded above suggest that females can reach maturity at ML >400 mm. Extrapolating from the limited size, age and maturity range in this sample the data suggest that maximum mantle length and full maturity would be reached at, or somewhat before, 2 yr after hatching depending on sex. Assuming the squid complete their life cycle in the same season of the year that they start, there is probably some reduction in the growth rate in the latter part of the life cycle if the squid live for 2 yr. Given the scatter in the size at age data, some of the relatively large squid could reach 400 to 500 mm ML within 1 yr after hatching whilst the smaller squid might only reach about 300 mm ML after 1 yr.

Back-calculations of individual hatch dates, from age and date of capture, indicated that hatching of the squid in the 1995 samples extended from May to October 1994, i.e. during late-autumn and winter, with a maximum in August of that year (Fig. 8).

In 1995 males and females recruited into the fishery at an age of about 6 mo. The maximum age of squid caught, estimated from counts of microgrowth increments in the statolith, was 330 and 357 d for males and females respectively. Given the relatively immature reproductive status of females, these data are not inconsistent with the hypothesis that the life span of *Martialia hyadesi* is greater than 1 yr (Rodhouse 1991, Rodhouse et al. 1994). However, the question of the life span of *M. hyadesi* remains open and needs to be addressed by studies on mature/spawing specimens.

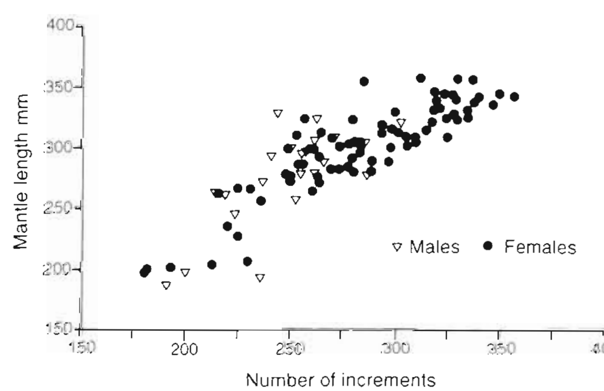


Fig. 7. *Martialia hyadesi*. Relationship between the number of daily microgrowth increments (n = 65) in the statolith and mantle length

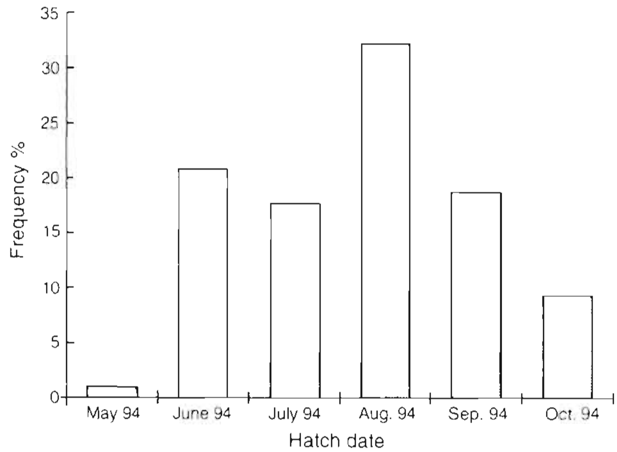


Fig. 8. *Martialia hyadesi*. Seasonality in hatching back-calculated from age of squid sampled from the 1995 fishery

Diet of *Martialia hyadesi* in 1995

A total of 9 prey species, together with unidentifiable remains from the 3 main categories, fish, crustaceans and cephalopods, were present in the stomach contents of *Martialia hyadesi*. The occurrence index (OCI) and frequency of occurrence (F) data, along with published information on the habitat of the prey species identified, are summarised in Table 1. The diet of *M. hyadesi* in the samples was mostly species of mesopelagic fish and epipelagic crustaceans characteristic of open ocean and shelf break communities.

The small sample of *Martialia hyadesi* collected from the *Loligo gahi* fishery had been feeding on crustaceans *Euphausia vallentini* and *Themisto gaudichaudii* and squid *L. gahi*. These data are not included in Table 1.

Oceanography: SST and oceanographic variability

The SST image of the region around the Falklands Islands illustrates the complex surface hydrography of the region (Fig. 9). It shows the frontal region associated with the Patagonian Shelf break and mesoscale features at the front where the *Martialia hyadesi* concentrations occurred in 1995. Comparison of the information in Figs. 2 & 4 with Fig. 9 shows the squid were caught in the area where on 21 April a stream of relatively cool water (~7°C) was apparently flowing westwards along the shelf break north of the Falkland Islands. The image also shows the warm South Atlantic subtropical gyre to the northeast and the APF to the south. The APFZ lies in the area between the shelf break front, the subtropical gyre and the APF.

The monthly SST OI time series between November 1981 and July 1996 for the grid cell 59° 30' W, 49° 30' S and monthly anomalies (monthly SST OI time series minus average seasonal climate) are shown in Fig. 10. Extreme anomalies lie outside the pair of horizontal lines representing 2 standard deviations, i.e. $y = x + 2$ SD and $y = x - 2$ SD, where SD is the standard deviation of the anomalies.

Three periods of extreme positive anomalies are apparent: in March 1985, December 1989 to March 1990 and December 1993 to January 1994. Three periods of extreme negative anomalies are also apparent: these occurred approximately 24 or 25 mo after the positive anomalies. However, the last of these negative anomalies is not so extreme and lies above the line $y = x - 2$ SD; also the timing of the negative anomalies is less well defined than the positive anomalies. The *Martialia hyadesi* 'events' all occurred in the period

Table 1. *Martialia hyadesi*. Prey items in the stomach contents at Falkland Islands Conservation Zones (FICZ and FOCZ). n: no. of stomachs in which taxon was found; OCI: occurrence index; F: frequency of occurrence (%); O: oceanic; MP: mesopelagic; BP: bathypelagic; EP: epipelagic. Information on habitats of prey items obtained from sources shown

Prey item	n	OCI	F	Habitat	Source
Fish (total)	(228)	(43.8)	(68.1)	–	–
Krefftichthys anderssoni	136	26.1	40.6	O-MP	Williams & McEldowney (1990)
Protomyctophum bolini	2	0.4	0.6	O-MP	Williams & McEldowney (1990)
Protomyctophum choriodon	17	3.3	5.1	O-MP	Williams & McEldowney (1990)
Gymnoscopelus nicholsi	45	8.6	13.4	O-MP	Williams & McEldowney (1990)
Notothenia squamifrons	1	0.2	0.3	O-MP-BP	Williams & McEldowney (1990)
Unidentified fish	27	5.2	8.1	–	–
Crustaceans (total)	(211)	(40.4)	(63.0)	–	–
Euphausia vallentini	126	24.2	37.6	O-EP	Brinton & Antezana (1981)
Themisto gaudichaudii	71	13.5	23.0	O-EP	Kane (1966)
Unidentified crustaceans	14	2.7	4.2	–	–
Cephalopods (total)	(82)	(15.8)	(24.5)	–	–
Martialia hyadesi	77	14.8	23.0	O-MP	Nesis (1987)
Gonatus antarcticus	1	0.2	0.3	O-MP	Nesis (1987)
Onychoteuthid	1	0.2	0.3	–	–
Unidentified cephalopods	3	0.6	0.9	–	–

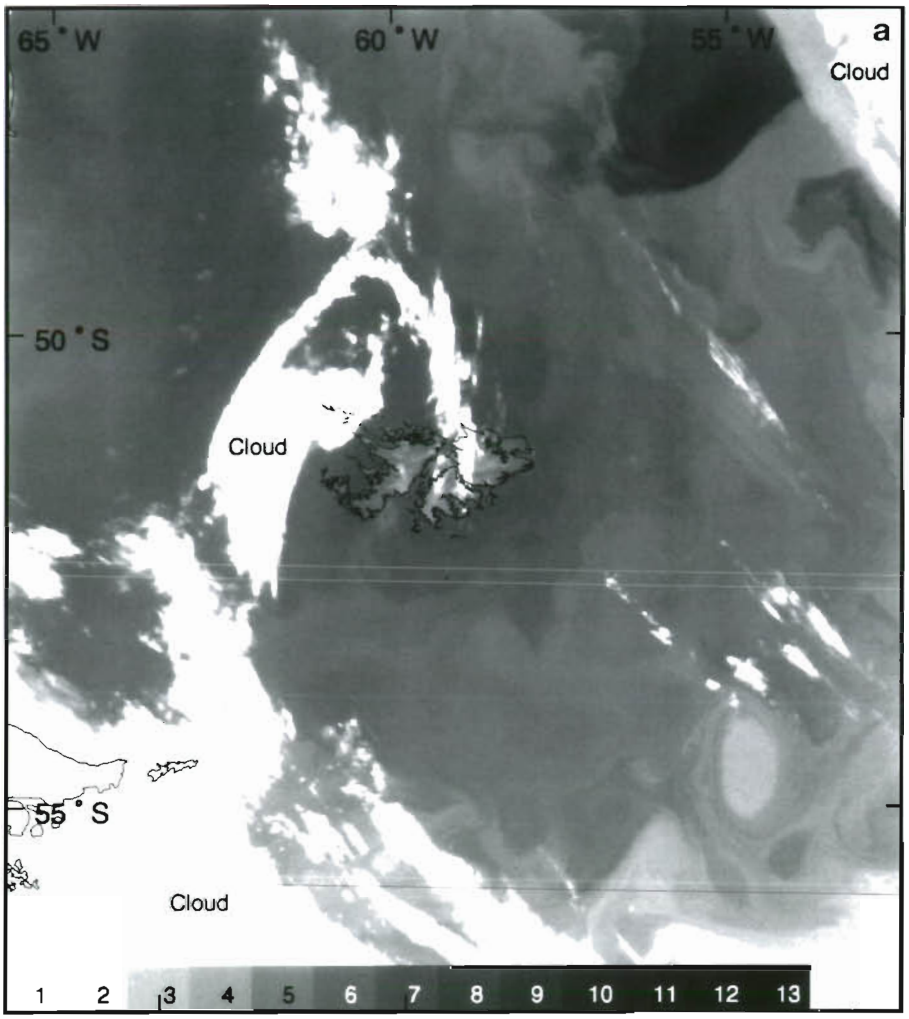
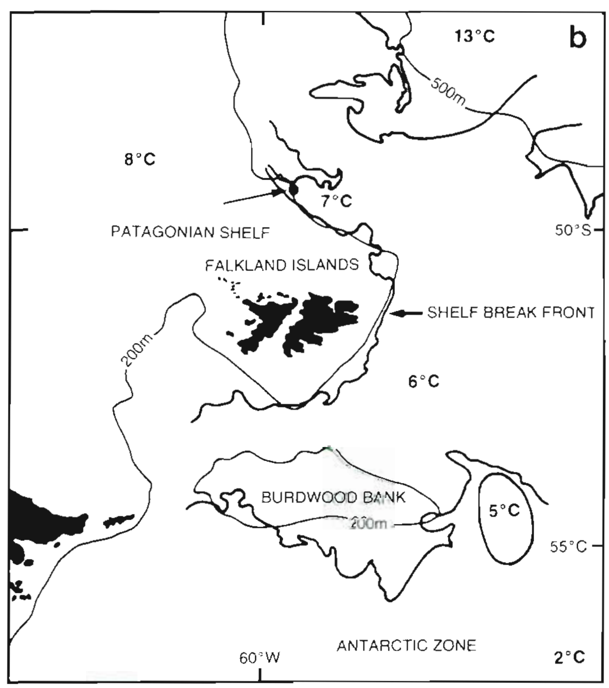


Fig. 9. (a) Remotely sensed, infrared (sea surface temperature) image of the Patagonian Shelf and oceanic region around the Falklands Islands, captured at 09:30 h Z on 21 April 1995: taken from the ARIES (Antarctic Reception of Imagery for Environmental Studies) database; (b) Traced land masses, bathymetry and isotherms illustrating surface oceanography including mesoscale features at the Patagonian Shelf edge north of the Falkland Islands. (Position where the historical SST OI data set was extracted is indicated by an arrow)



between positive and negative anomalies, some 4 to 15 mo after a positive and 6 to 10 mo before a negative anomaly.

Teleconnections with large-scale oceanographic variability

SST anomaly data (NCAR Data Center, Boulder, Colorado, USA) from the eastern Pacific Ocean 0° to 10° S, 80° to 90° W show the warm ENSO events of 1982/83, 1987 and 1992 (Fig. 10) which were followed by cold, La Niña events in 1985, 1988 and 1994/95. The recent La Niña event, which has continued into 1996, has been associated with a dramatic reduction in catches of the ommastrephid *Dosidicus gigas* (jumbo flying squid) in the Peruvian fishery (Yamashiro et al. in press) and it is perhaps noteworthy that the 1986, 1989/90 and 1995 '*Martialia hyadesi* events' in the South Atlantic followed the cold, La Niña events in the eastern Pacific. Warm events in the South Atlantic fol-

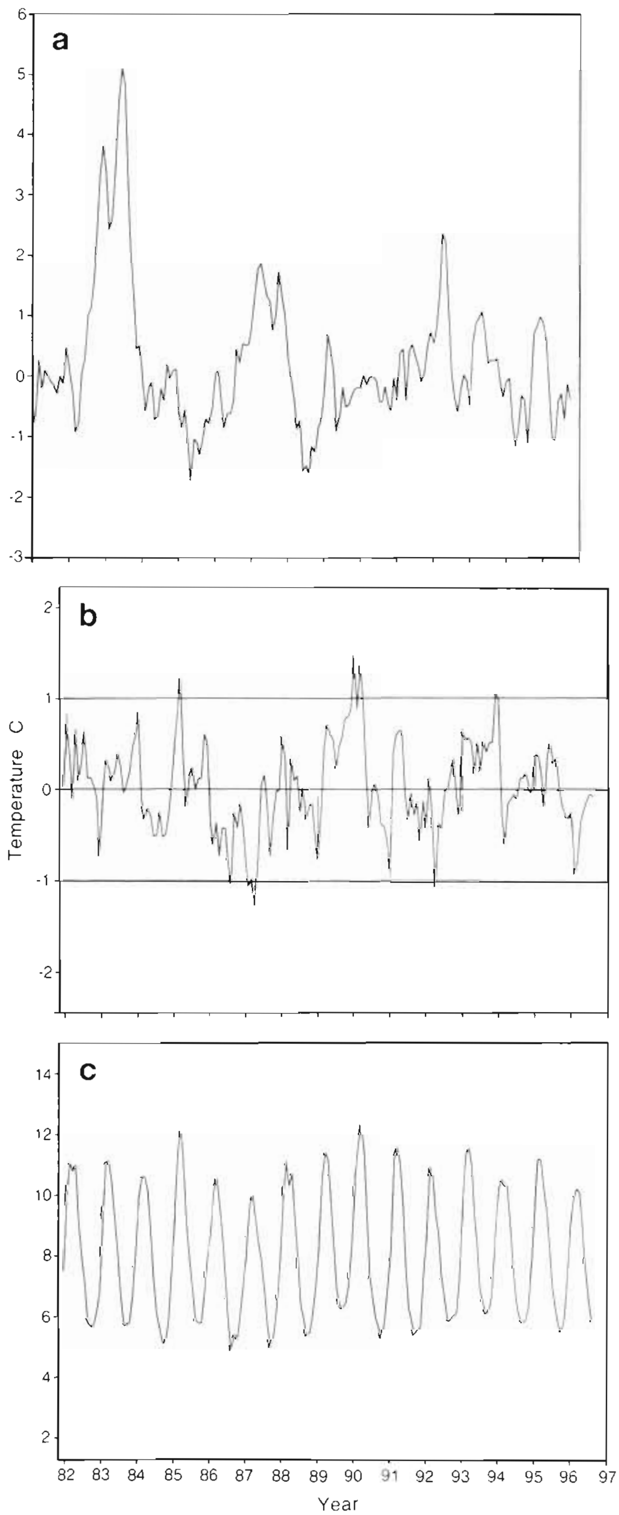


Fig. 10. (a) Sea surface temperature anomaly data (NCAR Data Center, Boulder, Colorado) from the eastern Pacific Ocean 0° to 10° S, 80° to 90° W. (b) Monthly anomalies (upper and lower horizontal lines indicate ±2 standard deviations) and (c) monthly sea surface temperature optimum interpolation (SST OI) time series between November 1981 and July 1996 for the grid cell 59° 30' W, 49° 30' S (tic marks indicate beginning of year labelled; data set in (a) commences 1 yr earlier)

low some 24 to 30 mo after those in the Pacific and cold events in the South Atlantic follow some 12 to 24 mo after those in the Pacific.

The interval between warm and cold SST anomalies in the middle panel of Fig. 10 also approximate the 4 to 5 yr period of the Antarctic circumpolar wave (ACW) in several physical variables described by White & Peterson (1996) and which relate to the circumpolar precession of anomalous sea ice extent in the Antarctic (Murphy et al. 1995).

DISCUSSION

Over the last decade *Martialia hyadesi* has appeared on the edge of the southern Patagonian Shelf in sufficient numbers to generate a fishery on 3 occasions. The data for the 1995 fishery indicate that there is no evidence that *M. hyadesi* makes significant incursions over the shelf, remaining largely outside the 250 m contour in the cool APFZ waters of the Falkland Current. Here *M. hyadesi* preys on macroplanktonic/micronektonic members of the oceanic mesopelagic and epipelagic community. Variability in the distribution of *M. hyadesi* may therefore be related to variability in the oceanic system off the shelf edge.

A profile of the population from the 1995 fishery in the FICZ/FOCZ indicates that the squid appeared in the fishery at an age of about 6 to 12 mo when feeding, growing and maturing, but when females were still at an early stage of maturity. Male *Martialia hyadesi*, in common with *Illex argentinus* (Rodhouse et al. 1995), mature earlier than females and, judging from sex ratios, are partially segregated from females during the exploited phase of the life cycle.

The normal life span of *Martialia hyadesi* in the South Atlantic remains to be fully resolved. Our data seem to be consistent with a 2 yr life cycle assuming some reduction in growth rate towards the end of the 2 yr. Although no large, mature female specimens were recorded in the 1995 fishery, mature specimens of large size have occasionally turned up in the Falklands fishery in recent years. It is not known, however, whether these represented a distinct cohort of large, mature squid which would indicate a different year class. There was no evidence of bimodality in the 1995 data or in earlier data (Rodhouse 1991, Rodhouse et al. 1994). Large, mature squid are apparently not generally available to the fishery as it operates in the South Atlantic. In common with other ommastrephids, growth patterns of *M. hyadesi* are probably variable and plastic and further data on life span and growth are needed to clarify the picture.

In common with *Illex argentinus* in the South Atlantic (Haimovici et al. in press), peak hatching time for the *Martialia hyadesi* population, sampled by the fishery in summer, is the austral winter of the previous year. Presumably winter spawning has evolved in both species to optimise the match between timing of the critical paralarval and juvenile phases with seasonality in the plankton. The observations of mature females, coupled with the records of small numbers of post-hatching juveniles on the Patagonian Shelf edge (Rodhouse et al. 1992a), show that some spawning takes place in the vicinity of the Falkland Islands. Knowledge of the life cycle of *M. hyadesi* is incomplete and information is particularly needed on the latter part of the life cycle, on spawning biology and paralarval, juvenile and pre-recruitment biology.

In 1995 concentrations of exploited *Martialia hyadesi* were associated with mesoscale oceanographic features on the shelf break front separating shelf water from the APFZ water of the Falkland Current. This front is a region of high primary and secondary productivity supporting several squid and fish stocks (Bertolotti et al. 1996). Association of *M. hyadesi* with mesoscale frontal processes is consistent with behaviour observed in the APFZ to the north of South Georgia (Rodhouse et al. 1996).

The behaviour of the *Martialia hyadesi* stock over the decadal time scale represented by FIG Fisheries Department data, Japanese catch data and catches reported to FAO and the SST OI analysis reveals apparent links with environmental variability. Catch rates (Fig. 2) suggest a relationship with anomalies in the oceanographic regime which are likely to be linked to large-scale variability such as ENSO and the ACW.

The large-scale SST OI data integrate the mesoscale spatial and temporal variability in the region so that large-scale patterns remain evident (Fig. 10). The mechanism by which seasonal and interannual variability in the regional oceanography affects the *Martialia hyadesi* stock is not understood. Oceanographic variability could affect the population during one or more of a number of critical periods, for example altered hydrographic conditions may affect the stock during egg development, hatching, juvenile development, migration, sexual maturation, or spawning. Furthermore, such effects may be more important during the life span of the parent generation, rather than that of the current generation. Such effects may occur at a place or time remote from where and when the squid are exploited. Considering the potential mobility of *M. hyadesi*, environmental influences may be exerted in areas remote from the Falklands Plateau.

Given the occurrence of '*Martialia hyadesi* events' between warm and cold anomalies in the South Atlantic, 2 hypotheses are suggested. Firstly, warm conditions preceding the appearance of the squid may favour the reproductive success of the parent generations or the early life cycle stages of the generations which recruit. Alternatively, *M. hyadesi*, which is associated with the cool waters of the APFZ, may recruit in exceptional numbers into the region near the Patagonian Shelf edge during the phase preceeding a cold anomaly. This would represent the reverse situation to that described by Dawe & Warren (1993) for *Illex illecebrosus* in the northwest Atlantic which is a relatively warm-water species that is adversely affected by cold events associated with the Labrador Current. The 2 hypotheses for variability in *M. hyadesi* in the South Atlantic are not mutually exclusive and could be tested by comparative studies if there were more information on the life cycle.

Knowledge of relations between ommastrephid squid populations, their food and mesoscale oceanographic features, and of the links between the dynamics of these mesoscale features and large-scale oceanographic variability (whether manifested as ENSO events or the ACW) would greatly assist in understanding the variability in short-lived squid populations that respond rapidly to environmental change. Understanding these links might in turn assist short-term forcasting of catch levels in the fisheries for these notoriously unpredictable, but increasingly valuable, invertebrate resources.

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