

Large and Meso-Scale Distribution of the Ommastrephid Squid *Martialia hyadesi* in the Southern Ocean: A Synthesis of Information Relevant to Fishery Forecasting and Management

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ABSTRACT. The seven star flying squid, *Martialia hyadesi*, is a Southern Ocean ommastrephid with an oceanic distribution that extends to the edge of the shelves and slopes of continents and islands. Its range is circumpolar and it is generally associated with the Antarctic Polar Frontal Zone. It has been caught in commercial quantities in the Atlantic sector but is only recorded in smaller numbers from the Indian Ocean and Pacific sectors in scientific samples, the gut contents of predators and in mass strandings on island shores. It has only occasionally been found in commercial catches outside the Atlantic sector. In the northern part of its range in the South Atlantic, commercial catches are highly variable and apparently linked to large-scale oceanographic variability. *Martialia hyadesi* appears to concentrate in frontal areas where characteristics of the bathymetry generate meso-scale oceanographic features. Such concentrations have been observed at shelf breaks and in the deep ocean near a submarine ridge. Predator data confirm the circumpolar distribution of the species and its relationship with the APFZ. Grey-headed albatrosses appear to forage for *M. hyadesi* in the region of meso-scale oceanographic features associated with the bathymetry of submarine ridges and the shelves of oceanic islands. In the medium future, improved understanding of oceanographic variability of the Southern Ocean may provide the basis for long term forecasting in a fishery for the species. In the nearer future, improved knowledge of the behaviour of the species in relation to meso-scale oceanography may provide the basis for short-term forecasting of the location of shoals based on remotely sensed images of surface oceanography. The life cycle of *M. hyadesi* is poorly understood and, in view of increased commercial interest in the species in recent years, and its conservation value in the CCAMLR area, there is a need for more information on the location of spawning and feeding grounds and seasonal migrations.

Key Words: distribution, fishery forecasting, Southern Ocean, squid

Introduction

The seven star flying squid, *Martialia hyadesi* Rochebrune and Mabile, 1889, is a large ommastrephid from the Southern Ocean. It was a little known species until about a decade ago when it appeared in the new squid fishery in the Southwest Atlantic. It was then identified in the gut contents and regurgitations of predators at South Georgia

and was subsequently redescribed on the basis of new material (Rodhouse and Yeatman 1990). An analysis of the Antarctic cephalopod fauna suggested that the species was the one most likely to be exploited commercially in the Antarctic in the medium term (Rodhouse 1990). Subsequently there have been exploratory fishing ventures that have confirmed the presence of commercial concentrations in the South Georgia area (Rodhouse 1991; González and Rodhouse 1998).

This short review considers the pattern of distribution throughout the Southern Ocean as determined

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by direct sampling and from samples of the diet of predators, mostly those breeding on oceanic islands. It examines the limited data available on distribution in relation to the meso-scale oceanography in the sub-Antarctic range of the species and considers the possible use of this knowledge for fishery forecasting.

Large-Scale Distribution

Data on large-scale, global, distribution patterns in *Martialia hyadesi* come from commercial and exploratory fisheries and from scientific sources (Table 1). Most information is from the South Atlantic where the international fleet targeting *Illex argentinus* and *Loligo gahi* either sometimes redirect fishing effort to *M. hyadesi*, or take the species as an occasional by-catch.

Position data from the sources in Table 1 have been loaded onto Arc/Info version 7.0.2 (ESRI), a geographic information system (GIS) used at the British Antarctic Survey for analysis of Southern Ocean fisheries (Trathan *et al.* 1993). Individual locations of all samples from the literature cited in Table 1 are shown plotted with bathymetry, major frontal systems and the maximum/minimum extent of sea ice in Figs 1-3. *Martialia hyadesi* is a circumpolar, oceanic species with a range that extends to the slopes of continents and islands (Fig. 1). The species is rarely found over shelves but it may concentrate near the shelf slope. Occasional strandings on island shores where the slope lies close to the land (O'Sullivan *et al.* 1983; Nolan *et al.*, in press; C. Buxton, pers. comm.) probably result from exceptional weather/oceanographic conditions. The species is closely associated with, but not confined to, the Antarctic Polar Frontal Zone (APFZ) that lies between the Antarctic Polar Front (APF) and the sub-Antarctic Front (SAF) (Fig. 2). The APFZ extends furthest north, and is broadest, in the south west Atlantic in the region of the Falkland Current where the SAF lies parallel to the edge of the Patagonian Shelf (Peterson and Whitworth 1989). *Martialia hyadesi* has never been recorded south of

Table 1. Sources of position data for the large-scale GIS plots of *Martialia hyadesi* distribution in the Southern Ocean based on material from scientific nets, commercial trawls, commercial jigs and mass strandings

Sector	References
Atlantic Ocean	Rochebrune and Mabile (1889) Castellanos (1967) Nesis and Nigmatullin (1972) Brunetti <i>et al.</i> (1990) Rodhouse (1991) Rodhouse <i>et al.</i> (1992; 1996) Coggan <i>et al.</i> (1996) González and Rodhouse (1996) Arkhipkin and Silvanovich (1997) González <i>et al.</i> (in press) Rodhouse P.G. (unpubl. data)
Indian Ocean	Piatkowski <i>et al.</i> (1991)
Pacific Ocean	O'Sullivan <i>et al.</i> (1983) Uozumi <i>et al.</i> (1991) Alexeyev (1994)

the maximum extent of sea ice cover (Fig. 3). In the region of the APFZ it dominates a cephalopod community that replaces epipelagic fish (Rodhouse and White 1995).

The large-scale distribution of the cool water *Martialia hyadesi* is probably influenced by large scale oceanographic variability, especially at the edge of its range. Catches of *M. hyadesi* in the fishery at the edge of the Patagonian Shelf have been highly variable over the decade up to 1995 and there have only been three or four years when substantial numbers have been caught. The years of large catches have coincided with the onset of negative SST anomalies in the area (González *et al.* 1997). However, it is not obvious how these oceanographic events influence *M. hyadesi*. There are two alternative, but not mutually exclusive, hypotheses for a mechanism: either a warm event favours the reproductive success of a generation giving rise to a strong recruitment in the next generation as the ensuing cold event develops at the edge of the geographical range, or the species is able to extend its range to the Patagonian Shelf edge early in the

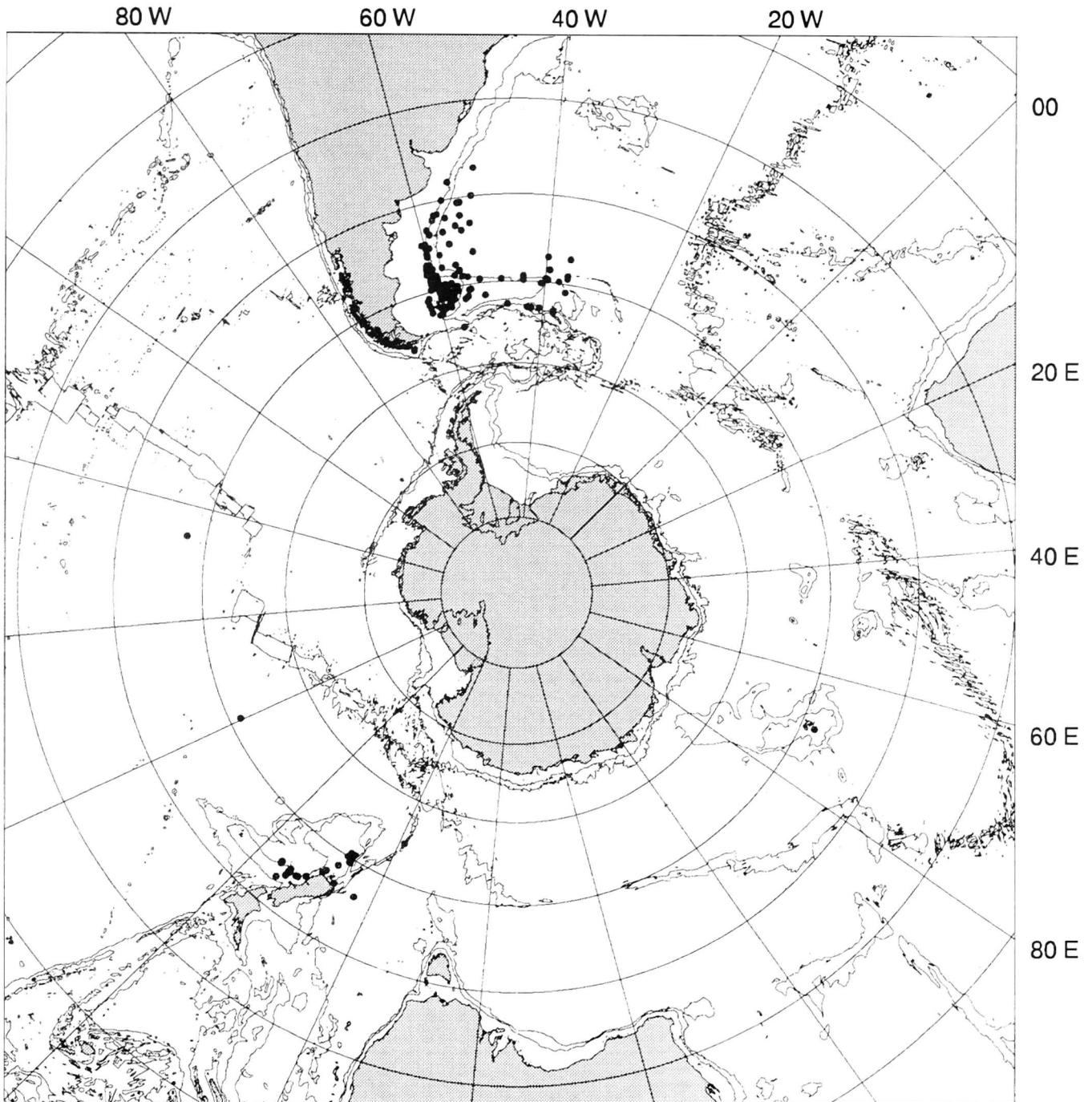


Fig. 1. Map of the Southern Ocean showing the locations of *Martialia hyadesi* samples caught by nets and jigs in relation to bathymetry.

sequence of a cold event. In either case the oceanographic effects probably influence *M. hyadesi* via its prey. There seem to be teleconnections between the oceanographic anomalies in the south Atlantic, which effect *M. hyadesi*, and ENSO events in the Pacific. The south Atlantic anomalies may also be associated with the sub-decadal Antarctic circumpolar wave (ACW) described by White & Peterson

(1996) and the circumpolar precession of anomalous sea ice extent in the Antarctic (Murphy *et al.* 1995).

Meso-Scale Distribution

Information on meso-scale distribution of *Martialia hyadesi* comes from studies in the south west

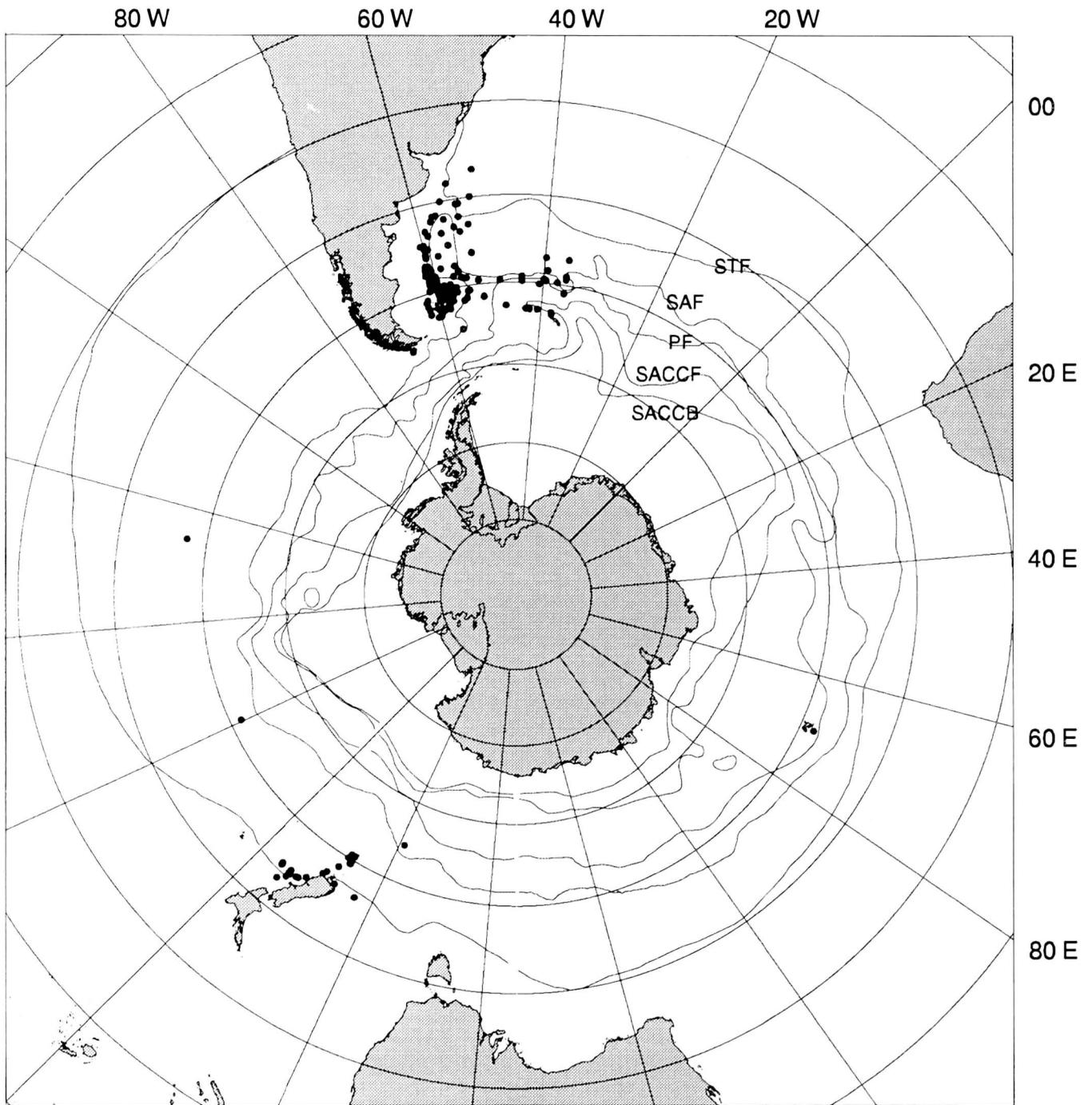


Fig. 2. Map of the Southern Ocean showing the locations of *Martialia hyadesi* samples caught by nets and jigs in relation to major frontal systems (STF: Subtropical Front; SAF: sub-Antarctic Front; PF: Polar Front; SACCF: Southern Antarctic Circumpolar Current Front; SACCB: Southern Antarctic Circumpolar Current Boundary).

Atlantic. This is an area with a high incidence of meso-scale eddies, with dimensions measured in tens of kilometers (Peterson and Whitworth 1989), which are generally known to be features where oceanic production processes are stimulated (Mann and Lazier 1991) and which are implicated in the generation of phytoplankton blooms (Whitehouse *et*

al. 1996) and zooplankton concentrations (Atkinson *et al.* 1990) to the south of the APF in the south west Atlantic. Figure 4 shows a series of such eddies to the west of South Georgia. Recent research has demonstrated concentrations of *M. hyadesi* feeding on mesopelagic fishes and epipelagic crustaceans associated with an eddy structure in the APFZ

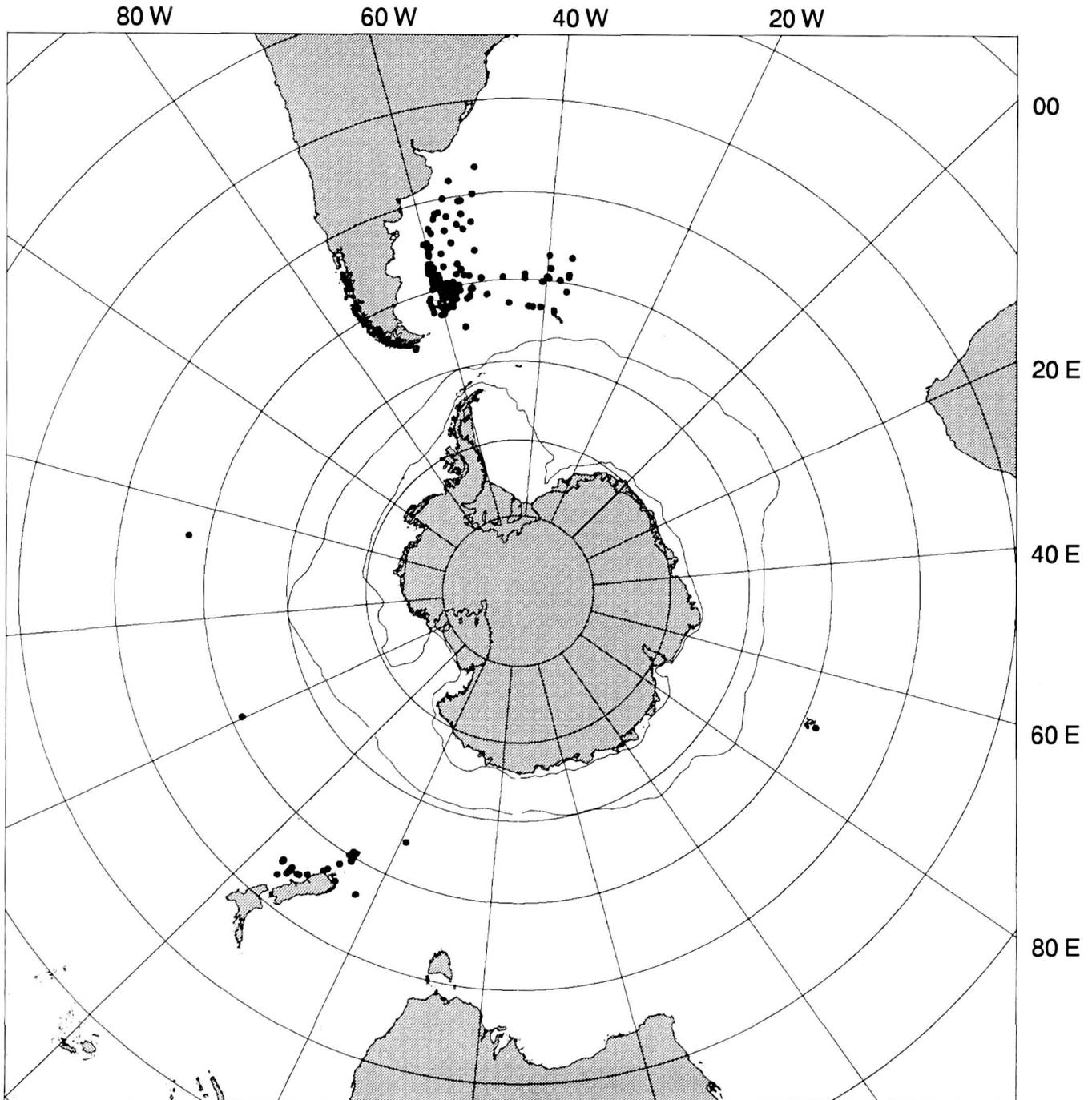


Fig. 3. Map of the Southern Ocean showing the locations of *Martialia hyadesi* samples caught by nets and jigs in relation to the maximum and minimum extent of sea ice.

which was sampled using research and commercial nets (Rodhouse *et al.* 1996).

Martialia hyadesi concentrations also appear to be associated with meso-scale oceanographic features at the interface of the open ocean and the slope. The unusually high catches taken on the edge of the Patagonian Shelf in 1995 were associated with meso-scale features where the SAF runs parallel to the

north/south orientated continental slope (González *et al.* 1997). Similarly, in the austral winter of 1996 *M. hyadesi* was found in high densities close to the South Georgia shelf edge near the 1000 m bathymetric contour (González and Rodhouse, submitted), an area where the long-line fishery for the Patagonian toothfish, *Dissostichus eleginoides* is also concentrated (Croxall and Prince 1996).

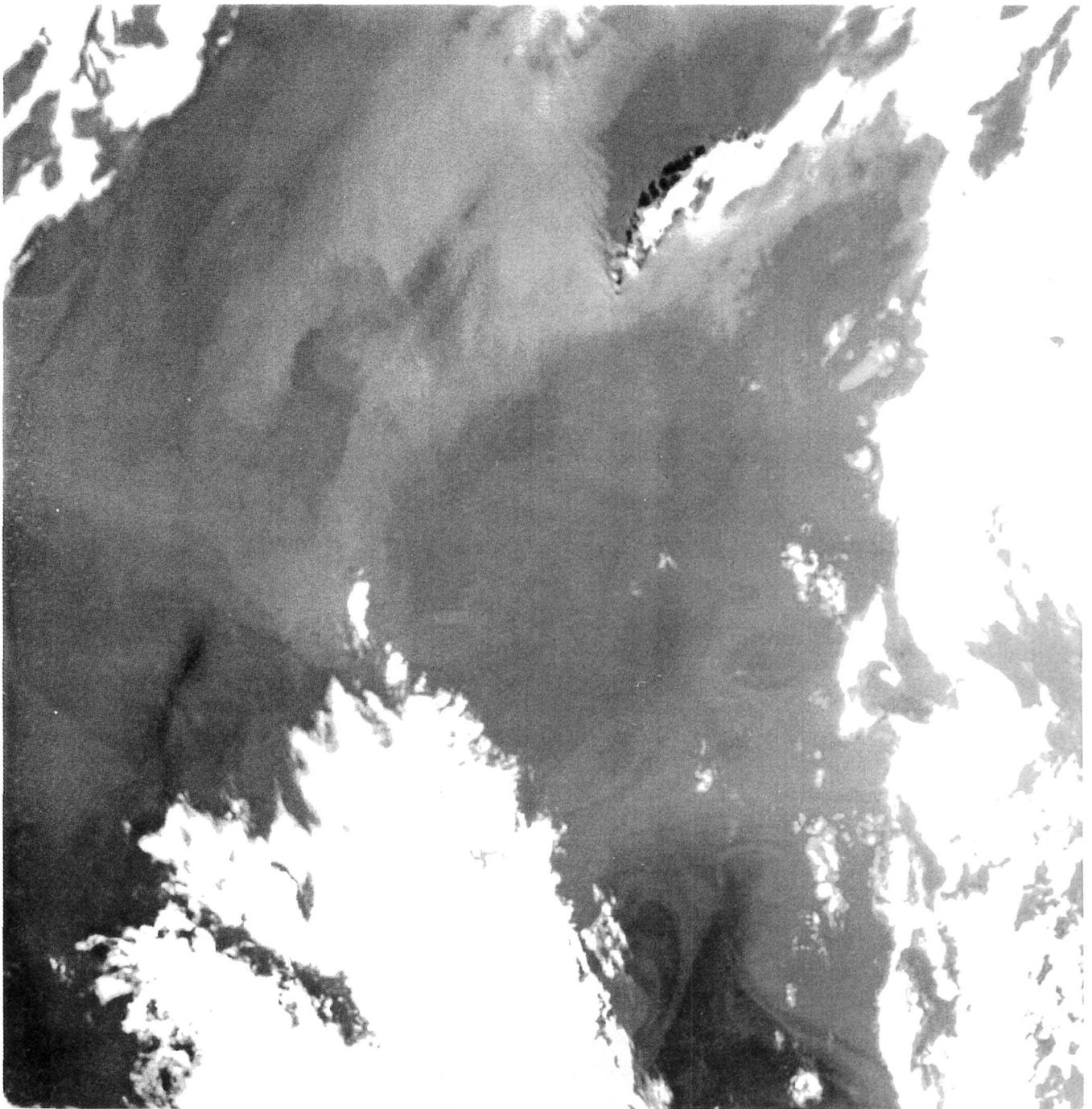


Fig. 4. Satellite sea surface temperature image (AVHRR) of the south west Atlantic showing meso-scale eddies to the west of South Georgia (20:30 GMT, 3 February 1994).

A common feature of these observations has been that the meso-scale features with which *Martialia hyadesi* concentrations have been associated are found in the vicinity of bathymetric features. In the case of the open ocean at the APFZ north of South Georgia these were deep features on the North Scotia Arc, elsewhere at they were associated with the rise of the slope. Records of *M. hyadesi* close to the sub-Antarctic Kerguelen Islands and Macquarie

Island (Cherel and Weimerskirch 1995; O'Sullivan *et al.* 1983) suggest that concentrations may be present in association with bathymetric features in the Indian Ocean and Pacific sectors too. The implication of this apparent connection between bathymetry, meso-scale oceanography and *M. hyadesi* is that the squid may concentrate in more or less predictable areas.

Table 2. Predators of *Martialia hyadesi* recorded from the Atlantic, Indian Ocean and Pacific sectors of the Southern Ocean

	Atlantic Ocean sector	Indian Ocean sector	Pacific Ocean sector
Seabirds	<i>Diomedea chrysostoma</i> ^a <i>Diomedea melanophrys</i> ^b <i>Diomedea exulans</i> ^c <i>Phoebetria palpebrata</i> ^d <i>Procellaria aequinoctialis</i> ^e <i>Macronectes halli</i> ^f <i>Macronectes giganteus</i> ^f <i>Aptenodytes patagonica</i> ^g <i>Eudyptes chrysolophus</i> ^h	<i>Diomedea chrysostoma</i> ^t <i>Diomedea melanophrys</i> ^{l,t} <i>Diomedea exulans</i> ^t <i>Diomedea chlororhynchos</i> ^t <i>Phoebetria fusca</i> ^w <i>Phoebetria palpebrata</i> ^w <i>Aptenodytes patagonicus</i> ^{m,q,r}	<i>Aptenodytes patagonicus</i> ^s <i>Eudyptes schlegeli</i> ^u <i>Eudyptes chrysocome</i> ^v
Seals	<i>Mirounga leonina</i> ⁱ <i>Arctocephalus gazella</i> ^j		<i>Mirounga leonina</i> ^o
Whales		<i>Hyperoodon planifrons</i> ⁿ	
Fish	<i>Dissostichus eleginoides</i> ^k		<i>Allothenus fallai</i> ^p

Sources: ^aRodhouse *et al.* (1990); ^bRodhouse and Prince (1993); ^cRodhouse *et al.* (1987); ^dThomas (1982); ^eCroxall *et al.* (1995); ^fHunter (1983); ^gRodhouse (unpubl. data); ^hReid (unpubl. data); ⁱRodhouse *et al.* (1992); ^jNorth (1996); ^kGonzález and Rodhouse (submitted); ^lCherel and Weimerskirch (1995); ^mCherel *et al.* (1996); ⁿSlip *et al.* (1995); ^oGreen and Burton (1993); ^pYatsu (1995); ^qAdams and Klages (1987); ^rBrown *et al.* (1990); ^sHindell (1988a); ^tRidoux (1994); ^uHindell (1988b); ^vCooper *et al.* (1990); ^wCooper and Klages (1995)

Predator Data

Martialia hyadesi has been recorded in the gut contents of predators (seabirds, seals, whales and fish) from locations throughout the Southern Ocean (Table 2). Seabirds and seals have been sampled ashore while breeding and moulting. Data from fish have been gathered from commercial or research fishery samples while the whale data are scant and come from strandings.

The most detailed information about predation on *Martialia hyadesi* is available from South Georgia (Atlantic sector). Here, reliable census data for predator population sizes are also available (e.g. Croxall *et al.* 1990; Prince *et al.* 1994; Boyd *et al.* 1996) enabling estimates of total predator consumption of *M. hyadesi* in the Scotia Sea area to be made (Rodhouse *et al.* 1993; Rodhouse 1997). Estimates range from a conservative 245,000 tonnes per year to an upper estimate of 550,000 tonnes if less reliable data are included in the calculation (Rodhouse 1997).

In the Indian Ocean sector predators from the Kerguelen Islands, Marion Island, the Crozet archipelago and Heard Island have been found to include *Martialia hyadesi* in their diet and in the Pacific sector predators from Macquarie have similarly been shown to take *M. hyadesi*. These locations are all close to the APFZ, confirming the general conclusion, based on data from other sources, that the species is associated with this large-scale oceanographic feature.

Satellite-tracked squid predators from South Georgia including grey-headed and black-browed albatrosses (*Diomedea chrysostoma* and *D. melanophrys*) apparently forage for *Martialia hyadesi* at the APFZ (Prince *et al.*, in press) where they are located in meso-scale eddies (Rodhouse *et al.* 1996). At the Kerguelen Islands black-browed albatrosses preying on *M. hyadesi* forage near the shelf break and over a submarine bank beyond the slope (Cherel and Weimerskirch 1995), suggesting that they exploit similar meso-scale distribution patterns as the predators from South Georgia.

Discussion

Although far from adequate for a detailed account of the distribution of *Martialia hyadesi*, the data currently available allow some broad conclusions to be drawn. The species is found throughout the Southern Ocean associated with the APFZ. Most records come from the Southwest Atlantic where the APFZ is widest and where fisheries for other squid mean that it is caught by commercial vessels from time to time. At the meso-scale, distribution is associated with eddies that are probably generated by the bathymetry of submarine ridges and island slopes and in this context one of the most important areas for the species identified so far is the Scotia Sea, especially in the vicinity of South Georgia. Data from predators breeding at South Georgia highlight this conclusion.

The life cycle and migrations of *Martialia hyadesi* are poorly known. Although most commercial catches have been taken near the edge of the Patagonian Shelf these are intermittent and apparently associated with large-scale oceanographic anomalies in the northern part of the species range. Commercial-scale catches near the APF in summer (Rodhouse 1991; Rodhouse *et al.* 1996) and near the South Georgia slope in winter (González and Rodhouse, in press) support the simple hypothesis that there is a southwards migration during the austral winter to feeding grounds where they appear to be preyed on by toothfish. There are few data on larval and juvenile distribution patterns or the distribution of ripe, spawning or spent adults that would indicate the location of spawning grounds.

At large spatial and temporal scales, variability in the distribution of the *Martialia hyadesi* stock in the South Atlantic seems to be related to large scale oceanographic variability. In the longer term, as our understanding of the physical processes develop, we may be able to predict fisheries on these scales. In the shorter term, as our knowledge of the relationships between meso-scale processes and the behaviour of *M. hyadesi* improves short term prediction of meso-scale distribution may become possi-

ble, based on the use of remote sensing imagery of surface oceanography.

Given the difficulty of scientific sampling for this highly active, aggregated species which inhabits one of the remotest parts of the world's oceans, there are only limited opportunities for increasing our knowledge. However, if a commercial fishery were to commence in the Scotia Sea, as seems likely in the medium term, then every effort should be made to capitalise on the opportunity of developing close collaboration between science and industry arising from the mutual interest of the international scientific and fishing communities in effectively managing this resource in the CCAMLR area.

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References

- Adams N.J. and Klages N.T. 1987. Seasonal variation in the diet of the king penguin (*Aptenodytes patagonicus*) at sub-Antarctic Marion Island. *J. Zool. Lond.* **212**: 303-324.
- Alexeyev D.O. 1994. New data on the distribution and biology of squids from the Southern Pacific. *Ruthenica* **4**: 151-166.
- Arkipkin A.I. and Silvanovich N.V. 1997. Age, growth and maturation of the squid *Martialia hyadesi* (Cephalopoda, Ommastrephidae) in the south-west Atlantic. *Antarct. Sci.* **9**: 373-380.
- Atkinson A., Ward P., Peck J.M., and Murray A.W.A. 1990. Mesoscale distribution of zooplankton around South Georgia. *Deep-Sea Research* **37**: 1213-1227.
- Boyd I.L., Walker T.R., and Poncet J. 1996. Status of southern elephant seals at South Georgia. *Antarct. Sci.* **8**: 237-244.
- Brown C.R., Klages N.T., and Adams N.J. 1990. Short and medium-term variation in the diets of penguins at Marion Island. *S. Afr. J. Antarct. Res.* **20**: 13-20.
- Brunetti N.E., Ivanovic M.L., and Rossi G.R. 1990. Argentine final report of the Southwestern Atlantic survey. Unpublished report. Instituto Nacional de Investigacion Y Desarrollo Pesquero, Playa Grande s/n, 7600 Mar del Plata, Argentina.
- Castellanos Z. 1967. Rehabilitacion del Genero *Martialia* Roch. et Mab. 1887. *Neotropica* **13**: 1-12.

- Cherel Y., Ridoux V., and Rodhouse P.G. 1996. Fish and squid in the diet of king penguin chicks, *Aptenodytes patagonicus*, during winter at sub-Antarctic Crozet Islands. *Mar. Biol.* **126**: 559-570.
- Cherel Y. and Weimerskirch H. 1995. Seabirds as indicators of marine resources: black browed albatrosses feeding on ommastrephid squids in Kerguelen waters. *Mar. Ecol. Prog. Ser.* **129**: 295-300.
- Coggan R.A., Nolan C.P., and George M.J.A. 1996. Exploratory deepsea fishing in the Falkland Islands, SouthWestern Atlantic. *J. Fish. Biol.* **49** (suppl. A): 298-310.
- Cooper J., Brown C.R., and Gales R.P. 1990. Diets and dietary segregation of crested penguins (*Eudyptes*). In: Davis L.S. and Darby J.T. (eds), *Penguin Biology*. Academic Press, San Diego. pp. 131-156.
- Cooper J. and Klages N.T. 1995. The diets and dietary segregation of sooty albatrosses (*Phoebastria* spp.) at sub-Antarctic Marion Island. *Antarct. Sci.* **7**: 15-23.
- Croxall J.P., Hall A.J., Hill H.J., North A.W., and Rodhouse P.G. 1995. The food and feeding ecology of the white-chinned petrel *Procellaria aequinoctialis* at South Georgia. *J. Zool. Lond.* **237**: 133-150.
- Croxall J.P. and Prince P.A. 1996. Potential for interactions between wandering albatrosses and longline fisheries for Patagonian toothfish at South Georgia. *CCAMLR Science* **3**: 101-110.
- Croxall J.P., Rothery P., Pickering S.P.C., and Prince P.A. 1990. Reproductive performance, recruitment and survival of wandering albatrosses *Diomedea exulans* at Bird Island, South Georgia. *J. Anim. Ecol.* **59**: 773-794.
- González A.F. and Rodhouse P.G. 1996. Research fishery for the squid *Martialia hyadesi* at South Georgia conducted by the Korean registered vessel *Ihn Sung 101* (June 1996): Scientific Observers Report (WG-FSA-96/21).
- González A.F., Trathan P.N., Yau C., and Rodhouse P.G. 1997. Interactions between oceanography, ecology and fishery biology of the ommastrephid squid *Martialia hyadesi* in the South Atlantic. *Mar. Ecol. Prog. Ser.* **152**: 205-215.
- González A.F. and Rodhouse P.G. 1998. Fishery biology of the seven star flying squid *Martialia hyadesi* at South Georgia during winter. *Polar Biol.* **19**: 231-236.
- Green K. and Burton H.R. 1993. Comparison of the stomach contents of southern elephant seals, *Mirounga leonina*, at Macquarie and Heard Island. *Mar. Mammal Sci.* **9**: 10-22.
- Hindell M.A. 1988a. The diet of the king penguin *Aptenodytes patagonicus* at Macquarie Island. *Ibis* **130**: 193-203.
- Hindell M.A. 1988b. The diet of the royal penguin *Eudyptes schegeli* at Macquarie Island. *Emu* **88**: 219-226.
- Hunter S. 1983. The food and feeding ecology of the giant petrels *Macronectes halli* and *M. giganteus* at South Georgia. *J. Zool. Lond.* **200**: 521-538.
- Mann K.H. and Lazier J.R.N. 1991. *Dynamics of Marine Ecosystems*. Blackwell, Oxford. 466 pp.
- Murphy E.J., Clarke A., Symon C., and Priddle J. 1995. Temporal variation in Antarctic Sea-ice: Analysis of a long term fast-ice record from the South Orkney Islands. *Deep-Sea Res.* **42**: 1045-1062.
- Nesis K.N. and Nigmatullin C.M. 1972. Demersal squids from the Patagonian Falkland area. *Trudy Atl. NauchnoIssled. Inst. Rybn. Okeanogr.* **42**: 170-175.
- Nolan C.P., Strange I., Alesworth E., and Agnew D. In press. A stranding of the ommastrephid squid *Martialia hyadesi* on New Island, Falkland Islands. *S. Afr. J. Mar. Sci.*
- North A.W. 1996. Fish in the diet of Antarctic fur seals (*Arctocephalus gazella*) at South Georgia during winter and spring. *Antarct. Sci.* **8**: 155-160.
- O'Sullivan D.B., Johnstone G.W., Kerry K.R., and Imber M.J. 1983. A mass stranding of squid *Martialia hyadesi* Rochebrune and Mabile (Teuthoidea; Ommastrephidae) at Macquarie Island. *Pap. Proc. Royal Soc. Tasmania* **117**: 161-163.
- Peterson R. and Whitworth T. 1989. The Subantarctic and Polar Fronts in relation to deep water masses through the Southwestern Atlantic. *J. Geophys. Res.* **94**(C8): 10817-10838.
- Piatkowski U., Rodhouse P.G., and Duhamel G. 1991. Occurrence of the cephalopod *Martialia hyadesi* (Teuthoidea: Ommastrephidae) at the Kerguelen Islands in the Indian Ocean sector of the Southern Ocean. *Polar Biol.* **11**: 273-275.
- Prince P.A., Rothery P., Croxall J.P., and Wood A.G. 1994. Population dynamics of black-browed and grey-headed albatrosses *Diomedea melanophrys* and *D. chrysostoma* at Bird Island, South Georgia. *Ibis* **136**: 50-71.
- Prince P.A., Croxall J.P., Trathan P.N., and Wood A.G. In press. The pelagic distribution of South Georgia Albatrosses and their relationship with fisheries. In: Robertson G. (ed.), *Albatross Ecology and Conservation*. Surrey Beatty and Sons, Chipping Norton, Australia
- Ridoux V. 1994. The diets and dietary segregation of seabirds at the sub-Antarctic Crozet Islands. *Mar. Orn.* **22**: 1-192.
- Rochebrune A.T. and Mabile J. 1889. Mollusques. in Mission scientifique du Cap Horn 1882-1883, *Zool. VI* (2): 1143.
- Rodhouse P.G. 1990. Cephalopod fauna of the Scotia Sea at South Georgia: potential for commercial exploitation and possible consequences. In: Kerry K. and Hempel G. (eds), *Ecological Change and the Conservation of Antarctic Ecosystems*. Proc. 5th SCAR Symp. Antarct. Biol. Springer-Verlag, Berlin. pp. 289-298.
- Rodhouse P.G. 1991. Population structure of *Martialia hyadesi* (Cephalopoda: Ommastrephidae) at the Antarctic Polar Front and the Patagonian Shelf, South Atlantic. *Bull. Mar. Sci.* **49**: 404-418.
- Rodhouse P.G. 1997. Precautionary measures for a new *Martialia hyadesi* (Cephalopoda, Ommastrephidae) fishery in the Scotia Sea: An ecological approach. *CCAMLR Science*
- Rodhouse P.G., Arnbom T.R., Fedak M.A., Yeatman J., and Murray A.W.A. 1992. Cephalopod prey of the southern elephant seal, *Mirounga leonina* L. *Can. J. Zool.* **70**: 1007-1015.
- Rodhouse P.G., Clarke M.R., and Murray A.W.A. 1987. Cephalopod prey of the Wandering Albatross *Diomedea exulans*. *Mar. Biol.* **96**: 1-10.
- Rodhouse P.G., Croxall J.P., and Prince P.A. 1993. Towards an assessment of the stock of the ommastrephid squid

- Martialia hyadesi* in the Scotia Sea: data from predators. In: Okutani T., O'Dor R.K., and Kubodera T. (eds), *Recent Advances in Cephalopod Fisheries Biology*. Tokai Univ. Press, Tokyo. pp. 433-440.
- Rodhouse P.G. and Prince P.A. 1993. Cephalopod prey of the black-browed albatross *Diomedea melanophrys* at South Georgia. *Polar Biol.* **13**: 373-376.
- Rodhouse P.G., Prince P.A., Clarke M.R., and Murray A.W.A. 1990. Cephalopod prey of the grey-headed albatross *Diomedea chrysostoma*. *Mar. Biol.* **104**: 353-362.
- Rodhouse P.G., Prince P.A., Trathan P.N., Hatfield E.M.C., Watkins J.L., Bone D.G., Murphy E.J., and White M.G. 1996. Cephalopods and mesoscale oceanography at the Antarctic Polar Front: Satellite tracked predators locate pelagic trophic interactions. *Mar. Ecol. Prog. Ser.* **136**: 37-50.
- Rodhouse P.G., Symon C., and Hatfield E.M.C. 1992. Early life cycle of cephalopods in relation to the major oceanographic features of the southwest Atlantic. *Mar. Ecol. Prog. Ser.* **89**: 183-195.
- Rodhouse P.G. and White M.G. 1995. Cephalopods occupy the ecological niche of epipelagic fish in the Antarctic Polar Frontal Zone. *Biol. Bull.* **189**: 77-80.
- Rodhouse P.G. and Yeatman J. 1990. Redescription of *Martialia hyadesi* Rochbrune and Mabile, 1889 (Mollusca: Cephalopoda) from the Southern Ocean. *Bull. Br. Mus. nat. Hist. (Zool.)* **56**: 135-143.
- Slip D.J. Moore, G.J., and Green K. 1995. Stomach contents of a southern bottlenose whale, *Hyperoodon planifrons*, stranded at Heard Island. *Mar. Mammal. Sci.* **11**: 575-584.
- Thomas G. 1982. The food and feeding ecology of the light-mantled sooty albatross at South Georgia. *Emu* **82**: 92-100.
- Trathan P.N., Murphy E., Symon C., and Rodhouse P.G. 1993. Ecological and oceanographic relationships in the Southern Ocean. *GIS Europe* **2**: 34-36.
- Uozumi Y., Forch E.C., and Okutaki T. 1991. Distribution and morphological characters of immature *Martialia hyadesi* (Cephalopoda: Oegopsida) in New Zealand waters. *New Zealand J. Mar. Freshwater Res.* **25**: 275-282.
- White B.W. and Peterson R.G. 1996. An Antarctic circum-polar wave in surface pressure, wind, temperature and sea-ice extent. *Nature* **380**: 699-702.
- Whitehouse M.J., Priddle J., Trathan P.N., and Brandon M.A. 1996. Substantial open-ocean phytoplankton blooms to the north of South Georgia, South Atlantic, during summer 1994. *Mar. Ecol. Prog. Ser.* **140**: 187-197.
- Yatsu A. 1995. The role of slender tuna, *Allothenus fallai*, in the pelagic ecosystems of the South Pacific Ocean. *Japan. J. Ichthyol.* **41**: 367-377.

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