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Distribution and abundance of the squid *Moroteuthis ingens* (Cephalopoda: Onychoteuthidae) in the Falkland Islands region of the South Atlantic

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Abstract The distribution and abundance of the onychoteuthid squid Moroteuthis ingens were assessed for the Patagonian Shelf in the Falkland Islands region. Catch records from the commercial fishery and a research cruise were recorded from 1988 to 1996. Sampling included benthic, pelagic and semi-pelagic trawls and jigging. Moroteuthis ingens was recorded from 1,414 stations out of a total of 9.060 stations with 79.9% of all positive stations being from benthic trawls. Catch size ranged up to approximately 3,000 kg. The length frequency analysis and maturity indices suggested a major recruitment onto the shelf in September with a movement off the shelf during winter. There appears to be a lack of mature females on the Patagonian Shelf, indicating that females migrate into deeper offshore water to spawn. Observations of predation on Moroteuthis ingens on the Patagonian Shelf, along with a literature review, revealed that at least 4 mammal, 17 bird and 13 fish species prey on this squid.

Introduction

The waters above the Patagonian Shelf support a huge biomass of fish and cephalopods which sustains an international multispecies fishery (Csirke 1987). In the last decade this fishery has continued to be of significant

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Present addresses: ¹Seafish (Falklands) Ltd. P.O. Box 1, Stanley, Falkland Islands ²Synergy Information Systems Ltd., 14 Ross Road West, Stanely, Falkland Islands international interest. Research has recently expanded in the region and has included a survey of the species present in deep water between 500 and 1,000 m (Coggan et al. 1996). There is also increasing attention being given to the potential oil and gas reserves on the Patagonian Shelf (see Coggan et al. 1996; Hirst and Rodhouse 1996). The continued importance of fish stocks on the Patagonian shelf and the potential for future oil exploration and extraction highlight the need for continued biological studies in this region.

In the past few years there has been increasing interest in South Atlantic cephalopods and the role that they play in the food web (e.g. Rodhouse et al. 1992, 1994, 1996; Okutani 1994). The ommastrephid squid *Illex argentinus* and the loliginid squid *Loligo gahi* are especially abundant in the Falkland Islands region and have both been targeted by fisheries for a number of years (e.g. Csirke 1987; Hatfield and Rodhouse 1991). However, it has become apparent that a third species, *Moroteuthis ingens*, is also relatively common on the Patagonian Shelf (Jackson et al. 1997, see also Jackson 1997).

Moroteuthis ingens has been recorded previously in the Falkland Islands region (e.g., Filippova 1969, 1972; Clarke 1980; Rodhouse 1991), as well as off Argentina (Arkhipkin and Bizikov 1991). However, this species has not been the focus of detailed studies, possibly due to its lack of commercial importance. Although this is a noncommercial species, it is ecologically important around the Falkland Islands and other regions of the Southern Ocean. Moroteuthis ingens has proven to be important in the diets of many vertebrate predators as represented by the presence of beaks in stomach contents (e.g., Jackson 1995, Clarke 1996; Croxall and Prince 1996; Klages 1996; Weimerskirch et al. 1997). Due to the high levels of tissue ammonia, this species may float after death and therefore be important in the diet of scavenging seabirds (Lu and Williams 1994).

This study was undertaken to gain a better understanding of the distribution and important biological parameters of this species in the Patagonian Shelf region. The Falkland Islands Government Fisheries 162

Department observer program provided the mechanism to gather a substantial body of data on *Moroteuthis ingens* over a number of years. This provided information on important features of distribution, abundance and maturation. The data allowed us to postulate on the possible life history and migration patterns of *Moroteuthis ingens*.

Materials and methods

Records of *Moroteuthis ingens* were made from 1988 to 1996 by Falkland Islands Government Fisheries Department observers onboard commercial fishing vessels in the Falkland Islands region of the Patagonian Shelf. This included recording the presence of squid and roughly estimating the order of magnitude of the catch. All fishing methods were sampled including commercial benthic, pelagic, and semi-pelagic trawls and jiggers. Stations were spread throughout the important commercial fishing areas where the squid *Loligo gahi, and Illex argentinus*, and fish *Merluccius hubbsi*, *Merluccius australis, Micromesistius australis* and other commercial species are targeted. In addition, data were available from a short deep-water bottom trawling cruise undertaken by the *Heroya Primero*, which sampled a number of stations around 1000 m during October 1994 (see Coggan et al. 1996).

Fishing gear and mesh sizes varied. However, the benthic trawls that were most commonly used sampled the bottom 4 m. Semipelagic trawls were deployed very close to the bottom and had much larger mouth openings (generally over 20 m). Semi-pelagic tows generally targeted single-species aggregations, resulting in huge catches of many tens of tons (e.g. *Micromesistius australis*). Bycatch in these tows was therefore reduced and less likely to be noticed by solo observers. The pelagic trawls were only used on the Patagonian Shelf prior to 1991. Most stations were inside the Falkland Islands Interim Conservation and Management Zone (FICZ) but some were in the Falklands Outer Conservation Zone (FOCZ) and a few were in international waters to the north of the FOCZ (see Coggan et al. 1996). All work on commercial vessels was opportunistic and depended on the time available after essential work on commercial target species had been completed. Although records were taken from 1988, increased work was focused on *Moroteuthis ingens* after June 1993 when observers were specially requested to record this species diligently. Therefore, between 1988 and 1993 the amount of effort put into recording the catch of *Moroteuthis ingens* was minimal and it would have been underrecorded. Moreover, emphasis was not given to recording the presence of bycatch species in commercial trawls until after 1991; this is also a significant factor influencing the under-recording of *Moroteuthis ingens* prior to that year.

Samples that were taken for length frequency analyses were random and dorsal mantle length (ML) was measured to the half centimeter below. Sex, length and maturity stage were recorded using a modified Lipinski scale (after Juanico 1983; Sauer and Lipinski 1990). Mature individuals in this study (stage 5) are equivalent to mature stage 3 individuals in Jackson (1997), although some stage 4 (maturing) males in this study (with only some spermatophores present) would have been included as stage 3 in Jackson (1997). The majority of measurements were made on fresh specimens on board ship. However, some specimens were frozen and were taken back to the laboratory for more detailed analysis. Mantle length for these specimens was included in the length frequency data, but no correction was made for possible mantle length changes due to freezing.

From 1993 to 1996, attention was also given by staff of the Falkland Islands Government Fisheries Department to opportunistically recording the predation on *Moroteuthis ingens*. Therefore, where possible, stomach content analysis was undertaken for selected large teleost predators captured from commercial trawls (this is summarised in Table 4).

Results

Occurrence of Moroteuthis ingens in commercial stations

Data were available from a total of 9,060 stations from 1988 to 1996 between depths of 25 and 1,025 m

Table 1 Depth distribution for all sampling stations where observations were made for the presence of *Moroteuthis ingens* on the Patagonian Shelf

Depth	Benthic t	rawl	Jigging		Pelagic t	rawl	Semi-pela	agic trawl	Total	%
(m)	Count	%	Count	%	Count	%	Count	%	count	
25	13	0.1	9	0.1					22	0.2
75	55	0.6	32	0.4					87	1
125	1092	12.1	404	4.5	55	0.6	99	1.1	1650	18.2
175	3215	35.5	948	10.5	167	1.8	288	3.2	4618	51
225	1284	14.2	69	0.8	47	0.5	80	0.9	1480	16.3
275	436	4.8	25	0.3	24	0.3	68	0.8	553	6.1
325	173	1.9	4	0.04	28	0.3	97	1.1	303	3.3
375	55	0.6	3	0.03	33	0.4	37	0.4	128	1.4
425	50	0.6	3	0.03	8	0.1	29	0.3	90	1
475	32	0.4	4	0.04	12	0.1	42	0.5	90	1
525	9	0.1	1	0.01	2	0.02	8	0.1	20	0.2
575	3	0.03	2	0.02					5	0.1
625			2	0.02					2	0.02
675	4	0.04							4	0.04
725	2	0.02							2	0.02
775	1	0.01							1	0.01
875	3	0.03							3	0.03
1025	3	0.03							3	0.03
Total	6430	71	1506	16.6	376	4.2	748	8.3	9060	100

(Table 1). *Moroteuthis ingens* was recorded at 1,414 stations representing 15.6% of all stations (Table 2). The catch sizes of *Moroteuthis ingens* estimated from the 1,414 stations were: 1,028 stations < 10 kg, 352 < 100 kg, 26 < 500 kg, 6 < 1,000 kg, and 2 between 1,000 and 3,000 kg. The maximum estimated catch was 3,000 kg. The exceptionally large catches occurred in the second half of 1993 and were from semi-pelagic trawls. These very large catches of *Moroteuthis ingens* exceeded the weight of all previous records.

Composition of commercial samples

The commercial stations that were observed included 376 pelagic trawls, 748 semi-pelagic trawls, 1,506 jigging stations and 6,430 benthic trawls (Table 1). The sampling was generally undertaken around 200 m on the Patagonian Shelf with the most sampling taking place between 125 and 375-m depth (Fig. 1). The majority of recorded occurrences of Moroteuthis ingens (79.9%) were from benthic trawls; 11.5% and 8.5% of the total positive-recorded stations were from jigging and semipelagic trawls respectively, while only 1 pelagic trawl out of 376 recorded Moroteuthis ingens (Table 2). The distribution of positive stations (out of the total 9,060 stations) for each sampling type were: 17.6% benthic trawls, 16.0% semi-pelagic trawls, 10.8% jigging trawls and 0.27% pelagic trawls. These records can only represent the minimum number of stations where catches of Moroteuthis ingens were recorded, for the reasons discussed above, with the semi-pelagic and pelagic stations probably representing the greatest degree of underrecording.

The underrecording of *Moroteuthis ingens* prior to 1991 was apparent by the low number of positive stations for each fishing season from 1988 to 1996 (Table 3). The low number of positive catches is espe-

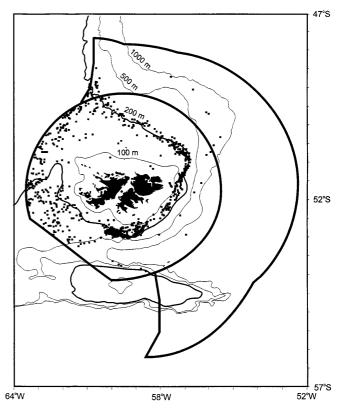


Fig. 1 Map of the distribution of positive stations where *Moroteuthis ingens* was captured on the Patagonian Shelf

cially notable from 1988 to 1991. Positive catches of approximately 20–35% may be more representative. However, there does appear to be a substantial increase in the abundance of *Moroteuthis ingens* during season 1 of 1994 with over 65% of observed stations recording the presence of the squid. We suspect that this increase is real and represents a year of unusually high abundance of *Moroteuthis ingens* on the Patagonian Shelf.

Depth	Benthic t	rawl	Jigging		Pelagic tr	rawl	Semi-pela	agic trawl	Total	%
(m)	Count	%	Count	%	Count	%	Count	%	count	
75	7	0.5							7	0.5
125	189	13.4	20	1.4	1	0.1	10	0.7	220	15.6
175	574	40.6	133	9.4			30	2.1	737	52.1
225	193	13.6	9	0.6			4	0.3	206	14.6
275	99	7	1	0.1			22	1.6	122	8.6
325	35	2.5					44	3.1	79	5.6
375	6	0.4					8	0.6	14	1
425	6	0.4					2	0.1	8	0.6
475	3	0.2							3	0.2
525	5	0.4							5	0.4
675	4	0.3							4	0.3
725	2	0.1							2	0.1
775	1	0.1							1	0.1
875	3	0.2							3	0.2
1025	3	0.2							3	0.2
Total	1130	79.9	163	11.5	1	0.1	120	8.5	1414	100

Table 2 Depth distribution for all sampling stations where there were positive catches of Moroteuthis ingens on the Patagonian Shelf

Length frequency

Length frequency data were available for 4,205 individuals (1,430 males, 2,775 females) that covered the 4 quarters of the year Jan. to Mar., Apr. to Jun., Jul. to Sept., Oct. to Dec. (Fig. 2). While this is somewhat arbitrary, it corresponds to the fishing seasons in the year and to the routine data collection undertaken by the Falkland Islands Government Fisheries Department. Data collection was not extensive in some months, e.g. very little fishing is undertaken in June/July. Furthermore, August (which is a heavily fished month) does not have any records of Moroteuthis ingens catches. The data suggest that there is some recruitment during the second quarter, April to June (the small mode in the second quarter are all juveniles captured along with larger individuals during April), with a large recruitment in the third quarter, July to September. All the recruits in the third quarter are from September. There appears to be a modal progression commencing in September through to the second quarter (April to June). Interestingly, by the third quarter when sampling commences for the *Loligo gahi* fishing season in August, virtually all the large adult individuals have disappeared from the Patagonian Shelf. There appears to be a general abundance of large squids on the Patagonian Shelf from late in the year during the fourth quarter (October) to early winter, with a lack of larger squids through much of the winter until a major juvenile recruitment occurs in September. The bimodal distribution shown in most quarters of the year, along with the observed recruitment in September and April, suggest two spawning periods, one in summer and one in winter.

Table 3 Percentage of positive catches of *Moroteuthis ingens* from the Patagonian Shelf from 1988 to 1996. Season 1 is January/June; season 2 is July/December

Year	Season	Number of stations	Number with <i>M. ingens</i>	Percent with <i>M. ingens</i>
1988	1	1296	4	0.31
1988	2	284	12	4.23
1989	1	601	1	0.17
1989	2	447	20	4.47
1990	1	1000	79	7.90
1990	2	333	7	2.10
1991	1	475	46	9.68
1991	2	273	9	3.29
1992	1	472	86	18.20
1992	2	363	54	14.88
1993	1	634	223	35.17
1993	2	599	132	22.04
1994	1	535	348	65.05
1994	2	398	96	24.12
1995	1	551	151	27.40
1995	2	326	58	17.79
1996	1	473	88	18.60
Total		9060	1414	

Maturity

Maturity stage data were also taken for the 4,205 individuals discussed above (Fig. 3). These data also revealed some interesting trends. There were no records of any spent males or females (stage 6) during the course of this study. Stage 1–4 males covered a relatively wide size range in ML with stage 2–4 males particularly abundant. In contrast, there were relatively few stage 5 males recorded (only 21 in comparison to 494 stage 4 males). It is possible that the large mature males migrate off the shelf to deeper water. However, the stage 4 males do have spermatophores present and are therefore likely to be mating.

The situation with females is much more extreme and interesting (Fig. 3). The majority of females (81.9%) were immature stage 2. This was followed by a marked decline in the number of females from stage 2 through to stage 5, with numbers dropping from 2,272 to 1. The one stage 5 mature female was an observer record that was not confirmed and may have been a mis-identification. The data reveal a lack of mature females on the Patagonian Shelf. This lack of mature and spent females

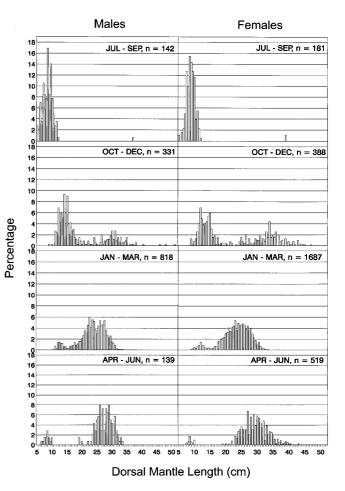
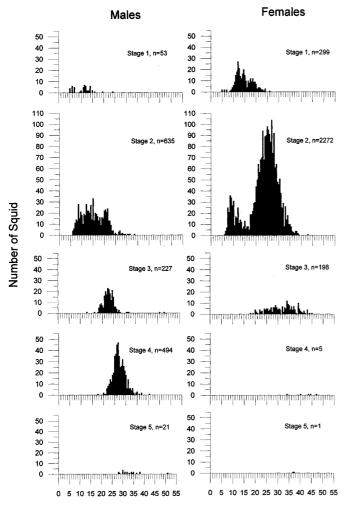


Fig. 2 Length frequency distribution of 4,198 individuals of *Moroteuthis ingens* captured on the Patagonian Shelf grouped according to the 4 quarters of the year

strongly suggests a migration off the Patagonian Shelf to spawn.

Discussion

This study presents the most comprehensive data set on the distribution of *Moroteuthis ingens* on the Patagonian Shelf. The data set also provides a useful comparison to what is known of the biology of this species in New Zealand waters. Both *Moroteuthis robusta* in the North Pacific (Smith 1963; Roper and Young 1975) and *Moroteuthis ingens* in the South Pacific (Lipinski and Linkowski 1986; Jackson 1993) have been suggested as having a demersal existence due to their predominance in bottom trawls. Jackson (1993, 1994) suggested that, in New Zealand waters, *Moroteuthis ingens* spends its early



Dorsal Mantle Length (cm)

Fig. 3 Length frequency distribution of each maturity stage of male and female individuals of *Moroteuthis ingens* captured on the Patagonian Shelf

juvenile phase in the epipelagic zone and then migrates to a demersal existence later in the life-cycle.

Moroteuthis ingens appears to have a close association with the bottom on the Patagonian Shelf and is common around 200 m and even shallower. However, the fact that Moroteuthis ingens was also captured in semi-pelagic trawls and even jigs suggests that it does move off the bottom, although these specimens could have been captured in close association with the bottom (i.e., semi-pelagic trawls are deployed close to the bottom). The jigged individuals were captured in a relatively shallow water depth of around 200 m. Observers on board jiggers have noted that as the jigs are lifted off the bottom during the course of the night, the catch of Moroteuthis ingens ceases, which again suggests that this species is not moving far off the bottom. Based on the abundance of the neritic Loligo gahi and Moroteuthis. ingens in the diet of both the pilot whale (Globicephala melaena) and bottlenose whale (Hyperoodon planifrons) at Tierra del Fuego, Clarke and Goodall (1994) suggested that these whales were possibly feeding entirely on the continental shelf. This was based on their assumption that *Moroteuthis ingens* may move into shallow water or live close to islands. Our study supports this assumption due to the abundance of Moroteuthis ingens in shallow shelf waters in association with L. gahi.

We cannot draw any conclusions for the South Atlantic population regarding the epipelagic-demersal migration of this species as suggested by Jackson (1993). No paralarval *Moroteuthis ingens* were captured in extensive cephalopod plankton sampling in this region by Rodhouse et al. (1992). However, net avoidance could account for this as cephalopod juveniles generally are difficult to sample with nets (Wormuth and Roper 1983). Furthermore, despite the huge abundance of *Loligo gahi* on the Patagonian Shelf, extensive net sampling produced relatively small numbers of individuals of this species (Hatfield and Rodhouse 1994).

The length frequency data along with the maturation data revealed that the population of *Moroteuthis ingens* on the Patagonian Shelf is not static and possibly undergoes extensive migrations off the shelf. The lack of mature females on the Patagonian Shelf is interesting compared to the depth distribution of this species in New Zealand waters. Jackson (1997) found that mature and spent females were only encountered in water depths off New Zealand greater than 740 m. Above this depth in New Zealand, all females (including individuals with a large body size) are immature. This suggests that an ontogenetic downward migration takes place in New Zealand for spawning. This appears to be what is happening in the Falkland Islands region as well. The marked decline in female abundance from stage 2 probably represents a migration to deeper water off the shelf. Moroteuthis ingens is a terminal spawner with females undergoing dramatic tissue breakdown in association with development of the large ovary (Jackson and Mladenov 1994). Therefore, there may be a metabolic advantage in females migrating to cooler water to spawn.

Species common name	Species scientific name	Feeding mode	Location	References
Mammals Southern elephant seal Southern bottlenose whale	Mirounga leonina Hyperoodon planifrons	Deep diving Deep diving	Macquarie Is., Heard Is. South Africa	Green and Burton 1993; Slip 1995 Sekiguchi et al. 1992
Pilot whale	Globicephala melaena	Deep diving	Argentina, Patagonia	Clarke and Goodall 1994 Clarke and Goodall 1994,
Sperm whale	Physeter macrocephalus	Deep diving	Argentina South Georgia New Zealand	Crespo et al. 1994 cited in Clarke 1996 Pascoe et al. 1990 Rodhouse 1990 Clarke 1980, 1986
Birds Emperor penguin King penguin	Aptenodytes forsteri Aptenodytes patagonicus	Deep diving Deep diving	Antarctica (Indian Ocean sector) Crozet Islands	Robertson et al. 1994 Cherel and Ridoux 1992; Cherel and 1002 1006
Gentoo penguin Magellanic penguin Yellow-eyed penguin	Pygoscelis papua Spheniscus megallanicus Megadyptes antipodes	Diving Diving Diving	Falkland Islands Falkland Islands New Zealand	Cuerci et al. 1999 Thompson 1989 van Heezik 1990a, b
Rockhopper penguin	Eudyptes chrysocome	Diving	Falkland Island New Zealand	Thompson 1989 Cooner et al 1990
Fiordland crested penguin Snares crested nenouin	Eudyptes pachyrhynchus Fudwntes robustus	Diving	New Zealand New Zealand	Cooper et al. 1990; van Heezik 1990b Cooper et al. 1990;
Little penguin Sooty albatross	Eudyptula minor Phoebetria fusca	Diving Surface	New Zealand Marion Island	van Heezik 1990b Berruti and Harcus 1978;
Wandering albatross	Diomeda exulans	Surface	South Georgia, Marion Island, New Zealand, Prince Edward, Macquarie, Crozet Island	Cooper and Klages 1995 Rodhouse et al. 1987; Rodhouse 1990; Imber 1992; Cooper et al. 1992; Ridoux 1994 cited in Croxall and Prince
Grey-headed albatross	D. chrysostoma	Surface	Prince Edward Island	1996, Cooper et al. 1992; Weimerskirch et al. 1997 Hunter and Klages 1989 cited in
Buller's albatross Royal albatross Thin-billed prion Northern giant petrel	D. bulleri D. epomophora Pachyptila belcheri Macronectes halli	Surface Surface Surface Surface	New Zealand New Zealand Falkland Islands Crozet Islands	Cloxall and Frince 1990 West and Imber 1986 Imber 1991 Thompson 1989 Ridoux 1994 cited in Croxall and
Grey petrel	Procellaria cinerea	Surface	Crozet Islands	Prince 1996 Ridoux 1994 cited in Croxall and Prince 1996

Table 4 (contd.)				
Species common name	Species scientific name	Feeding mode	Location	References
Fish				
Porbeagle shark	Lanna nasus	Epipelagic	Falkland Islands	Current study
Ray	Bathyraja griseocauda	Benthic	Falkland Islands	Current study
Ray	Bathyraja meridionalis	Benthic	Falkland Islands	Current study
Ray	Bathyraja papilionifera	Benthic	Falkland Islands	Current study
Hoki	Macruronus novaezelandiae	Pelagic	New Zealand,	Clark 1985; current study
			Falkland Islands	
Hake	Micromesistius australis	Pelagic	New Zealand	Clark 1985
Southern common hake	Merluccius hubbsi	Pelagic	Falkland Islands	Current study
Ling	Genypterus blacodes	Demersal	Falkland Islands	Current study
Opah	Lampris immaculatus	Epipelagic	Falkland Islands	Current study
Orange roughy	Hoplostethus atlanticus	Bathypelagic	New Zealand	Rosecchi et al. 1988
Patagonian toothfish	Dissostichus eleginoides	Bathypelagic	Falkland Islands	Current study
Smallscaled cod	Paranotothenia microlepidota	Bathypelagic	New Zealand	Clark 1985
Slender tuna	Allothumus fallai	Epipelagic	South Pacific	Yatsu 1995
Squid				
4	Moroteuthis ingens	Demersal	Falkland Islands	Current study
	Illex argentinus	Pelagic	Falkland Islands	Current study

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Maturity in males does not appear to be related to depth in New Zealand waters (Jackson 1997). This also appears to be the situation on the Patagonian Shelf, although the dramatic decrease in stage 5 males may also represent a movement into deeper slope waters. The deep-water sampling in this study was limited and included only nine trawls deeper than 725 m. More extensive sampling would be needed to find the areas where mature females are migrating.

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This study also suggested that there is a movement of individuals off the Patagonian Shelf during some periods. The apparent lack of individuals in August on the Patagonian Shelf along with the pronounced recruitment of juveniles that occurs in September agree with a possible 1-year life span suggested for the species in New Zealand (Jackson 1997). The possible life history of this species probably involves: (1) a major recruitment onto the shelf in September; (2) growth throughout the year on the Patagonian Shelf; and (3) commencement of a winter migration of maturing females into deep water to spawn, possibly also followed by the mature males. Spawning and death would then occur in winter, which would account for the lack of individuals in August. Furthermore, there also appears to be a second smaller spawning in summer leading to a recruitment onto the shelf in April. However, the movements of this cohort are not clear as individuals from this hatching are apparently not on the shelf during August. Statolith ageing may help to identify more specific aspects of the timing of the life-cycle and migration of this species in the South Atlantic.

This research is the first data set to reveal how common this species is on the Patagonian Shelf. The possible role that Moroteuthis ingens might play in the Patagonian Shelf ecosystem as both predator and prev has not yet been considered and this highlights the need for continued study into the life-cycle of Southern Ocean cephalopods. It is likely that Moroteuthis ingens is an important species throughout much of the Southern Ocean. The data collected from predator stomachs on the Patagonian Shelf allowed us to assess the importance of Moroteuthis ingens as a prey species. In addition to these observations, we undertook a literature review to assess predation on Moroteuthis ingens throughout the Southern Ocean region (Table 4). This revealed that Moroteuthis ingens is preyed upon by a large number of vertebrate predators in many sectors of the Southern Ocean. At least 4 mammal, 16 bird and 12 fish species prey on Moroteuthis ingens. In addition, Moroteuthis ingens is cannibalistic and is preved upon by the pelagic squid Illex argentinus. For some species (such as the king penguin, southern elephant seal and southern opah in some regions) Moroteuthis ingens forms an important part of the diet.

Recent detailed foraging studies of wandering albatrosses (Weimerskirch et al. 1997) further emphasises the importance of this squid in the diet of these sea birds as *Moroteuthis ingens* was demonstrated to be one of the most important prey items for these birds in the Crozet Islands. Cephalopods are now recognised as both significant predators (Rodhouse and Nigmatullin 1996) and prey of many marine vertebrates (e.g., Clarke 1996 Croxall and Prince 1996; Klages 1996; Smale 1996). Further research will help to establish the role of *Moroteuthis ingens* in the South Atlantic and other regions in the Southern Ocean where it occurs.

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