Chapter 3

Illex argentinus

M. Haimovici,[1] N.E. Brunetti,[2] P.G. Rodhouse,[3] J. Csirke[4] and R.H. Leta[5]

[1] *Departmento de Oceanografia, Fundaçao Universidade de Rio Grande, Cx Postal 474, Rio Grande RS 96.200, Brazil*
[2] *lnstituto Nacional de lnvestigación y Desarollo Pesquero, Casilla de Correo 175, Mar del Plata 7600, Argentina*
[3] *British Antarctic Survey, Natural Environment Research Council, High Cross, Madingley Road, Cambridge CB5 9BG, United Kingdom*
[4] *FAO, Viale delle Terme di Caracalla, Rome 00100, Italy*
[5] *lnstituto Nacional de Pesca, Constituyente 1497, Montevideo 11200, Republica Oriental del Uruguay*

Abstract: The Argentinean short-finned squid, *Illex argentinus*, is distributed along the shelf and slope in the western South Atlantic from 22° to 54°S. Since 1977 catches by a local and an international fleet increased by two orders of magnitude from c. 7 000 to > 700 000 t y^{-1}. The species is associated with the Subtropical Convergence of the Brazil and Falkland (Malvinas) Currents. Three or four stocks are identified: the summer-spawning stock (SSS), the south patagonic stock (SPS), the Bonaerensis-northpatagonic stock (BNS) and the southern Brazil stock (SBS), which may be a northern continuation of the BNS. Surveys of the shelf and adjacent oceanic waters from 29° to 54°S have covered most of the year. Mature and spawned specimens, and rhynchoteuthion paralarvae of *I. argentinus*, have been found in summer over the northern Patagonian Shelf and in winter and spring from 29° to 38°S, mainly off the Río de la Plata and along southern Brazil. Evidence suggests that the SPS, which supports the major fishery, makes a spawning migration northward to the confluence of the Brazil and Falkland (Malvinas) Currents, and paralarvae are subsequently carried to the confluence. The life span of *I. argentinus* is *c.* one year. Females grow faster and reach a larger size than males, and there is evidence that within a cohort, specimens hatching in warmer conditions have higher overall growth rates. Mantle length at maturity ranges from 142 to 250 mm for males and from 195 to 330 for females. Squid from the SSS are the smallest at maturity and those from the SPS are the largest. Potential fecundity could be as high as 750 000 in the largest females if spawning is intermittent and all eggs that attain a major axis of >0.05 mm at first maturity undergo complete vitellogenesis and are released. Crustacea are the major prey of *I. argentinus* in the southern part of the species range and fish increase in importance towards the north. It is preyed on by the most abundant demersal fishes of the patagonian Shelf. Off Argentina and Uruguay *Merluccius hubbsi* is a major competitor with *I. argentinus* for *Engraulis anchoita* as well as being predator and prey at different ontogenetic stages. In southern Brazil it is preyed upon by various species of tuna and the serranid *Polyprion americanus*. Future research should focus on the biology of the early ontogenetic stages, on gene flow among stocks and on the impact of the fishery for *I. argentinus* on other commercial species.

1   Introduction

The Argentinean short-finned squid, *Illex argentinus* (Castellanos, 1960), is a neritic-oceanic species distributed along the continental shelf and slope in the western South Atlantic from approximately 22° to 54°S and is most abundant between 35° and 52°S (Castellanos 1964, Leta 1981, Otero *et al.* 1981, Brunetti 1981, 1988, Sato and Hatanaka 1983, Hatanaka 1986, Haimovici and Pérez 1990).

The species was first taken by Argentina and Uruguay as a by-catch of the hake trawl fishery and total annual catches were initially low (less than 5 900 t in 1977) (Brunetti 1990a). Later a large-scale fishery started to develop on the Argentinean and Uruguayan shelf, around the Falkland (Malvinas) Islands and in international waters along the Patagonian slope. Catches of all squid species by trawlers and jiggers of several countries increased from 75 000 t in 1978 to more than 760 000 t in 1987. Since then squid catches have shown some variability with a slight decreasing trend, although catch totals have always been well

above the 500 000 t per year. Most of these catches are *Illex argentinus*, which is by far the most abundant squid species in the southwest Atlantic. Reported catches of *I. argentinus* increased from 73 000 t in 1978 to at least 540 000 t in 1987 and 590 000 t in 1993, although actual figures are probably higher since there is a large proportion of squid catches not identified at the species level (Fig. 3.1).

The ecological importance of the short-finned squid off Argentina was first noted by Angelescu *et al.* (1958) in a study of the biology and trophic relations of the hake. They referred to *I. argentinus* as *Ommastrephes bartrami*, before Castellanos (1960) identified it as a new species. Catchable stock size was estimated to be several hundred thousand t following a bottom trawl survey by the R/V *Walter Herwig* in 1966 (Hempel 1970 cited in Yesaki 1973). Despite its fishery potential the biology of *I. argentinus* received little attention until the late 1970s. Increased demand for squid as food then raised interest in the distribution, abundance and life cycle of the species. Since the late 1970s several international surveys have taken place and extensive data sets have been acquired by research and commercial fishing vessels. This chapter reviews available information on the distribution, life history and population dynamics of the species.

2   Oceanographic conditions

Illex argentinus is associated with the subtropical convergence formed by the Brazil and Falkland (Malvinas) Currents (Fig. 3.2). The Brazil Current flows poleward along the continental margin of South America as part of the western boundary current of the South Atlantic subtropical gyre. South of 36°S, after its confluence with the Falkland (Malvinas) Current, it leaves the edge of the shelf and turns southeast towards
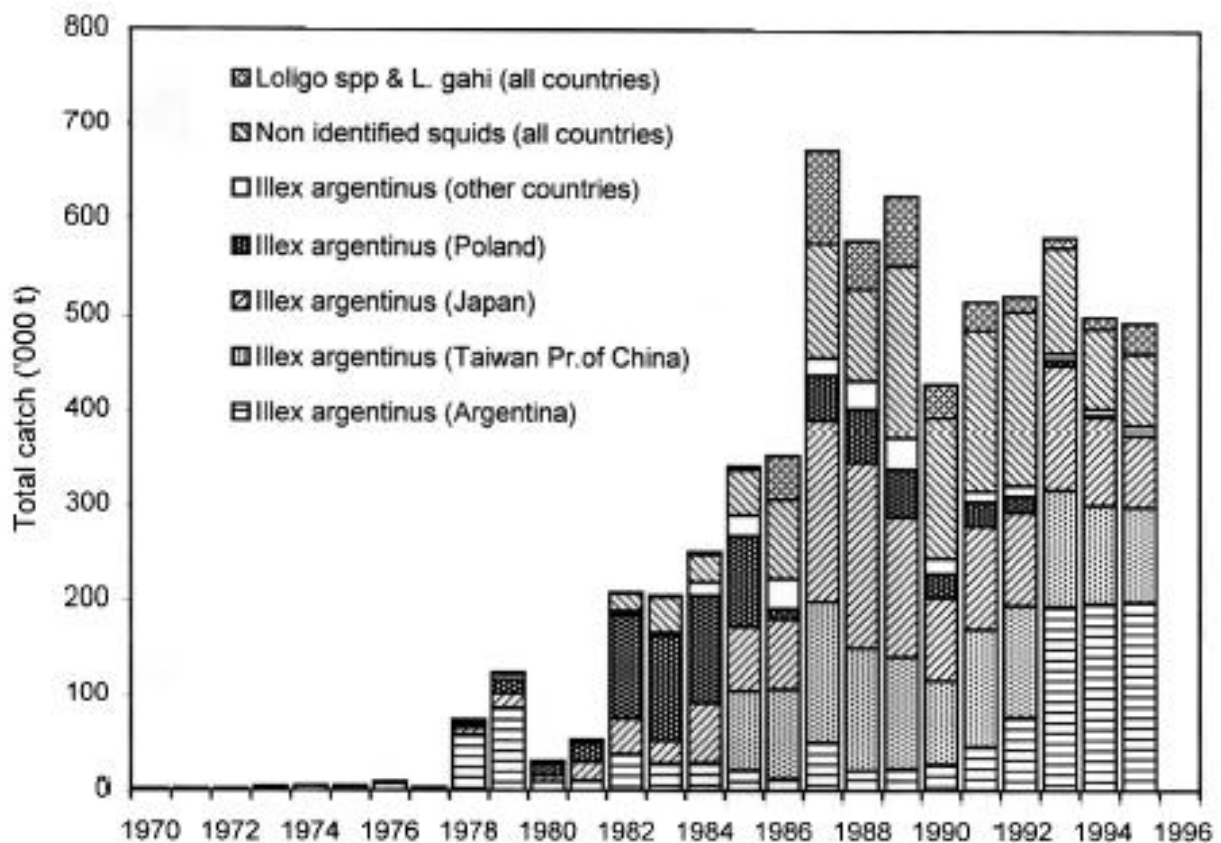
Figure 3.1. Nominal catch of *Illex argentinus* and other selected squid species in the southwest Atlantic, by main fishing country in '000 t per year, 1970-1995 (Csirke 1987, Brunetti 1990a, FAO 1997)
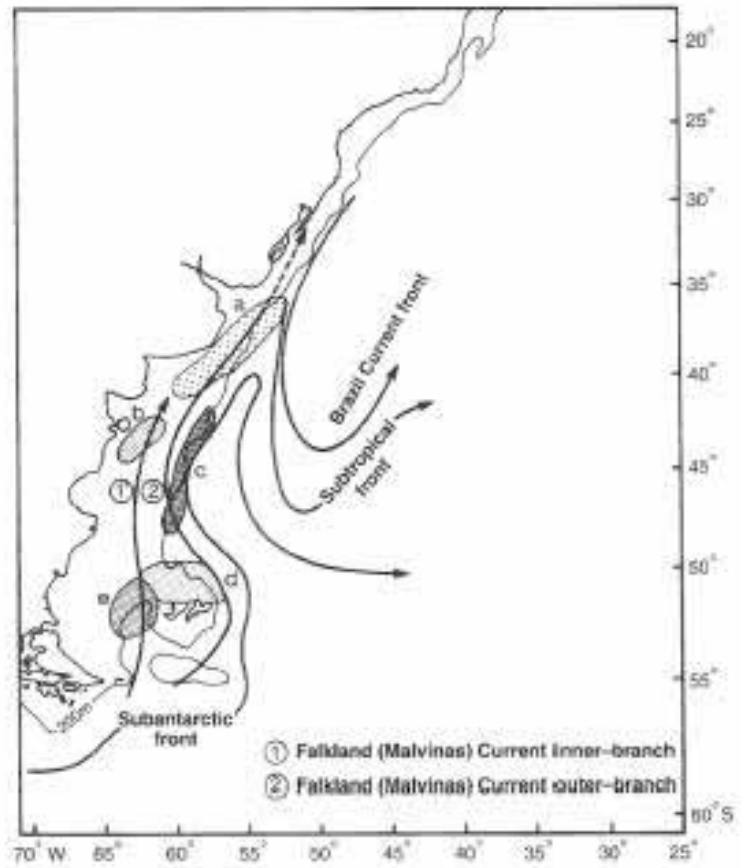
Figure 3.2. Current pattern in the distribu-
-tion range of *Illex argentinus* in the
southwestern Atlantic (modified from
Peterson 1992) and main fishing
grounds of *I. argentinus* (Csirke 1987,
Brunetti 1990a) (Fishing areas are
described in text.)

deeper water (Olson *et al.* 1988, Peterson 1992). The meridional displacement of the warm water is accompanied by the intermittent formation of meanders and anticyclonic warm-core eddies (Legeckis and Gordon 1982) within longitude 50°-55°W and latitude 38°-46°S. These warm-core eddies may be quasi-stationary for several months and reach latitudes as far south as 49°S. Off southern Brazil and Uruguay the temperature and salinity of the Brazil Current varies between 18° and 24°C and 34.5 and 36.0 ‰ (Thomsen 1962). The front of the Río de la Plata estuary is characterized by relatively high temperatures and low salinity and spreads over the more saline Brazil and Falkland (Malvinas) Current waters between 34° and 37°S as shown in Leta (1992). The cold Falkland (Malvinas) Current, which originates as a branch of the Antarctic Circumpolar Current, flows northward off Argentina in two branches. An eastern branch, *c.* 100 km wide, flows over the continental slope. A less saline western branch, the Patagonian Current, flows over the shelf at depths of 100-200 m northward to nearly 38°S (Brandhorst and Castello 1971, Fedulov *et al.* 1990). In winter, water originating from the Patagonian Current reaches the shelf of southern Brazil as far north as 30°S and is known locally as the inner branch of the Falkland (Malvinas) Current (Castello *et al.* 1991) (Fig. 3.2).

The mixing of the cold Falkland (Malvinas) Current with the Brazil Current, the influence of these currents on coastal waters and the presence of wann-core eddies generate areas of high plankton production in different areas at different times throughout the range of *I. argentinus*. Off southern Brazil in winter, areas of high productivity have been found on the shelf associated with the northward movement of nutrient-rich coastal waters originating from the runoff of the Río de la Plata and from the inner branch of the Falkland (Malvinas) Current (Hubold 1980a, Castello *et al.* 1991, Ciotti *et al.* 1995). Partial upwelling of cold waters along the continental slope and shelf from Conceição (31°45'S) to Santa Marta Grande (28°30'S) increases the availability of nutrients in this region (Hubold 1980a, 1980b, Lima *et al.* 1996). In winter and spring, high zooplankton concentrations have been found in the frontal zone between the Brazil and Falkland (Malvinas) Currents offshore and these are also associated with upwelling of cold water (Hubold 1980a).

The boundary between the waters of the shelf and the Falkland (Malvinas) Current is manifested as a shelfbreak front where high phytoplankton biomass occurs throughout spring and summer (Podestá 1990). A second bloom occurs on the shelf in the fall and phytoplankton biomass remains high into late April along the shelf break. This may in turn elevate zooplankton concentrations in the subsequent winter months (Hubold 1980b, Podestá 1990). Productivity is also enhanced by cold waters flowing over the shelf, particularly along submarine canyons. Stronger upwelling occurs from 37° to 42°S, to the south of 46°S and around the Falkland (Malvinas) Islands (Angelescu and Prenski 1987).

On the north Patagonian Shelf in summer, tidal fronts between stratified waters offshore and well-mixed waters inshore have been described (Glorioso 1987) and these are associated with high summer production (Angelescu and Prenski 1987).

3   The fishery

Landing statistics for *I. argentinus* are given by Csirke (1987), Brunetti (1990a) and the FAO Fishery Statistics Yearbooks (FAO 1997). Official catch statistics from some main fishing countries such as Japan, Korea, the Russian Federation, Spain and the former Soviet Union provide information on squid catches in Area 41 only by major taxonomic groupings, which may include *I. argentinus* as well as *Loligo gahi*, *Martialia hyadesi* and other minor species. Therefore, there is some degree of uncertainty regarding the final figures of total catch by species, although a large proportion of the non-identified squids is likely to be *I. argentinus* (Figure 3.1, see also Table 3.7).

Until 1977 *I. argentinus* was only captured by Argentina and Uruguay as a by-catch in their hake fishery, with total annual catches below the 8 300 t per year. Catches showed a sharp increase, reaching 73 000 and 122 000 t in 1978 and 1979 respectively, mainly due to the full-scale operation of Argentinean trawlers transferred from the traditional hake fishery to squid. Japanese and Polish trawlers also contributed to the increase in squid catches in the area (Sato and Hatanaka 1983). Catches decreased in 1980 and 1981 but increased again reaching 300 000 t in 1985. In the following years catches grew further as total squid catches in the FAO fishing area 41 reached a maximum of 760 000 t, mostly of *I. argentinus*, in 1987 and 1989. It is estimated that catches of this species had reached total catches well over 600 000 t in 1987, 1988, 1989, 1991, 1992 and 1993.

Illex argentinus has been fished in several regions within its distribution range, as shown in Fig. 3.2:
- a)   along the shelf and shelf break of common Argentinean/Uruguayan waters from 35° to 40°S, from March to August, by trawlers of both countries, though mainly as a by-catch of the hake *Merluccius hubbsi* fishery. This fishery targets pre-reproductive concentrations of winter and spring spawners;
- b)   along the north Patagonian Shelf between 42° and 44°S to depths of around 100 m, from December to February, by the Argentinean trawl fleet targeting mature and spawning specimens of the coastal summer-spawning group;
- c)   along the shelf break from 42° to 48°S, from December to September but mostly between February and July, by trawlers and jiggers of several countries including Japan, Poland, the former Soviet Union, the former East Germany (since 1978/79) and more recently by Cuba, Bulgaria, Korea and Spain. This fishery targets pre-reproductive concentrations of the south-patagonic group of *I. argentinus*;
- d)   around the Falkland (Malvinas) Islands from February to July but mostly between March and June; and
- e)   in recent years some fishing of subadults of the same group has taken place on the southern Argentinean shelf before they move offshore.

In 1984 and 1985, 10-15 percent of the total catch was taken by Argentinean and Uruguayan trawlers on the shelf from northern Patagonia to the Río de la Plata front, 45-50 percent offshore to the north of 48°S, and 40-45 percent around the Falkland (Malvinas) Islands south of 48°S. Annual fluctuations in the abundance of the southern group have been observed, and variability is greater in the Falkland (Malvinas) Islands region than elsewhere (Csirke 1987). This may be because the region lies at the southern extremity of the species' range, causing the squid here to be more subject to environmental variability.

4   Distribution

Illex argentinus is found off Argentina at bottom temperatures of 2.1-13.5°C, but mainly at 4-12°C (Brunetti 1988). Off southern Brazil juveniles occurred from 12 to 17°C and maturing and spawning specimens from 4 to 12°C (Haimovici and Pérez 1990). Paralarvae are rarely found in surface water temperatures under 12°C.

As in other ommastrephid squids, *I. argentinus* in the southwest Atlantic is divided into different groups or stocks. Each has its own reproductive season and adult size is adapted to the annual production cycles, which differ among regions. Based on information about distribution of early life stages, juveniles and adults, Brunetti (1988) distinguished three main spawning stocks in the southern range of the distribution of *I. argentinus*. She named them the summer-spawning stock (SSS), the south patagonic stock (SPS) and the Bonaerensis-northpatagonic stock (BNS). Less is known about the northern range of the distribution of the species, but clear evidence of spawning has been found in winter and spring as shown in Haimovici and Pérez (1990) and Haimovici *et al.* (1995). It is not clear whether this is an extension of the BNS or a separate fourth stock that could be called the southern Brazil stock (SBS).

4.1 Distribution of early life stages

Since the late 1970s, several surveys for paralarvae and juveniles of *I. argentinus* have been undertaken along the shelf and adjacent oceanic waters off Brazil, Uruguay and Argentina. Table 3.1 lists the paralarval surveys and Fig. 3.3 shows the regions surveyed in the austral summer, autumn, winter and spring, indicating where paralarvae of *I. argentinus* have been found.

On the continental shelf off southern Brazil, paralarvae of *I. argentinus* have been found in the plankton from late autumn to late spring but were absent from summer samples. They occurred in approximately 30 percent of 482 hauls by bongo nets between July and November (Table 3.1). They were present in association with the western boundary of the Brazil Current and subsurface upwelling of subtropical waters on the shelf edge. They rarely occurred in coastal and subantarctic waters at temperatures under 12°C. They were absent in summer samples. An inverse relation between paralarval size and water depth over which they were caught suggests that hatching takes place along the slope over deeper water (Haimovici *et al.* 1995, Vidal and Haimovici *unpubl. data*). Juveniles of 30-100 mm ML (mantle length) have been caught with bottom trawls year-round at 80-200 m depth on the outer shelf (Haimovici and Andriguetto 1986, Haimovici and Pérez 1990).

Leta (1987, 1992) reports on surveys by the R/V *Lamatra* from 1979-1982 on the Argentinean-Uruguayan Common Fishing Zone (AUCFZ). In summer he found low numbers of paralarvae on the mid-shelf (37°08'-38°45'S, 63-69 m depth and 19.1-20°C). In autumn 1979 some larvae occurred on the outer shelf from 37° to 39°S. In three consecutive winters paralarvae were abundant and occurred to the north of 37°S at temperatures from 9.9 to 19.1°C; higher catches were taken in the winter of 1982 in the western boundary of the Brazil Current and subtropical front waters at 12.1-16.9°C with salinities of 34.8-35.2 ‰. In November-December 1989, the German vessel Meteor surveyed the oceanic front of the Río de la Plata

(35°56'-36°35'S) from its mouth to the continental slope using a BIOMOC net (1 m^2, 300 µm mesh). Low densities of paralarvae were found in the upper 50 m layer (Leta 1992).
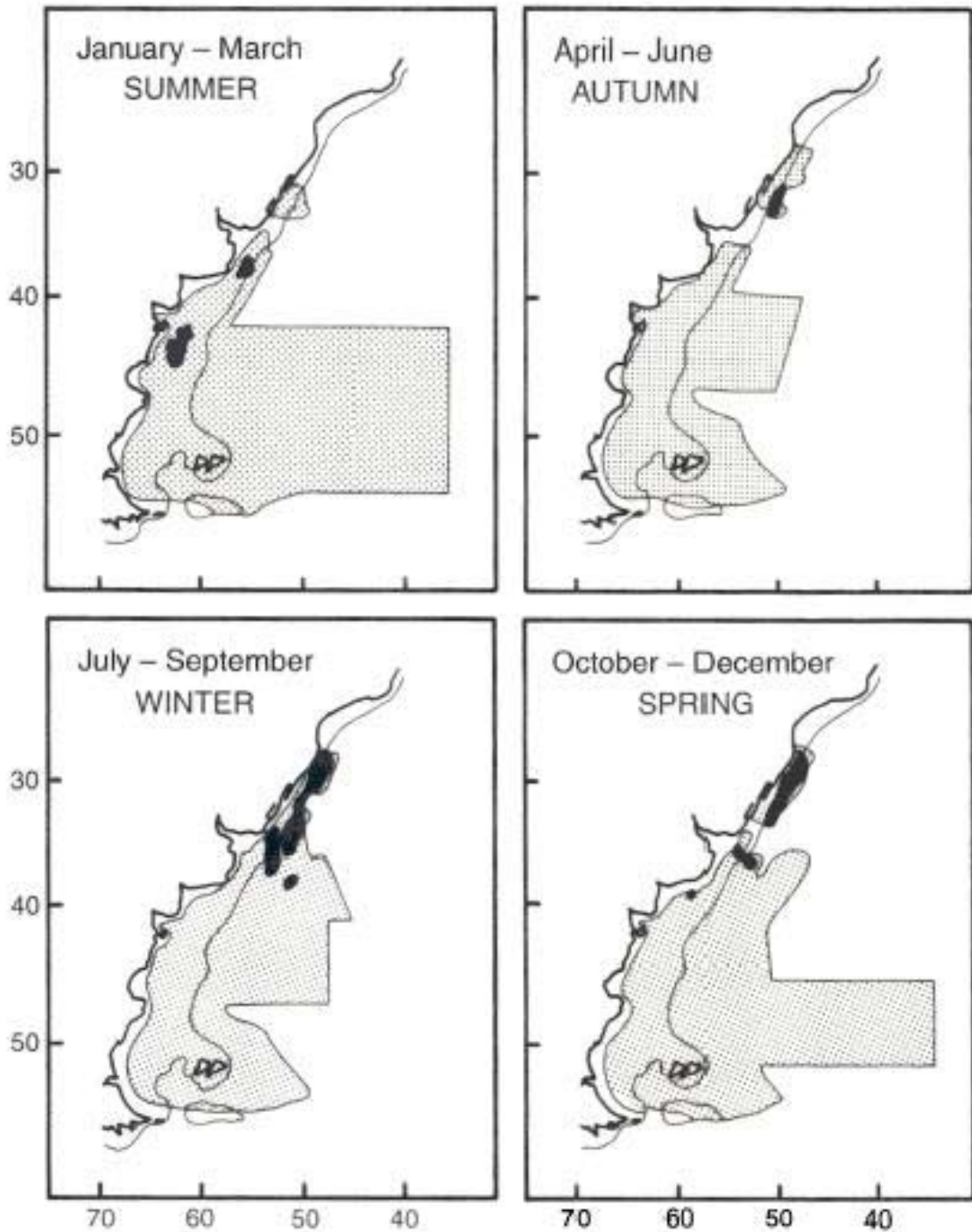
Figure 3.3. Grey = area covered by paralarvae surveys in different seasons, black = areas where paralarvae of *Illex argentinus* were found; summarized from Leta 1987, 1992, Brunetti 1990b, Brunetti and Ivanovic 1992, Rodhouse *et al.* 1992, Parfeniuk *et al.* 1992, Haimovici *et al.* 1995, Vidal and Haimovici *unpubl. data*

Table 3.1. Summary of *Illex argentinus* paralarvae surveys

References to research vessels, gear and haul duration	Survey dates	Latitude range (°S)	Number of stations		Number of paralarvae				
					per haul		per 100 m³		
			total	with paralarvae	min.	max.	total	min.	max
Brunetti (1990)[a]	Monthly 1978/79	35-55	698	15	1	91	219	-	-
Leta (1992)[b]	Dec. 1979	34-39	24	4	-	-	-	-	-
Leta (1992)[b]	Dec.-Mar. 1980	34-39	27	4	-	-	-	1	3
Leta (1992)[b]	Aug.-Sept. 1980	34-39	34	6	-	-	-	0.4	3
Leta (1992)[b]	Jul.-Aug. 1981	34-39	79	6	-	-	-	0.4	34
Leta (1992)[b]	Aug.-Sept. 1992	34-39	71	3	-	-	-	3	14
Leta (1992)[c]	Nov.-Dec. 1989	36-36	25	-	-	-	-	0.2	0.8
Brunetti and Ivanovic (1992)[d]	Aug.-Sept. 1989	35-45	59	5	-	-	-	-	-
Parfeniuk et al. (1992)[e]	Apr.-May 1989	40-47	40	0	-	-	-	-	-
Parfeniuk et al. (1992)[f]	Aug.-Oct. 1988	36-47	164	2	-	-	-	-	-
Parfeniuk et al. (1992) and Brunetti and Rossi (1990)[g]	Nov. 1989- Feb. 1990	42-	172	0	-	-	-	-	-
Haimovici et al. (1995)[h]	April 1980	29-	33	0	0	0	0	0	0
Haimovici et al. (1995)[h]	August 1980	29- 34	88	55	1	47	382	1.25	14.9
Haimovici et al. (1995)[h]	Nov. 1980	33- 34	92	14	1	5	21	0.08	5.06
Haimovici et al. (1995)[h]	Nov. 1981	32- 34	59	6	1	2	9	0.07	0.69
Haimovici et al. (1995)[h]	Nov. 1982	29- 34	100	30	1	11	73	0.1	1.89
Vidal and Haimovici[j]	Oct. 1987	31- 34	52	20	1	232	329	0.13	41
Vidal and Haimovici[j]	Feb. 1990	31- 34	49	0	0	0	0	-	-
Vidal and Haimovici[j]	Jun.-Jul. 1991	31- 34	51	17	1	20	78	1.2	80
Vidal and Haimovici[j]	Sept. 1988	31- 34	51	10	1	5	21	0.08	5.17
Vidal and Haimovici[j]	Nov. 1989	28- 29	40	16	-	-	-	-	-
Rodhouse et al. (1992)[k]	Oct. 1990	35-52	44	0	0	0	0	-	-
Rodhouse et al. (1992)[k]	Oct. 1991	35-52	35	1	0	1	1	-	-

[a] R/V *Walter Herwig*, 330 µm mesh bongo net oblique 0-100 m, over shelf and slope

[b] R/V *Lamatra*, 300-500 µm mesh bongo, oblique 11-215 m on shelf waters

[c] R/V *Meteor*, 36°S, multiple opening/closing net (BIOMOC) mesh 300 µm, shelf

[d] R/V *Kaiyo Maru*, 330 µm mesh bongo, oblique, shelf to oceanic waters

[e] R/V *Orcher*, bongo net, 5' horizontal hauls at 10, 20, 30, 40 m, oceanic

[f] R/V *Evrika*, bongo 5' horizontal hauls at 1, 5, 10, 20, 30, 50 m, oceanic

[g] R/V *Evrika*, 330 µm bongo oblique hauls, 0-100 m, oceanic

[h] R/V *Atlantica Sul*, 330 µm mesh bongo, 5' oblique hauls, 0-200 m, shelf

[i] R/V *Atlantica Sul*, 330 µm bongo, 5' oblique hauls 0-200 m, shelf and slope (*unpubl. data*)

[j] R/V *Atlantica* Sul, 1 mm mesh, 8 m2 rectangular midwater trawl (RMT), shelf (*unpubl. data*)

[k] R/V *Falklands Protector*, 335 µm bongo, 30' surface hauls, shelf, slope and oceanic

Brunetti (1990b) analysed 687 samples of plankton collected with a bongo net by the R/V *Shinkai Maru* and R/V *Walter Herwig* throughout an annual cycle between latitudes 36° and 55°S out to the 1 000 m isobath. Only 15 samples included rhynchoteuthion paralarvae, and except for one sample from November at 39°S, all were caught from January to March in the north Patagonian Shelf (43°-46°S) between 80 and 116 m, where water temperature down to 50 m depth was > 14°C.

The former Soviet Union R/V *Orcher* surveyed the oceanic region between 40°30' and 47°S and as far as 51S during April and May 1987. No paralarvae were found but juveniles were caught at most stations (Parfeniuk et al. 1992).

Figure 3.4. (opposite) Distribution, spawning and hatchery grounds and migratory patterns (arrows) of the south patagonic (SPS), Bonaerensis-northpatagonic (BNS) and summer spawning (SSS) stocks of *Illex argentinus*; paralarval abundances are given in individuals per trawl; adults are given in individuals per square nautical mile. (modified from Brunetti 1988)

The former Soviet Union R/V *Evrika* surveyed the oceanic region between 36°30' and 47°30'S and as far as 35°W during August-October 1988. Only five paralarvae were caught at two stations at the southern edge of the Brazil Current (36°30'S, 49°10W and 37°30'S, 47°44'W). Juveniles of 12-46 mm ML and up to 2-3 months old, according to statolith readings (Anon 1989), were caught at 27 stations, mostly between 36°30' and 47°30'S, in the mixed zone between subantarctic and subtropical waters surrounding the warm meanders and eddies originating from the Brazil Current (Brunetti and Rossi 1990, Parfeniuk *et al.* 1992).

The R/V *Evrika* surveyed the oceanic region between 41° and 54°S and as far as 35°W from November 1989 to February 1990. No paralarvae were found, but juveniles of 40-160 mm ML were frequent and occasionally abundant (Parfeniuk *et al.* 1992).

Analysis of the former Soviet Union surveys led Parfeniuk *et al.* (1992) to conclude that eggs and hatchlings of *I. argentinus* are transported towards oceanic waters by both the Falkland (Malvinas) Current (summer-spawning) and Brazil Current (winter-spawning). Juveniles develop during the first 2-3 months of the life cycle, feeding in frontal subantarctic water masses, and then move from offshore warmer waters to colder shelf waters.

A cruise by the Japanese R/V *Kaiyo Maru* to study the winter-spring hatchery areas surveyed the shelf, slope and open sea between 35° and 50°S and west of 50°W. A few paralarvae were found in the tropical waters of the Brazil Current, close to the Brazil-Falkland (Malvinas) confluence, and in the frontal zone between the Brazil Current and shelf waters, and always at temperatures over 14°C. Large numbers of juveniles (10-110 mm ML) were found in subantarctic waters (6-10°C) over the shelf. These were probably migrating southward from the hatchery grounds, and thus following the zooplankton concentrations on which they were feeding (Brunetti and Ivanovic 1992).

Rodhouse *et al.* (1992) found a single paralarva of *I. argentinus* at 35°S in two spring surveys off the 200-mile limit along the Patagonian Shelf and around the Falkland (Malvinas) Islands. These surveys were in October/November of 1990 and 1991, several months after the spawning peak of the SPS, but no juveniles were caught at any of these offshore stations.

Taking all the surveys that have been reported, a total of over 2 000 bongo net hauls have sampled a large geographical area and all seasons of the year (Fig. 3.3). From 570 hauls off Brazil, 27 percent caught *I. argentinus* paralarvae, almost all in winter and spring. Elsewhere, off Uruguay and Argentina, only 3 percent caught *I. argentinus* paralarvae, mostly from summer samples on the north Patagonian Shelf and from winter and spring in the Río de la Plata front. Paralarvae were usually found at water temperatures over 12°C and up to 20°C. Highest densities were caught along the slope off the Río de la Plata (36°S) in winter and off Santa Marta Cape (29°S) in spring.

4.2 Seasonal changes in the distribution of juveniles and adults

In the northern part of the range of *I. argentinus*, off southern Brazil, juveniles of 60-160 mm ML have been caught year-round in bottom trawls along the outer shelf and upper slope from 100 to 350 m depth. Adults are more frequent in deeper water. Small mature squid are found in summer and autumn, large
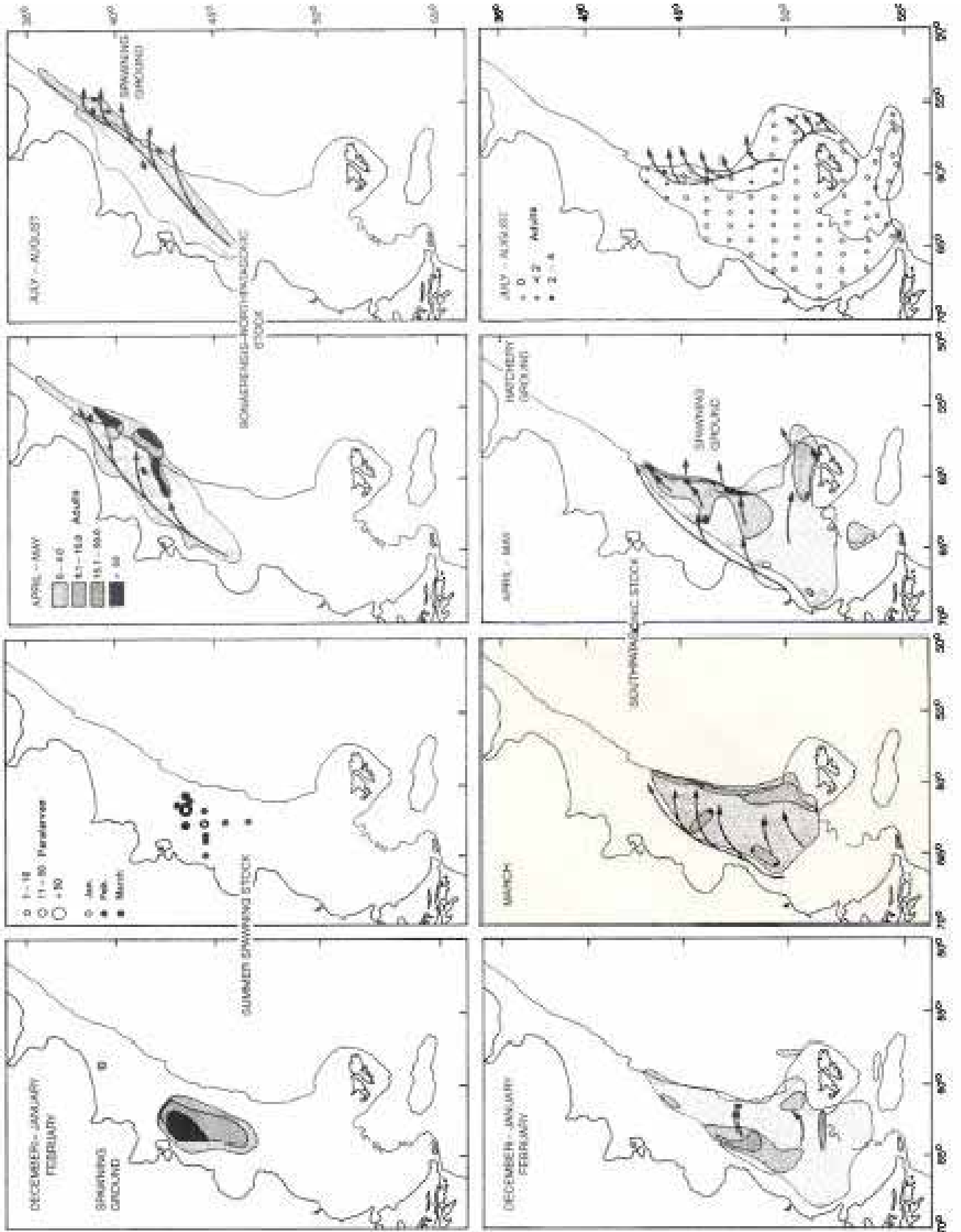
mature squid are found in winter, and in spring both mature and spawned specimens are frequent (Santos and Haimovici 1996). Adults have been more abundant in spring surveys (Haimovici and Pérez 1990).

In the southern part of the species range, during autumn, large squid concentrations are found along the outer shelf and continental slope. South of 44°S most of these concentrations are found from March to May and they correspond to the SPS. Squid aggregations north of 44°S to the Río de la Plata front, during May to July, are recognized as being part of the BNS. In the case of both stocks the squid are adult (180-370 mm ML) and are either starting to mature or are already mature (stages IV and V). This is the phase immediately prior to migration off the shelf (Fig. 3.4). Parfeniuk *et al.* (1992) found juveniles off the Patagonian Shelf in oceanic waters up to longitude 51°W.

In winter, to the south of the Río de la Plata front, both the outer shelf and the continental slope are dominated by cold water flowing from the south towards the northeast. At this time the juvenile squid start to migrate from offshore hatchery grounds to the intermediate Bonaerensis-northpatagonic shelf, where both feeding and breeding grounds are located in winter and spring. A cohort of juveniles (10-60 mm ML) has been found inhabiting oceanic areas off Argentina in August-September (Brunetti and Rossi 1990, Parfeniuk *et al.* 1992). This cohort was carried from the oceanic region towards the hatchery ground by the Brazil Current north of the Brazil-Falklands (Malvinas) confluence (Brunetti and Rossi 1990). During winter, no prereproductive aggregations are found south of 44°S, indicating that the individuals of the SPS have finished their spawning migration. North of 43°S some aggregations remain; these belong to the BNS, which complete their spawning migration by late August or September. Members of the SSS, 70-140 mm ML in size and thus 3-4 months old, are also caught in winter north of 44°S on the intermediate shelf (Brunetti 1981, 1988, Hatanaka 1986, Brunetti and Pérez Comas 1989b).

In spring, thermal stratification starts in the Bonaerensis-northpatagonic area (35°-46°S). The influence of cold waters decreases. Greater numbers of squid are found at depths of 50-100 m than during winter, and these include juveniles, preadults and adults (Brunetti 1981, Hatanaka 1986). The juveniles (10-110 mm ML), from the SPS, migrate southward in spring following the zooplankton concentrations on which they feed (Hatanaka 1988, Brunetti 1988, Brunetti and Ivanovic 1992). They are pelagic and usually complete their migration into the feeding area and their recruitment to the bottom by the end of spring. The preadults (150-220 mm ML) are summer spawners starting sexual maturation. The adults are large (230-350 mm ML) and are either reproductive or spent spring spawners (October-November). Juveniles up to 160 mm have been found in oceanic waters from 41° to 48°S (Parfeniuk *et al.* 1992).

During summer, *I. argentinus* is caught at depths of 50-200 m (mainly at 80-150 m). Two areas of high density have been found. In the first, in the Bonaerensis-northpatagonic area, there are small-sized adults (150-250 mm ML) of the SSS (see spawning stocks). The second high-density area in summer occurs between 46 ° to 49 ° S, on the southern shelf area where squids of the SPS feed during January and February. By then, the size ranges from 170 to 290 mm ML. Most females are immature (stage II =49 percent and III=24 percent), but most males are starting their gonadal maturation (stage III=38 percent and IV=46 percent). Some of them begin the reproductive migration towards the outer shelf (Brunetti and Pérez Comas 1989b, Rodhouse *et al.* 1995, Uozumi and Shiba 1993). In summer, strong thermal stratification of the water within the Bonaerensis-northpatagonic area is established. The rhynchoteuthion paralarvae of the SSS, found in the upper warm layer, are caught during February and March (Brunetti 1990b). South of 47°S the water is colder and there is slight thermal stratification, which affects only a narrow zone between the coast and the 100 m isobath. In January, juveniles (30-140 mm ML) have been caught in oceanic waters from 42° to 44°S (Parfeniuk *et al.* 1992).

4.3 Spawning stocks

Along the continental slope of southern Brazil between 27° and 34°S pre-reproductive and reproductive concentrations, including mature, fertilized and spawned adults, have been found from early winter to midspring (July-October). These spawners of the SBS attain large sizes: 200-270 mm ML (males) and 240-356 mm ML (females) (Haimovici and Pérez 1990, Santos and Haimovici 1996). Rhynchoteuthion paralarvae have been found only from late autumn to late spring, but juveniles, maturing and mature specimens have been found year round (Haimovici and Andriguetto 1986, Haimovici and Pérez 1990, Haimovici *et al.* 1995). Adult *I. argentinus* are frequent in the diet of several abundant predators of the slope in the winter and spring (Santos 1992). These squid spawn on the slope in the Brazil Current to the north of the subtropical front. Partial upwelling of subtropical water over the shelf from Rio Grande (32 ° S) to the north (Castello and Moller 1977, Lima *et al.* 1996) contributes to the retention of para larvae in the region. The same phenomenon has been observed by Weiss *et al.* (1988) for *Maurolicus muelleri*, a small mesopelagic fish that spawns over the shelf break of southern Brazil but whose larvae are found over the shelf but not in oceanic waters or to the south. Paralarvae of *I. argentinus* found in the surface waters of the Brazil Current are probably transported southward; they may contribute to recruitment to other stocks and at least some of them seem to return to spawn off southern Brazil (Santos and Haimovici 1996).

Figure 3.4, modified from Brunetti (1988) and including information from Otero *et al.* (1981), Brunetti (1981, 1988), Hatanaka *et al.* (1985) and Hatanaka (1988), summarizes the movements of stocks to the south of 35°S. Small-sized adults (150-250 mm ML) from the SSS in pre-spawning condition (stages IV and V) and spawning concentrations (stages (VI-VIII) are found on the intermediate and outer shelf of the Bonaerensis-northpatagonic area between 42° and 46°S from December to February (Brunetti 1981, 1988, Hatanaka 1986, Koronkiewicz 1986, Nigmatullin 1989). Spent individuals appear by February and it has been estimated that this group completes spawning within a single short period of about 30-60 days.

Pre-reproductive concentrations of the SPS are found along the outer shelf and slope south of 44°S (Fig. 3.4). These concentrations are mostly found between March and May with some inter-annual variation (Otero *et al.* 1981, Brunetti 1988, Hatanaka *et al.* 1985, Koronkiewicz 1986, Brunetti and Pérez Comas 1989b, Nigmatullin 1989, Rodhouse *et al.* 1995, Uozumi and Shiba 1993). These squids are adults (ML 180-370 cm) and are either starting to mature or are already mature (stages III, IV and V). In July-August the SPS has finished the spawning migration and there are no catches on the outer shelf and slope. There is little information about the location of the spawning ground of this stock, but it has been suggested that it may spawn in the Falkland (Malvinas) Current (Koronkiewicz 1986, Brunetti and Ivanovic 1992, Rodhouse *et al.* 1992), with the eggs and paralarvae being subsequently carried northward toward the front with the Brazil Current. However, there are no data to substantiate this suggestion and it has also been suggested that spawning may occur in the warm waters of the Brazil Current (Hatanaka *et al.* 1985), where rhynchoteuthions have been found.

Pre-reproductive concentrations of the BNS occur on the outer shelf, 35°-43°S, from April to September (Brunetti 1988). After completing maturation, they migrate towards oceanic waters, where mating and spawning take place. A small number of both fertilized and spent individuals are therefore found on the shelf break between 36° and 37°30'S (Schuldt 1979, Brunetti and Pérez Comas 1989a). The adults of this stock are 200-350 mm ML and the spawning grounds may be close to the western side of the Brazil-Falkland (Malvinas) Current confluence.

Juveniles of both the SPS and the BNS migrate eastward towards the intermediate shelf, where both breeding and feeding groups are located in winter and spring. Later, there is a migration of preadult and adult squid in summer and autumn towards the regions of pre-reproductive concentrations and the, as yet, unlocated spawning grounds. The movement of these two stocks are not synchronized and there is a difference of about two months between them.

Data on tissue energy content and estimated rates of energy consumption during the migration of the winter-spawning SPS from the feeding grounds to the spawning grounds have been used to calculate the endurance of squid if they do not feed during migration (Clarke *et al.* 1994). Maximum endurance was estimated at 14 and 21 days respectively for males and females. Arkhipkin (1993) estimated that successive waves of squid migrate at 23-29 km d^{-1} from the feeding to the spawning grounds, so for a migration of up to 2 000 km, the energy reserves in the squid tissues would not be sufficient to fuel the migration. The squid must therefore feed during the migration. They do not grow during this time (Arkhipkin 1993) so all consumption is apparently used to fuel the high locomotory costs of swimming.

Illex argentinus modifies its vertical distribution pattern with ontogeny. The juveniles are epiplanktonic. They enter the neritic zone off Argentina together with other juvenile forms of the subantarctic macrozooplankton, and are distributed in the upper 25-40 m of the water column. During spring they range from 20 to 160 mm ML and are found on the intermediate shelf. Then they start their recruitment to the bottom, which is complete when the squid are over 180 mm ML. By this time they perform diel migrations, scattering for feeding during the night and moving close to the bottom during the day (Brunetti 1988).

The spawning grounds of the SPS and the BNS stocks have still not been precisely determined. Plankton surveys have shown that the distribution of the early life stage of *I. argentinus* is restricted to temperatures over 12-14°C, i.e. to the northern part of the subtropical convergence and warm-water eddies that move southward. The exception to this is the SSS, the paralarvae of which occur in heated shelf waters in summer. Several authors suggest that spawning might take place somewhere along the slope in the Falkland (Malvinas) Current, from whence the egg masses could be transported towards the Brazil Current and return in it (Brunetti and Ivanovic 1992, Rodhouse *et al.* 1992). Hatanaka *et al.* (1985) suggested that spawning takes place in the Brazil Current waters, and this has been confirmed by Haimovici *et al.* (1995) and Santos and Haimovici (1996). Parfeniuk *et al.* (1992) proposed that paralarvae might develop in the quasi-stationary warm oceanic eddies and juveniles move across the front into the Falkland (Malvinas) Current and then disperse over the shelf. At present, clear evidence of spawning is available only for the northpatagonic summer-spawning and the southern Brazil winter- and spring-spawning groups.

Besides the four major stocks, other minor spawning events occur. Small numbers of mature fertilized females have been found in late summer and autumn off southern Brazil (Haimovici and Pérez 1990) and some paralarvae have been found at different times of the year on the intermediate shelf between 37° and 40°30'S (Brunetti 1990a, Leta 1987, 1992). It is also worth noting that a few immature *I. argentinus* up to 186 mm ML were caught by jiggers carrying out exploratory fishing for *Martialia hyadesi* at the Antarctic Polar Frontal Zone (52°46'S, 47°01'W) in February 1990 (Rodhouse 1991).

5   Growth and life span

Life span and growth of cohorts of *I. argentinus* have been studied by Hatanaka (1986), Koronkiewicz (1986) and Brunetti (1981, 1988) from modal or mean length progression, and by Rodhouse and Hatfield (1990a), Arkhipkin (1990), Arkhipkin and Scherbich (1991) and Uozomi and Shiba (1993) by ageing individuals from counts of daily increments on ground statolith sections (see Chapter 8).

Using ML modal progression analysis, Hatanaka (1986) concluded that the species has a one-year life span, and Koronkiewicz (1986) suggested a 12-18 month life cycle. Daily increment counts subsequently showed that the life span of *I. argentinus* is approximately one year, which is similar to other coastal and shelf ommastrephids. Rodhouse and Hatfield (1990a) counted up to slightly over 360 increments (days) on statoliths and Arkhipkin (1990) up to 380. Both studies showed considerable variability in age at onset of sexual maturation among squids from the same cohort and between different seasonal cohorts. Arkhipkin (1990) found that in summer, females of 260-300 d were mature (two specimens of 375 and 380 d had

spawned). In the winter, mature females were aged 300-310 d and spawned females were 330-340 d. Uozurni and Shiba (1993) validated daily growth-ring formation in the statolith by demonstrating a slope of *c.* 1 in the regression between dates of catch and number of growth rings.

Growth rates of immature males and females are similar, but after the onset of sexual maturation, male growth rate is comparatively slower than that of females. Arkhipkin (1990) estimated that after 200 days, males grew one third more slowly than females. Rodhouse and Hatfield (1990b) estimated the instantaneous relative growth rate (G_i, weight) to be 1.5 percent for females and 1.2 percent for males aged between 150 and 350 days.

If the life span is one year for all cohorts, maturity and maximum size provide indices of growth for the different regions and seasons. Brunetti (1981, 1988) and Hatanaka (1986) observed contrasting growth rates in winter slope spawners and summer shelf spawners, the winter spawners on the slope attaining a larger size than the summer spawners on the shelf.

Statolith ageing methods have allowed back-calculation of individual birth dates and estimates of the growth of specimens born in different months. Rodhouse and Hatfield (1990a) sampled only winter spawners, hatched mainly between May and August, and found fast growth rates in males and females that hatched later in the season; the same observation was made by Uozumi and Shiba (1993). Arkhipkin (1990) observed faster growth for squid hatched in late winter (August) compared to those hatched in early winter (June). Interannual differences in growth were also recorded. Furthermore, Arkhipkin and Scherbich (1991) studied the statoliths of squid hatched in all four seasons and caught in winter and spring in the outer shelf, slope and oceanic adjacent waters off Argentina, and also found intra- and inter-group variations in growth rate (*see Chapter 8*).

Variability in growth rates among cohorts of the winter spawners, which sustain most of the *I. argentinus* fishery, may be explained by variability in the length of the period in which the juveniles grow in less productive waters of low temperatures. Environmental conditions during the feeding period of juveniles, and at the onset of maturity in adults, are considered to be of prime importance in determining final size of *I. argentinus* (Arkhipkin and Scherbich 1991, *see Chapter 8*).

The von Bertalanffy growth model has been fitted to ML frequency data by Hatanaka (1986) for the dominant winter offshore spawning cohort of the Argentinean shelf (ML males = 26.48 cm [1-exp(-0.28[t-0.44])] and ML females = 34.13 cm [1-exp(-0. 18[t-0.27])]) where t is time in months. Brunetti and Ivanovic (1990) obtained values for k ranging from 0.18 to 0.23 using monthly ML distributions of commercial landings of the Argentinean trawl fishery (36°-44°S) in 1981, 1983 and 1986. Linear models were fitted by Koronkiewicz (1986) to trawl and jig catches by the Polish fleet from the Patagonian and the Falkland (Malvinas) Shelves between 46° and 51°S, and a mean growth rate of 0.8 mm d^{-1} for females and 0.6 mm d^{-1} for males was calculated for the winter cohort caught in the fishing season of December 1983 to June 1984. Rodhouse and Hatfield (1990a), Arkhipkin (1990) and Arkhipkin and Scherbich (1991) observed an almost linear increase in mantle length with the number of daily increments in the statolith when data are pooled by month of birth. Uozomi and Shiba (1993) suggested that a midpoint of growth may exist. They applied a logistic model to their data, but the fit did not prove consistently better than for the linear model.

6 Reproduction

6.1 Reproductive system and gantetogenesis

The reproductive system of *I. argentinus* has been described by Schuldt (1979). In females it consists of a single ovary and two oviducts. A pair of nidamental and a pair of oviducal glands are associated with the

distal part of the oviducts. The ovary consists of a central core of muscular connective tissue, a cortical zone with protogonia, and a very thin epithelium, where the future ovarian follicle cells originate. The ectodermal part of the ducts gives rise to the oviductal glands. Ovarian development begins at a small size; differentiating oocytes can be found in specimens as small as 100 mm ML. Oogenic stages develop centrifugally, in clusters. Oogenesis has been divided into seven stages:

1) oocytes with a single nucleolus;
2) oocytes with many nucleoli;
3) oocytes with nucleoli degeneration;
4) oocytes without nucleoli and with follicle cells surrounding them;
5) oocytes without nucleoli and penetration of follicle cells into the oocyte producing flap-like projections;
6) oocytes in incipient vitellogenesis; and
7) oocytes in advanced vitellogenesis.
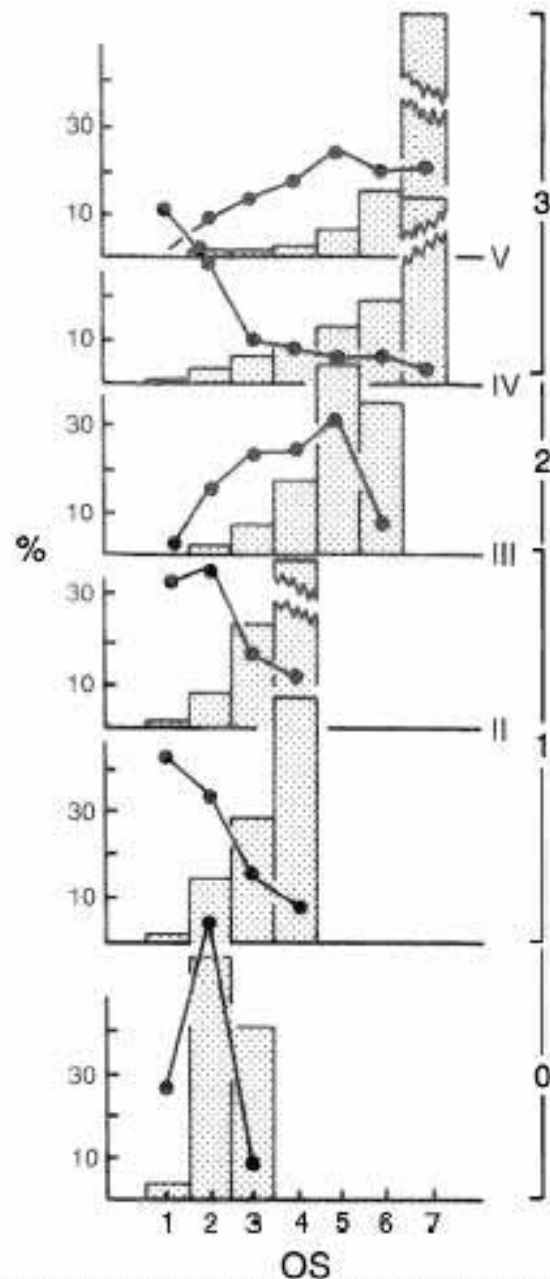
Figure 3.5. Distribution by maturity stage; lines = percent, bars = percent in volume, OS = oogenic stages, arabic numbers = ovary-nidamental stages, roman numbers = ovary stages (adapted from Schuldt 1979)

Table 3.2. Maturity scales for male and female *Illex argentinus* (adapted from Schuldt 1979)

	Immature	Maturing	Mature	
Females	Previtellogenesis	Vitellogenesis	Advanced vitellogenesis	
Ovary stages	O I II	III	IV V	
Nidamental index	<0.15 0.15-0.20	0.20-0.30	0.30-0.35 >0.35	
Nidamental stages	I II	III	IV V	
Nidamental stages	1	2	3	
Males				
Spermatophoric sac storage	I	II	III	
Hectocotylus index	<0.3	0.3-0.4	>0.45	
Hectocotylus stages	I	II	III	

Table 3.3. Approximate correspondence among maturity scales for females of *Illex argentinus* (IG= 100 x nidamental gland length/mantle length)

Brunetti (1990c)		Nigmatullin (1989) (modified from Burukovsky *et al.* 1984)		Lipinski (1979)	
I.	Immature mean IG = 13	I-II	Formation and development IG = 0.3 to 16	I.	Juvenile
II.	Immature mean IG = 21	III.	Beginning of maturation IG = 12 to 24	II.	Immature
III.	Maturing mean IG = 27	IV.	Physiological maturation IG = 18 to 34	III.	Preparatory
IV.	Early mature mean IG =38	V_1.	Beginning of functional maturation IG = 25 to 42	IV.	Maturing
V.	Advanced mature mean IG =45	V_2.	Mean functional maturation IG = 40 to 50	V.	Mature
VI.	Fertized mean IG =46	V_3.	Pre-spawning and beginning of spawning IG = 36 to 48		
VII.	Spawning mean IG =45	VI.	Spawning IG = 36 to 48		
VIII.	Spent mean IG =39	VII.	Spent IG = 35 to 42		Spent

The male reproductive system consists of a single, median testis. Immature spermatocytes gradually develop into mature spermatozoa within the seminiferous tubules of the testis. The spermatozoa are encapsulated within spermatophores, which are stored in the spermatophoric (Needham's) sac until mating occurs. Schuldt (1979) has described the spermatogenesis of *I. argentinus* in the three stanzas of the species' life cycle: juvenile (70-90 mm ML), preadult (maturing) and adult (mature, >220 mm ML). In juveniles the

seminiferous tubules are not developed and only spermatogonia are present. In preadults commencing maturation, the tubules are clearly developed (220 µm high). There are many primary spermatocytes, some secondary spermatocytes, and spermatids. In individuals larger than 220 mm ML, which are all mature, the tubules are 330 µm high and have many spermatids and spermatozoa in the centre.

6.2 Maturity scales

On the basis of histological features and using stereometric analysis, Schuldt (1979) proposed a six-stage scale of ovary maturity (O-V) for *I. argentinus* females. Oocyte number and volume were used to assign stages of ovarian maturity. The ratio between nidamental gland length and mantle length (nidamental index) was also used to obtain a nidamental scale of five stages (I'- V') which correlated with the ovary scale (Table 3.2). Nidamental stages were assigned to histological ovary stages (Fig. 3.5).

For males, Schuldt (1979) defined a three-stage scale (I-III) based on the spermatophoric sac. He found a positive correlation between the hectocotylus index (hectocotylus length/arm length) and spermatophoric (prostate) gland length (Table 3.2).

A clear definition of the maturity stages in both sexes is vital for the discrimination of different spawning populations. Macroscopic and easy-to-interpret scales, based on morphological features, gonado-somatic and nidamental indexes, are necessary. Three scales are commonly used for *I. argentinus* proposed by Lipinski (1979), Nigmatullin (1989, modified from Burukovsky *et al.* 1984) and Brunetti (1990c) (Table 3.3). There is good agreement between the three, but the last two scales are more detailed for mature specimens.

Brunetti's scale includes seven stages in males and eight in females, is based on Schuldt's histological stages, morphological features, gonad indexes and nidamental indexes, and includes "mating", "spawning" and "spent" categories. Stage VI is defined by spermatophore release in males and the presence of spermatophores in females. Spawning females are classified as stage VII, whereas post-spawning are classified as stage VII in males, but VIII in females. Spent females have large and flaccid nidamental glands, or the glands are absent, the oviducts are distended and empty, and the ovary shows the muscle-connective core with small groups of mature ova. In both sexes the mantle condition is poor and flaccid. The weight of the body, reproductive system and digestive system is significantly lower (Santos and Haimovici 1996). The spent squid are sometimes trawled up dead.

Nigmatullin's (1989) scales include seven stages each for females and males, and takes into account accumulation of sexual products, characteristics of the gonads and accessory glands, eggs, spermatophoric complex, nidamental gland indices and fertilization.

6.3 Relative growth and maturation

Rodhouse and Hatfield (1990b), Hatfield *et al.* (1992) and Rodhouse and Hatfield (1992) have studied the absolute and relative growth of *I. argentinus* in relation to sexual maturation and examined the production of gonad and soma, at different stages of maturation. Their data showed that growth and maturation occurred simultaneously during most of the time that the squid were found on the feeding grounds over the outer southern Patagonian Shelf. During maturation of the males, the mass of the gonads, the accessory reproductive organs and the head increases and the mass of the viscera decreases relative to mantle length, but there is no significative change in the mass of the digestive gland relative to mantle length.

During the course of female maturation there is an increase in the mass of the gonad and accessory reproductive organs. The mass of the mantle, head and viscera declines by small amounts and the mass of the

Table 3.4. Summary of characteristics of the four proposed main spawning stocks of *Illex argentinus*

	Stocks			
	Summer spawning (SSS)	South patagonic (SPS)	Bonaerensis-northpatagonic (BNS)	Southern Brazil (SBS)
Spawning grounds[a]	Intermediate shelf, 42°–47°S[b]	Slope, north of 44°S under the Malvinas (Falklands) or Brazil Current[b,c,d]	Slope, north of 38°S, under the Malvinas (Falklands) or Brazil Current[b,e]	Slope, between 27°S and 34°S, under the Brazil Current[f,g,h]
Spawning season	Summer (Dec to Feb)[b]	Late autumn and winter (April to Aug)[b]	Winter to early spring (July to Sept)[b]	Winter and spring (July to Nov)[f,g,h]
Size at maturity (mm)	Mean ML at maturity[b] ♂ = 141.7 mm ♀ = 195.1 mm	Mean ML[c] ♂ = 250, r = 190–300 ♀ = 330, r = 250–350	Mean ML at maturity[b] ♂ = 202.9 mm ♀ = 241.0 mm	Ranges of ML at maturity[f,h] ♂ = 200 – 290 ♀ = 240 – 360
Total maturing egg counts	m=101 000 (n=4) r=82 000–148 000 ML=173–192 mm[i]	113 835–246 098[c] 600 000–750 000 ML=330–370 mm[i]		m=180 240 (n=10) r=92 996 – 294 320 ML=294 – 336 mm[h]
Oviduct maturing egg counts	m=18 544 (n=27) r=1 479 – 47 395, ML r=190–255mm[b] m=20 000 (n=4)[i]	m=90 121 sd = 14 816 (n=12) min=20 000; max: 100 000[i]	m=59 644 (n=94) r=14 580 – 137 768 ML = 210–350 mm[b]	m=118 470 (n=10) r= 51 548 – 233 956 ML = 294 – 336 mm[h]
Hatchery grounds	North Patagonian Shelf[j]	Probably along the slope in the Falkland (Malvinas) Current (see text)	Probably along the slope near the subtropical convergence[j]	Southern Brazilian shelf and slope[f,g,h]

m = mean, r = range, n = number, sd = standard deviation, ML = mantle length
[a] inferred from fertilized females and recently spawned paralarvae
[c] Rodhouse and Hatfield 1990b
[f] Haimovici and Pérez, 1990
[e] Schuldt (1979)
[i] Laptikhovsky and Nigmatullin 1992

[b] Brunetti 1988, Brunetti *et al.* 1991
[d] Koronkiewicz, 1986
[g] Haimovici *et al.* 1995
[h] Santos and Haimovici 1996
[j] Brunetti 1990b

digestive gland increases slightly relative to the mantle length. The combined effect of these changes is a small decline in the mass of the total soma of the "standard" relative to mantle length, but this is not statistically significant. When immature and fully mature females are compared, the mantle mass of mature squid is less than that of immature squid by a small, but significant amount. This decline is not associated with degradation of the mantle muscles for re-allocation of resources to gonad growth, at least while the squid are still on the feeding grounds around the Falkland (Malvinas) Islands (Hatfield *et al.* 1992, Rodhouse and Hatfield 1992). The energy and nutrient resources for squid maturation are derived from the diet in both sexes. The proportional investment of body mass in reproductive and accessory reproductive organs predicted for a fully mature male is less than a half that of a female.

6.4 Fertilization

In *I. argentinus*, spermatophores are transferred to the mantle cavity and attached to the base of the gills, around the oviducal glands or rarely to the mantle. Males have either the right or left fourth arm hectocotylized (Castellanos 1964, Schuldt 1979). Mating does not appear to happen until the hectocotylus is more than 50 percent modified and able to roll. Males only copulate with mature females. Fertilized females (stage VI) often have groups of spermatophores attached in different places as a result of several copulations (Brunetti 1988, Laptikhovsky and Nigmatullin 1992). It is probable that implantation of spermatophores provides the stimulus for females to spawn within a few days, as has been shown for *Illex illecebrosus* (O'Dor 1983, *see Chapter 5*).

6.5 Size at maturity

Available information on size at maturity in different regions and seasons is presented in Table 3.4. Brunetti (1988) and Brunetti *et al.* (1991) have analysed size composition and gonado-somatic indexes as a function of maturity stage in the winter spawners of the BNS, and the SSS during the pre-reproductive and reproductive seasons. In both stocks males mature before females and females complete maturation in about one month. Mantle length at maturity was found to be larger in the winter-spring spawners. Off southern Brazil, Haimovici and Pérez (1990) observed that the sizes of mature males and fertilized females were smaller in late summer and autumn than in winter and spring (Table 3.4). Rodhouse and Hatfield (1990b) observed mature female squid above 250 mm and usually over 280 mm ML.

6.6 Fecundity

There are several estimates of individual fecundities of *I. argentinus* (Schuldt 1979, Brunetti *et al.* 1991, Rodhouse and Hatfield 1990b, Laptikhovsky and Nigmatullin 1992, Santos and Haimovici 1996) (Table 3.4). Brunetti *et al.* (1991) suggested that eggs present in the oviducts of fully mature and copulated females are the only ones to be evacuated during spawning, but a significant number of oocytes in advanced stage of vitellogenesis (12.5-25.6 percent, mean 21.5 percent) remain in the ovary after spawning. However, Laptikhovsky and Nigmatullin (1992, 1993) have proposed that spawning in *I. argentinus* is intermittent and includes 70-80 percent of all the oocytes that attain a diameter over 0.05 mm.

Brunetti *et al.* (1991) observed a weak correlation of positive sign between fecundity and ML, and fecundity and weight, but found that the nidamental weight (NW) was a reliable index of fecundity (F) for both stocks:

$$F_{SSS} = (0.254 * NW^{1.427}) * 10^3 \quad r^2 = 0.466$$
$$F_{BNS} = (0.7534 * NW^{1.240}) * 10^3 \quad r^2 = 0.774$$

Comparisons of fecundity among stocks are difficult because inconsistent methods of counting have been used. Only the mature ova present within the oviducts of copulated mature females were counted by Schuldt (1979) and Brunetti *et al.* (1991). On the other hand Rodhouse and Hatfield (1990b), Laptikpovsky and Nigmatullin (1992) and Santos and Haimovici (1996) measured and counted eggs in both ovaries and oviducts, but in some cases Rodhouse and Hatfield included females that were not fully mature. Oviduct egg count estimates range from 50 000 for the small summer patagonic spawners to over 250 000 eggs for the large winter and spring spawners along the slope (Brunetti *et al.* 1991). Fecundity estimates by Laptikhovsky and Nigmatullin (1992) including 70-75 percent of all vitellogenic eggs over 0.05 mm, ranged from 60 000 to 400 000. In southern Brazil oviduct fecundity may reach 240 000 eggs, and the total number of vitellogenic eggs in the ovary and oviducts may reach 300 000 (Santos and Haimovici 1996) (Table 3.4).

6.7 Early life stages

There are no data on egg masses and embryonic stages of *I. argentinus*. Rhynchoteuthion paralarvae of this species have been described by Leta (1987), Brunetti (1988, 1990b), Haimovici *et al.* (1995) and Vidal (1994), and scanning electron micrographs have been published by Rodhouse *et al.* (1992). The smallest paralarvae, at hatching, are 1 mm ML. In the initial stages, usually <1.4 mm ML, the head is often retracted into the rounded mantle which has big chromatophores. The eyes are visible through the transparent mantle (Fig. 3.6). As size increases the body becomes relatively long and the mantle becomes cylindrical. The third and fourth arm pairs are vestigial at ML < 1.9 mm but at 5.8 mm they are well developed and the arm formula is 2.3.1.4. The proboscis is robust in small paralarvae and becomes relatively thin with growth; it has eight suckers of equal size at the distal end. Separation of the tentacles starts at a ML of 2.5 mm and is completed at ML 6.5-8 inm. Six large chromatophores, arranged like petals, are present on the dorsal side of the head and two big chromatophores are present ventro-laterally, behind the eyes (Fig. 3.6). The fins are present from the earliest stages when they are small and terminal; they become quadrangular and located dorsally at ML 6.5 mm. Vidal (1994) observed two discontinuity points in the relative growth of the paralarvae and juveniles under 55 mm ML: up to 14 mm there is rapid development of arms, suckers and fins, and the separation of the tentacles is not accompanied by other morphometric changes; in the second stage (14-28 mm ML), tentacles and clubs develop rapidly; and in the third stage (>28 mm ML) the body elongates.
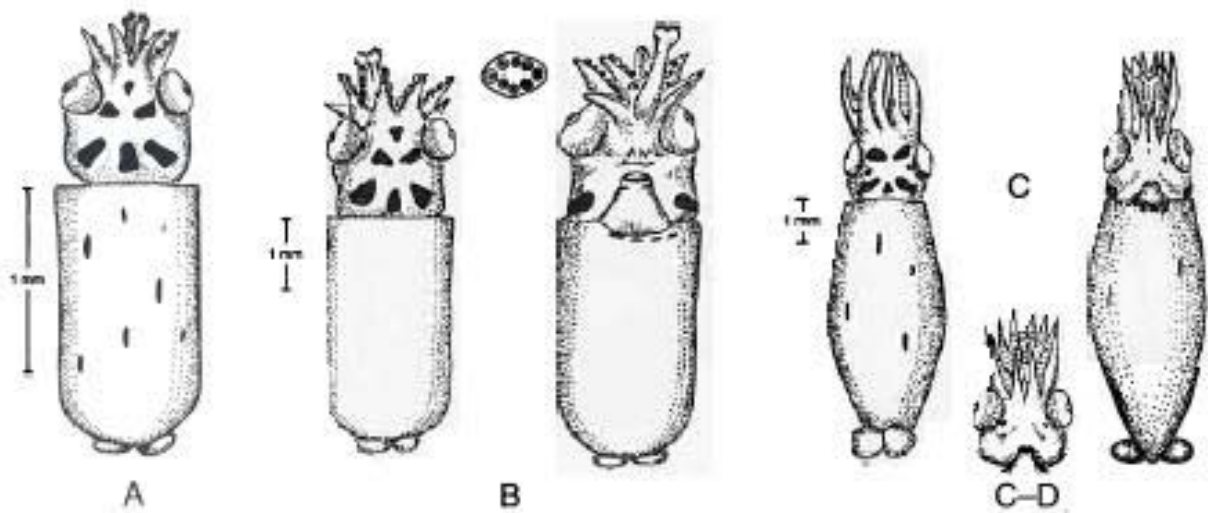

Figure 3.6. Rhynchoteuthion larvae of *Illex argentinus* (from Brunetti 1990b); a = 1.34 mm ML, b = 3.13 mm ML, c = 5.85 mm ML

TABLE 3.5. List of identified prey from the stomach contents of *Illex argentinus*

Prey items	Shelf	Slope	<35°S	35°-45°	>45°	Sources
FISHES	X	-	-	-	X	a
Engraulidae	X	-	-	X	-	b
Engraulis anchoita	X	X	-	X	X	c,d
Macrouridae	X	-	-	X	-	d,e
Mictophidae	X	X	-	X	X	d,e,f,g
Diaphus dumerilii	-	X	X	-	-	h
Scianidae	X	-	-	X	-	e
Stemoptychidae						
Maurolicus muelleri	-	X	X	-	-	h
Merlucciidae						
Merluccius hubbsi	X	X	X	X	-	d,h
CEPHALOPODS						
Argonautoidae						
Argonauta sp	X	-	X	-	-	h
Enoploteuthidae	X	-	X	-	-	h
Ornmastrephidae						
Illex argentinus	X	-	X	X	X	a,c,g,h
Spirulidae						
Spirula spirula	X	-	X	-	-	h
CRUSTACEANS						
Arnphipoda						
Themisto gaudichaudii	X	X	-	X	X	a,g,i
Copepoda	X	-	X	X	-	a,h
Oncaea media	X	-	X	-	-	h
Decapoda	X	X	X	-	-	h
Munida gregaria	X	-	-	-	X	a
Peneidae	X	-	-	X	-	c
Euphausiacea	X	X	-	X	X	a,c,g
Euphausia sp	-	X	-	-	X	i
Mysidacea	X	-	X	X	-	c,h
OTHERS						
Chaetognatha	-	X	-	-	X	i

Sources:
[a] Koronkiewicz 1986
[b] Castellanos 1964
[c] Leta 1981
[d] Angelescu and Prenski 1987
[e] Klyuchnik and Zasypkina 1972
[f] Nigmatullin 1989
[g] Ivanovic and Brunetti 1994
[h] Santos and Haimovici (*in press*)
[i] Tshchetinnikov and Topal1991
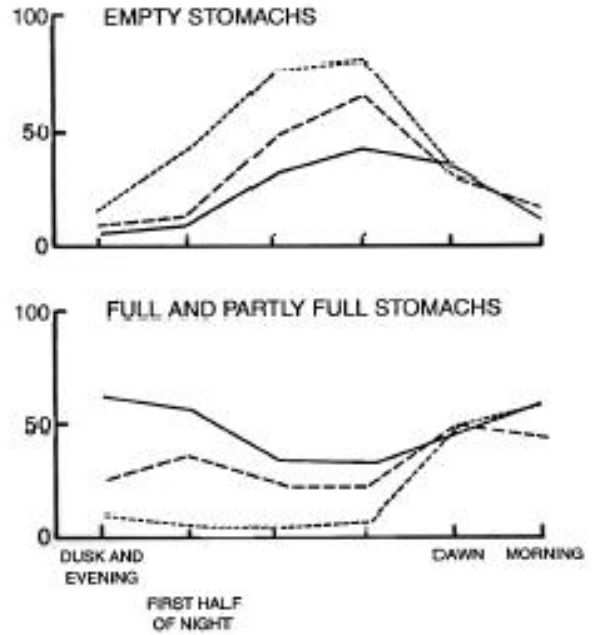
Figure 3.7 Diel feeding rhythm of *Illex argentinus* in different concentrations of macrozooplankton; ─ = dense;---- = rare; ….. = absent (redrawn from Koronkiewicz 1986)

7   Trophic relations

7.1 Diet and feeding

The diet and feeding habits of *I. argentinus* throughout its range have been studied by several authors cited in Table 3.5, where identified prey items are listed. In the southern part of its range the main prey of young and maturing squids were crustaceans, including the amphipod *Themisto gaudichaudii*, the lobster krill *Munida gregaria*, euphausids of the genera *Euphausia*, and Chaetognaths. Fish, mainly young hake, anchovy and myctophids, and squid, including *I. argentinus*, become more important for the larger sizes (Koronkiewicz 1986, Angelescu and Prenski 1987, Nigmatullin 1989, Tshchetinnikov and Topa1 1991, Ivanovic and Brunetti 1994).

In the region off northern Argentina and Uruguay, Angelescu and Prenski (1987) found that young hake, (*M. hubbsi*) and *Engraulis anchoita* are important prey. Leta (1981) found that of the crustaceans the mysidaceans, euphausiaceans, hyperiid amphipods and peneid decapods occur in the diet. Bony fishes of the families Sciaenidae, Myctophidae and Macrouridae have been reported by Klyuchnik and Zasipkna (1972, in Leta 1981). Fishes are more important in this region compared with the southern part of its range (Ivanovic and Brunetti 1994).

Off southern Brazil, *I. argentinus* occurs mostly on the upper slope and, besides pelagic crustaceans, the diet includes small hake, myctophids and cephalopods (Santos and Haimovici *in press*). In this area fish appear to be of greater importance than in the southern part of the range. Evidence of cannibalism was found in 18.5 percent of the 313 stomach contents examined. Cannibalism was found to occur at all sizes but was higher in juveniles under 120 mm ML.

Diel vertical migrations and feeding behaviour are related. Koronkiewicz (1986) observed that squidfeeding on macroplankton increases before dawn and continues during the daytime close to the bottom. At dusk the squid migrate upwards in the water column and when macroplankton is abundant they feed intensively in the first half of the night (Fig. 3.7).

Table 3.6. List of predators of *Illex argentinus* from southern Brazil[a]

Predators	No. of stomachs examined	Occurence[b]	Predators	No. of stomachs examined	Occurence[b]
Demersal pelagic fishes			Pelagic fishes		
Merlucciidae			Istiophoridae	220	*
Merluccius hubbsi	231	*	Lamnidae		
Pomatomidae			*Isurus oxyrinchus*	19	*
Pomatomus saltatrix	164	*	Scombridae		
Serranidae			*Thunnus albacares*	343	**
Polyprion americanus	>100	***	*Thunnus alalunga*	101	**
Sparidae			*Thunnus obesus*	73	***
Pagrus pagrus	362	*	Xiphiidae		
Sphymidae			*Xiphias gladius*	195	***
Sphyma lewini	8	**			
Trichiuridae			Marine mammals		
Trichiurus lepturus	490	*	Physeteridae		
			Kogia breviceps	2	*
Marine birds			*Physeter macrocephalus*	1	*
Spheniscidae			Otariidae		
Sphesniscus magellanicus	>100	*	*Arctocephalus tropicalis*	3	*

a adapted from Santos 1992
b * = infrequent; ** = frequent; *** = very frequent
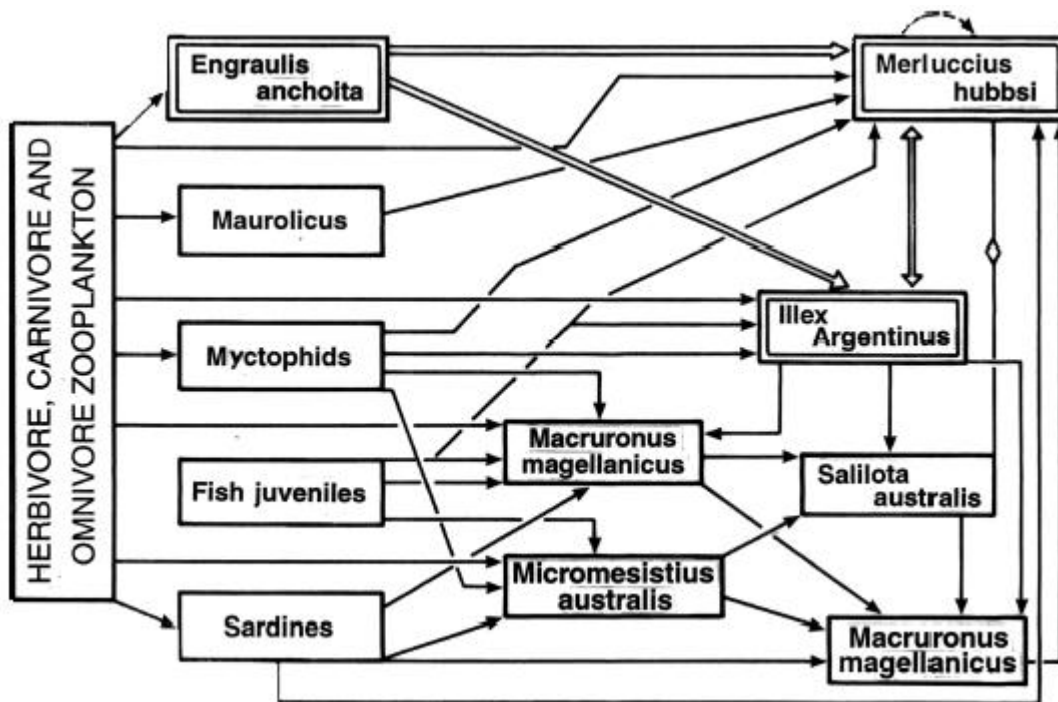
Figure 3.8. Trophic relations in the demersal pelagic communities in the Argentinean Sea; double lines = the relationship between the short-finned squid *Illex argentinus*, the anchovy Engraulis anchoita and the hake *Merluccius hubbsi* (adapted from Angelescu and Prenski 1987)

Nigmatullin (1989) describes two vertical migration patterns, one for immature and maturing specimens (on the bottom in daytime and near the surface at night) and a second for pre-spawning and spawning squid (near the bottom at night and in the water column up to 200-300 m feeding on myctophids in the acoustic scattering layer in daytime). Observations from a submersible by Moiseev (1991) confirmed midwater daytime concentrations but did not find squid near the bottom at night, perhaps because his observations were in April, when little spawning takes place along the Patagonian slope.

As other neritic ommastrephids, *I. argentinus* feeds successively on copepods, euphausids and to a lesser degree, amphipods and other planktonic invertebrates. Diet then shifts with growth to micronectonic fishes and cephalopods thus moving from the third to the fifth trophic level (Angelescu *et al.* 1958, Nigmatullin and Shukhgálter 1990).

7.2 Predation

Information on predation on *I. argentinus* is available from an analysis of the stomach contents of 46 fish, marine mammals and penguins from southern Brazil summarized in Table 3.6, which is adapted from Santos (1992). *Illex argentinus* is an important prey for the tuna *Thunnus obesus*, the swordfish *Xiphias gladius*, the demersal serranid *Polyprion americanus*, and to a lesser degree for *T. alalunga* and *T. albacares*.

Angelescu and Prenski (1987) found that *I. argentinus*, hake (*M. hubbsi*) and *E. anchoita* from a complex trophic system in the demersal-pelagic community. Both squid and hake feed on anchovy, squid prey on young pelagic hake, and older hake feed on all sizes of squid. Thus, the hake is competitor, predator and prey of *I. argentinus* (Fig. 3.8). Hake appear to feed more intensely on squid in the southern part of its range from January to July and in the northern part from April to June.

I. argentinus appears to be a very important link in the food web of the southern Patagonian Shelf. L.B. Prenski (Instituto Nacional de Investigación y Desarrollo Pesquero, Argentina, *unpubl. data*) examined the trophic relations on the shelf off Argentina from 46° to 55°S during the summer and estimated that *I. argentinus* represented 38 percent of the food of the fish of the region.

7.3 Parasites

The first reference to the parasites of *I. argentinus* was by Threlfall (1970), who studied the helminths in specimens landed in Mar del Plata in April, 1969 and almost certainly fished on the Buenos Aires Province or north Patagonian Shelf as a by-catch of the hake trawl fishery. He reported two genera of tetraphyllidean cestodes (*Phyllobothrium* and *Pelichnibothrium*) and two nematodes (one unidentified and an anisakid). In the same fishing area, Sardella *et al.* (1990) later added a third plerocercoid larvae of the genus *Dinobothrium*.

Nigmatullin and Shukhgálter (1990) describe a study of the helminth parasites of *I. argentinus* from the outer shelf and adjacent oceanic waters from latitudes 45° to 47°S. From January to June in the years 1982 to 1987 they sampled specimens from 13-380 mm ML and collected twelve species: four cestodes (two types of *Phyllobothrium* sp, *Pelichnibothrium speciosum* I and *Hepatoxylon trichiuri*), two trematodes (*Derogenes varicus* and *Hirudinella ventricosa*) and six nematodes (*Porrocaecum* sp I, *Contracaecum* sp I, *Anisakis simplex* I, *Anisakis* sp I (II), *Hysterothylacium* sp I, *Spinitectus* sp I). They consider this to be a relatively rich helminth fauna by comparison with other squids, but *I. argentinus* is only part of the parasitic system, especially for *Phyllobothrium* sp (I) III in all seasons and to a lesser degree for *Phyllobothrium* sp I (II) for the summer- and autumn-spawned squid and for both *Anisakis* for the winter-spawned squid.

In the upper slope of southern Brazil, from 27° to 34°S, Santos (1992) sampled digestive tract parasites of squid of 34-356 mm ML in all seasons and found at. least three genera of cestodes of the family Phyllobothridae, nematodes of the family Anisakidae and trematodes of the family Didymozoidae.

Some information on the trophic relations of *I. argentinus* can be inferred from the existence and intensity of infestation by parasites. Nigmatullin and Shukhgálter (1990) state that throughout the species' geographical range the cartilaginous fishes, which are the final hosts of cestodes (in particular *Phyllobothrium* sp III), and marine mammals, which are the fmal hosts of nematodes (in particular *Anisakis* spps), are the major predators of *I. argentinus*. In the northern part of its distribution, tunas and xiphoid fishes (final hosts of didymozoids) are the most important predators (Santos 1992).

Helminth assemblages may serve as stock markers in widespread squid species such as *Ommastrephes bartrami* in the northern Pacific (Bower and Margolis 1991). This may depend on the trophic web and the final hosts of each parasite type. Groups of *I. argentinus* spawning at different times of the year in the southern range of the distribution are not separable by their parasites. Specimens hatched at different times of the year are caught in the same regions (Arkhipkin and Scherbich 1991) and their parasitic composition is generally similar (Nigmatullin 1989). On the other hand, immature and maturing *I. argentinus* caught in all seasons off southern Brazil are frequently infected by didymozoids, which are absent in the colder waters beyond the subtropical convergence. Among mature specimens, only those caught in autumn are infected by didymozoids. On the other hand, large mature and spawning specimens caught in winter and spring had no didymozoid parasites. This suggests that most of the winter and spring spawners off Brazil are migrants that feed and grow in colder waters to the south and migrate north to the waters of the Brazil Current to spawn (Santos and Haimovici 1996).

8   Stock assessment and management

Several methods have been applied at different times to assess the state of the *I. argentinus* stock in the southwest Atlantic. The spatial coverage, reliability and level of complexity of these estimates also vary with time and with the availability of fisheries and resources survey data.

Long before any directed squid fishery started in the area there was already some evidence that the short-finned squid (*Illex* sp.) was an important species in terms of abundance, and was capable of yielding total catches in the order of several hundreds of thousands of tons per year (Gulland 1971). Commercial interest in the squid stocks in the area started to build in the mid-1970s, and resource surveys conducted in the years that followed allowed the first direct assessments of the so far under-exploited or virtually unexploited *I. argentinus* population.

The total biomass and from there the potential yield of *I. argentinus* was estimated with the swept area method using data from trawl surveys conducted on board the R/V *Walter Herwig* (1978), *Shinkai Maru* (1978/79) and *Dr Holmberg* (1981/82) (FAO 1983). Different estimates of total biomass proposed by different authors based on these sets of trawl data ranged from 60 000 to 2.6 million t. These would correspond to the virgin stock size given that the stock was virtually unexploited. The higher estimates were derived from the 1978/79 cruises by the R/V *Shinkai Maru* and ranged from 635 968 t (Otero *et al.* 1981) to 2 605 000 t (Sato and Hatanaka 1983) for the same catch data using different methods of grouping and analysis. Based on the same data Sato and Hatanaka (1983) proposed a figure of 1 303 000 t as a possible virgin stock size and estimated a potential annual yield of 482 000 t.

In 1983 an FAO ad hoc Working Group (FAO 1983) was conyened to review the fishery resources assessment data and information available for the area. The Working Group estimated the total *I. argentinus* biomass to be around 230 000 t and found no signs of the stock being fully or heavily exploited.

Csirke (1987), using additional fisheries data, estimated fishing mortality and stock size by virtual population analysis and analysed yield-per-recruit and stock-recruitment relationships of the exploited *I. argentinus* population. The available data included monthly landings and size compositions provided by Poland (1978-85), Japan and Argentina (1979-1985) and total reported landings by country. The results included estimates of F (fishing mortality) that gave annual values ranging from 0.3 to 2.4, and monthly estimates of total biomass (corresponding to the minimum biomass that would explain the catches obtained) ranging from 35 000 to 370 000 t. The maximum biomass values were reported for 1979.

The main conclusions in Csirke (1987) were that no overfishing existed until 1985, that inter-annual variability in this period was very high (x 10), and that no single value of fishing mortality or effort could maximize the total annual yield and minimize the risk of a collapse of the fishery. As a precautionary measure to prevent overfishing and stock depletion he suggested that a conservative minimum spawning stock size be defmed and agreed upon below which no fishing would be allowed. It was also suggested that this minimum safe level be set somewhere between 1 and 1.5 times the mean value of the lower estimated spawning stock sizes observed to date in 1980 and 1983. While proposing that fishing effort and fishing mortality be reduced when poor year classes are detected (e.g. from monitoring biomass or catch-per-unit-effort estimates) and that fishing be halted if the observed or projected spawning stock size falls below the above mentioned safe level, it was also suggested that fishing pressure could be augmented when recruitment is high. He suggested that with this strategy, under average conditions, the escapement or surviving spawning stock could be set at 20 to 25 percent of the expected virgin spawning stock size (corresponding more or less to yearly F values between 1.6 and 1.4). He also added that F and annual catches could be increased further allowing a lower spawning stock escapement (as low as 8 percent) in years when recruitment is particularly high, whereas the stock should be protected by increasing the spawning stock escapement to about 40 percent in years with poor recruitment. This can only be achieved by drastically reducing fishing effort, fishing mortality (F) and expected annual catches during poor years.

Rosenberg *et al.* (1990) developed an assessment methodology applicable to the *I. argentinus* fishery based on a modified Leslie-DeLury analysis that follows the decay in abundance of squid cohorts during the fishing season. Their analyses were geared to providing the required information for an effort-limited regulation system to manage these resources, and while discussing some of the possible management targets based on constant spawner escapement and constant proportional escapement, they suggested that constant proportional escapement (i.e. constant harvest rate) is simpler to apply. They reported that since 1987 the fishery around the Falkland (Malvinas) Islands has been managed using the proportional escapement method and controlling effort by licenses, with a conservative target of 40 percent escapement (Beddington *et al.* 1990), and estimated that in 1987 the exploited stock in that area reached a total biomass level around 170 000 t.

Later, Basson *et al.* (1996) extended previous work based on the standard Leslie-DeLury analysis by considering migration between adjacent fishing grounds. By applying the new methodology and using more updated data and information they undertook a retrospective assessment of the *I. argentinus* fishery to the south of 45°S for the period 1987-1991, and used estimates of recruitment and spawning stock biomass to derive a threshold for spawning biomass and revised proportional escapement levels. They estimated annual spawning stock biomass values ranging from 26 000 to 66 000 t when using their best fitting runs, and from 64 000 to 109 000 t when using a more conservative approach based on results which give the highest spawning stock biomass estimates. Regarding the stock-recruitment relationship, they noted that with the first set of estimates, the lowest spawning stock biomass (26 411 t in 1989) was associated with the lowest estimated recruitment (1 208 millions in 1990), while only a slightly higher spawning stock biomass (31 545 t in 1987) was associated with the highest estimated recruitment value (3 457 millions in 1988). It is also worth noting that although, as indicated above, the intended escapement target for this fishery was originally set at a conservative 40 percent, Basson *et al.* (1996) estimates suggest that the percentage proportional escapements actually applied ranged from 8.7 percent (in 1987) to 32.1 percent (in 1990).

9   Fisheries data

Fisheries data available for *I. argentinus* exists for different periods of time, in various formats and in different levels of detail depending on the reporting fishing country. While fisheries data from some reporting countries may include yearly and monthly catch data, length frequency data, fishing effort, fishing area, etc., and might even be complemented with information on mean weight, sexual maturity and other biological observations, other countries may only report total annual squid catches for the whole Area 41, without further details regarding specific fishing grounds or differentiation by species.

The most important and simplest fisheries data to collect for any exploited fish population is the total catch. FAO has been collecting total annual catches by species since 1950 on a world-wide basis, and a summary of the annual catches of *I. argentinus* and other squid species caught in the southwest Atlantic by country is provided in Table 3.7 (see also Figure 3.1). Further details of the other available fisheries data is provided in the several reports that analyse this data for assessment purposes such as, for instance, in FAO (1983), Csirke (1987), Beddington *et al.* (1990), Rosenberg *et al.* (1990) and Basson *et al.* (1996).

10   Discussion

The data presented in this review show that, except for the small north Patagonian summer-spawning stock, there is a strong link between the larger spawning groups and the subtropical convergence. The early life stages develop in warm waters and the juveniles and subadults are adapted to the production cycles on the shelf and slope break at different latitudes. Summer shelf-spawners spawn at higher latitudes than the main spawning groups along the slope in winter and spring.

It has been suggested that large current systems sustain large populations of squid and that such systems provide a powerful selection regime for larger individuals (O'Dor 1992). Large squid can migrate between highly productive areas, where the feeding grounds are located in regions of cold currents, and spawning grounds, from which egg masses can be carried to warmer and productive regions where paralarvae can develop. It is suggested that egg masses are transported towards the Brazil-Falkland (Malvinas) convergence from both the north and the south. Spawning probably occurs in the Falkland (Malvinas) Current and Brazil Current over a latitudinal range of 2 000 km, from early winter to late spring. The protracted spawning of larger squids over an extensive slope area contributes to the abundance of the species.

High concentrations of paralarvae have been found in winter off Uruguay and southern Brazil and in spring off southern Brazil (Leta 1992, Haimovici *et al.* 1995). The subtropical front and southward-moving eddies in winter appear to be the main areas for paralarval development for the squid recruited on the Patagonian Shelf. Unfortunately the timing of oceanic surveys to date may not have been optimal for a conclusive test of these hypotheses (Brunetti and Ivanovic 1992, Rodhouse *et al.* 1992, Parfeniuk *et al.* 1992).

The SPS sustains the most important fishery but it has been shown that all the stocks are important in the ecology of the respective regions. Fishing on *I. argentinus* is intense and pursued by an international fleet. As has already happened with other ommastrephid squid stocks, a collapse of the fishery in the future, due to unfavourable environment and intense fishing, cannot be ruled out. As *I. argentinus* is an annual species, its abundance is determined by recruitment in the same year as cohorts are hatched. Considerable inter-annual variability in abundance and timing has been observed for at least the southern stock (Csirke 1987, Uzuomi and Chiba 1993). Its abundance is related to its ability to respond quickly to favourable combinations in space and time in an unpredictable environment. The degree to which the stocks mix is an important research question because the time of recovery of any overfished stock in the future may depend on the contribution of recruits from the other stocks.

Table 3.7. Nominal annual catch of selected squid species groups fished in the southwest Atlantic, in thousand metric tonnes, by main fishing country or area, years 1950-95[a]

Species or species group / Fishing country or area	1950-59	1960-69	1970-79	1980-89	1990	1991	1992	1993	1994	1995
Argentine short-finned squid (*Illex argentinus*)[b]										
Argentina	0	1	17	25	28	46	77	194	197	199
Bulgaria	0	0	0	2	6	4	6	1	1	1
Chile	0	0	0	0	0	4	2	1	0	0
Cuba	0	0	0	2	2	0	0	0	0	0
Germany	0	0	0	5	7	0	0	0	0	0
Poland	0	0	0	17	25	26	17	6	2	0
Spain	0	0	0	3	1	1		1	3	4
Taiwan Pr. of China	0	0	0	57	88	124	117	124	104	100
Uruguay	0	0	1	3	1	2	2	4	2	4
Sub total	*0*	*1*	*18*	*114*	*157*	*207*	*223*	*330*	*310*	*310*
Squids non-identified (Loliginidae & Ommastrephidae)[c]										
Estonia	0	0	0	2	12	12	7	0	0	0
France	0	0	0	0	0	0	0	0	2	7
Japan[d]	0	0	2	82	87	109	99	132	93	76
Korea Rep.[d]	0	0	0	38	111	178	211	129	79	124
Latvia	0	0	0	3	11	18	11	5	6	2
Lithuania	0	0	0	3	15	28	19	15	3	0
Poland[d]	0	0	2	51	0	0	0	0	0	0
Russian Fed.	0	0	0	8	55	66	77	47	24	12
Spain	0	0	0	21	45	36	66	39	47	54
Ukraine	0	0	0	2	11	10	4	5	3	
USSR	0	1	0	18	0	0	0	0	0	0
Sub total	*0*	*1*	*4*	*228*	*347*	*456*	*494*	*371*	*257*	*275*
Patagonian squid (*Loligo gahi*)										
Falkland (Malvinas) Islands	0	0	0		6	1	2	1	5	22
Poland	0	0	0	5	6	7	9	4	1	0
Subtotal	*0*	*0*	*0*	*5*	*12*	*8*	*11*	*5*	*6*	*22*
Common squid (*Loligo* spp.)[e]										
Argentina	0	0	0	0	0	0	0			
Brazil	0	0	1		1	1			1	
Bulgaria	0	0	0	1	0	0	0	0	0	0
Greece	0	0	0	1	6	3	0	0	0	0
Italy	0	0	0	0	1	1	0	0	0	0
Japan	0	0	0	15	9	3		1	0	2
Korea Rep	0	0	0	0	0	8	0	0	0	0
Portugal	0	0	0		5	3		2	2	4
United Kingdom	0	0	0	2	1	2	0	0	1	2
Subtotal	*0*	*0*	*1*	*22*	*24*	*22*	*5*	*5*	*6*	*10*
Sevenstar flying squid (*Martialia hyadesi*)[f]										
Taiwan Pr. of China	0	0	0	1	11	1	1	1	0	23
Subtotal	*0*	*0*	*0*	*1*	*12*	*1*	*1*	*1*	*0*	*24*
Total (all squids)	0	3	23	371	552	695	734	713	579	641

[a] Data from Csirke 1987, FAO 1997, FISHBASE, in FAO web page in http:\\www.fao.org
[b] Falkland (Malvinas) Islands, France, Netherlands, Portugal and United Kingdom report zero catch of category *I. argentinus*
[c] Germany, Israel and Italy report zero catch of category "squid non-identified"
[d] Most if not all of the catches reported as general Ommastrephidae by these countries prior to 1986 were found to correspond to *I. argentinus* (Csirke 1987).
[e] Germany and Netherlands report zero catch of category *Loligo* spp.
[f] Argentina, Falkland (Malvinas) Islands, Poland and Spain report zero catch of *M. hyadesi*

Nigmatullin (1987) discusses two alternative hypotheses on stock structure: 1) a single population system with a long spawning season and a high level of genetic mixing or alternatively, 2) several distinct groups that are in the process of invading new habitats. Strong evidence in favour of the first hypothesis has been found using statolith ageing methods. Arkhipkin (1990) concluded that due to the wide spawning age range and overlapping of spawning seasons and biotopes, groups of *I. argentinus* are not genetically isolated and represent intra-populational units. In fact, some spawning in other seasons and areas besides those mentioned also occurs. Large adults were found spawning (stages V-VIII) in low numbers in October-November on the inner shelf from 38° to 39°S. Rhynchoteuthion paralarvae have been found in the same area and season (Brunetti 1981, Hatanaka 1985). It is not known if they are the remains of Bonaerensis-northpatagonic spawners or a different stock. Small mature males and females and fertilized females have been found in southern Brazil in late summer and early autumn (Haimovici and Pérez 1990). Arkhipkin and Scherbich (1991) found squid hatched in all four seasons and were caught in winter and spring in the outer shelf, slope and adjacent oceanic waters off Argentina.

The second hypothesis cannot be discounted, as non-random distribution of genotypes and an overall deficit of heterozygotes has been found in isoenzyme studies of squid of the southern stock (Carvalho *et al.* 1992, *see Chapter 10*), suggesting that partial reproductive isolation occurs among samples from adjacent fishing grounds.

Future research should include early winter oceanic surveys for paralarvae and juveniles in the subtropical front area, and genetic studies on the four main stocks proposed in this paper. The SPS sustains the most important fishery. Recent catches are larger that those predicted some years ago (Sato and Hatanaka 1983, FAO 1983, Csirke 1987). It should be noted however that these earlier estimates were done when the fishery was still developing and the *I. argentinus* was considered under-exploited or very lightly exploited throughout all of its distribution range, and some stock units were probably still unexploited. It is known that most assessments based on fisheries data are fishery and/or exploited stock specific, i.e. are specific for that portion of the population actually exploited in and by the area and fishery covered by the data. Retrospective assessments of these earlier years should therefore take into account the effects of the continuous build-up of the fishing pressure in those years, changes in the location and expansion of the area or fishing grounds being exploited and other changes in the fishing strategy and practices that might have incorporated new stock subunits into the original exploited stock unit being assessed. When available, revised formulas and growth and mortality parameters used to estimate potential yields from biomass estimates should also be used. The relationship between the apparent boom in the *I. argentinus* fishery and the development of fisheries on its predators or competitors should also be examined. The impact of the squid fishery on other commercial species also deserves the consideration of future research and management policies.

References

ANGELESCU, V., GNIERI, F.S. & NANI, A. 1958. La merluza del mar Argentino (biologia e taxonomia). Servicio de Hidrografia Naval, Buenos Aires, Documento H 1004, 224 pp. (+ 4 maps and 14 plates).

ANGELESCU, V. & PRENSKI, L.B. 1987. Ecologia trofica de la merluza comi'in del Mar Argentino (Merlucciidae, *Merluccius hubbsi*). Parte 2. Dinámica de la alimentación analizada sobre la base de las condiciones ambientales, la estructura y lag evaluaciones de los efectivos en su area de distribución. *Contrib. Inst. Nac. Invest. Desarrollo Pesq.* Mar del Plata, Argentina, No. 561, 205 pp.

ANON. 1989. *Informe sabre la primera expedición sovietico-argentina en el Atlantico Sudoccidental a bordo del B/I "EVRIKA: (agosto-octubre 1988).* AtlantNIRO, Kaliningrad, 215 pp.

ARKHIPKIN, A.I. 1990. Age and growth of the squid (*Illex argentinus*). *Frente Marítimo*, 6(A): 25-35. (*in Spanish*)

ARKHIPKIN, A.I. 1993. Age, growth, stock structure and migratory rate of prespawning short-finned squid, *Illex argentinus* based on statolith ageing investigations. *Fish. Res.*, 16: 313-338.

ARKHIPKIN, A.I. & SCHERBICH, ZH.N. 1991. Intraspecific growth and structure of the squid, *Illex argentinus* (Ommastrephidae) in winter and spring in the Southwestern Atlantic. *Scientia Marina*, 55: 619-627. (*in Spanish*)

BASSON, M., BEDDINGTON, J.R., CROMBIE, J.A., HOLDEN, S.J., PURCHASE, L.V. & TINGLEY, G.A. 1996. Assessment and management of annual squid stocks: the *Illex argentinus* fishery in the Southwest Atlantic as an example. *Fish. Res.*, 28: 3-29.

BEDDINGTON, J.R., ROSENBERG, A.A., CROMBIE, J.A. & KIRKWOOD, G.P. 1990. Stock assessment and the provision of management advice for the short fm squid fishery in Falkland Islands waters. *Fish. Res.*, 8: 351-365.

BRANDHORST, N. & CASTELLO, J.P. 1971. Evaluación de los recursos de anchoita (Engraulis anchoita) frente a la Argentina y Uruguay. I. Las condiciones oceanograficas, sinopsis del conocimiento actual sobre la anchoita y el plan para su evaluación. *Proy. Des. Pesq. Ser. Infs. Tec.* Mar del Plata, No. 29, 63 pp..

BOWER, S.M. & MARGOLIS, L. 1991. Potential use of helminth parasites in stock identification of flying squid, Ommastrephes bartami, in North Pacific waters. *Can. J. Zool.*, 69: 1124-1126.

BRUNETTI, N. E. 1981. Length distribution and reproductive biology of *Illex argentinus* in the Argentine Sea (April 1978-April 1979). *Contrib. Inst. Nac. Invest. Desarrollo Pesq.* Mar del Plata, Argentina, (383): 119-127. (*in Spanish*)

BRUNETTI, N.E. 1988. Contribución al conocimiento biologico-pesquero del calamar argentino (Cephalopoda, Ommastrephidae, *Illex argentinus*). Trabajo de Thesis presentado para optar al Grado de Doctor en Ciencias Naturales, Universidad Nacional de La Plata, 135 pp.

BRUNETTI, N.E. 1990a. The evolution of the *Illex argentinus* (Castellanos, 1960) fishery. Informes Tecnicos de Investigación Pesquera, *Consejo Superior de Investigaciones Cientificas*, Barcelona, No.155, 19 pp.

BRUNETTI, N.E. 1990b. Description of Rhynchoteuthion larvae of mex argentinus from summer spawning subpopulation. *J. Plankton Res.*, 12: 1045-1057.

BRUNETTI, N.E. 1990c. Escala para la identificación de estadios de madurez sexual del calamar, (*Illex argentinus*). *Frente Marítimo* 7(A): 45-52.

BRUNETTI, N.E. & IVANOVIC, M.L. 1990. Calamar (*Illex argentinus*). In Muestreo bioestadistico de desembarques del puerto de Mar del Plata. Periodo 1980-1985. M.B. Cousseau, ed. *Contrib. Inst. Nac. Invest. Desarrollo Pesq.* Mar del Plata, Argentina, (585): 185-219.

BRUNETTI, N.E. & IVANOVIC, M.L. 1992. Distribution and abundance of early life stages of squid (*Illex argentinus*) in the south-west Atlantic. *ICES J. Mar. Sci.*, 49: 175-183.

BRUNETTI, N.E. & PÉREZ COMAS, J.A. 1989a. Abundance, distribution and population composition of squid resource in Uruguayan-Bonaerensis waters in May, September and November, 1986 and in March and May, 1987. *Frente Marítimo*, 5(A): 39-59. (*in Spanish*)

BRUNETTI, N.E. & PÉREZ COMAS, J.A. 1989b. Abundance, distribution and population structure of squid (*Illex argentinus*) of the south patagonic shelf waters in December 1986 and January-February 1987. *Frente Marítimo*, 5: 61-70. (*in Spanish*)

BRUNETTI, N.E. & ROSSI, G.R. 1990. Informe preliminar sobre la campana argentina-soviet en el B/I EVRIKA (agosto-octubre 1988). INIDEP. Info Tec. No 1, 31 pp.

BRUNETTI, N.E., IVANOVIC, M.L., LOUGE, E. & CHRISTIANSEN, H.E. 1991. Reproductive biology and fecundity of two stocks of the squid (*Illex argentinus*). *Frente Marítimo*, 8(A): 73-84. (*in Spanish*)

BURUKOVSKY, R, FROERMAN, Yu.M. & NIGMATULLIN, M. 1984. Reproductive biology and scale of maturity stage of reproductive system of female squid (*Illex illecebrosus*). NAFO SCR Doc., No. 120, Serial no. 917, 4 pp.

CASTELLANOS, Z.J.A. DE 1960. Una nueva especie de calamar Argentino *Ommastrephes argentinus* sp. nov. (Mollusca, Cephalopoda). *Neotropica*, 6(20): 55-58.

CASTELLANOS, Z.A. 1964. Contribución al conocimiento biologico del calamar argentino *Illex illecebrosus* argentinus. *Bol. Inst. Biol. Mar. Mar del Plata*, 8: 4-33.

CASTELLO, J.P. & MOLLER, 0.0. 1977. Sobre as condições oceanográficas no Rio Grande do Sul. *Atlántica*, Rio Grande, 2: 1-119.

CASTELLO, J.P., DUARTE, A., MOLLER, 0.0., NIENCHESKI, F., ODE-BRECHT, C., WEISS, G., HABIAGA, R.P., BELLOTTO, V.R., KITZMAN, D., SOUTO, C., DE SOUZA R.B., CIOTTI A.M., FILLMAN G., SCHWINGEL P.R., BERSANO J.C., CIRANO, M., FREIRE, K., LIMA JR, I., MELLO, R., MONTEIRO, A., REsGALLA JR, C., SOARES, I. & SUZUKI, M. 1991. On the importance of coastal and sub-Antarctic waters for the shelf ecosystem off Rio Grande do Sul. Anais do II Simpósio de Ecossistemas da Costa Sul e Sudeste Brasileira. Estrutura, Função e Manejo. Pub.Academia de Ciências de Sao Paulo, Brazil, 71(1): 112-129.

CARVALHO, G., THOMPSON, A. & STONER, A.L. 1992. Genetic diversity and population differentiation of the shortfm squid *Illex argentinus* in the south-west Atlantic. *J. Exp. Mar. Biol. Ecol.*, 158: 105-121.

CIOTTI, A.M., ODERBRECH, C, FILLMAN, G & MOLLER, 0.0. 1995. Freshwater outflow and subtropical convergence on phytoplanckton biomass on the southen Brazilian continental shelf. *Continental Shelf Res.*, 15: 1737-1756.

CLARKE, A, RODHOUSE, P.G. & GORE, D.J. 1994. Biochemical composition in relation to the energetics of growth andsexual maturation in the ommastrephid squid *Illex argentinus*. *Phil. Trans. R. Soc. Lond. B.*, 344: 201-212.

CSIRKE, J. 1987. The Patagonian fishery resources and the offshore fisheries in the South-West Atlantic, FAO Fisheries Technical Paper, No. 286. Rome, 75 pp.

FAO 1983. Informe del grupo ad-hoc de trabajo sobre los recursos pesqueros de la plataforma continental patagónica. Roma, 7-11 Febrero 1983. Report of the ad hoc Working Group on fishery resources of the Patagonian Shelf. Rome, 7-11 February 1983. FAO Info Pesca/FAO Fish. Rep. No. 297, Rome, 83 pp.

FAO 1997. Yearbook of fishery statistics. Catches and Landings. Vol 80. FAO, Rome, 713 pp.

FEDULOV, P.P., REMESLO, A. V., BURYKIN, S.N. & POLISHCHUK, J.A. 1990. Variabilidad de la Corriente de Malvinas. *Frente Marítimo*, 6(A): 121-127.

GLORIOSO, P. 1987. Temperature distribution related to shelf-sea fronts on the Patagonian Shelf. *Continental Shelf Res.*, 7: 27-34.

GULLAND, J.A. 1971. The fish resources of the ocean. Fishing News (Books) Ltd., West Byfleet, UK, 255 pp.

HAIMOVICI, M. & ANDRIGUETTO Fo, J.M. 1986. Cefalopodes costeiros capturados na pesca de arrasto do litoral sul do Brasil. *Arq. Biol. Tecnol.*, 29: 473-495.

HAIMOVICI, M. & PÉREZ, J.A.A. 1990. Distribution and sexual maturation of the Argentinean squid, *Illex argentinus* off southern Brasil. *Scientia Marina*, 54: 179-185. (*in Spanish*)

HAIMOVICI, M. & PÉREZ, J.A.A. 1991a. A coastal cephalopod fauna of southern Brazil. *Bull. Mar. Sci.*, 49: 221-230.

HAIMOVICI, M., VIDAL, E.A.G. & PÉREZ, J.A.A. 1995. Larvae of *Illex argentinus* from five surveys on continental shelf of southern Brazil. *ICES Mar. Sci. Symp.*, 199: 414-424.

HATANAKA, H. 1986. Growth and life span of short-finned squid, *Illex argentinus*, in the waters off Argentina. *Bull. Japan. Soc. Sci. Fish.*, 52: 11-17.

HATANAKA, H. 1988. Feeding migration of short-finned squid *Illex argentinus* in the waters off Argentina. Nippon Suisan Gakkashi, 54: 1343-1349.

HATANAKA, H., KAWAHARA, S., UOZUMI, Y. & KASAHARA, S. 1985. Comparison of life cycles of five ommastrephid squids fished by Japan: Todarodes pacificus, *Illex illecebrosus*, *Illex argentinus*, *Nototodarus sloani sloani*, and *Nototodarus sloani gouldi*. *NAFO Sci. Council Studies*, 9: 59-68.

HATFIELD, E.M.C., RODHOUSE, P.G. & BARBER, D.L. 1992. Production of soma and gonad in maturing female *Illex argentinus* (Mollusca: Cephalopoda). *J. Mar. Biol. Assoc*. UK, 72: 281-291.

HUBOLD, G. 1980a. Hydrography and plankton off Southern Brazil and Río de la Plata, August-November, 1977. *Atlántica*, Rio Grande, 4(1): 1-22.

HUBOLD, G. 1980b. Second report on hydrography and plankton off Southern Brazil and Río de la Plata; Autumn Cruise: April-June 1978. *Atlántica*, Rio Grande, (1): 23-42.

IVANOVIC, M.L. & BRUNE1TI, N.E. 1994. Food and feeding of *Illex argentinus*. *Antarctic Sci.*, 6: 185-193.

KLYUCHNIK, T.S. & ZASYPKINA, V.A. 1972. Some data on Argentine squid *Illex argentinus* Castellanos, 1960. *Tr. Atl. Nauchno-Issled Inst. Rhybn. Khoz. Okeanogr.*, 42: 190-192. (as cited in Leta 1981)

KORONK1EWICZ, A. 1986. Growth and life cycle of squid *Illex argentinus* from Patagonian and Falkland Shelf and Polish fishery of squid for this region, 1978-1985. ICES C.M. 1986/K:27, 25 pp.

LAPTIKHOVSKY, V.V. & NIGMATULLIN, CH.M. 1992. Caracteristicas reproductivas de machos y hembras del calamar (*Illex argentinus*). *Frente Marítimo*, 12: 23-38.

LAPTIKHOVSKY, V.V. & NIGMATULLIN, CH. 1993. Egg size, fecundity, and spawning in females of the genus *Illex* (Cephalopoda: Ommastrephidae). *ICES J. Mar. Sci.*, 50: 393-403.

LAGECKIS, R. & GORDON, A. 1982. Satellite observations of the Brazil and Falkland currents, 1975 to 1976. *Deep-Sea Res.*, 29: 375-401.

LETA, H.R. 1981. Aspectos biológicos del calamar *Illex argentinus*. Proyecto URU/78/005, FAO/PNUD, 50 pp.

LETA, H.R. 1987. Descripción de los huevos, larvas y juveniles de *Illex argentinus* (Ommastrephidae) y juveniles de *Loligo brasiliensis* (Loliginidae) en la zona comun de pesca Argentino-Uruguaya. Publ. Cient. INAPE, 1(1):1-8.

LETA, H.R. 1992. Abundance and distribution of *Illex argentinus* rhynchoteuthion larvae (Cephalopoda, Ommastrephidae) in the waters of the Southwestern Atlantic (Argentine-Uruguayan common fishing zone). *S. African J. Mar Sci.*, 12: 927-941.

LIMA, D.I., GARCIA, C.A.E. & MOLLER, 0.0. 1996. Ocean surface processes on the southern Brazilian shelf: Characterization and seasonal varia.bility. *Continental Shelf Res.*, 16: 1307-1319.

LIPINSKI, M. 1979. Universal maturity scale for the commercially important squids (Cephalopoda: Teuthoidea). The results of maturity classification of the *Illex illecebrosus* (Lesueur, 1821) populations for the years 1973-1977. ICNAF Res. Doc., No. 38, Serial 5364, 40 pp.

MOISEEV, S.I. 1991. Observations of the vertical distribution and behaviour of the nektonic squids using manned submersibles. *Bull. Mar. Sci.*, 49: 446-456.

NIGMATULLIN, CH.M. 1987. Ecological niche of the oceanic squids of the family Ommastrephidae: ontogenetic and evolutionary aspects. *In Molluscs. Results and perspectives of their investigations*, p. 92-94. VIII All-Union Symposium on Molluscan Study 7-9 April, Nauka Press, Leningrad. (*in Russian*)

NIGMATULLIN, CH. M. 1989. Mass squids of the South-West Atlantic and brief synopsis of the squid (*Illex argentinus*). *Frente Marítimo*, 5(A): 71-81. (*in Spanish*)

NIGMATULLIN, CH. M. & SHUKHGALTER, O.A. 1990. Helminthofauna and ecological aspects of the parasitary relations of the squid (*Illex argentinus*) in the Southwest Atlantic. *Frente Marítimo*, 7(A): 57-68. (*in Spanish*)

O'DOR, R.K. 1983. *Illex illecebrosus. In* P.R. BOYLE, ed. *Cephalopod life cycles* Vol. I, p. 175-199. London, Academic Press.

O'DOR, R.K. 1992. Big squid in big currents. *S. African J. Mar. Sci.*, 12: 225-235.

OLSON, D.B., PODESTA, G.P., EVANS, R.H. & BROWN, O.B. 1988. Temporal variation in the separation of the Brazil and Malvinas currents. *Deep-Sea Res.*, 35: 1971-1990.

OTERO, H.O., BEZZI, S.I., PERROTA, R., PÉREZ COMAS, J.A., SIMONAZZI, M.A. & RENZI, M.A. 1981. Los recursos pesqueros demersales del mar argentino. Parte 111- Distribución, estructura de la población, biomassa y rendimiento potencial de la polaca, el bacalao austral, la merluza de cola y del calamar. *Contrib. Inst. Nac. Invest. Desarrollo Pesq.* Mar del Plata, Argentina, No.383: 28-41.

PARFENIUK, A.V., FROERMAN, Yu. M. & GOLUB, A.N. 1992. Particularities in the distribution of the squid juveniles *Illex argentinus* in the area of the Argentine hollow. *Frente Marítimo*, l2(A): 105-111. (*in Spanish*)

PETERSON, R.G. 1992. The boundary currents in the western Argentine Basin. *Deep-Sea Res.*, 39: 623-644.

PODESTA, G.P. 1990. Migratory pattern of the Argentina hake *Merluccius hubbsi* and oceanic processes in the Southwestern Atlantic Ocean. *Fish. Bull.*, 88: 167-177.

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. & HATFIELD, E.M.C. 1990a. Age determination in squid using statolith growth increments. *Fish. Res.*, 8: 323-334.

RODHOUSE, P.G. & HATFIELD, E.M.C. 1990b. Dynamics of growth and maturation in the cephalopod *Illex argentinus* de Castellanos, 1960 (Teuthoidea: Ommastrephidae). *Phil. Trans. Royal Soc. Lond.* B, 329: 229-241.

RODHOUSE, P.G. & HATFIELD, E.M.C. 1992. Production of soma and gonad in maturing male *Illex argentinus* (Mollusca: Cephalopoda). *J. Mar. Biol. Assoc.* UK, 72: 293-300.

RODHOUSE, P.G., SYMON, C. & HATFIELD, E.M.C. 1992. Early life cycle of cephalopods in relation to the major oceanographic features of the southwest Atlantic Ocean. *Mar. Ecol. Progr. Ser.*, 89: 193-195.

RODHOUSE, P.G., BARTON, J., HATFIELD, E.M.C., & SYMON, C. 1995. *Illex argentinus*: life cycle, population structure, and fishery. *ICES Mar. Sci. Symp.*, 199: 425-432.

ROSENBERG, A.A., KIRKWOOD, G.P., CROMBIE, J.A. & BEDDINGTON, J.R. 1990. The assessment of stocks of annual squid species. *Fish. Res.*, 8: 335-349.

SANTOS, R.A. 1992. Relações tróficas do calamar argentino *Illex argentinus* (Castellanos, 1960) (Teuthoidea: Ommastrephidae) no sul do Brasil. Tese de mestrado. Funda~ao Universidade do Rio Grande, Rio Grande-RS, 83 pp.

SANTOS, R.A. & HAIMOVICI, M. 1996. Reproductive biology of the winter-spring spawners of *Illex argentinus* (Cephalopoda: Ommastrephidae) off southern Brazil. *Scientia Marina* 61: 53-64.

SANTOS, R.A. & HAIMOVICI, M. *in press*. Food and feeding of the short-finned squid *Illex argentinus* (Cephalopoda:Omastrephidae) off southern Brazil. *Fisheries Research*.

SARDELLA, N.H., ROLDAN, M.I. & TANZOLA, D. 1990. Helmintos parasitos del calamar (*Illex argentinus*) en la subpoblación bonaerense-norpatagonica. *Publ. Tec. Mix. Fr. Mar.*, 7: 53-56.

SATO, T. & HATANAKA, H. 1983. A review of assessment of Japanese distant -water fisheries for cephalopods. *In* J. F. CADDY, ed. *Advances in assessment of world cephalopod resources*, p. 145-180. FAO Fisheries Technical Paper No. 231. Rome.

SCHULDT, M. 1979. Contribución al conocimiento del ciclo reproductor de *Illex argentinus*. Comisión de Investigaciones Científicas de la Provincia de Buenos Aires, Monographias 10: 1-110.

THOMSEN, H. 1962. Masas de agua características del Océano Atlántico (Parte Sudoeste). Servicio de Hidrografía Naval, Secretaria de Marina, Buenos Aires, Publ. 11621: 1-27.

THRELFALL, W. 1970. Some helminth parasites from *Illex argentinus* (Cephalopoda: Ommastrephidae). *Can. J. Zool.*, 48: 195-198.

TSHCHETINNIKOV, A.S. & TOPAL, S.K. 1991. La composición de la dieta de los calamares *Illex argentinus* y *Loligo patagonica* en el litoral argentino. Resúmenes del VIII Simposio Científico, Comisión Técnica Mixta del Frente Marítimo, Montevideo, 27 pp.

UOZUMI, T. & SHIBA, C. 1993. Growth and age composition of *Illex argentinus* (Cephalopoda: Oegospsida) based on daily increment counts in statoliths. *In* T. OKUTANI, R.K. O'DOR & T. KUBODERA, eds. *Recent advances in cephalopod fisheries biology*, p. 591-605, Tokai University Press, Tokyo.

VIDAL, E.A.G. 1994. Relative growth of paralarvae and juveniles of *Illex argentinus* (Castellanos, 1960) in southern Brazil. *Antarctic Sci.*, 6: 275-282.

WEISS, G., HUBOLD, G. & BONECKER, A.C.T. 1988. Egg and larvae of *Maurolicus muelleri* (Gmelin, l789)(Teleostei, Sternoptychidae) in the southwest Atlantic. *Meeresforschung* 32(1): 53-60. Hamburg.

YESAKI, M. 1973. Sumário dos levantamentos de pesca exploratória ao largo da costa sul do Brasil e estimativa da biomassa de peixe demersal e potencial pesqueiro. Dóc. Téc. SUDEPE-PDP/T, Rio de Janeiro, 1: 1-27.