

## Food and feeding of *Illex argentinus*

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**Abstract:** The diet and feeding behaviour of *Illex argentinus* were determined from analysis of stomach contents of squid caught during four bottom trawl surveys carried out over the Bonaerensis (34–40°S, autumn–winter 1991) and Patagonian (45–55°S, summer–autumn 1992) shelves of Argentina. Crustaceans, mainly *Themisto gaudichaudii* and, to a lesser extent, euphausiids were the most important components of the diet in both areas and years, although there were considerable geographical differences in the relative proportion of the main prey. In the Patagonian area, during summer and autumn of 1992, almost all squid preyed on crustaceans (percentage occurrence = 85.29%), followed by squid (11.76%) and fish (2.94%). On the Bonaerensis shelf, during autumn and winter of 1991, crustaceans were most important by percentage occurrence (56.96%), but fish and squid accounted for a large proportion of the diet (29.41% and 13.62% respectively). Myctophids were prevalent among the fish and cannibalism was on *I. argentinus* juveniles. Changes in diet composition with squid size demonstrated the opportunistic nature of *I. argentinus* feeding. Although large squids were able to catch large prey (fish, squid), they also fed on small crustaceans when available, especially in the Patagonian area. The relative abundance of different prey organisms probably determined the diet. In both areas and both years *I. argentinus* fed mostly during daylight hours, starting in the morning and reaching a maximum in the afternoon. No difference in feeding behaviour was observed between the sexes.

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**Key words:** *Illex argentinus*, food, feeding, crustaceans, fish, cannibalism

### Introduction

*Illex argentinus* is the most important cephalopod species in the southwest Atlantic (27–55°S) where it plays a principal role in the ecosystem (Angelescu & Prenski 1987, Brunetti 1988). Knowledge of feeding ecology by this squid is thus an important aspect of the study of this system. Koronkiewicz (1980, 1986) analysed the diet of adult squid caught by jigging vessels in the south Patagonian waters of the continental shelf and slope outside the Argentine Economic Zone, in the period December–July of several years. The diet of juveniles and subadults (80–170 mm ML) caught on the continental slope between 45–46°30'S during the spring of 1988 has been described (Anon. 1989) and the diet and trophic relationships of juveniles and adults off southern Brazil were analysed by Aguiar dos Santos (1992).

This paper describes the feeding behaviour and diet of *Illex argentinus* in two regions of the Argentine continental shelf: the Bonaerensis area (34–40°S) during autumn–winter of 1991, and the Patagonian area (45–55°S) in summer and autumn of 1992.

### Materials and methods

Material was collected during four bottom-trawl research cruises by the RV *Cap. Oca Balda* in the Bonaerensis region (34–40°S) during autumn and winter of 1991, and the RV *Dr. E. L. Holmberg* in the Patagonian area (45–55°S) during summer and autumn of 1992 (Fig. 1).

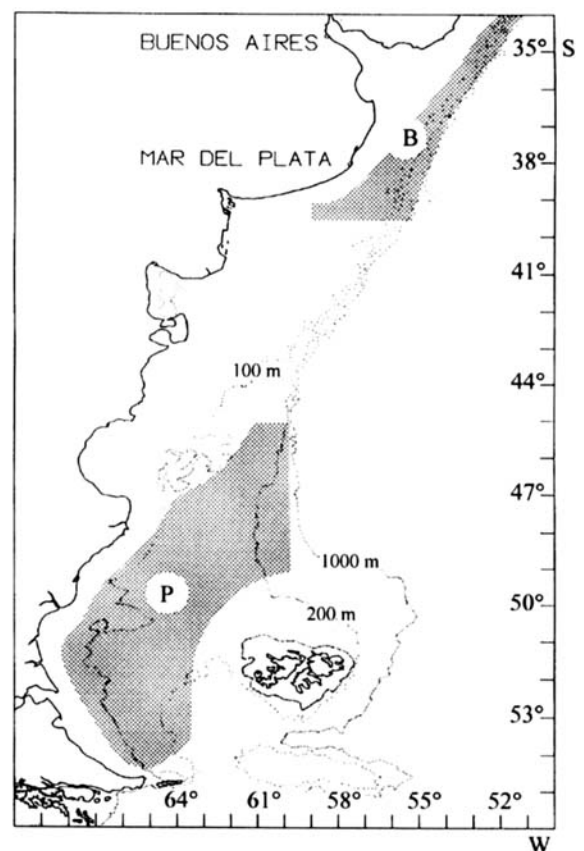


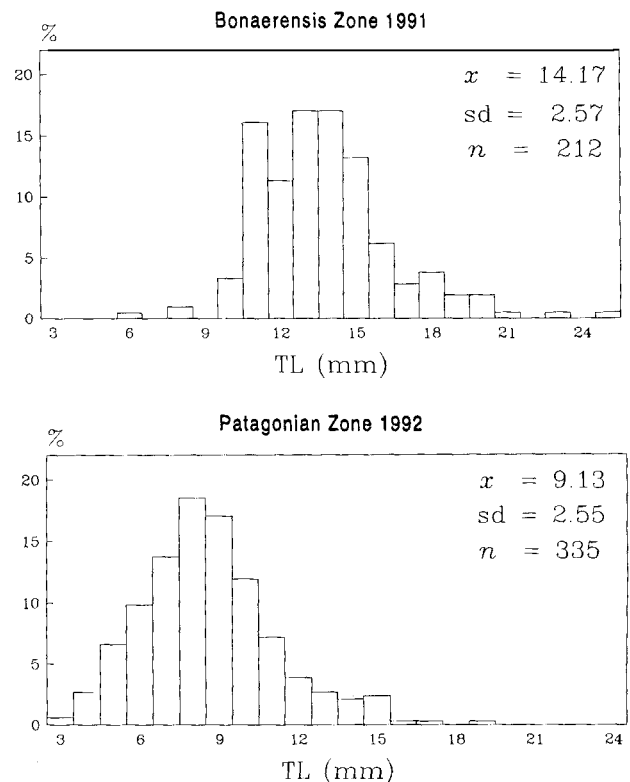
Fig. 1. Location of sampling areas: B, Bonaerensis zone (Autumn and winter 1991), P, Patagonian zone (summer and autumn 1992).

**Table I.** List of food items found in stomachs of *Illex argentinus* and number of squids with each item during autumn and winter 1991 in the Bonaerensis zone (B) and, summer and autumn 1992 in the Patagonian zone (P).

Food items	No. of squids with each item			
	B-autumn	B-winter	P-summer	P-autumn
<b>Phylum Crustacea</b>				
<b>Order Amphipoda</b>				
<i>Themisto gaudichaudii</i>	113	5	85	121
<i>Hyperoche medusarum</i>	1	–	–	–
<i>Cylopus magellanicus</i>	1	–	–	–
<i>Primno macropa</i>	3	–	8	–
<b>Order Euphausiacea</b>				
<i>Euphausia lucens</i>	21	18	25	63
<i>Euphausia lucens</i>	10	9	7	22
<i>Nematoscelis megalops</i>	3	–	1	–
<i>Thysanoessa gregaria</i>	5	–	3	–
<b>Phylum Mollusca</b>				
<b>Class Cephalopoda</b>				
<i>Illex argentinus</i>	25	10	–	–
<i>Loligo gahi</i>	–	–	10	22
<i>Loligo sanpaulensis</i>	10	2	–	–
<b>Phylum Chordata</b>				
<b>Class Osteichthyes</b>				
<b>Family Myctophidae</b>				
<i>Gymnoscopelus nicholsi</i>	33	5	–	–
<i>Protomyctophum tenisoni</i>	11	22	–	–
<i>Lampichthys procerus</i>	9	12	–	–
<b>Family Engraulidae</b>				
<i>Engraulis anchoita</i>	7	–	–	–
<b>Unidentified fish</b>				
Otolith "A"	1	–	–	–
Otolith "B"	1	–	–	–
Otolith "C"	–	2	–	–
Otolith "D"	–	1	–	–
Otolith "E"	–	–	1	–
<b>Miscellaneous</b>				
<b>Phylum Bryozoa</b>				
Phylum Crustacea	12	–	–	–
Subclass Copepoda				
<i>Calanus propinquus</i>	–	–	1	–
Class Ostracoda				
Family Cytheridae	–	–	1	–
Class Malacostraca				
Order Isopoda	–	–	–	–
Suborder Valvifera	1	–	–	–
<b>Phylum Insecta</b>				
Class Coleoptera				
Family Anobiidae	2	–	–	–
No. of squids examined	192	54	104	168

Dorsal mantle length (ML), weight, sex, maturity stage, following the eight stage scale of Brunetti (1990), and stomach fullness were recorded for all individuals of each sample. Stomach fullness (RD) was rated using a four point scale proposed by Amaratunga & Durward (1978): 0 = empty, 1 = half full, 2 = full, 3 = distended.

Contents of 518 frozen stomachs were examined under a binocular microscope. Prey items were counted and identified to the lowest taxonomic level possible. Measurements, such as amphipod eye diameter, otolith length, squid beak rostral length



**Fig. 2.** Percentage distribution of the estimated sizes (TL: total length) of *Themisto gaudichaudii* preyed by *Illex argentinus* in the Bonaerensis and Patagonian zones.

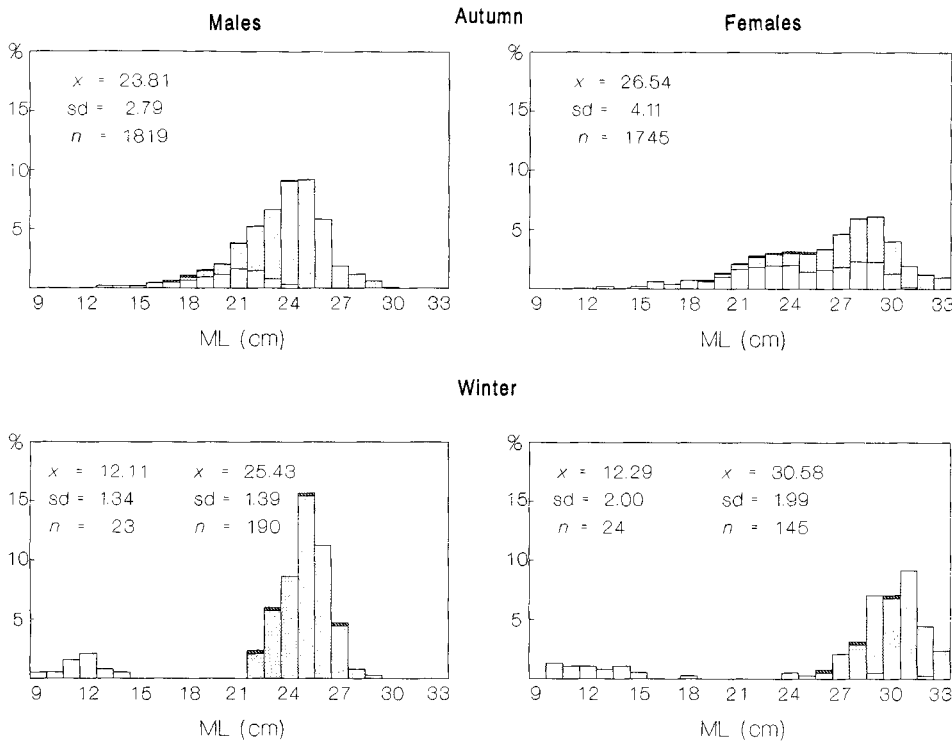
and statolith length, were made using an ocular micrometer with a precision of 0.01 units, and transformed to mm. A variety of relationships were used to estimate prey size e.g. eye diameter-total length for *Themisto gaudichaudii* and upper/lower beak rostral length-mantle length for *Illex argentinus* (Ivanovic, unpublished data).

Analysis of the diet utilized two indices: percentage occurrence and a dominance index (Hyslop 1980, Breiby & Jobling 1985). Percentage occurrence (PO) of a given prey is the proportion of the total number of fed squid that had eaten that prey:  $PO = (A/N) * 100$ , where A is the number of stomachs containing prey 'a' and N the total number of stomachs with food. The dominance index (DI) was determined by subjectively assessing the prey type dominating the biomass in each gut examined. The dominance index for each prey type was calculated as  $DI(a) = (A/N) * 100$ , where A is the number of guts in which prey type 'a' was dominant and N the total number of guts analysed for this purpose.

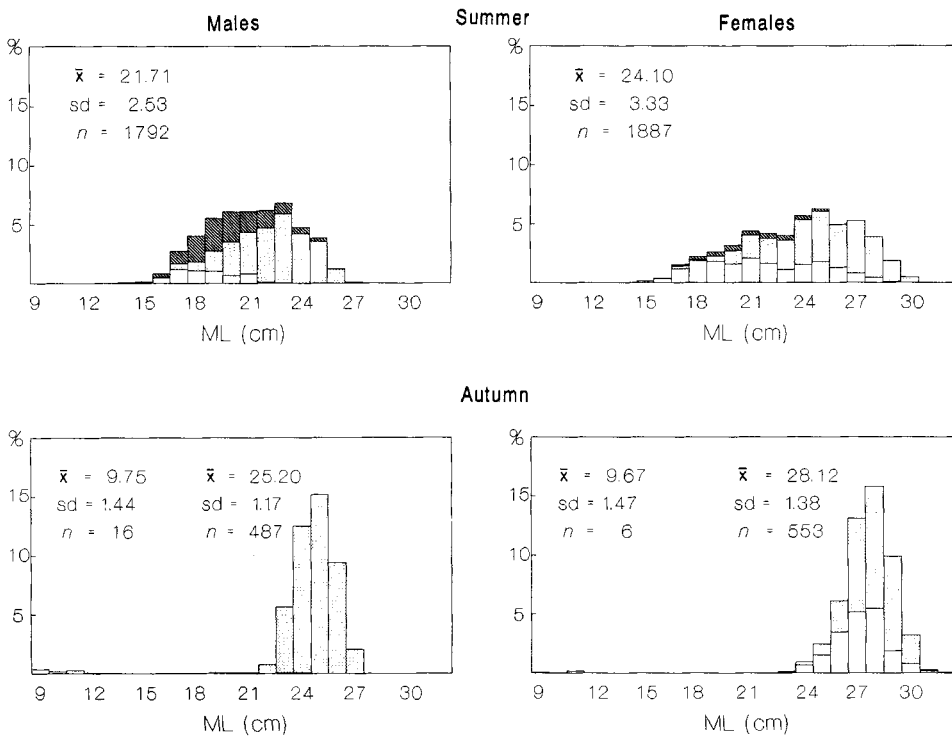
## Results

### Diet

Food consisted of four major groups of prey that could be classified by size: small crustaceans (mostly amphipods and euphausiids) and large fish and squid (Table I). The principal



**Fig. 3.** Percentage distribution of mantle lengths and maturity stages by size of squid caught during autumn and winter of 1991 in the Bonaerensis zone. (Maturity stages I-III: empty; IV-V: broken lines; VI-VIII: solid lines).

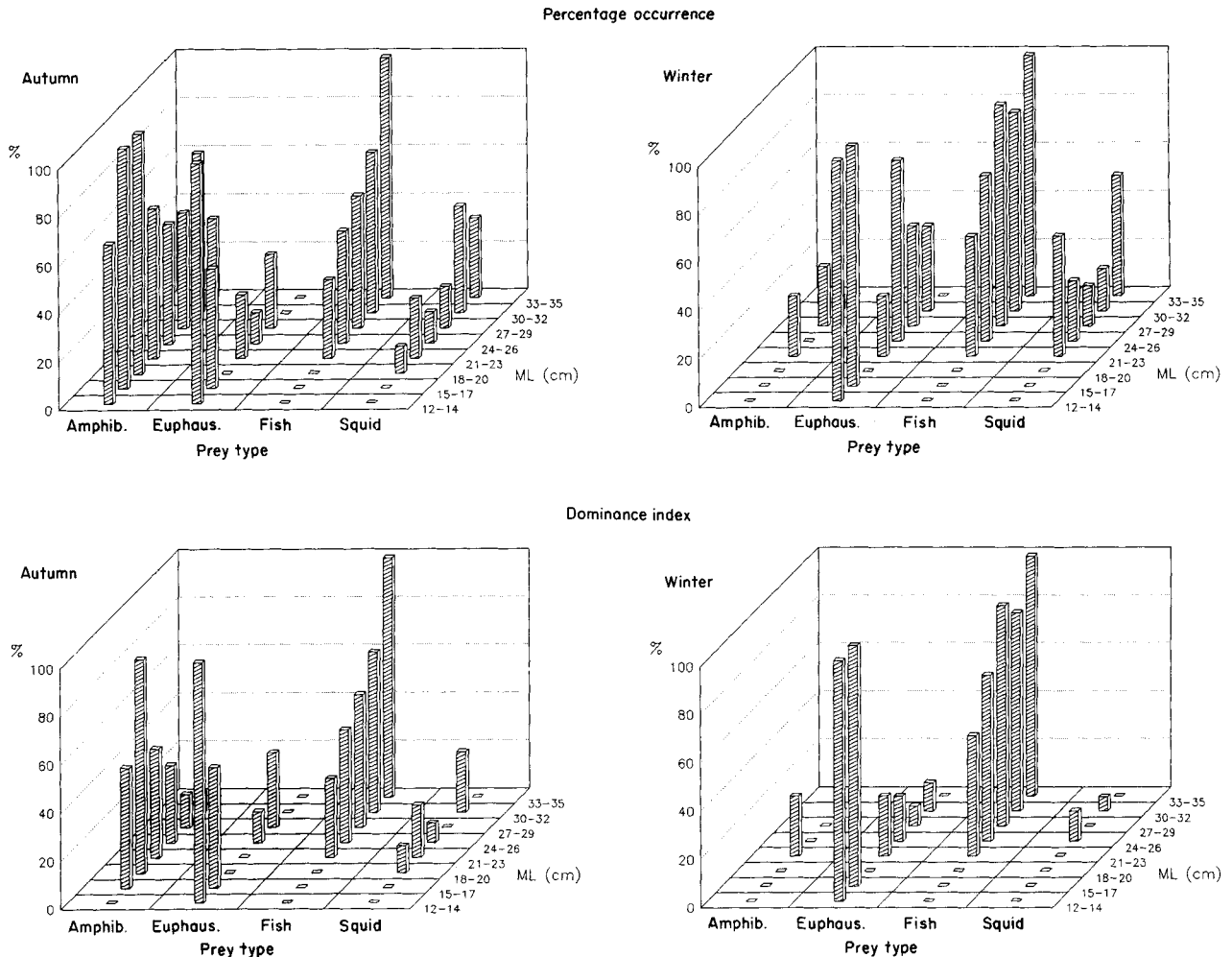


**Fig. 4.** Percentage distribution of mantle lengths and maturity stages by size of squid caught during summer and autumn of 1992 in the Patagonian zone. (Maturity stages I-III: empty; IV-V: broken lines; VI-VIII: solid lines).

amphipod was the hyperiid *Themisto gaudichaudii*; other species only occurred occasionally. Identification was based on structures such as heads, eyes, pereopods and uropods, which did not suffer much change in the stomach. Estimated size of specimens showed that those preyed on in the Bonaerensis zone (autumn–winter 1991) were larger than those from the Patagonian

region (summer–autumn 1992) (Fig. 2).

Euphausiids were the frailest components of the stomach contents, making species identification difficult, and often impossible. However, three species were identified from a few complete specimens: *Euphausia lucens*, *Nematoscelis megalops* and *Thysanoessa gregaria*. No measurements could be taken



**Fig. 5.** Changes in the dietary composition of *Illex argentinus* with mantle length (ML) in the Bonaerensis region during autumn and winter of 1991.

because of the advanced state of digestion.

Fish were mainly represented by myctophids. Three species were identified from otoliths: *Gymnoscopelus nicholsi* and *Protomyctophum tenisoni*, which were the most abundant, and *Lampichthys procerus*. Five other otolith types, probably myctophids, could not be identified, but were only found occasionally. Estimated size of fish consumed was 50–140 mm (total length). Squid from the Bonaerensis shelf had also fed on smaller quantities of *Engraulis anchoita*, identified from scales as otoliths were absent.

Squid were less important in the diet. In the Patagonian zone only one species, *Loligo gahi*, was consumed. In the Bonaerensis zone *Loligo sanpaulensis* was found occasionally and there was a high proportion of cannibalism on juveniles. Squid were easily recognized from beaks, statoliths and pens. Some paralarval (5–7 mm ML) and small juvenile (8–12 mm ML) *Illex argentinus* were found whole in stomachs and ML measured directly. Estimated size (from beaks) of juveniles consumed was

20–110 mm ML ( $\bar{x} = 5.70$ ;  $sd = 1.70$ ;  $n = 47$ ) in autumn, and 50–130 mm ML ( $\bar{x} = 7.58$ ;  $sd = 1.58$ ;  $n = 34$ ) in winter.

#### Diet in relation to squid size

Percentage frequency distribution of ML and maturity stage by squid size from each zone and season are shown in Figs 3 & 4. To test if the relative proportion of the four categories of food changed with squid size, percentage occurrence and dominance index were analysed by mantle length. Squid size, ranging between 90–350 mm ML, were grouped into 30 mm interval (Figs 5 & 6). In the Bonaerensis zone in 1991 there was a change in the diet composition of squid at c. 200 mm ML. Squid below that size ate only crustaceans, whereas larger specimens also fed on fish and squid. The dominant crustaceans were amphipods and euphausiids during autumn, and almost exclusively euphausiids in winter. Fish was always dominant in squid larger than 200 mm ML.

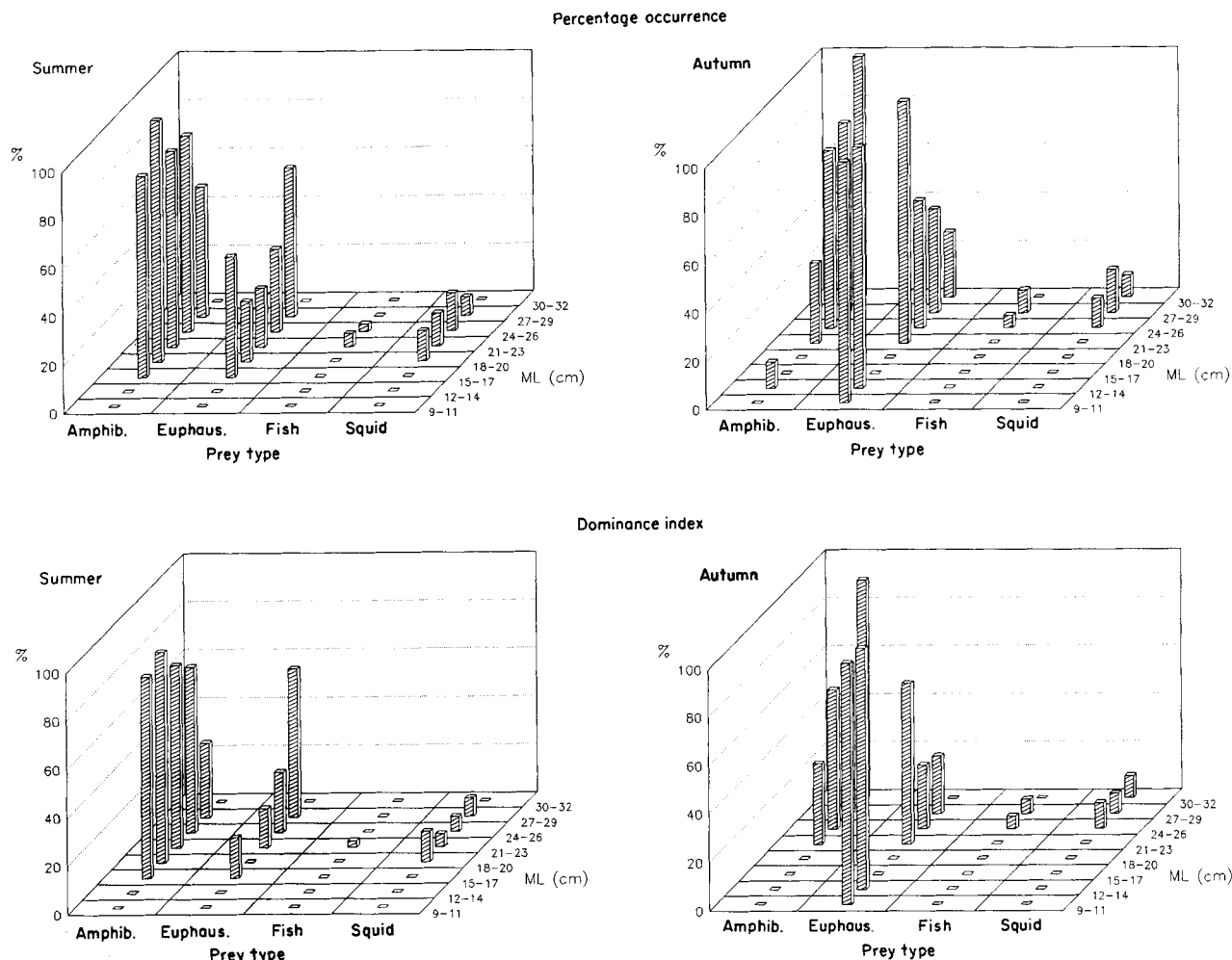


Fig. 6. Changes in the dietary composition of *Illex argentinus* with mantle length (ML) in the Patagonian region during summer and autumn of 1992.

In the Patagonian region during 1992, squid of all sizes mainly ate crustaceans, although the largest (> 200 mm ML) consumed small quantities of squid and fish. The dominant prey was euphausiids in squid 90–140 mm ML in autumn, and amphipods for larger squid during both seasons. Fish and squid were relatively unimportant in the diet, compared with the situation in the Bonaerensis region.

*Diet in relation to time of day*

Dietary analysis, by the percentage occurrence and dominance index of prey at 2 h intervals, revealed that all prey types were consumed during the whole day in both areas and years (Fig. 7). There was no strong evidence of a change in dietary composition with time of day, although within the bonaerensis region during 1991, consumption of crustaceans seemed higher in the morning, whereas that of fish and squid appeared to be higher in the afternoon. In the southern area squid consumed crustaceans during daylight and squid (*Loligo gahi*) at dusk and dawn.

*Diet in relation to geographical area and year*

There were strong differences in dietary composition between the Bonaerensis zone in 1991 and the Patagonian zone in 1992 (Fig. 7). In the Bonaerensis area in 1991 (autumn–winter) the prey with highest percentage occurrence were amphipods (36.84%) and fish (29.41%), while euphausiids and squid were eaten in lesser amounts (20.12% and 13.62% respectively). Most predation on squid was through cannibalism of juveniles.

In the Patagonian area in 1992 (summer–autumn) highest percentage occurrence (85.29%) was attributed to crustaceans, mainly *Themisto gaudichaudii* (60.66%) and to a lesser extent euphausiids (24.63%). Squid, exclusively *Loligo gahi* was of secondary importance (11.76%). Fish were eaten only occasionally (2.94%).

Diet diversity was higher in the northern area (1991) than the southern (1992) (Table I).



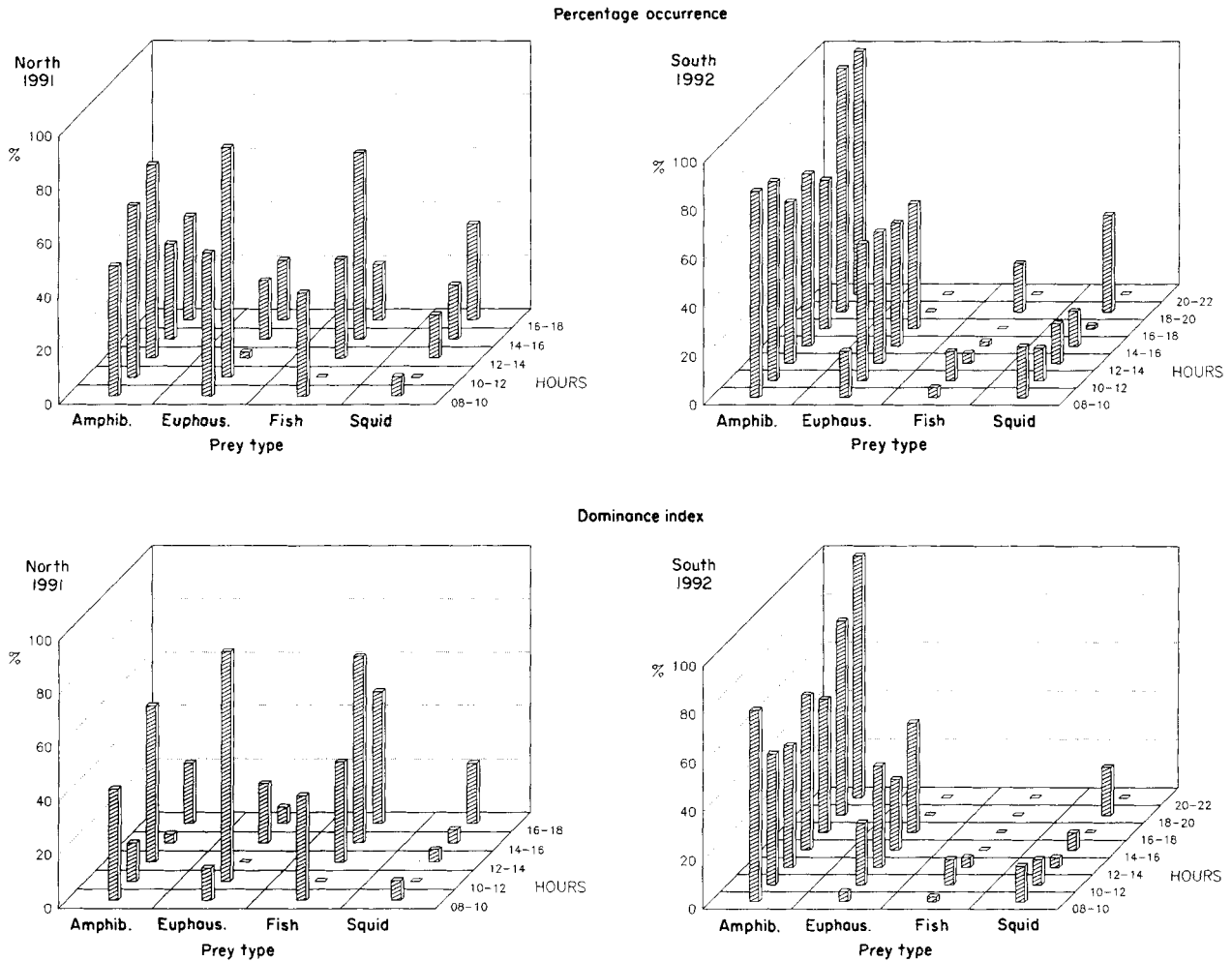


Fig. 7. Changes in the dietary composition of *Illex argentinus* with time interval in the Bonaerensis region (north) in autumn–winter 1991 and in the Patagonian region (south) in summer–autumn 1992.

#### Diel variation in feeding

Diel changes in feeding behavior were analysed at 2 h intervals during daylight on each cruise, usually between 06h00–18h00, with the exception of the Patagonian zone in summer, when the sampling period was 06h00–22h00 (Figs 8 & 9). There were no samples from the Bonaerensis zone in winter for 10h00–12h00.

Highest percentage of empty stomachs (RD: 0) was observed during early morning in all cases (06h00–08h00). Proportion of stomachs with some food (RD: 1) increased with time, peaking at 14h00–16h00 (Bonaerensis zone) and 08h00–12h00 (Patagonian zone). During autumn, in both regions, the proportion of full and distended stomach records (RD: 2 & 3) increased together with the proportion of RD 1 records, but RD 1 records predominated except for the interval 16h00–18h00. During summer, in the southern region, there were more RD 3 and 2 than RD 1 records between 12.00–14.00, showing a higher feeding intensity than in autumn.

The results show that squid fed intensively during daylight,

especially from noon onward, when more than 50% of the individuals had food in their stomachs.

#### Feeding behavior in relation to sex and maturity stage

Presence/absence of food was analysed by sex for three phases of the life cycle: immature–maturing (stages I–III), mature (stages IV–V), and spawning–post-spawning (stages VI–VIII) (Fig. 10). The Bonaerensis area was examined in autumn and the Patagonian area in summer because of differences in the number of squid of different maturity stages available for study in the two areas in the two seasons (Figs 3 & 4).

There was no difference in feeding activity between males and females in either area. There were no differences among the three maturity phases in the southern area, but immature squids from the north always (from 08h00) had a higher percentage of stomachs with food indicating longer and more intense feeding activity.

Mature and spawning–post-spawning squid from the south

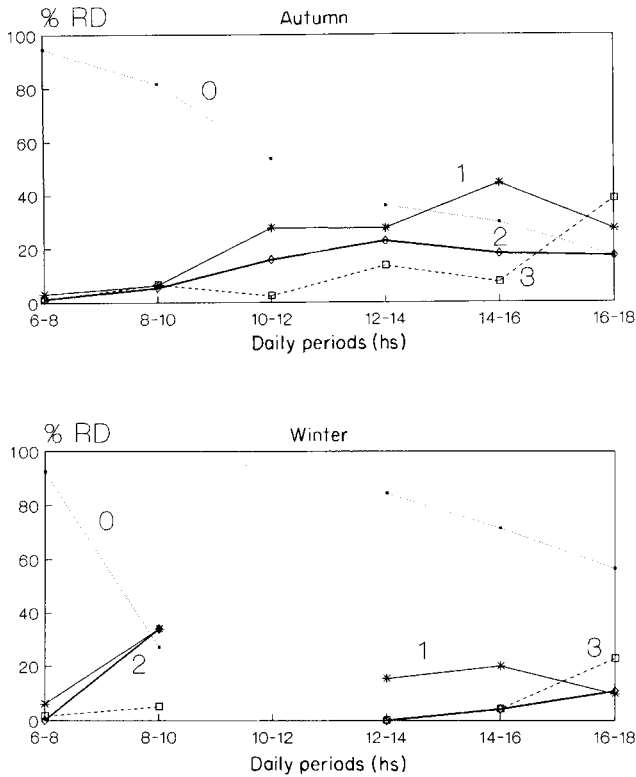


Fig. 8. Percentage distribution by hours of the four stomach repletion degrees (RD: 0,1,2,3) in the Bonaerensis zone during autumn and winter of 1991.

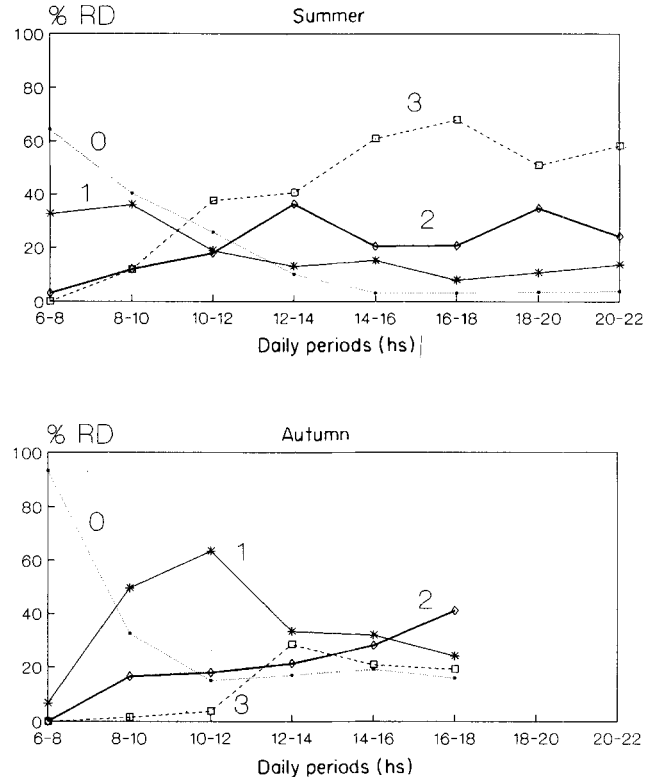


Fig. 9. Percentage distribution by hours of the four stomach repletion degrees (RD: 0,1,2,3) in the Patagonian zone during summer and autumn of 1992.

corresponded to the summer spawning stock, whereas immature and maturing individuals (stage I-III) came from the autumn spawning stock (Brunetti 1988). Squid of the summer spawning stock, when mature, and the autumn spawning stock when maturing, have similar sizes, 150–250 mm ML so we compared different maturity stages but approximately comparable sizes, and found no differences in feeding activity. In the north, where the abundance of spawning and post-spawning squid was low, squid size increased with maturity stage, especially in males. Different feeding activity between the maturity phases in this area might therefore have been due mainly to size effects rather than to maturity effects.

*I. argentinus* appears to feed during its entire life cycle, since stomachs with food were present in spawning and post-spawning individuals (maturity stages VI-VIII).

**Discussion**

Stomach contents were often well digested, making it difficult to identify species for quantitative study, but the qualitative indices used here provide useful data on the feeding behaviour of *I. argentinus*. The subjective dominance index provides valuable comparative information about composition of the diet, in spite of its limitations.

The diet of *I. argentinus* throughout its range is characterized by a low diversity of prey items, including crustaceans, fish and squid (Koronkiewicz 1980, 1986, Anon. 1989, Aguiar dos Santos 1992). In many cephalopod species prey changes during growth and with season or habitat (Boucher-Rodoni *et al.* 1987). Our analysis suggests size-related change in diet of squid from the Bonaerensis zone in 1991. This trend agrees with that observed by Aguiar dos Santos (1992), who found that diet of the subadult and adult squid off southern Brazil consisted mainly of fish and squid, whereas that of the juveniles consisted of crustaceans (copepods, mysids and decapods). Similar behaviour has been reported for other ommastrephid squids. Vinogradov & Noskov (1979) found that nearly 50% of the diet of large and small *I. illecebrosus* consisted of crustaceans, the remainder being squid in the smaller individuals (100–180 mm ML) and fish in the larger (190–250 mm ML). For the same species, Amaratunga *et al.* (1979), Amaratunga (1983) and Froerman (1984) reported that there is a size-related change in the diet, at around 200 mm ML. Specimens below that size feed principally on euphausiids, the largest squid feed on fish. Sanchez (1982) found that *I. coindetii* also changes diet from euphausiids to fish with size. O’Sullivan & Cullen (1983) reported that small *Nototodar* *gouldi* fed preferently on crustaceans but large specimens were more likely to eat cephalopods. Breiby &

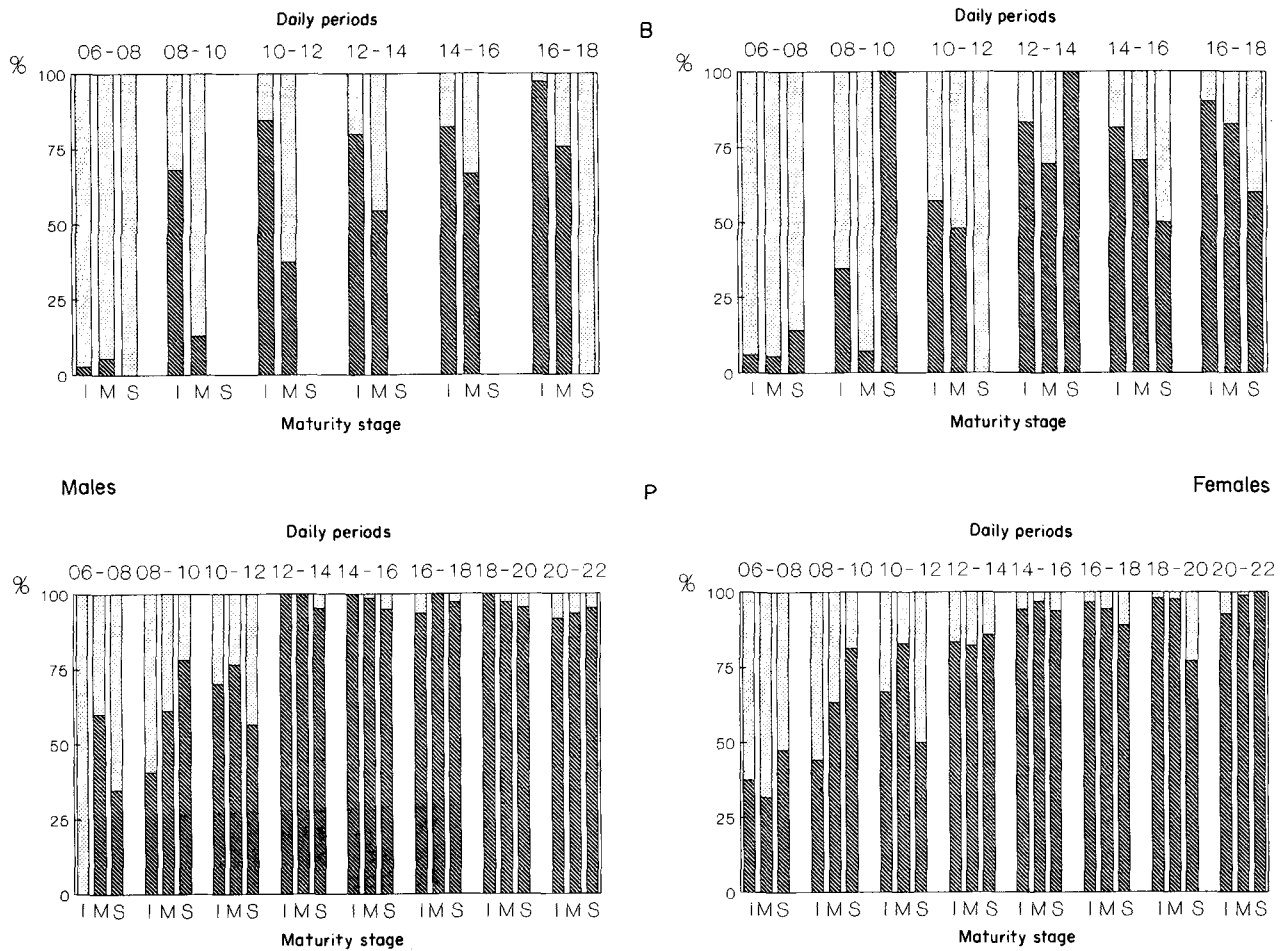


Fig. 10. Percentage distribution of squid stomachs with food (solid lines) and without food (broken lines), by maturity stage (I. immature, M. mature, S. spawning-postspawning), sex and hours. B. Bonaerensis zone in autumn 1991, P. Patagonian zone in summer 1992.

Jobling (1985) observed a similar pattern in *Todarodes sagittatus* with a change in the diet at 330 mm ML.

Conversely, size-related change in diet was not evident in *I. argentinus* from the Patagonian region, where even the largest squids ate almost exclusively amphipods. In the same area, during summer and autumn of several years, Koronkiewicz (1980, 1986) found that they had eaten principally crustaceans (*Munida gregaria* larvae) and low quantities of fish and squid. Food of juveniles (80–170 mm ML) from the Patagonian slope was found to be euphausiids (*Euphausia* sp), and to a lesser extent the hyperiid, *Themisto gaudichaudii* (Anon. 1989).

Our results demonstrate the opportunistic nature of *I. argentinus* feeding, similarly reported elsewhere for many cephalopod species (Lipinski 1992). Although large squids can capture large prey, as in the northern area in 1991, the relative abundance of different prey organisms probably determined the diet. The main prey available in the southern area in 1992 appears to have been crustaceans and in those samples there was no difference in the diet between juveniles and adults.

In both regions and both years *I. argentinus* fed mostly during daylight, when near the seabed, starting in the morning and reaching a maximum in the afternoon. Koronkiewicz (1986) observed that feeding activity was most intense during daytime, beginning at dawn and declining from dusk with a minima in the second half of the night. This conflicts with Aguiar dos Santos (1992) who showed that off southern Brazil lowest feeding activity (33.5%) occurred between 12h00–18h00 and highest (69.1%) during night (18h00–01h00). Amaratunga *et al.* (1979) reported that *I. illecebrosus* feeds during the day, with highest intensity between 13h00 and 24h00 and a maximum in the period 15h00–17h00. This is similar to observations in the present study.

There was no difference in feeding behaviour of *I. argentinus* between the sexes and feeding usually continued after spawning. Similar results were reported for mature individuals of *Nototodaros gouldi* (O'Sullivan & Cullen 1983) which continued to feed, but less intensively than immature squid. The authors proposed that this behaviour was due to the size of the individuals



rather than maturity stage. Laboratory experiments on *I. illecebrosus* showed that, in this species, fully mature females continued feeding until a few days before spawning (O'Dor 1983).

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