NOTE

Diet of spring and summer spawning groups of *Illex argentinus* inhabiting coastal waters in San Matias Gulf (northern Patagonia, Argentina)

Augusto César Crespi-Abril^{1,*}, Maria Magdalena Trivellini²

¹Centro Nacional Patagónico (CENPAT-CONICET), Boulevard Brown s/n, Puerto Madryn 9120, Chubut, Argentina ²Universidad Nacional de la Patagonia San Juan Bosco, Boulevard Brown s/n, Puerto Madryn 9120, Chubut, Argentina

ABSTRACT: To study the diet of 2 coastal spawning groups of *Illex argentinus*, we analyzed the stomach contents of 3645 specimens (10 to 36 cm in mantle length). More than half (58%) of observed stomachs were empty. There were no differences in the prey consumed between specimens of different sex and maturity stages. Additionally, no differences were observed in the diet among individuals belonging to either the summer or spring spawning groups. The most frequent prey item was fishes (0.79 frequency of occurrence), followed by cephalopods (0.18) and lastly by crustaceans (0.09). The seasonal variation of empty stomach frequency and the mean stomach fullness revealed that squids fed more actively in spring and summer and mainly preyed upon small pelagic fishes.

KEY WORDS: Illex argentinus · Near-shore waters · Diet · Cephalopods

- Resale or republication not permitted without written consent of the publisher

INTRODUCTION

Squids generally play a key role in marine ecosystems, as predators, due to their high rates of consumption (Rodhouse & Nigmatullin 1996), and as prey, since most top predators consume them (Smale 1996, Clarke 1986, Croxall & Prince 1996, Klages 1996). Argentine shortfin squid *Illex argentinus* (Castellanos, 1960) is not an exception to this rule and is an important link in the trophic web of the Argentinean shelf community (Angelescu & Prenski 1987, Ivanovic 2000, Santos & Haimovici 2001, Koen-Alonso & Yodzis 2005). However, the diet of this species changes among regions along its geographical distribution range (Ivanovic & Brunetti 1994, Santos & Haimovici 1997, Ivanovic 2000, Bazzino & Quiñones 2001, Mouat et. al 2001, Laptikhovsky

gentinusregions were neglected. Thus, San Matias Gulf pro-
vides an opportunity to study the diet of Argentine
shortfin squid in coastal regions since 2 major spawn-
ing groups — spring spawning group (SpSG) and
summer spawning group (SSG) — coexist in these
waters (Crespi-Abril et al. 2008). In the present study,
we describe the diet of *I. argentinus* in the San
Matias Gulf through direct observation of stomach
contents as a first attempt to understand the trophic
role of the species in near-shore habitats.

2002); thus the role that *I. argentinus* plays in the trophic web may change among regions as well. At

present, all research of *I. argentinus* diet has been

conducted with specimens caught on the outer shelf

and slope south of 26°S (Ivanovic & Brunetti 1994,

Santos & Haimovici 1997, Bazzino & Quiñones 2001,

Mouat et. al 2001, Laptikhovsky 2002), and coastal

MATERIALS AND METHODS

Samples were obtained with 21 surveys while onboard trawling from vessels which were operating in the San Matias Gulf (42°S, 64.5°W) between June 2005 and October 2007. Tows were conducted during the day with a bottom trawl net (120 mm mesh size) at approx. 4 knots within the deep range, 90 to 150 m. A total of 3645 individuals of both spawning groups (1516 SSG and 2129 SpSG) were collected and were preserved chilled for posterior dissection in the laboratory. During dissection, the stomach of each individual was extracted and supplementary biological information of each specimen was recorded: dorsal mantle length to the nearest cm, sex, and macroscopic maturity condition (Nigmatullin 1989). To analyze the data, maturity stage (I to VII) was grouped into 3 categories as defined by Laptikhovsky & Nigmatullin (1993): immature individuals (stages I and II), physiologically mature individuals (stages III and IV), and functionally mature individuals (stages V, VI and VII).

Stomachs were analyzed under $60 \times \text{magnification}$, and the hard structures found in the contents were stored and used for prey identification to species level. To determine what the species consumed, identification keys (Clarke 1986, Boschi et al. 1992, Gosztonyi & Kuba 1996, Volpedo & Echeverría 2000) and reference material were used. In the cases of stomachs without hard structures, tissue remains (i.e. muscle, gladius, crystalline, exoskeletons) were used to assign prey into main categories such as fishes, cephalopods or crustaceans. Additionally, for each specimen the stomach fullness (SF) was recorded following the scale proposed by Amaratunga & Durward (1978): 0 = empty, 1 = half full, 2 = full, 3 = distended.

A generalized linear model (GLM) was fitted to data (McCullagh & Nelder 1998) to compare the frequency of prey consumed using the maturity condition of individuals, spawning group and sex as covariates. In this model, the dependent variable was the frequency of stomachs corresponding to each category of the covariates and was assumed to follow a Poisson distribution. The function used to link the linear predictor with the mean value of the Poisson probability distribution was a logarithm. The linear predictor of the model is the following: $\eta = \alpha G + \beta MS$ + χS + δP where, η = linear predictor, logarithm of the expected value (number of stomach in each category of the covariates) of a Poisson distribution, G = categorical factor 'spawning group', MS = categorical factor 'maturity condition', S = categorical factor 'sex', P = categorical factor 'prey item', α , β , χ , δ = coefficients of the linear model. The significance of each covariate in the model was tested using a likelihood ratio (Wald test, McCullagh & Nelder 1998). For each prey item, the frequency of occurrence (FO) was calculated as: FO = N_i/N , where N_i = number of stomachs with prey item 'i', N = number of stomachs analyzed.

RESULTS

Sizes of the individuals analyzed ranged from 10 to 36 cm (Fig. 1). The number of individuals without prey in the stomach was similar between spawning groups and sexes (Table 1; chi-square test, p > 0.05). The variation of the *FO* of empty stomachs presented a marked seasonality with the highest values in autumn and winter (Fig. 2).

Differences in the mean *SF* were not significant when comparing between sexes (Student's *t*-test, p > 0.05) or both spawning groups (Student's *t*-test, p > 0.05). This value presented a seasonal variation (ANOVA, p < 0.05) with the highest values in summer and spring (Fig. 2). Stomachs with food were more than 50% of the total analyzed, but only 20% of them presented hard structures that allowed prey identification to species level. Four species were identified in this study (Table 1): 2 fishes (*Engraulis*)



Fig. 1. *Illex argentinus.* Size structure and maturity condition of the individuals analyzed. White columns: immature individuals; gray columns: physiologically mature individuals; black columns: functionally mature individuals. SpSG: Spring Spawning Group; SSG: Summer Spawning Group

Table 1. Illex argentinus. Stomach contents, frequency of occurrence (no. of stomachs with prey item/total no. of stomachs) of each prey item, and number of stomachs empty and with food. SpSG: spring spawning group; SSG: summer spawning sroup

Food items	—— Sp Female	SG— Male	——SS Female	SG—— e Male
Fishes				
Gymnoscopelus nicholsi	0.0108	0.0099	0.0119	0.018
Engraulis anchoita	0.0157	0.0175	0.023	0.009
Unindentified fishes	0.1579	0.267	0.101	0.1544
Cephalopods				
Illex argentinus	0.0112	0.0193	0.0121	0.0184
Loligo sanpaulensis	0.0063	0.0197	0.003	0.0048
Unindentified cephalopods	0.0121	0.0242	0.0404	0.0144
Crustaceans				
Unidentified crustaceans	0.0103	0.0049	0.0013	0.002
Individuals				
Filled stomachs	1270	859	740	776
Empty stomachs	343	563	273	381

anchoita and Gymnoscopelus nicholsi) and 2 cephalopods (Illex argentinus and Loligo sanpaulensis). The prey items fishes and cephalopods were present in all size classes (Fig. 3).

The results of the GLM showed that individuals of different sexes (Wald test, df = 1, p > 0,.05), maturity condition (Wald test, df = 2, p > 0.05) or spawning



Fig. 2. Illex argentinus. Seasonal variation of (A) the frequency of occurrence (no. of empty stomachs/total no. of stomachs) of empty stomachs and (B) the stomach fullness (means \pm SE) (0 = empty, 1 = half full, 3 = distended) of individuals

group (Wald test, df = 1, p > 0.05) consumed a similar number of each prey item (Fig. 4). Thus, the seasonality of the diet was analyzed considering all data together. Additionally, the model revealed that each prey item was consumed in different proportions (Wald test, df = 2, p < 0.05), with fishes the most frequent (FO = 0.79), followed by cephalopods (0.18), and, lastly, by crustaceans (0.09). Although



Fig. 3. Illex argentinus. Frequency of occurrence of prey consumed by males and females for each spawning group and size class (see Table 1 for definitions). Grey columns: fishes; white columns: cephalopods



Fig. 4. *Illex argentinus.* Frequency of occurrence of prey consumed by males and females for each spawning group and maturity stage (see Table 1 for definitions). White columns: immature individuals; grey columns: physiologically mature individuals; black columns: functionally mature individuals. Ceph: cephalopods; Cr: crustaceans, F: fishes



Fig. 5. *Illex argentinus.* Seasonal variation of the frequency of occurrence (see Table 1) of prey consumed by individuals (sexes and seasonal groups combined). Black columns: fishes; gray columns: cephalopods; white columns: crustaceans

fishes were more important year round, the FO of each prey item in the diet of *Illex argentinus* varied among seasons (Fig. 5). Fishes were more represented in the stomachs in summer and spring (chisquare, df = 3, p < 0.05) than in autumn and winter (Fig. 5) when cephalopod consumption was higher (chi-square, df = 3, p < 0.05; Fig. 5). Crustaceans were found in the diet sporadically and mainly in autumn (Fig. 5).

DISCUSSION

Nigmatullin (2005) mentioned that squids obtained from netting gear could have non-natural food items (gear food) in their stomachs as a consequence of an artificially increased encounter rate with the catch community species. This kind of food can be easily recognized in the stomach contents since it is fresh or slightly digested. Thus, recently consumed species must be considered separately from the diet analysis to avoid overestimating the prey spectrum (Nigamtullin 2005). In the present study, no evidence of gear food was observed in the stomachs analyzed since all the prey items were in an advanced degree of digestion (tissues were mainly minced without skin covering).

The selective ingestion of soft parts by squids makes the identification of the prey consumed difficult (Bradbury and Aldrich, 1969, Rodhouse & Nigmatullin 1996), but it is possible to recognize higherlevel taxons (i.e. fishes, mollusks, and crustaceans) by observing the structural differences in soft tissue. In the present study, 5 species could be identified in the stomach contents of *Illex argentinus*. The prey spectrum consumed by squids in San Matias Gulf is low when compared with previous studies conducted with individuals from the outer shelf and slope (Ivanovic & Brunetti 1994, Santos & Haimovici 1997, Mouat et al. 2001).

Illex argentinus is an opportunistic predator, and its diet varies along the continental shelf and slope, depending on the availability of potential prey (Ivanovic & Brunetti 1994). In the San Matias Gulf, individuals of both spawning groups, regardless of size class, fed on the same prey with a predominance of fishes. These results are consistent with those reported for squids inhabiting the northern region of the species distribution (Ivanovic & Brunetti 1994, Santos & Haimovici 1997, Bazzino & Quiñones 2001) and contrary to those reported for squids of the southern region, where the most consumed prey are pelagic crustaceans (e.g. *Themisto gaudichaudii*) (Ivanovic & Brunetti 1994, Mouat et al. 2001, Ivanovic 2000, Laptikhovsky 2002).

Cannibalism in species of the genus *Illex* is interpreted as an advantageous mechanism for maintaining energy within the population in situations of food scarcity (Mauer & Bowman 1985, O'Dor 1998, Ibáñez & Keyl 2010). In San Matias Gulf, cannibalism was observed in 33% of stomachs containing cephalopods, which represent 6% of the total of the stomachs with food. This value is low in comparison to those reported by Ivanovic & Brunetti (1994) and by Santos & Haimovici (1997) for individuals captured in the North Patagonic shelf and southern Brazil (10 and 15% of stomachs with prey contained *I. argentinus*, respectively), and it could reflect a higher food availability inside the Gulf than in shelf waters.

The seasonal variation of both the frequency of empty stomachs (Fig. 2A) and the mean value of stomach fullness (Fig. 2B) revealed that squids fed more intensively in spring and summer. During these seasons, fishes increased in the diet significantly (Fig. 5). In coastal waters, Engraulis anchoita is the most abundant pelagic fish and concentrates inside the San Matias Gulf and waters of the adjacent inner shelf (reaching more than 0.7 million tons of spawning biomass), in order to reproduce during spring and summer (Sánchez & Ciechomski 1995, Pájaro 1998, Pájaro et al. 2008). This reproductive aggregation represents an important peak of available prey that squid may be actively consuming. In autumn and winter, when individuals of *E. anchoita* migrate from coastal regions to the mid shelf, fishes decrease in frequency in the diet of Illex Argentinus, which feeds upon alternative preys (i.e. cephalopods and crustaceans). The diet of *I. argentinus* inside the San Matias Gulf is independent of the spawning season of the individuals. The change in the frequency of occurrence of prey food items found in I. argentinus

stomachs can be explained by the opportunistic feeding behavior of this species, reflecting the availability of prey in coastal waters (Ivanovic & Brunetti 1994).

Acknowledgements. We thank P. Sgarlatta, M. Dherete and S. Fernandez for the help provided during the sampling processing. Thanks also to P. Barón and E. Morsan for their comments during the work and to the reviewers whose observations helped to improve the paper. A special thanks for G. Nagel who helped with the text in English.

LITERATURE CITED

- Amaratunga T, Durward RD (1978) Standardization of the data collection for the short-finned squid, *Illex illecebrosus*. ICNAF Selected Papers 5:37–41
- Angelescu V, Prenski LB (1987) Ecología trófica de la merluza común del Mar Argentino (Merlucciidae, Merluccius hubbsi). Parte II. Dinámica de la alimentación analizada sobre la base de las condiciones ambientales, la estructura y las evaluaciones de los efectivos en su área de distribución. Contrib INIDEP 561
- Bazzino G, Quiñones RA (2001) Feeding of *Illex argentinus* (Cephalopoda: Ommastrephidae) in the Argentine-Uruguayan common fishing zone. Gayana (Zool) 65: 181–192
- Boschi EE, Fischbach CE, Iorio MI (1992) Catálogo ilustrado de los crustáceos estomatópodos y decápodos marinos de Argentina. Frente Marit 10:7–94
- Bradbury HE, Aldrich FA (1969) Observations on feeding on the squid *Illex illecebrosus* (LeSueur, 1821) in captivity. Can J Zool 47:913–915
- Clarke MR (1986) A handbook for the identification of cephalopod beaks, 1st edn. Clarendon Press, Oxford
- Crespi-Abril AC, Morsan EM, Barón PJ (2008) Contribution to understanding the population structure and maturation of *Illex argentinus* (Castellanos, 1960): the case of the inner-shelf spawning groups in San Matias Gulf (Patagonia, Argentina). J Shellfish Res 27:1225–1231
- Croxall JP, Prince PA (1996) Cephalopods as prey. I. Seabirds. Phil Trans R Soc Lond B 351:1023–1043
- Gosztonyi A, Kuba L (1996) Atlas de huesos craneales y de la cintura escapular de peces costeros patagónicos. Plan de Manejo Integrado de la Zona Costera Patagónica – Fundación Patagonia Natural (Puerto Madryn, Argentina)
- Ibáñez CM, Keyl F (2010) Cannibalism in cephalopods. Rev Fish Biol Fish 20:123–136
- Ivanovic M (2000) Alimentación y relaciones tróficas del calamar *Illex argentinus* en el ecosistema pesquero. PhD thesis. Universidad Nacional de Mar del Plata
- Ivanovic ML, Brunetti NE (1994) Food and feeding of *Illex* argentinus. Antarct Sci 6:185–193
- Klages NT (1996) Cephalopods as prey. II. Seals. Philos Trans R Soc Lond B 351:1045–1052

Koen-Alonso M, Yodzis P (2005) Multispecies modeling of

Editorial responsibility: Hans Heinrich Janssen, Oldendorf/Luhe, Germany

some components of the marine community of northern and central Patagonia, Argentina. Can J Fish Aquat Sci 62:1490–1512

- Laptikhovsky V (2002) Diurnal feeding rhythm of the shortfin squid *Illex argentinus* (Cephalopoda: Ommastrephidae) in the Falkland waters. Fish Res 59:233–237
- Laptikhovsky V, Nigmatullin ChM (1993) Egg size, fecundity, and spawning in females of the genus *Illex* (Cephalopoda: Ommastrephidae). ICES J Mar Sci 50: 393–403
- Mauer RO, Bowman RE (1985) Food consumption of squids (*Illex illecebrosus* and *Loligo pealei*) off the Northeastern United States. NAFO Sci Counc Stud 9:117–124
- McCullagh P, Nelder JA (1998) Generalized linear models, 2nd edn. Chapman & Hall, New York, NY
- Mouat B, Collins MA, Pompert J (2001) Patterns in the diet of *Illex argentinus* (Cephalopoda: Ommastrephidae) from the Falkland Islands jigging fishery. Fish Res 52: 41–49
- Nigmatullin ChM (1989) Las especies del calamar más abundantes del Atlántico sudoeste y sinopsis sobre ecología del calamar *Illex argentinus*. Frente Marit 5: A7–81
- Nigmatullin ChM 2005. Towards the correct methodology of cephalopod feeding study: review of some neglected problems. Libro de resumenes III Simposio Internacional sobre calamares del Pacifico y II Taller Internacional SOBRE CALAMARES (28 Noviembre to 2 Deciembre 2005, Lima, Peru). Resumen No 34. IMARPE, Callao
- O'Dor RK (1998) Squid life-history strategies. In: Rodhouse P, Dawe E, O'Dor RK (eds) Squid recruiment dynamics: the genus *Illex* as a model, the commercial *Illex* species and influences on variability. FAO Fish Tech Pap 376, Rome
- Pájaro M (1998) El canibalismo como mecanismo regulador denso-dependiente de mortalidad natural en la anchoíta argentina (*Engraulis anchoita*). Su relación con las estrategias reproductivas de la especie. PhD thesis. Universidad Nacional de Mar del Plata
- Pájaro M, Martos P, Leonarduzzi E, Macchi GJ, Diaz MV, Brown D (2008) Estrategia de puesta de la anchoíta (*Engraulis anchoita*) en el Mar Argentino y Zona Común de Pesca Argentino-Uruguaya. Informe Técnico INIDEP. 11/08
- Rodhouse PG, Nigmatullin ChM (1996) Role as consumers. Philos Trans R Soc Lond B 351:1003–1022
- Sánchez RP, Ciechomski JD (1995) Spawning and nursery grounds of pelagic fish species in the sea-shelf off Argentina and adjacent areas. Sci Mar 59:455–478
- Santos RA, Haimovici M (1997) Food and feeding of the short-finned squid *Illex argentinus* (Cephalopoda: Ommastrphidae) off Southern Brazil. Fish Res 33:139–147
- Smale MJ (1996) Cephalopods as prey. IV. Fishes. Philos Trans R Soc Lond B 351:1067–1081
- Volpedo AV, Echeverría DD (2000) Catálogo y claves de otolitos para la identificación de peces del Mar Argentino: 1. Peces de importancia económica. Editorial, Dunken, Buenos Aires

Submitted: November 17, 2010; Accepted: October 19, 2011 Proofs received from author(s): December 7, 2011