Journal of the Marine Biological Association of the United Kingdom, 2008, 88(4), 793–798.
doi:10.1017/S0025315408001227 Printed in the United Kingdom

Feeding ecology of *Enteroctopus megalocyathus* (Cephalopoda: Octopodidae) in southern Chile

CHRISTIAN M. IBÁÑEZ[1] AND JAVIER V. CHONG[2]

[1]Instituto de Ecología y Biodiversidad, Departamento de Ciencias Ecológicas, Facultad de Ciencias, Universidad de Chile, PO Box 563, Santiago, Chile, [2]Departamento de Ecología Costera, Facultad de Ciencias, Universidad Católica de la Santísima Concepción, P.O. BOX 297, Concepción, Chile

In this research we studied the diet of Enteroctopus megalocyathus *from three principal locations of the octopus fishery (Ancud, Quellón and Melinka) in southern Chile. The gastric contents of 523 individuals, collected between October 1999 and September 2000, were examined and statistically analysed. Diet composition was described using detrended correspondence analysis and analysed as a function of predator gender, body size and fishing area. Food items were found in ~50% of the octopuses examined and a total of 14 prey items were recognized. The diet of* E. megalocyathus *consisted primarily in brachyuran and anomuran crustaceans, fish and conspecifics. The diet differed in composition between fishing zones and mantle length of the specimens and size of octopuses varied between locations. After adjusting for octopus mantle length, diet composition was found to be different between fishing areas. Large octopuses fed on large crabs at Ancud, while in Quellón and Melinka small octopuses fed mainly on small crustaceans. There were no differences in prey composition between the gender and the size of octopuses was a better predictor of the variance in the diet composition (16%) than the fishing zone (6%). Cannibalism may become an important issue when food is scarce and/or at high population density.*

Keywords: diet, *Enteroctopus megalocyathus*, cannibalism, Chile

Submitted 24 August 2007; accepted 29 November 2007

INTRODUCTION

Incirrate octopods of the family Octopodidae are typically benthic cephalopods that live in crevices and caves where they hide from predators, including conspecifics (Roper *et al.*, 1984; Aronson, 1986). Common prey items for most species include clams, snails, fish and crustaceans and it may include up to 55 different species as reported for *Octopus bimaculatus* Verrill 1883 (Ambrose, 1984). Thus, octopuses have been considered generalist predators of the third or fourth trophic level in marine communities (Guerra, 1978; Ambrose & Nelson, 1983; Summers, 1983; Rodhouse & Nigmatullin, 1996).

Some studies have shown that the trophic habits of octopuses vary among geographical locations. For example, the diet of *O. vulgaris* Cuvier 1797 from Portugal shows that fish are the common prey in two of the three locations studied, while crustaceans are more important in the other location (Rosa *et al.*, 2004). This shows that shifts in the diet of octopuses may occur over a relatively small geographical scale even in different locations with similar habitats. As an additional case, *O. vulgaris* from South Africa change their diet between closer locations (Smith, 2003).

Some octopus species show ontogenetic changes in their diets, where juveniles of *Octopus bimaculatus* feed mainly on small crustaceans, while adults consume a wide variety of benthic invertebrates (Ambrose, 1997). Smale & Buchan (1981) reported similar ontogenetic variations in the diet of *Octopus vulgaris* from the coasts of South Africa. In this case, juveniles feed mainly on the bivalve *Perna perna* (Linnaeus, 1758), whereas larger individuals feed on crustaceans and other molluscs. This demonstrates that prey diversity increases in relation to body size of octopuses (Smale & Bucham, 1981; Smith, 2003).

Generally, female incirrate octopuses attach their eggs to the roof of caves and care for them until hatching and during this period they do not feed (Roper *et al.*, 1984; Cortez *et al.*, 1995; Rocha *et al.*, 2001). Moreover, Cortez *et al.* (1995) reported that differences in diet between mature females and males of *Octopus mimus* Gould 1852 may be due to differences in nutrient and energetic requirements.

Enteroctopus megalocyathus (Gould, 1852) is distributed along the southern coasts of South America, in both the Pacific and Atlantic Oceans. The range extends from Chiloé Island (~42°S) in the Pacific (Rocha, 1997), to the Gulf of San Matías in the Atlantic (42°S) (Ré, 1998). The species can be found in hard-bottom habitats from the lower intertidal zone to 140 m depth (Ré, 1998), and still much about their biology and ecology remains unknown. The fishery of this species in southern Chile is carried out by free-diving fishermen who capture the octopus with gaffs (Rocha & Vega, 2003). Octopus catches in southern Chile began to be recorded in 1991, with a maximum of 765 tons recorded in 2003

Corresponding author:
C.M. Ibáñez
Email: christianibez@yahoo.com

(SERNAPESCA, 2003). At present, the *E. megalocyathus* catch in southern Chile is approximately 500 tons per year (SERNAPESCA, 2002, 2003, 2004).

In this study we examined: (a) the composition in the diet of *E. megalocyathus* from different fishing areas with similar habitats; (b) potential changes in the diet composition in relation to body size; and (c) differences in the diet as a function of sex.

MATERIALS AND METHODS

Samples were obtained from three principal sites of landings in southern Chile around Chiloé Island: Ancud (41°47′S 74°28′W), Quellón (43°07′S 73°37′W) and Melinka (43°50S 74°28′W; Figure 1). Samples were not taken at the same time in all locations and the information is summarized in Table 1. The octopuses were collected by commercial divers, at depths between 20–30 m, using surface air supply (HOOKA), and brought frozen to the laboratory for further analysis. In the laboratory sex determination was performed and the dorsal mantle length (DML, cm), total length (TL, cm) and total weight (TW, g) were recorded. The digestive tracts were removed and frozen (−15°C) for diet analysis.

As octopuses only ingest small pieces of their prey, gut analysis only revealed the hard parts of the gastric contents. The difficulty in identifying individual prey prevented us from determining all prey items to species level, but all prey were identified to the lowest taxonomic level. We estimated the frequency of occurrence of a prey species (O%): the ratio (%) between the numbers of stomachs with a specific type of prey present divided by the total number of digestive tracts with any type of food present (Hyslop, 1980). Number of prey (N%) was calculated as the percentage of a specific prey type divided by the total number of prey in all food categories (Hyslop, 1980). To ascertain the number of a specific prey type present in a single stomach we considered otoliths for fish, beaks for octopuses, and chelae and/or eyes for crustaceans. Weight of prey (W%) is the total weight of a prey item as a percentage of the total weight of all prey present in a sample (Hyslop, 1980).

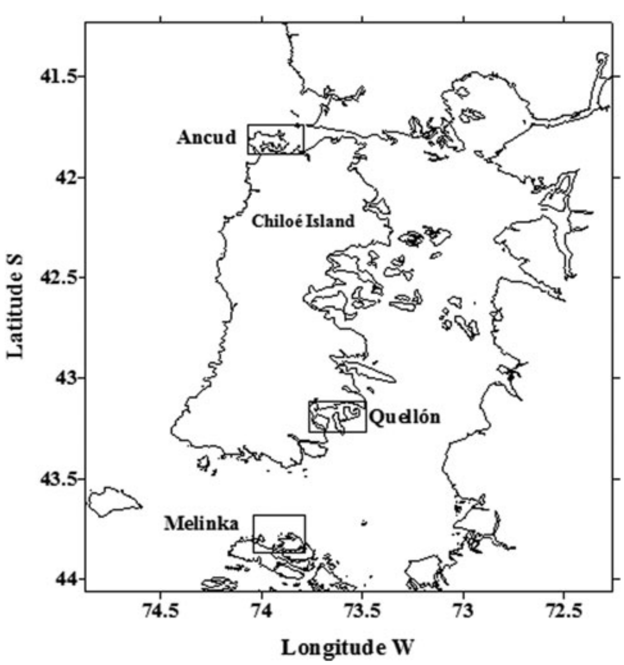

Fig. 1. Map showing the study area and the locations where octopuses were collected (indicated by squares).

Table 1. Number of stomachs with food contents (Stomachs) and empty stomachs of *Enteroctopus megalocyathus* at three sampling locations from southern Chile, from October of 1999 to September of 2000.

Date	Ancud		Quellón		Melinka	
	Stomachs	Empty	Stomachs	Empty	Stomachs	Empty
October 1999					32	17
November 1999	33	18	15	5	23	12
December 1999	28	17	30	18	27	13
January 2000	41	13	24	12	25	9
February 2000	26	12	10	6		
March 2000	10	3			27	14
April 2000			27	16		
May 2000			26	13	33	19
June 2000					19	7
July 2000	11	6	17	9		
August 2000						
September 2000	23	10	16	7		
Total	172	79	165	86	186	91

Dietary composition was described by means of an ordination carried out on the presence–absence matrix of prey–predators, with a detrended correspondence analysis (DCA; Jongman *et al.*, 1995) following Muñoz *et al.* (2002) and Pardo-Gandarillas *et al.* (2004). This method allows the simultaneous display of samples and species in a reduced space (Jongman *et al.*, 1995). Prey whose frequencies of occurrence were less than 5% in the whole sample were not included in the analysis, because the DCA is sensitive to species that occur only in a few stomach contents and modified the scores of the ordination (Jongman *et al.*, 1995). Compositional gradients of this ordination are expressed as standard deviation units (×100) of replacement of taxa along the gradient. A total of 218 specimens were considered in the analyses, after discarding those whose mantle and organs were destroyed (without sex and size data) by the fishing method (gaff hooks) (see Tables 1, 2 and Figure 2).

Generalized linear models (GLMs; Agresti, 2002) were used to analyse variations in the diet composition (DCA axis) and the relative importance of different variables in explaining those variations. The differences of octopus sizes between locations were tested by means of ANOVA, and Tukey *a posteriori* tests (Zar, 1984). Two-way ANOVAs on the scores of the DCA were carried out with sampling locations and sex as factors (Zar, 1984). A one-way ANOVA on the residuals of the regression between DCA scores with DML was carried out to test the statistical significance of dietary differences between locations, in order to correct for the eventual effect of the octopuses' size on the diet composition.

RESULTS

Fifty-two per cent out of 523 octopuses examined had food contents in their digestive tracts. The DML, of octopuses that had food contents, ranged from 8 to 28 cm (39 to 130 cm TL) and total weight (TW) varied between 304 and

Table 2. Prey items found in *Enteroctopus megalocyathus* stomach contents at three sampling locations from southern Chile, considering the whole sample.

	Ancud (n = 93)			Quellón (n = 79)			Melinka (n = 95)		
Prey	O%	N%	W%	O%	N%	W%	O%	N%	W%
TELEOSTEI	25.8	5.9	7.7	25.3	5.5	11.6	9.5	2.0	8.5
BRACHYURA	26.9	2.1	9.7	25.3	3.3	20.8	18.9	1.9	10.1
CANCRIDAE	9.7	0.8	15.1	12.7	1.6	15.8	4.2	0.4	8.1
Cancer setosus	1.1	0.1	0.3	5.1	0.6	0.8	1.1	0.1	0.7
Cancer coronatus	5.4	0.4	6.1	1.3	0.2	5.2	1.1	0.1	2.2
Eggs of crabs	11.8	0.9	34.8	5.1	0.6	10.8	1.1	0.1	0.4
XANTHIDAE									
Homalaspis plana	9.7	0.8	15.4	13.9	1.7	16.4	5.3	0.5	16.8
ANOMURA									
GALATHEIDAE									
Munida subrugosa	2.2	0.2	0.4	25.3	5.8	9.4	34.7	9.5	38.2
Munidopsis sp.	3.2	0.9	0.4	1.3	0.2	0.1			
PORCELLANIDAE									
Petrolisthes tuberculosus	1.1	0.1	0.05	2.5	0.5	1.1	1.1	0.3	2.0
MACRURA									
ALPHEIDAE									
Synalpheus spinifrons	2.2	0.2	0.1	1.3	0.3	0.01	1.1	0.1	0.03
MOLLUSCA									
GASTROPODA									
NASSARIDAE									
Nassarius gayii	1.1	0.1	0.003	2.5	0.3	0.002	2.1	0.3	0.02
CEPHALOPODA									
OCTOPODIDAE									
Enteroctopus megalocyathus	14.0	1.1	7.9	6.3	0.8	7.0	8.4	0.8	9.3
Eggs of *E. megalocyathus*	29.0	86.4	2.1	12.7	78.5	1.0	11.6	83.8	3.5
Total number and weight of prey		1163	1561.76		633	1199.73		980	697.36

O, occurrence; N, number; W, weight; n, number of stomachs with food.

5537 g. The DML was different between locations (ANOVA, $F_{(2,\ 215)} = 13.94$, $P < 0.001$; Figure 2), mainly because octopuses from Ancud were larger in DML than at Melinka (Tukey test, $P < 0.001$).

The diet of *E. megalocyathus* consisted predominantly of crustaceans, molluscs, and teleost fish (Notothenioidei) (Table 2). The high presence of both eggs and body parts of conspecifics indicates an important degree of cannibalism (Table 2). In the stomach contents of *E. megalocyathus* we often found one (72%) and two (23%) prey species and rarely they feed on three (4%) or four (1%) prey species. When the octopuses fed on two prey species these were principally fish and crabs. In some cases we found octopus crops full of eggs of crabs with or without fragments of *Homalaspis plana*, for this reason we considered the eggs of crabs as another prey. The more important prey (>25%) in terms of occurrence were Teleostei, Brachyura and eggs of octopus in Ancud; Teleostei, Brachyura and *Munida subrugosa* in Quellón; and *M. subrugosa* in Melinka (Table 2). In the three fishing areas eggs of octopuses were the more important prey in number (>75%) (Table 2), while in terms of weight eggs of crabs, Brachyura and *M. subrugosa* (>20%) were the principal prey in Ancud, Quellón and Melinka, respectively (Table 2).

Eigenvalues of DCA ordination of fourteen prey taxa and 218 octopuses were $\lambda_1 = 0.89$, $\lambda_2 = 0.74$ and $\lambda_3 = 0.32$ from the first to the third axis (compositional gradients) respectively. The two first compositional gradients account for 24.39% of the total inertia, a measurement of the association among the predators and prey. For this reason the information was insufficient to find a significant association ($\chi^2_{2398} = 2158.03$, $P = 0.99$), indicating that in light of the available information, the analysed octopuses form a very homogeneous feeding group. Some patterns, however, were identified from the dimensional graphs, because some prey were positioned at the extremes of the first compositional gradient, but other prey were positioned at the extremes of the second compositional gradient (Figure 3A). Simultaneous display of the composition of octopuses from the three fishing areas (Figure 3B) revealed more variation between fishing areas in the second compositional gradient than in the first.

There were no significant changes in first compositional gradient in the regression analyses, according to DML in the whole data set (first DCA axis, $r^2 = 0.01$, $F_{(1,\ 216)} = 3.22$, $P = 0.07$). Along the second DCA axis we found significant differences according to DML in dietary composition ($r^2 = 0.10$, $F_{(1,\ 216)} = 24.50$, $P < 0.001$), which explained 16% of the variance, because some octopuses fed on rare prey (Figure 4). In Ancud the largest octopuses fed on large crabs *Cancer coronatus* and conspecifics, and the smallest fed on *Homalaspis plana*, eggs of crabs and eggs of octopuses (Figure 4A). In Quellón and Melinka small octopuses fed mainly on small crustaceans *Synalpheus spinifrons* (Milne-Edwards, 1837) and *Munida subrugosa*, while the largest fed on crabs and conspecifics (Figure 4B, C).

A two-way ANOVA on the residuals of the regression between second DCA scores with DML showed differences between locations (second DCA axis, $F_{(2,\ 215)} = 7.38$, $P = 0.0008$), which explained 6% diet composition variation.

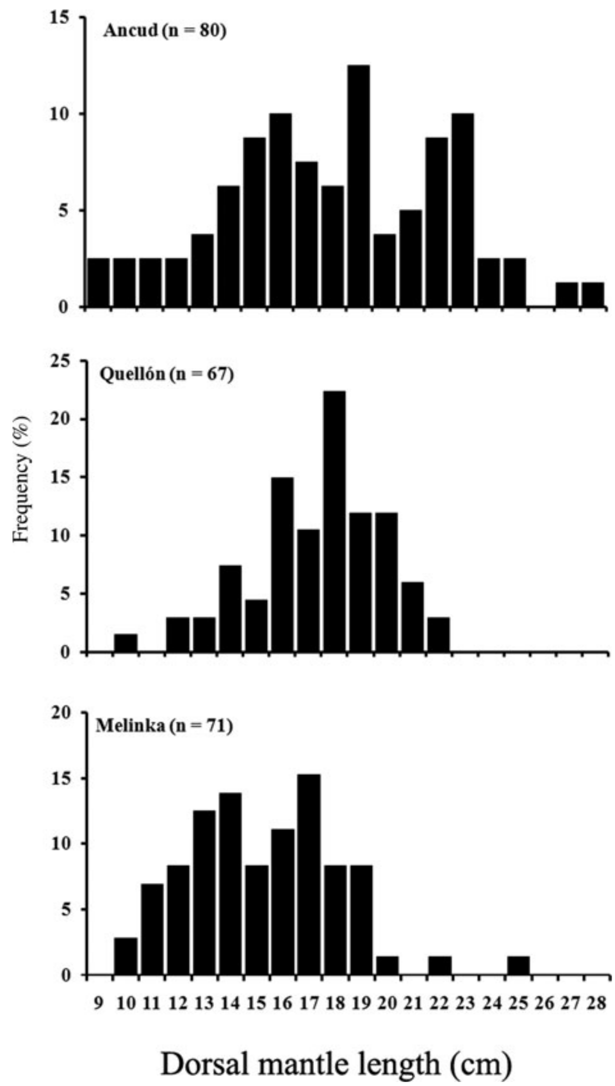

Fig. 2. Size–frequency distribution of octopus dorsal mantle length (cm) in each location.

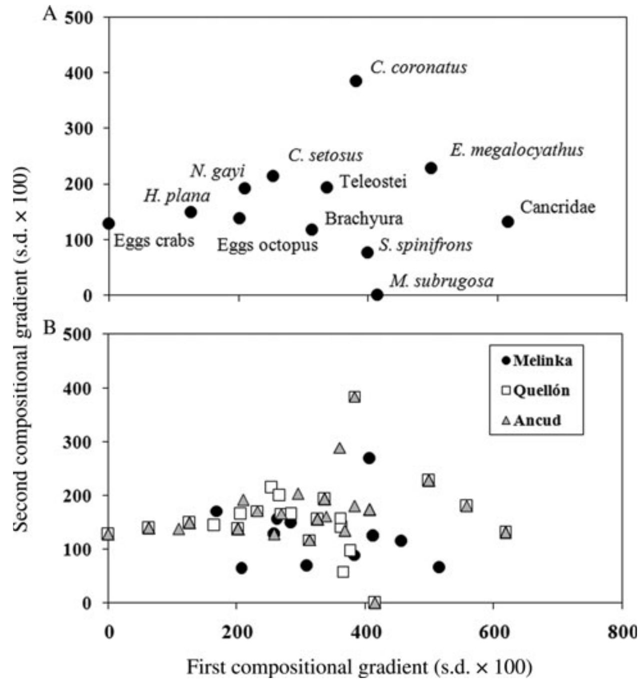

Fig. 3. Position of twelve prey taxa (A) found in stomach contents of *Enteroctopus megalocyathus* in a two-dimensional space according to a detrended correspondence analysis (DCA) carried out in 218 predators (B). The units of DCA axes are standard deviations (×100) of the turnover rate of taxa in the gradient.

Munida subrugosa was found in the gastric contents of octopuses from Melinka 30 times more than it was in octopuses from Ancud and Quellón (Table 2). There were no significant changes in dietary composition in relation to octopuses sex (second DCA axis, $F_{(1,\ 216)} = 2.89$, $P = 0.09$), and with the interaction between octopuses sex and locations (second DCA axis, $F_{(2,\ 215)} = 0.0$, $P = 0.99$).

DISCUSSION

The diet of *E. megalocyathus* consisted of benthic organisms including brachyuran and anomuran crabs, nassarid snails, octopuses and fish, similar for other species. The DML of octopuses proved to be a better predictor of the variance in the diet composition (16%) than the fishing zone (6%). These low percentages are due to these octopuses forming a very homogeneous feeding group.

The significant differences in the diet composition of *E. megalocyathus* among the three locations, was presumed due to the variations in occurrence of some prey items among locations, like *Munida subrugosa*. This variation could be due to differences in prey abundance between sites, but unfortunately no information on this is available for our study area. The diets of *Enteroctopus dofleini* (Wülker, 1910) and *O. bimaculatus* are influenced by food preferences and availability in the environment (Ambrose, 1984; Vincent *et al.*, 1998). Rare prey were excluded from the analyses because they modified the scores of the ordination (see Materials and Methods). Including rare prey could show more differences among locations, but can bias the scores of the ordination too.

Enteroctopus megalocyathus showed significant changes in its diet in relation to body size. The smallest octopuses fed on small crustaceans while the largest fed on large crabs and conspecifcs in all locations. However, further studies with a wider range of octopus sizes, including juvenile octopuses ($<$5 cm DML), are needed to determine whether prey composition changes with size or age. On the other hand, the sex of octopuses had no effect on the diet variations of *E. megalocyathus*, because male and female octopuses fed on the same prey organisms and at a similar rate, moreover females during their incubation period fed on fish, crabs and octopus eggs.

The gastric contents of *E. megalocyathus* show that this species is cannibalistic, as a large number of conspecific eggs and juveniles were found in the gut analysis. This is not unusual for octopuses and has been recorded in several species. An extreme case of cannibalism was reported for *O. maorum* Hutton 1880 from Tasmania, where the largest prey biomass (211.9 g) was represented by clusters of eggs and small individuals of the same species (Anderson, 1999; Grubert *et al.*, 1999). Cannibalism may be beneficial for survival of the individual in periods of food scarcity, and may reduce competition when resources are limited (Calow, 1998). It appears to be a density-dependent effect that increases when the abundance of adult octopuses increases

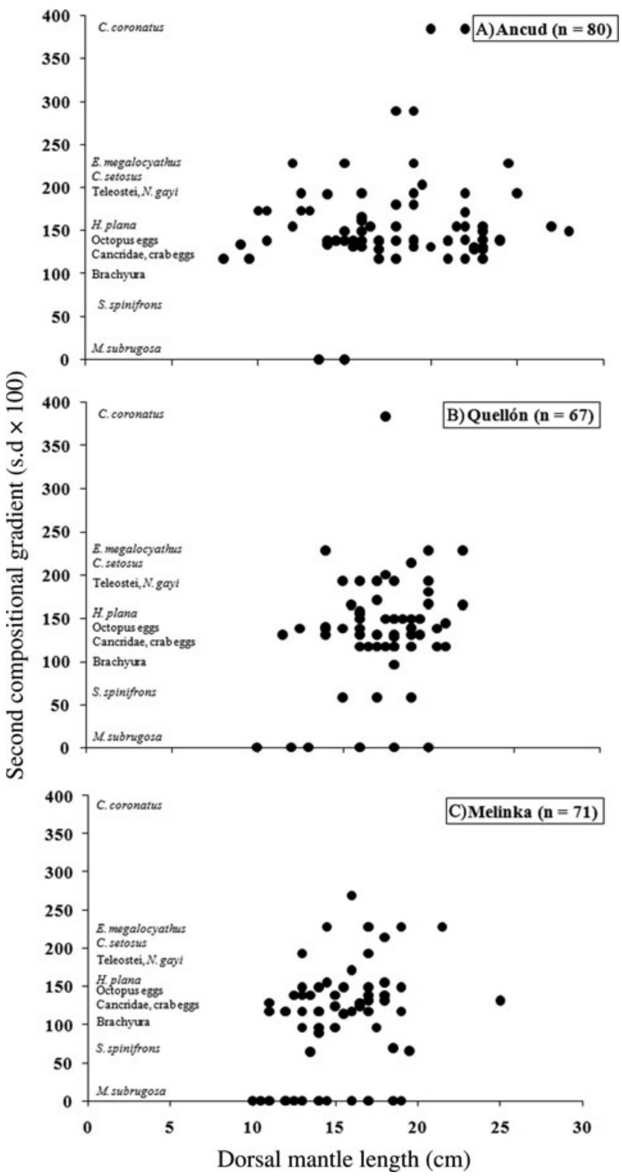

Fig. 4. Relationship between prey scores and octopus dorsal mantle length (cm) on the second compositional gradient of detrended correlation analysis from three locations of southern Chile: (A) Ancud, (B) Quellón and (C) Melinka.

raising the per capita rate of cannibalism (Aronson, 1986). Conspecific eggs are an important prey item in the diet of *E. megalocyathus*. This behaviour has also been reported in females of *O. tehuelchus*, *O. mimus* and *O. maorum* (Ré & Gómez-Simes, 1992; Cortez *et al.*, 1995; Grubert *et al.*, 1999). In the deep-sea octopus *Bathypolypus arcticus* maintained in aquaria, feeding was observed on non-viable (unfertilized) eggs (Wood *et al.*, 1998).

Given the range of prey items consumed by *E. megalocyathus* and their large body size (up to 100 cm TL) and high abundance, it appears to be an important predator in subtidal communities around the southern tip of South America. In some cases, octopus predation has been shown to have demonstrable effects on community structure in the subtidal zone (Ambrose & Nelson, 1983; Ambrose, 1986), but octopuses are generally not considered important predators in intertidal and shallow systems. Our results indicate that *E. megalocyathus* should be considered as an important part of the guild of subtidal predators in southern Chile.

ACKNOWLEDGEMENTS

We thank M. George-Nascimento, Mrs M.C. Pardo-Gandarillas and M. Canals for their help with the statistical analysis and valuable comments, and R.D. Sepúlveda, C. González and J.B. Wood for comments on the manuscript. This work was partially funded by the Fondo de Investigación Pesquera, FIP 99-20 to Javier Chong. C.M. Ibáñez was supported by a CONICYT doctoral fellowship.

REFERENCES

Agresti A. (2002) *Categorical data analysis*, 2nd edn. Hoboken, New Jersey: John Wiley & Sons, Inc.

Ambrose R.F. (1984) Food preferences, prey availability, and the diet of *Octopus bimaculatus* Verril. *Journal of Experimemtal Marine Biology and Ecology* 77, 29–44.

Ambrose R.F. (1986) Effects of octopus predation on motile invertebrates in a rocky subtidal community. *Marine Ecology Progress Series* 30, 261–273.

Ambrose R.F. (1997) *Octopus bimaculatus*. In Lang M. and Hochberg F.G. (eds) *Proceedings of the workshop on the fishery and market potential of octopus in California*. Washington: Smithsonian Institution, pp. 11–22.

Ambrose R.F. and Nelson B.V. (1983) Predation by *Octopus vulgaris* in the Mediterranean. *Marine Ecology PSZN* 4, 251–261.

Anderson T.J. (1999) Morphology and biology of *Octopus maorum* Hutton 1880 in northern New Zealand. *Bulletin of Marine Science* 65, 657–676.

Aronson R.B. (1986) Life history and den ecology of *Octopus briareus* Robson in a marine lake. *Journal of Experimental Marine Biology and Ecology* 95, 37–56.

Calow P. (1998) *The encyclopedia of ecology and environmental management*. London: Blackwell Science.

Cortez T., Castro B.G. and Guerra A. (1995) Feeding dynamics of *Octopus mimus* (Mollusca: Cephalopoda) in northern Chile waters. *Marine Biology* 123, 497–503.

Grubert M., Wadley V. and White R. (1999) Diet and feeding strategy of *Octopus maorum* in southeast Tasmania. *Bulletin of Marine Science* 65, 441–451.

Guerra A. (1978) Sobre la alimentación y el comportamiento alimentario de *Octopus vulgaris*. *Investigación Pesquera* 42, 351–364.

Hyslop E. (1980) Stomach content analysis—a review of methods and their application. *Journal of Fish Biology* 17, 411–429.

Jongman R.H.G., Ter Braaka C.J.F. and Van Tongeren O.F.R. (1995) *Data analysis in communities and landscape ecology*. New York: Cambridge University Press.

Muñoz G., Valdebenito V. and George-Nascimento M. (2002) La dieta y la fauna de parásitos metazoos del torito *Bovichthys chilensis* Regan 1914 (Pisces: Bovichthydae) en la costa de Chile centro-sur: variaciones geográficas y ontogenéticas. *Revista Chilena de Historia Natural* 75, 66–671.

Pardo-Gandarillas M.C., Garcías F. and George-Nascimento M. (2004) La dieta y la fauna de endoparásitos del pejesapo *Gobiesox marmoratus* Jenyns, 1842 (Pisces: Gobiesocidae) en el litoral central de Chile están conectadas pero no correlacionadas. *Revista Chilena de Historia Natural* 77, 627–637.

Ré M.E. (1998) Pulpos Octopódidos (Cephalopoda, Octopodidae). In Boschi E. (ed.) *El mar Argentino y sus Recursos Pesqueros 2*. Mar del Plata: Instituto Nacional de Investigación y Desarrollo Pesquero, Secretaría de Agricultura, Ganadería, Pesca y Alimentación, pp. 87–91.

Ré M.E. and Gómez-Simes E. (1992) Hábitos alimentarios del pulpo (*Octopus tehuelchus*). I. Análisis cuali-cuantitativos de la dieta en el intermareal de Puerto Lobos, Golfo San Matías (Argentina). *Frente Marítimo* 11, 119–128.

Rocha F. (1997) Cephalopods in Chilean waters, a review. *Malacological Review* 30, 101–113.

Rocha F.J., Guerra A. and González A.F. (2001) A review of reproductive strategies in cephalopods. *Biological Review* 76, 291–304.

Rocha F.J. and Vega M.A. (2003) Overview of cephalopod fisheries in Chilean waters. *Fisheries Research* 60, 151–159.

Rodhouse P.G. and Nigmatullin C.M. (1996) Role as consumers. *Philosophical Transactions of the Royal Society of London* 351, 1003–1022.

Roper C., Sweeney J. and Nauen C. (1984) Cephalopods of the World (FAO species catalogue volume 3), an annotated and illustrated catalogue of species of interest to fisheries. *FAO Fisheries Synopsis* 3, 1–127.

Rosa R., Marques A.M., Nunes M.L., Bandarra N. and Reis C.S. (2004) Spatial-temporal changes in dimethyl acetal (Octadecanal) levels of *Octopus vulgaris* (Mollusca: Cephalopoda): relation to feeding ecology. *Scientia Marina* 68, 227–236.

SERNAPESCA (2002) *Anuario estadístico de pesca*. Servicio Nacional de Pesca, Ministerio de Economía, Fomento y Reconstrucción, Chile.

SERNAPESCA (2003) *Anuario estadístico de pesca*. Servicio Nacional de Pesca, Ministerio de Economía, Fomento y Reconstrucción, Chile.

SERNAPESCA (2004) *Anuario estadístico de pesca*. Servicio Nacional de Pesca, Ministerio de Economía, Fomento y Reconstrucción, Chile.

Smale M. and Buchan P. (1981) Biology of *Octopus vulgaris* off the East Coast of South Africa. *Marine Biology* 65, 1–12.

Smith C.D. (2003) Diet of *Octopus vulgaris* in False Bay, South Africa. *Marine Biology* 143, 1127–1133.

Summers W.C. (1983) Physiological and trophic ecology of cephalopods. In Russell-Hunter W.D. (ed.) *The Mollusca, Volume 6 ecology*. London: Academic Press, pp. 261–279.

Vincent T.L.S., Scheel D. and Hough K.R. (1998) Some aspect of the diet and foraging behaviour of *Octopus dofleini* (Wulker, 1910) in its northernmost range. *Marine Ecology PSZN* 19, 13–29.

Wood J.B., Kenchington E. and O'Dor R.K. (1998) Reproduction and embryonic development time of *Bathypolypus arcticus*, a deep-sea octopod (Cephalopoda: Octopoda). *Malacologia* 39, 11–19.

and

Zar J.H. (1984) *Biostatistical analysis. Second edition*. New York: Prentice-Hall, Inc.

Correspondence should be addressed to:
Christian M. Ibáñez
Instituto de Ecología y Biodiversidad
Departamento de Ciencias Ecológicas, Facultad de Ciencias
Universidad de Chile, PO Box 563, Santiago, Chile
email: christianibez@yahoo.com