

# Ontogenetic and temporal fluctuations in feeding habits of the Chilean croaker *Cilus gilberti* (Perciformes, Sciaenidae) in southern Chile.

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Abstract: The natural diet of *Cilus gilberti* was investigated from samples collected between December 1997 and November 1998 in Southern Chile. This study showed the possible influence that seasonal changes and ontogenetic development of individuals may have on their feeding habits. The information was obtained by stomach contents analysis of 764 specimens caught by small scale fishery and comprising the whole legal capture size spectrum. Twenty six prey items (grouped in five major taxa) were found. Five month groups (Trophic Seasons, TS) were also identified. According to the quantitative analysis, *C. gilberti* behaves as an euryphagic, carnivorous species, feeding mainly on small fish (*Engraulis ringens* and *Strangomera bentincki*). During certain periods of the year, environmental changes can provoke a shift in prey importance toward small crustaceans (*Neotrypaea uncinata*) which increase dramatically in abundance during winter. The structure of the population adapts to changes in the environmental offer and maintains the ontogenetic organization, which includes a Ontogenetic Trophic Unit of middle sized fish (61-75 cm TL), that remains constant during most of the year, except during summer (december-january) and winter (june-july) periods.

Résumé: Variations ontogéniques et temporelles dans le régime alimentaire de Cilus gilberti (Perciformes, Sciaenidae) au sud du Chili. L'alimentation naturelle de Cilus gilberti a été étudiée à partir d'échantillons obtenus entre Décembre 1997 et Novembre 1998 au Sud du Chili. Cette étude met l'accent sur l'influence possible des changements saisonniers et de l'âge des individus sur les régimes alimentaires. Cette information a été obtenue grâce à l'analyse du contenu stomacal de 764 exemplaires capturés par pêche artisanale, comprenant toute la gamme des tailles autorisées. Vingt-six espèces de proies, appartenant à cinq taxons majeurs, ont été identifiées ainsi que cinq groupes mensuels saisonniers (saisons trophiques, TS). D'après l'analyse quantitative, Cilus gilberti a un comportement euryphage, carnivore, les proies principales étant des poissons de petite taille (Engraulis ringens et Strangomera bentincki). Au cours de certaines périodes de l'année, des changements du milieu environnant s'accompagnent de changements dans les catégories de proies, les plus importantes étant alors les petits crustacés (Neotrypaea uncinata) dont le nombre augmente beaucoup pendant l'hiver. La structure de la population s'adapte au passage d'une saison trophique à l'autre en maintenant l'organisation ontogénique qui permet aux poissons de taille moyenne de fonctionner comme une unité ontogénique constante, sauf pendant les périodes d'été (décembre– janvier) et d'hiver (juin – juillet).

Keywords: Cilus gilberti, feeding ecology, southern Chile.

# Introduction

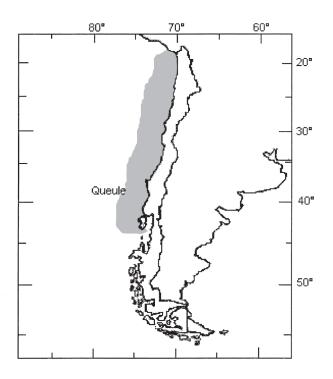
The diet of fish changes as they grow. Part of this is due to morphological and physiological changes that occur during the growth process. Research work directed to the study of such ontogenetic changes contributes to the knowledge of relationships developing within species as well as between different taxonomic groups, and is useful in order to understand the structure and dynamics of marine communities (Werner & Gilliam, 1984; Werner, 1986; Wootton, 1990; Silva, 1999). These aspects require the contribution of classic methods with statistical approaches, in order to elucidate seasonal and ontogenetic evolution within marine populations. The concept of Ontogenetic Trophic Units (OTU), introduced by Livingston (1982), is a good example of this. It can be used as a basis to distinguish length classes within a single species that feed mainly on the same prey, due to progressive changes in food consumption related to size variations. The essential idea of this approach is that taxonomic species do not behave as functional ecological units but, on the contrary, trophic ontogenetic changes describe a continuum in feeding habit changes (Stoner & Livingston, 1984).

This seems to be true for the Chilean croacker, Cilus gilberti (Abbott, 1899), an endemic Sciaenid fish of the South-eastern Pacific Ocean. Its distribution along the Chilean coast (Mann, 1954) goes from Iquique (20°13'S; 70°10'W) to Chiloé (43°06'S; 73°40'W) (see Fig. 1). Usually seen in inshore waters, this species is considered an important marine resource for human consumption. In spite of its economic importance, its biology is poorly known. In 1996, Toledo categorizes *Neomysis sopayi* Holmquist, 1957 as the main prey for C. gilberti in southern Chile. Recently, Chong et al. (2000) described the general food habits of this species further north, in the Talcahuano area (36°30'S-37°13'S), as predating mainly on *Engraulis ringens* Jenyns, 1842, Strangomera bentincki (Norman, 1936) and Mysid crustaceans. The present study describes the diet of C. gilberti in Southern Chile, during the 1997-1998 annual cycle. Feeding variations related to ontogenetic changes and seasonal response to changes in environmental conditions will be determined along the year as Ontogenetic Trophic Units and Trophic Seasons.

## **Materials and Methods**

#### Sampling

1236 stomachs from fish caught monthly between December 1997 and November 1998 were analysed. Samples were obtained from a small scale fishery at Queule (39°21'S; 73°14'W, Fig. 1), and therefore the lowest size limit corresponds to the smallest legal capture size (total



**Figure 1.** Geographic distribution of *C. gilberti* along the coast of Chile. The study area (Queule harbour) is indicated in black. **Figure 1.** Distribution géographique de *C. gilberti* le long de la

**Figure 1.** Distribution géographique de *C. gilberti* le long de la côte chilienne. La zone d'étude (Port de Queule) est signalée en noir.

length = 33 cm). For each individual, total length (TL), sex and total weight (TW) were registered before the stomach was removed. When regurgitation evidence was found, samples were not considered for further analysis. Stomach samples were preserved in 4% formaldehyde until their analysis (Holden & Raitt, 1974). Stomachs with contents were individually analysed and prey items were identified to the lowest possible taxonomic level. The total fish sample was then divided in 6 length classes of 7 cm each. Size intervals were defined as follows: G1 = 47 cm; G2 = 47-54 cm; G3 = 54-61 cm; G4 = 61-68 cm; G5 = 68-75 cm; G6 = 75 cm.

#### Data analysis

The Shannon & Wiener diversity index (H' =  $\sum_{i=1}^{\infty} -p_i \ln p_i$ , where  $p_i$  is the proportion of the species i in the community and s the number of species, Shannon & Weaver, 1949) was calculated using natural logarithm of the biomass to quantify the prey spectrum diversity. In spite of being a classic method to quantify species diversity (Berg, 1979), H' has an adequate sensitivity to detect changes in species diversity and provides a general indication of the relative magnitude of trophic specialization.

For each size group, numerical (%N), gravimetric (%W), frequency of occurrence (%F) methods (Berg, 1979; Hyslop, 1980) and the Geometric Index of Importance (GII, Assis, 1996) were applied. The later is based on a multivariate approach that combines some relative measures of prey quantification (RMPQ) which are %N, %F, %W in our case, in a n-dimensional space defined by as many orthogonal axes as quantification measures were used in the analysis. Following the author's procedure, the Geometric Index of Importance can be defined as the product between the magnitude of a prey vector, |P|, of each prey category, and a weighting coefficient C, calculated for any prey category considered (see Assis, 1996). Then, the GII can be resumed as follows:

 $\text{GII}_{j} = \frac{\binom{n}{\sum} Vi}{\sqrt{n}}^{j}$ , where Vi represents the value of the i'th parameter magnitude, corresponding to the prey j, and n is the number of magnitudes used in the analysis. Values of GII can oscillate between 0 and  $100 \text{ x} \sqrt{n}$  (for further details in the computation process, see Assis, 1996).

Prey classification (principal, secondary or occasional prey categories) was achieved using a graphic approach that considers the largest discontinuity in the decreasing sequence of points in the graph (Assis, 1996). Several authors (Mohan & Sankaran, 1988; Costello, 1990; Cortés, 1997) have pointed out that the use of a graphical representation of diet analysis can be easier to interpret. GII in particular, have a multivariate approach necessary to avoid techniques that can be dangerously redundant (Macdonald & Green, 1983; Cortés, 1997). Although the use of a particular analysis technique remains subjective (Hyslop, 1980), it has to be noted that we have already confronted this index with the Index of Relative Importance (Pinkas et al., 1971) and obtained satisfactorily accurate results from the former on the summer data set of C. gilberti (Fernández & Oyarzún, 2001).

After the diet composition of the population was determined, monthly GII values were calculated in order to define some trophic seasonality on the feeding habits of the croacker. Dissimilarity between months was calculated using Euclidean distances. The distance matrixes were then analysed using Multi Dimensional Scaling (MDS) analysis, allowing to group months into Trophic Seasons (TS). In this context, the concept of Trophic Season is defined as a period of time in which a trend of similar trophic behaviour is observed, and that do not necessarily correspond to a meteorological season of the year.

GII values were calculated for each prey within every length class, in order to define Ontogenetic Trophic Units (OTU). Dissimilarity between size classes was calculated using Euclidean distance matrixes for each Trophic Season. They were then analysed using MDS and the resulting groups were observed separately along the year in order to

elucidate an evolution in the ontogenetic structure of the population, as a response to possible changes in the environmental offer.

## **Results**

By the end of the sampling period, 1236 specimens have been analysed. From these, 61.8 % (n = 764) had stomach with food content, while 38.2 % (n = 472) were empty. Along the year (Table 1), the monthly sample number of caught specimens oscillated between 54 (February) and 161 (March). We also detected some variability in the frequency of empty stomachs, which exceeded 50 % in April and November (54.7 % and 50.4 % respectively) and was as little as 5.5 % and 9.1 % in June and August (Table 1). In spite of this, the annual distribution of stomach samples analysed seemed to be consistent enough to provide reliable results. Twenty six prey items were identified for the entire year, which are listed in Table 2.

**Table 1.** Species richness and H' diversity index of prey, total number of samples analysed and temporal distribution of empty stomach during the sampling period at Queule.

**Tableau 1.** Richesse spécifique et indice de diversité H' des proies, nombre total d'échantillons analysés et distribution temporaire du nombre d'estomacs vides au cours de la période d'échantillonnage à Queule.

Month	H'	Number of Prey items	Total sample number	Empty stomachs (%)	
December	0.74	9	100	39	
January	0.84	11	100	22	
February	0.72	4	54	44.4	
March	0.13	8	161	42.9	
April	0.67	6	128	54.7	
May	0.69	5	64	48.4	
June	1.32	12	91	5.5	
July	1.21	13	111	34.2	
August	0.8	6	66	9.1	
September	0.72	6	111	44.1	
October	0.95	8	125	44.8	
November	0.77	8	125	50.4	

#### Seasonality

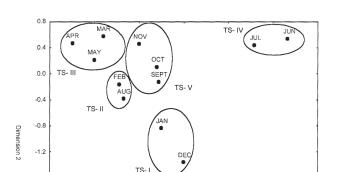
The H' index values were larger than 0.6 during the whole year (Table 1), except in March (H' = 0.13), when this index decreased due to dominance of anchovies in the stomach contents. Maximum values were registered in June and July, when a larger number of prey items were found in the stomachs, being *Neotrypaea uncinata* (H. Milne Edwards, 1837) the most abundant organism.

Once the MDS analysis was performed using the entire monthly data set, five major groups defining Trophic Seasons appeared (TS- I, II, III, IV and V, Fig. 2). Although

Table 2. General list of prey items identified in the stomachs of Cilus gilberti captured at the Queule harbour (Chile).

Tableau 2. Liste générale de espèces de proies identifiées dans les estomacs de Cilus gilberti capturés au port de Queule (Chili).

POLYCHAETA	Owenia cf. fusiformis
MOLLUSCA	Loligo gahi
	Ensis macha
	Nassarius dentifer
CRUSTACEA	Amphipoda n.i.
	Heterocarpus reedi
	Mysidae n.i.
	Pleuroncodes monodon
	Isopoda n.i.
	Pseudocorystes sicarius
	Cancer sp.
	Austropandalus grayi
	Neotrypaea uncinata
	Emerita analoga
	Pterygosquilla armata
	Euphausia mucromata
	Zoea larvae n.i.
	Megalopa larvae n.i.
UROCHORDATA	Thalia sp.
CHORDATA	Engraulis ringens



Strangomera bentincki

Leptonotus blainvillianus Paralichthys microps

Normanichthys crockeri

Odontesthes regia

Teleostei n.i.

Figure 2. MDS representation, showing month association based on diet composition. (Stress = 0).

0.4 Dimension 1

-0.2

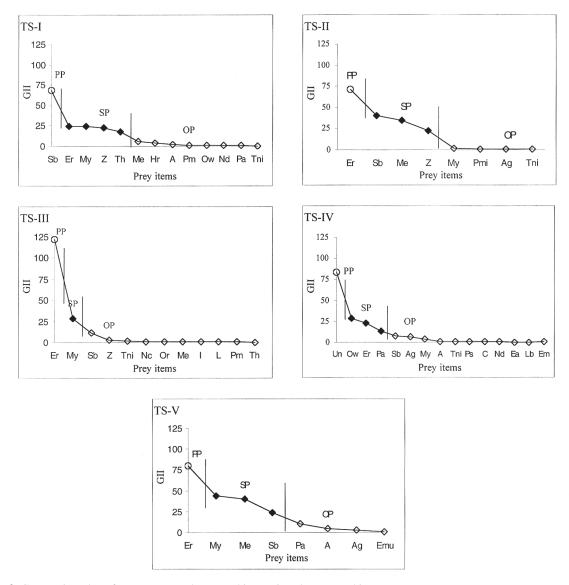
Figure 2. Représentation du MDS, montrant les associations de mois, d'après la composition du régime alimentaire (Stress = 0).

TS- II groups non consecutive months, it is assumed that the diet similarities between them are strong enough to result in a similar feeding behaviour during these periods. Fig. 3 shows the diet composition of the Chilean croacker during

each TS, according to the GII data. According to this, the croacker population at Queule can be characterized by having a low number of principal or secondary prey. However, a large number of occasional prey was a common feature in its feeding habits. During the summer (TS-I: December-January), the feeding importance of Strangomera bentincki seemed clear, even if its GII reached only 68.5. Four secondary items were preyed upon during this period, with GII values that oscillated around 20. Engraulis ringens, was possibly the most important item among these in energetic terms. In fact, it might be superior when compared to the rest of the secondary items that are either small (Mysid crustaceans, Zoea larvae) or hardly digested organisms (such as salps). It must be noted that, during the sampling period, salps were often found undigested in the fish stomachs. On the other hand, eight occasional prey were identified in the TS- I samples. During February and August (months clustered as TS- II, Fig. 3), GII values suggested a unique principal prey, E. ringens (GII = 71.2) and three secondary species of which GII values did not reach 40. Contrarily to the fact observed in TS-I, S. bentincki (GII = 40.5) was the most important secondary prey item, followed by megalop and zoea larvae, which probably do not represent a convenient energetic benefit for the fish. During TS- III, from March to May, anchovies were the absolute main prey, GII values reaching 122.46. During this trophic season, mysids seemed to be predated as a secondary alternative (GII= 28.8). Meanwhile, Strangomera bentincki showed very low GII values (GII= 11.4) and could only be classified as an occasional prey. The June-July period (TS-IV, Fig. 3) represents a change in prey consumption, mainly due to the presence of Neotrypaea uncinata as principal prey species (GII= 84.3). Three secondary prey were found. Among these, Owenia cf. fusiformis was the most important one (GII= 29), while Engraulis ringens did not reached a GII higher than 23. September, October and November (TS-V, Fig. 3), kept the general pattern of a unique principal prey (E. ringens). Mysids, Megalop larvae and S. bentincki (GII = 43.9, 40.3) and 24.1, respectively) were secondary prey during this period. Occasional prey were less numerous (4 items), and did not exceeded values of GII = 10.

## Ontogenetic Trophic Units

OTU's identified within each trophic season are presented in Fig. 4. During TS - I, the Cilus gilberti population showed two well-defined groups. First, individuals of length classes G3 and G4 (a wide range of specimens, measuring between 54 and 68 cm TL), were grouped. Then, we distinguished another group of two length classes (G5 and G6), relating to individuals larger than 68 cm TL. Individuals of length classes G1 and G2 (up to 54 cm TL) were not related to any other, and seemed to behave independently. During TS- II

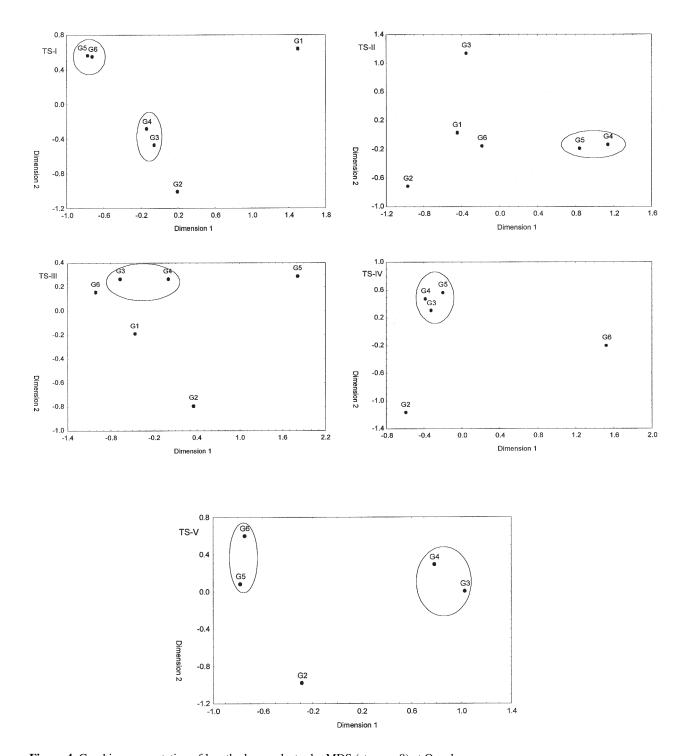


**Figure 3.** Geometric Index of Importance and prey ranking at Queule, per trophic season. **Figure 3.** Indice Géometrique d'Importance et classification des proies au Port de Queule, pour chaque saison trophique. PP: principal prey; SP: secondary prey; OP: occasional prey.

A: Amphipoda n.i.; Ag: A. grayi; C: Cancer sp.; Ea: E. analoga; Em: Ensis macha; Emu: E. mucromata; Er: E. ringens; Hr: H. reedi; I: Isopoda n.i.; L: Loligo gahi; Lb: L. blainvillianus; Me: Megalopa larvae n.i.; My: Mysidae n.i.; Nc: N. crockeri; Nd: N. dentifer; Or: O. regia; Ow: O. cf. fusiformis; Pa: P. armata; Pm: P. monodon; Pmi: P. microps; Ps: P. sicarius; Sb: S. bentincki sp.; Th: Thalia sp.; Tni: Teleostei n.i.; Un: N. uncinata; Z: Zoea larvae n.i.

(Fig. 4), length classes G4 and G5, were clustered in an OTU, grouping individuals between 61 and 75 cm TL. The rest of the population seemed to behave separately. During TS- III (March, May and April, Fig. 4), an identifiable OTU that groups length classes G3 and G4 (individuals between 54 and 68 cm TL) could be recognized as we saw during TS- I. During TS- IV, G3, G4 and G5 (individuals measuring between 54 and 75 cm TL, Fig. 4) were grouped in a single OTU, while individuals measuring less than 54

cm and more than 75 cm could not be included in any association and behaved independently. By the end of the year of sampling (TS- V, Fig. 4), we observed the same pattern than during TS- I. Once again, two OTU could be identified, grouping length classes G3 and G4 in the first one, and length classes G5 and G6 in the other. It has to be noted that the length distribution of each length class during every TS, keeps a general trend of larger numbers among middle sizes, while the extremes of the size spectrum



**Figure 4.** Graphic representation of length classes cluster by MDS (stress = 0) at Queule. **Figure 4.** Représentation graphique de l'association des classes de taille par MDS (stress = 0) au Port de Queule. G1: <47 cm; G2: 47-54 cm; G3: 54-61 cm; G4: 61-68 cm; G5: 68-75 cm; G6: >75 cm.

remain in low density (Table 3). With the exception of individuals larger than 68 cm TL during TS- I and larger than 75 cm TL during TS- V, all observed OTU had

acceptable numerical densities. During most of the annual cycle, middle length classes seem to behave as a single OTU (Table 3). This can be due to motility capacities related to

**Table 3.** Grouping of length classes into OTU, in each trophic season. n: number of samples on each length class.

**Tableau 3.** Groupement des classes de taille en OTU, dans chaque saison trophique. n: nombre d'échantillons dans chaque intervalle de taille.

TS-I		TS-II T		TS-III TS-IV		TS-V			
Length	n	Length	n	Length	n	Length	n	Length	n
class		class		class		class		class	
G1 (< 47 cm)	2	G1	5	G1	43	G1	0	G1	0
G2 (47-54 cm)	19	G2	5	G2	25	G2	2	G2	6
G3 (54-61 cm)	71	G3	26	G3	53	G3	47	G3	27
G4 (61-68 cm)	37	G4	25	G4	48	G4	78	G4	97
G5 (68-75 cm)	8	G5	21	G5	13	G5	31	G5	58
G6 (> 75 cm)	2	G6	8	G6	1	G6	1	G6	5

morphological ontogenetic development, since it is known that ontogenetic changes in trophic habits are produced in order to avoid some competition in one of the niche dimensions. The presence of *Neotrypaea uncinata* in TS- IV (which can be seen as a consequence of some possible niche perturbation), resulted in an OTU that includes not two but three middle length classes (individuals from 54 to 68 cm TL). According to this, size association did occur during the 1997-1998 year among the Queule population of *Cilus gilberti*, affecting the middle (and occasionally) bigger length classes.

## **Discussion**

According to our results, the Queule population of *Cilus gilberti*, behaves as a carnivorous euryphagic species of which the diet is composed mainly by a unique principal prey that can be replaced during the year by a small number of secondary prey and several items incorporated to the feeding spectrum by occasional hunt or incidental encounters. Their appearance in the feeding spectrum may be due to their abundance in the study area, and could eventually explain the trend of the H' index during the sampling period (Table 1).

Within the prey spectrum of this population, sardines (*Strangomera bentincki*) support its feeding habits only during TS- I (December-January, Fig. 3), while anchovies (*Engraulis ringens*) and other small organisms such as larvae and mysids are consumed as secondary prey items. This situation can change from March to May (Fig. 3, TS-II and TS- III), when the population feeds mainly on anchovy and secondarily on sardines, although mysids, zoea and megalop larvae are also strongly consumed. On the contrary, during TS- IV (June-July), the abundance of

Neotrypaea uncinata in the stomachs was the evidence of a dramatic change in the diet of the Chilean croaker. A polychaet (Owenia cf. *fusiformis*) and crustacean a (Pterigosquilla armata H. Milne Edwards, 1837) appeared secondary items during this trophic season. We think that this could be related to some fluctuations in food availability. Unfortunately, we did not perform an exploratory sampling of the environmental offer and the lack of this kind of data restrains a possible conclusion at this point. Between September and November (TS- V), the environ-mental situation seems to influence the feeding habits of Cilus gilberti toward the

consumption of *Engraulis ringens* on the first place, and mysids, that prevail as the most important secondary item.

Apparently, a changing environment offer (caused by seasonal fluctuations, geographical location or even by catastrophic events) could be able to provoke dramatic variations in C. gilberti feeding habits. In that context, winter (TS- IV) may be a key period of the year, as well as February and August may have been transitional months of the 1997-1998 annual cycle at Queule. But some of these observations differ from those made by other authors. Toledo (1996) analysed almost 150 specimens coming from southern Chile and found that C. gilberti predated mostly on Neomysis sopayi. Chong et al. (2000) focussed their study further north (Talcahuano area in central Chile) and found that *Emerita analoga* (Stimpson, 1857) was intensely predated by C. gilberti. In our case, the presence of nektonic fishes insures nutritional requirements, whenever they are available. Neotrypaea uncinata can replace them in winter (TS- IV), whether because of its relative abundance or higher availability. Since this species lives buried in the sea floor, its presence in the stomachs shows the capacity of the Chilean croaker to capture benthic items and we assume that the sucking ability developed by modern fish allows them to do so. In fact, the ability to protrude the jaw is a common feature in groups as advanced as the Sciaenidae family (Wootton, 1990). Protruding the jaw may also confer some advantage for obtaining benthic preys from otherwise inaccessible places (Alexander, 1967; Osse, 1985). Other benthic items present along the year, such as Owenia cf. fusiformis, Emerita analoga and benthic molluses caught by incidental encounters, may also be considered in the same way. Therefore, we can assume at this point that the Chilean croaker behaves as a well organized opportunistic predator. Along the year, the fish population adapts to fluctuations in the available food, but the size structure and ontogenetic diet organization do not. In spite of a low sample number in the younger (G1 and G2 specially during TS- IV and V) and larger stages (G5 and G6 during TS- I), our results illustrate the capacity of the Chilean croaker to exploit alimentary items coming from different depth ranges in the water column and trophic levels, taking epipelagic as well as benthic items. The variety of species used as food items, chosen either by size or by bathymetric location in the water column, suggests some diversification in predatory environments, which has already been pointed out by other authors (Valeria & Sanches, 1996) for other sciaenid species in Latin America.

#### Acknowledgements

We thank Mr. León Matamala (Universidad Austral, Chile) for his assistance during the sampling period. We are also indebted to Dr. Carlos Assis and an anonymous referee for their valuable comments on the manuscript. This research was supported by the project FIP 97-19.

#### References

- **Abbott J. F. 1899.** The marine fishes of Peru. *Proceedings of the Academy of Natural Sciences of Philadelphia*, **51**: 324-364.
- **Alexander R. McN. 1967.** The function and mechanism of the protrusible upper jaw of some actinopterygian fish. *Journal of Zoology*, **151**: 43-46.
- **Assis C. A. 1996.** A generalized index for stomach contents analysis in fish. *Scientia Marina*, **60** (2-3): 385-389.
- **Berg J. 1979.** Discussion of methods of investigating the food of fishes, with reference to a preliminary study of the prey of *Gobiusculus flavescens* (Gobiidae). *Marine Biology*, **50**: 263-273.
- **Cortés E. 1997.** A critical review of methods of studying fish feeding based on analysis of stomach contents: application to elasmobranch fishes. *Canadian Journal of Fisheries and Aquatic Sciences*, **54**: 726-738.
- Costello M. J. 1990. Predator feeding strategy and prey importance: a new graphical analysis. *Journal of Fish Biology*, 36: 261-263.
- Chong J., Cortés N. & Bustos R. 2000. Hábitos alimenticios de la corvina Cilus gilberti (Abbott 1899) (Pisces: Sciaenidae) frente a la costa de Talcahuano. Biología Pesquera 28: 29-35.
- **Fernández C. & Oyarzún C. 2001.** Trophic variations of the Chilean croacker *Cilus gilberti* during the summer period 1997-1998 (Perciformes, Sciaenidae). *Journal of Applied Ichthyology*, **17:**

- Holden M. & Raitt D. 1974. Manual of fisheries Science. Part 2.
  Methods of resource investigation and their application. FAO Fishery Technical Paper (M.Holden & D. Raitt eds), 115: 213 pp.
- Hyslop E. J. 1980. Stomach content analysis a review of methods and their application. *Journal of Fish Biology*, 17: 411-429
- **Livingston R. J. 1982.** Trophic organization of fishes in a coastal seagrass system. *Marine Ecology Progress Series*, 7: 1-12.
- **MacDonald J. S. & Green R. H. 1983.** Redundancy of variables used to describe importance of prey species in fish diets. *Canadian Journal of Fisheries and Aquatic Sciences*, **40**: 635-637.
- **Mann G. 1954.** *Vida de los peces en aguas chilenas.* Instituto de Investigaciones veterinarias: Santiago, Chile. 342 pp.
- Mohan M. V. & Sankaran T. M. 1988. Two new indices for stomach content analysis of fishes. *Journal of Fish Biology*, 33: 289-292.
- **Osse J. W. M. 1985.** Jaw protrusion, an optimization of the feeding apparatus of teleost? *Acta Biotheoretica*, **34**: 219-232.
- Pinkas L., Oliphant M. & Iverson L. 1971. Food habits of albacore, bluefin tuna and bonito in California Waters. Fish Bulletin. 152: 1-105.
- Shannon C. E. & Weaver W. 1949. The mathematical theory of communication. University of Illinois Press: Urbana, USA, 117 pp.
- **Silva A. 1999.** Feeding habits of John Dory, *Zeus faber*, off the Portuguese continental coast. *Journal of the Marine Biology Association of the United Kingdom*, **79**: 333-340.
- **Stoner A. W. & Livingston R. J. 1984.** Ontogenetic patterns in diet and morphology in sympatric spared fishes from seagrass meadows. *Copeia*, **1984**: 174-187.
- **Toledo H. 1996.** Alimentación de la "corvina" Cilus gilberti (Abbott, 1899) y su relación con el tamaño de la boca y las presas que consume. Tesis Magister en Ciencias Mención Zoología: Universidad Austral de Valdivia, Chile. 79 pp.
- Valéria C. & Sanches V. 1996. Food resources partitioning among sciaenid fishes (Perciformes, Sciaenidae) of the Flamengo Bay, Ubatuba, Southeastern Brazil. *Arquivos de Biología e Tecnología*, 39: 639-649.
- Werner E. E. & Gillian J. F. 1984. The ontogenetic niche and species interactions in size-structured populations. *Annual Review of Ecology and Systematics*, 15: 393-425.
- Werner E. E. 1986. Species interactions in freshwater fish communities. In: *Community Ecology* (J. Diamond and T.J. Case eds.), pp 344-357. Princeton University Press: Princeton.
- **Wootton R. J. 1990.** *Ecology of Teleost Fishes.* Fish and Fisheries series 1 (Chapman & Hall eds). London. 404 pp.