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First-feeding of hake (*Merluccius hubbsi*) larvae and prey availability in the North Patagonian spawning area – Comparison with anchovy *)

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Abstract

The diet of *Merluccius hubbsi* first-feeding larvae was analysed and related to food availability in stratified waters of the Patagonian spawning area. The gut contents of small larvae ranging from 2 to 4 mm SL, collected from five consecutive depth strata (upper 50 m of the water column), were examined. After dissection of the larvae, the prey items were stained with tolouidine blue. The feeding incidence, and the types, sizes and numbers of food particles per larvae were determined. The mean feeding incidence was 64.5 %. Food particles 45 to136 µm in width constituted the bulk of the prey ingested, which consisted of nauplii and early copepodites of the small copepod species frequently found in the sampling area. The most abundant taxa among the gut contents were *Paracalanus parvus*, *Oithona spp*., *Acartia tonsa* and members of Pseudocalanidae. The mean number of nauplii per larva was 4.4 times higher than the number of copepodites, but the volumetric ratio between the two groups was 1.4:1. The results of larval gut analysis were related to zooplankton distribution in the field. First-feeding strategies of hake and anchovy larvae growing in the area were compared.

Kurzfassung

Nahrungserstaufnahme von Seehechtlarven (*Merluccius hubbsi*) und Nahrungsangebot im patagonischen Laichgebiet. Ein Vergleich mit Sardellen.

Untersucht wurde der Mageninhalt erstmalig fressender Larven (2 bis 4 mm SL) aus fünf aufeinander folgenden Schichten (obere 50 m). Nach dem Sezieren der Larven wurden die Beuteorganismen mit Toluidin blau gefärbt. Fressrhythmus sowie Art, Größe und Anzahl der Nahrungspartikel jeder Larve wurden bestimmt. Die mittlere Futteraufnahme betrug 64,5 % Nahrungspartikel von 45 bis 136 µm stellten den hauptanteil der gefressenen Beute, bestehend aus Nauplien und frühen Copepoditen der kleinen Copepodenarten, die häufig im Sammelgebiet

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anzutreffen sind. Die häufigsten Taxa im Magen waren *Paracalanus parvus*, *Oithona* ssp; *Acartia tonsa* und Mitglieder der Psendocalanidae. Die mittlere Nauplienzahl pro Larve war 4.4 mal höher als die Zahl der Copepodite, aber das Volumenverhältnis zwischen den beiden Gruppen war 1.4:1. Die Ergebnisse der Magenuntersuchungen wurden zur Zooplanktonverteilung im Feld in Beziehung gesetzt. Die Strategien der ersten Nahrungsaufnahme von Seehecht und Sardellenlarven, die in dem Gebiet aufwachsen, werden verglichen.

Resumen

Se analizó la dieta de larvas de primera alimentación de *Merluccius hubbsi,* en relación con la disponibilidad de alimento en aguas estratificadas del área de desove patagónica. Se examinaron los contenidos digestivos de larvas pequeñas, de 2 a 4 mm de LE, colectadas en 5 estratos consecutivos de profundidad (50 m superiores de la columna de agua). Después de la disección las presas fueron teñidas con azul de tolouidina. Se determinó la incidencia trófica, el tipo, tamaño y número de partículas alimento por larva. La incidencia trófica media fue 64.5 %. Las partículas de ancho comprendido entre 45 y 136 µm constituyeron la mayor parte de las presas ingeridas, representadas por nauplii y primeros copepoditos de las especies pequeñas de copépodos frecuentemente encontradas en el área de estudio. Entre ellos, los más abundantes en los contenidos digestivos fueron *Paracalanus parvus*, *Oithona* spp., *Acartia tonsa* y miembros de Pseudocalanidae. El número medio de nauplii por larva fue 4.4 veces más alto que el número de copepoditos, pero la relación volumétrica entre estos items alimento fue 1.4:1. Los resultados obtenidos del análisis de contenidos digestivos fueron relacionados con la distribución del zooplancton en el medio. Se compararon las estrategias de primera alimentación adoptadas por las larvas de merluza y de anchoíta que coexisten en el área.

Introduction

Argentine hake (*Merluccius hubbsi*) is the most important species in the Argentine Sea fishery. The principal area of concentration of this species lies between 35° S and 48° S. Hake has two main spawning periods on the Argentine Shelf, depending on the geographical latitude. In the northern sector (35° to 38° S) it spawns during winter and in the southern sector (North Patagonia, 43° to 45° S) it spawns in late spring to early summer (Ehrlich and Ciechomski 1994). The spawning areas are associated with retention areas resulting from local oceanographic conditions (Ehrlich 1998).

This paper deals with the population of *Merluccius hubbsi* in the Patagonian area, which is characterised by the formation of tidal fronts between nearshore mixed waters and thermally stratified shelf waters (Carreto *et al.* 1981, Carreto *et al.* 1986). These frontal systems support a high biomass of phytoplankton (Carreto and Benavídes 1990) and microzooplankton (Viñas and Ramírez 1996; Möhlenkamp 1996) in the upper levels of the water column. The period of spawning of hake coincides with the seasonal development of the tidal fronts (from November to March). We analyse the first-feeding strategy of hake larvae in this ecosystem, taking into account that successful first-feeding is considered to be one of the main factors which determine the survival of fish larvae and, consequently, year-class strength (Hjort 1914; Cushing 1975 1990).

Although the larvae of Argentine hake are known to feed from the start on a wide spectrum of food particles (Ciechomski and Weiss 1974), the relative importance of the various prey items in the diet has not been established. The North Patagonian region is not only an important spawning and nursery ground for hake, but also for other fishes such as anchovy, *Engraulis anchoita* (Sánchez and Ciechomski 1995). Compared to hake, an anchovy larva has a relatively small mouth at first feeding. Thus the size of the food particles ingested is smaller (Viñas and Ramírez 1996).

Our primary objectives were: 1) to determine the prey composition in the gut contents of hake larvae; 2) to evaluate the relative importance of prey species and sizes; 3) to compare prey sizes in the guts with the size spectrum in the field, 4) to compare the first-feeding strategies of hake and anchovy larvae in the region.

Material and Methods

The samples were collected in the North Patagonian region during a cruise of RV "Meteor" (Germany) in December 1989. The survey was part of a SARP Project (Nellen 1990; Alheit *et al.* 1991).

Ichthyoplankton samples were taken at stations along four transects perpendicular to the coastline (Figure 1). At each station, 5 consecutive 10 m depth strata in the upper 50 m of the water column were sampled by oblique tows with a multiple opening/closing BIOMOC net (1 m^2 opening, 300 µm mesh size). The samples were preserved in 4 % formaldehyde solution.

Microzooplankton samples were collected at the same stations and depth levels used for the larvae with a multiple opening/ closing MULTINET, 0.25 m^2 mouth opening, equipped with a mesh size of 64 µm. In the laboratory all organisms smaller than 225 µm width were identified, counted and grouped into the size categories indicated in Figure 6 (see more details in Viñas and Ramírez 1996).

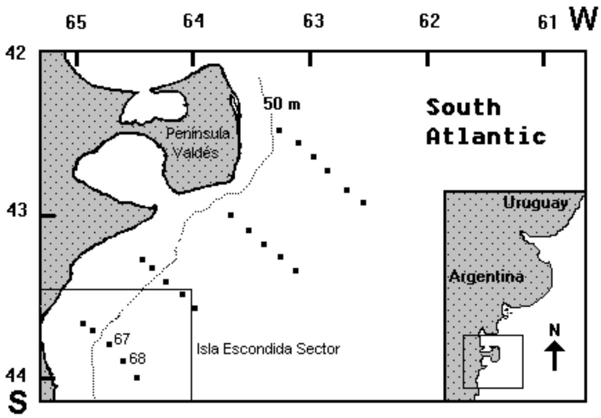


Figure 1: Location of the sampling stations in the North Patagonian region. Note that hake larvae were collected at stations 67 and 68.

Analysis concerning the gut contents of first-feeding anchovy larvae, the distribution of their microzooplanktonic prey in the field and the relationship between food items and feeding behaviour at different hydrographic conditions were previously published by Viñas and Ramírez (1996).

The gut contents of hake larvae were analysed out in samples from stations 67 and 68 of the southern transect (Figure 1). At the other stations, the larval concentrations were too low to allow analysis. The smallest "feeding larvae" (eyes completely pigmented, mouth and anus open) were taken at random from each sample and measured to standard length by means of an eye micrometer. The standard length shrinkage model proposed for silver hake (*M. bilinearis*) larvae by Fowler and Smith (1982) was used to estimate the size the larvae had had when alive.

A minimum of 30 larvae per sample were analysed whenever possible. The entire intestinal tract of each larva was dissected and opened. The feeding incidence for a given sample was determined as the percentage of larvae with at least one food item in the gut (Arthur 1976). The food particles were stained with a saturated solution of Toluidine Blue (0.25 %), and identified. The types of prey items and their abundances were determined to the lowest taxa possible. The total length and width of each prey item were determined under the microscope using a micrometer. Since the width of the prey is considered to be the critical dimension for ingestion of oblong organisms (such as copepods) by fish larvae (Hunter 1981), the prey items were grouped into 6 consecutive width categories (45–90 µm, 90–136 µm, 136–182 µm, 182–228 µm, 228–274 µm and 274–320 µm).

The volumetric biomass of each prey type was calculated according to Sumida and Moser (1980) by treating copepod eggs as spheres, and nauplii, copepodites and adults as ellipsoids. The general volumetric equation adopted was $V = 4/3\ \pi \times a \times b \times c$, where a, b and c are diameters along the three axes. The height of nauplii was assumed to be equal to the width. The height of the copepodite and adult stages was considered to be 95 % of the width, from data of Fernández Aráoz (1994).

The results are discussed in relationship to microzooplankton and mesozooplankton distribution in the field during the same cruise (Möhlenkamp 1996; Viñas and Ramírez 1996; Santos 1993). In order to compare the feeding strategies of hake and anchovy larvae, results published by Viñas and Ramírez (1996) and some of their original data were also used.

Results

Vertical distribution of hake larvae

The highest densities of early hake larvae were found in the Isla Escondida sector at the thermocline level (25 m) and below (Ehrlich 1998). In contrast, anchovy larvae were more frequently found associated with the upper mixed waters or the thermocline depth (Alheit *et al.* 1991).

Feeding incidence

The gut contents of 255 larvae in the size range of 2 to 4.5 mm SL (mean 2.75 ± 0.26) were examined. It was observed that larvae begin to feed before they complete absorption of the yolk. The mean feeding incidence at all sampling levels was 64.5 %. The two selected stations were sampled at midday on consecutive days. Despite this consistency in the timing of sampling, the highest feeding incidence and numbers of prey per larva (nauplii and copepodites) were found at station 68 (Table 1). In a general way, the number of prey per positive larvae ranged from 1 to 18, but almost 80 % of the larvae had 2 to 4 prey in their guts (Figure 2) with a mean value of 3.14.

Prey composition and size

Nauplii, copepodites and adult stages of small copepod species were the most common components in the diet. There were also small amounts of unidentified material, and copepod eggs were not observed. The numbers of prey items were not significantly correlated with larval length (Figure 3). Of the larvae with prey items in the gut, 79.4 % had

Table 1: Number of larvae studied (N), feeding incidence (F.i.), and number of total prey (P/L), nauplii (N/L) and copepodite stages (C/L) per larva. Percentage of larvae containing nauplii (% L with N) and copepodite stages (% L with C) in their guts.

	St. 67					St. 68				Total
	0–10	10–20	20–30	30–40	40–50	0–10	10–20	20–30	30–40	
N	30	5	30	33	31	16	30	50	30	255
F.i.	70	80	66.7	58.8	51.6	43.7	46.7	80	83.3	64.53
P/L	2	2.75	2.2	2.35	2.25	2.7	4.2	4.75	5.08	3.14
N/L	1.33	2.5	1.5	1.7	1.62	2.6	3.4	4.05	4.32	2.56
C/L	0.62	0.25	0.7	0.7	0.62	0.28	0.78	0.57	0.76	0.59
%L with N	61.9	100	70	70	68.7	85.7	78.6	87.5	92	79.38
%L with C	52.4	25	55	55	56.2	28.6	57.1	35	52	46.26

eaten nauplii, but only 46.35 % had eaten copepodites. The mean number of nauplii per larva (2.56) was 4.4 times higher than that of copepodites (0.59, Table 1), whereas the volumetric ratio between the two prey items was 1.4:1 (Figure 4).

Hake larvae ingest a wide size range of food particles when they start to feed. No significant relationship was observed between the length of the larvae and the size (length and width) of their prey (Figure 5). The size of food organisms ranged from 81 to 666 µm in length, while their width fluctuated between 36 and 311 µm (Table 2). More than 75 % of the prey were 45 to 136 µm in width (Figure 6), mostly consisting of copepod nauplii (Figure 7A). Few of these prey items could be identified to species level. However , it is assumed that they belong to the more common copepod species in the area (Ramírez 1981; Santos and Ramírez 1995; Viñas *et al.* 1992). The bulk of prey in 45 to 136 µm width class would therefore be composed of nauplii and early copepodites of small species (less than 1.5 mm total length) such as *Paracalanus parvus*, *Oithona helgolandica*, *O. nana*, *Acartia tonsa*, and of nauplii of *Ctenocalanus vanus* and *Drepano-*

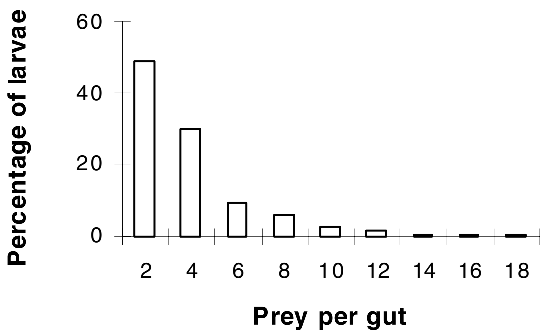


Figure 2: Percentage of first-feeding hake larvae containing given numbers of prey in their guts.

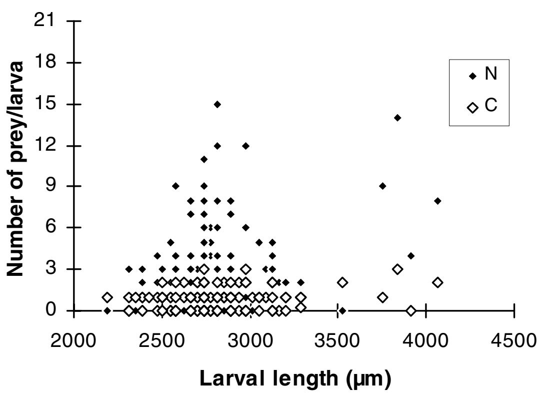


Figure 3: Numbers of prey at different larval size (N) nauplii, (C) copepodites 1 to 6.

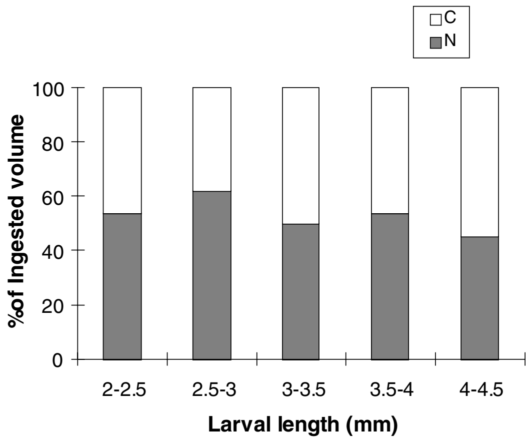


Figure 4: Percentage of the ingested volume of different prey. (N) nauplii, (C) copepodites 1 to 6.

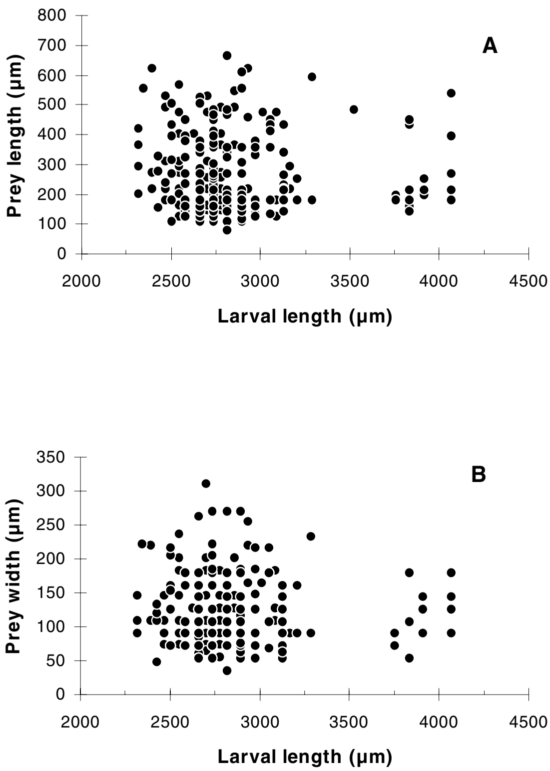


Figure 5: Relation of prey length (A) and prey width (B) to larval length.

pus forcipatus. Only the nauplius stages N1 and N2 of *Calanoides carinatus* and *Calanus australis* belonged to this width range (Figs. 7 B and 8 B).

The number and volume of ingested prey by hake and anchovy first-feeding larvae are shown in Figure 9. Hake larvae ingested almost twice as much prey biomass as did anchovy at first-feeding.

Discussion

In spite of the wide spectrum of prey sizes ingested by *M. hubbsi* larvae at first feeding, more than half of the volume ingested corresponded to copepod nauplii in the size range 45 to 136 µm (belonging mostly to small species). This is the first time that this prey item is reported in the diet of *M. hubbsi* larvae. However, in another species of the genus, *M. productus,* microzooplankton (copepod eggs and nauplii) have been found to be a predominant component in the gut contents (Sumida and Moser 1980) of the smallest larvae (3 to 3.9 mm SL).

Ciechomski and Weiss (1974) reported that the food of *M. hubbsi* larvae in the size range 2.4 to 18.0 mm SL was composed almost exclusively of adult copepods and, in a few cases, copepodite stages. On the other hand, the cuticles of small nauplii are very difficult to see unless they are stained (Viñas and Ramírez 1996). Hence, Ciechomski and Weiss (1974), who did not stain their samples, may have overlooked these prey items.

The main copepod species in the guts of the larvae were *Paracalanus parvus*, *Oithona* spp, *Acartia tonsa* and members of Pseudocalanidae, which confirms the findings of Ciechomski

Table 2: Length, width and volume of the principal prey items of first-feeding hake larvae.

	Nauplii stages			Copepodite stages		
	Length [μm]	Width [μm]	Volume [$10^6 μm^3$]	Length [μm]	Width [μm]	Volume [$10^6 μm^3$]
Max	622.20	270.00	137.34	666.00	311.10	182.94
Min	81.00	36.00	0.44	133.30	68.20	2.34
Mean	199.67	97.33	10.94	421.78	176.78	52.55
SD	80.53	33.98	15.87	95.83	44.56	36.13
N	281			58		

and Weiss (1974). These small copepod species (total length <1.5 mm) and their development stages dominated the plankton of the study area throughout the annual cycle, with the highest abundance of juvenile stages during spring (Ramírez 1981; Viñas *et al.* 1992; Santos and Ramírez 1995).

The diet of the first-feeding larvae of anchovy and hake growing in the region overlapped mainly in the 45 to 90 μm food size range (Figures 6 A and B). Microzooplankton within this size range were dominant in most of the stations of the "Meteor" cruise (Viñas and Ramírez 1996) except for stations 67 and 68 (Figure 6 C). This may be attributed to the impact of the predation by anchovy and hake larvae, or by ctenophores, which were very abundant in these stations (Mianzan 1993; Alheit *et al.* 1991;

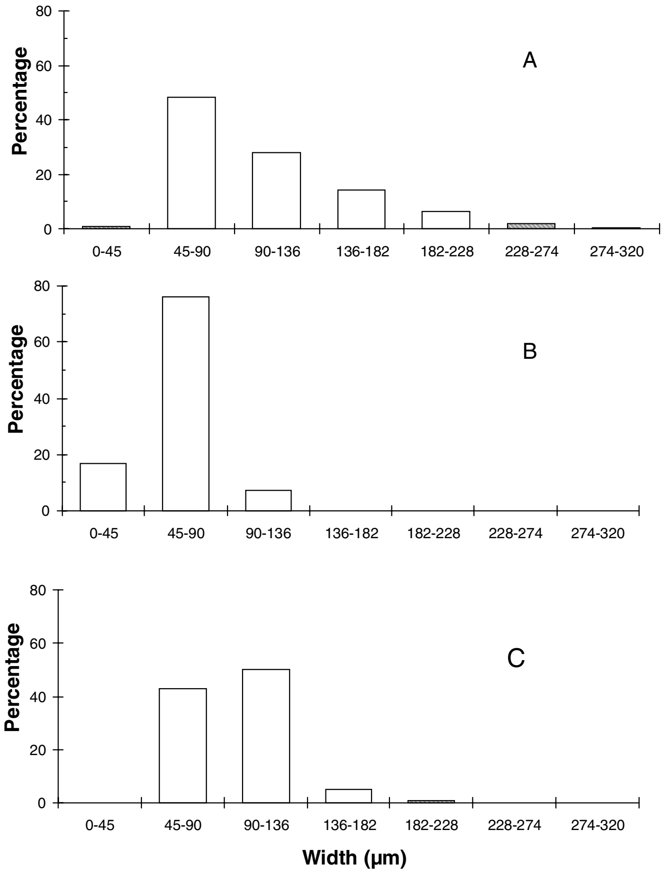
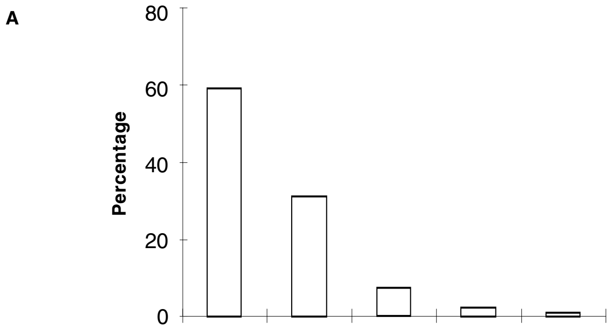


Figure 6: Size of food particles at first feeding in hake (A) and anchovy larvae (B), compared to microzooplankton availability in these size ranges (C). Anchovy and zooplankton data are from stations 67 and 68 of the 1989 "Meteor" cruise and were obtained by Viñas and Ramírez (1996). Note that microzooplankton data includes mostly eggs and nauplii of copepods.

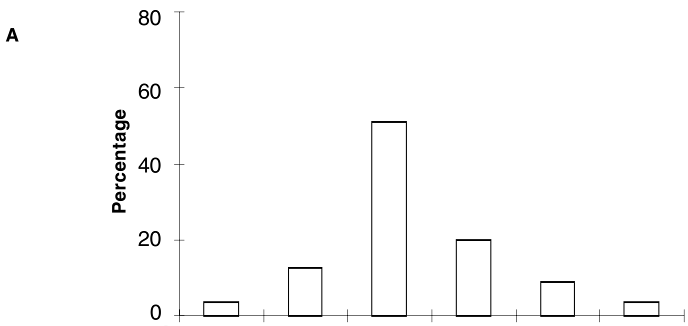


B

Width of prey [µm]

Species	45–90	90–136	136–182	182–228	228–274	Authors
Euterpina acutifrons	1–3	4–6				Haq (1965 a)
Oithona nana	1–6					Haq (1965 b)
Paracalanus parvus	1–4	5–6				Nichols and Thompson (1995)
Acartia tonsa	2–4	5–6				Conover (1956)
Calanoides carinatus		1–2	3–4	5–6		Björnberg (1972)
Pseudocalanidae	1–2	3–4	5–6			Nichols and Thompson (1995)

Figure 7: (A) Size (width) spectra of nauplii (1to 6) in hake guts. (B) Distribution of copepod nauplii (1 to 6) of the more common copepod species in different size classes classified by width. Nauplii width data were taken from different authors.



B

Width of prey [µm]

Species	45–90	90–136	136–182	182–228	228–274	274–320	Authors
E. acutifrons		1	2–3	4–6			Rao (1958)
O. nana	1–2	3	4–6	6			Grandori (1912)
O. helgolandica		1	2–4	5	6		Sabatini, com.pers.[1)]
P. parvus		1–2	3	4	5	6	Nichols and Thompson (1991)
A. tonsa		1–2 *)	3	4	5	6	Fernández Aráoz (1994)
C. carinatus						1–2 *)	
Pseudocalanidae			1–2	3	4	5	Nichols and Thompson (1991)

Figure 8: (A) Size (width) spectra of copepodites (1 to 6) in hake guts. (B) Distribution of copepodite stages (1 to 6) of the more common copepod species in the different size classes classified by mean cephalothorax width. Copepod width data were taken from different authors.
*) Estimated by the authors from data of Fernández Aráoz (1994), [1)] Sabatini, M.E. ,Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP), CC. 175, Mar del Plata, Argentina.

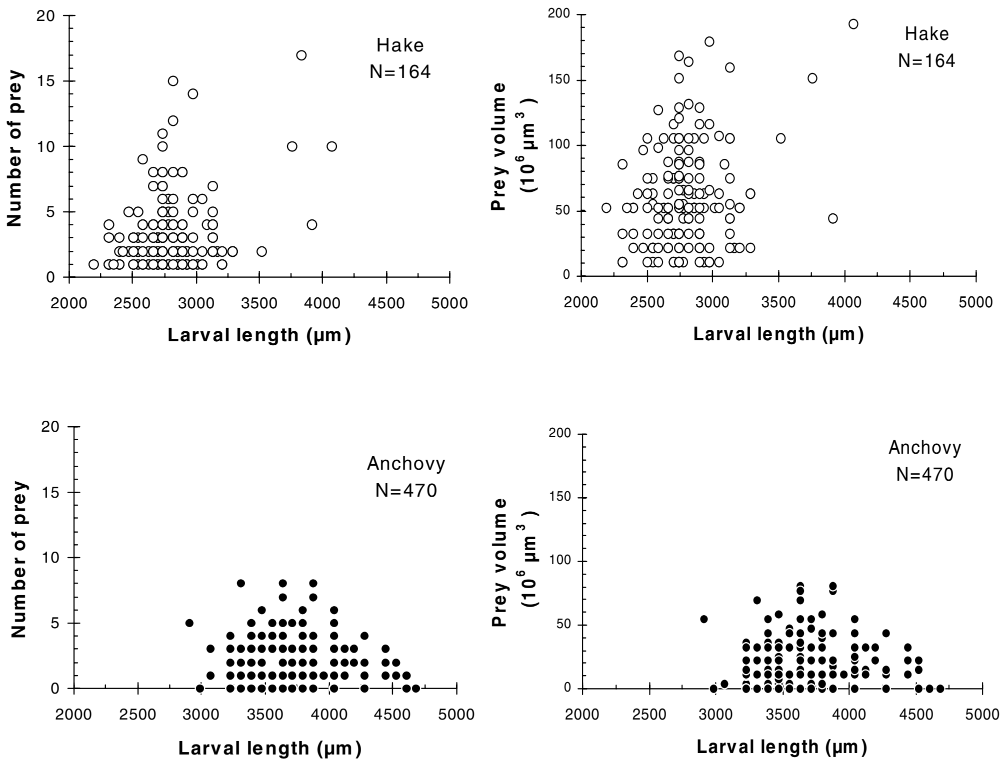


Figure 9: Relation of numbers and volume of prey ingested by first-feeding hake and anchovy larvae to larval size.

Ehrlich 1998). Therefore, the anchovy and hake larvae in the region compete for share this important food resource at first feeding. Similarly, Arthur (1977) observed that 70 µm in width nauplii were common in the first-feeding larval diets of Pacific sardine (*Sardinops sagax*), northern anchovy (*Engraulis mordax*) and jack mackerel (*Trachurus symmetricus*) living in the California current system. Houde and Alpern Lovdal (1984) also found that the average width of prey eaten by first-feeding larvae of more than 15 of the most common fish species in Biscayne Bay (Florida, USA) was 74 µm.

It has been observed in many regions that gadoid larvae also consume copepod nauplii as their earliest food, and indeed their growth and recruitment is sometimes correlated with the availability of this prey (Mullin and Cass-Calay 1997). In most cases, larvae feed in the upper ten meters of the water column, where the nauplii concentration can be quite high. Walleye pollock (*Theragra chalcogramma*) and pollock (*Pollachius virens*), for example, feed in water with concentrations of 20 to 144 nauplii per litre (Incze and Ainaire 1994; Napp *et al.* 1996). Larvae of Pacific hake (*M. productus)*, on the other hand, occur deeper in the water column where they may experience significantly lower concentrations of food (Mullin and Cass-Calay 1997). However, the maxi-

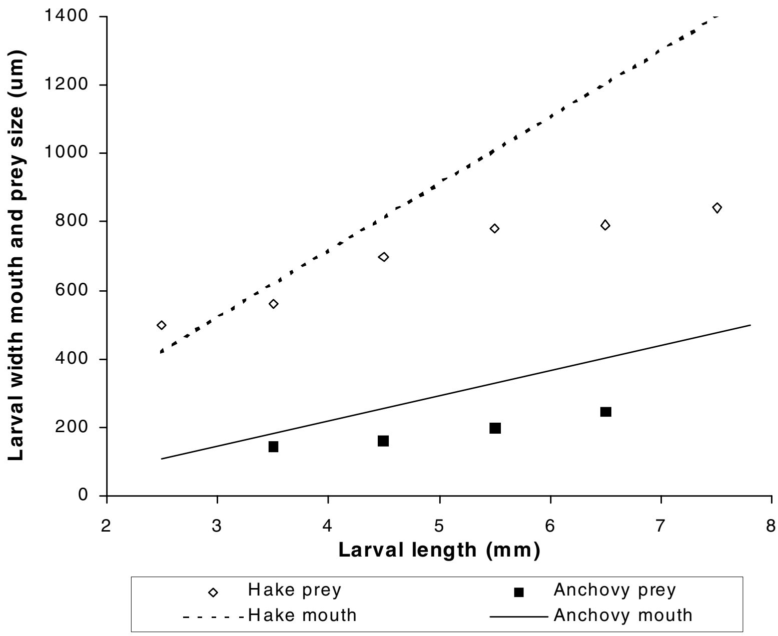


Figure 10: Relationship between the width of the mouth and the range of prey size in hake and anchovy larvae of different lengths (from Ciechomski and Weiss 1974).

mum growth rate of this species could be attained at concentrations of approximately 6 particles per litre (Cass-Calay 1997). Assuming that larvae of Pacific and Argentine hake grow at similar rates, the mean microzooplankton density recorded at stations 67 and 68 (about 13 particles per litre; Viñas and Ramírez 1996) should be sufficient to permit maximum larval growth.

The dominance of nauplii in the ingested food indicates that hake larvae are able to take advantage of small-scale patches of nauplii in the water column (Owen 1989). Nevertheless, they are also able to prey on larger prey.

The highest abundances of medium-sized copepods (*ca.* 1.3 mm total length, *e.g.*, *Drepanopus forcipatus, Ctenocalanus vanus*) and of large-sized copepods (> 2 mm in total length, *e.g. Calanoides carinatus*) were found at St. 67 and 68 (Möhlenkamp 1996; Santos 1993). This sector of Isla Escondida is the principed nursery ground of hake off Patagonia (Ehrlich 1998). It can be assumed that the growing larvae, having increasingly wider mouths (Ciechomski and Weiss 1974), could take advantage of the larger prey found in this area.

It has been observed that the massive summer spawning of hake in the Patagonian region occurs in thermally stratified waters. This is common in others species of *Merluccius* as well (Ehrlich 1998). From the scarce information available on the vertical distribution of hake and anchovy larvae in the region, it can be assumed that they inhabit different depth levels of the water column. Early hake larvae occurred more frequently at the thermocline level (25 m), or below (Ehrlich 1998). In contrast, anchovy larvae were more frequently found in the upper mixed waters or at thermocline depth (Alheit *et al.* 1991). In these layers, anchovy larvae may find dense patches of small prey (nauplii and eggs) for successful first-feeding. Hake larvae, on the other hand do not depend exclusively on such dense patches since they can feed also upon larger and less concentrated prey. These results confirm Bailey's (1982) opinion that the first-feeding period seems to be less critical for hake which have a wider choice of prey, than for other species of pelagic fishes, such as anchovy or jack mackerel, which depend on higher density patches of small prey.

An ability to consume relatively large prey is energetically advantageous to larvae and seems to be developed best in large-mouthed short-bodied species such as hake (Hunter 1981; Bailey 1982; Houde and Alpern Lovdal 1984).

The differences between the diet of anchovy and of hake could largely be explained by the accessibility of the prey to the size of the mouth of the fish. Ciechomski and Weiss (1974) have shown that for a given larval length (*eg.* 3.5 mm) the mouth of a hake larva is almost 3 times wider than that of an anchovy larva (Figure 10).

In conclusion, the first-feeding strategies favouring the survival and growth of early hake larvae include a capability to ingest a wide size range of food particles, an ability to take advantage of more abundant prey, such as copepod nauplii, and the capability to start feeding while still having yolk reserves.

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