

Food size selectivity and diet overlap in larvae of Clupeiform species from central Chile

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Abstract: The feeding behaviour of larvae of four Clupeiform fish species (*Sardinops sagax*, *Strangomera bentincki*, *Ethmidium maculatum* and *Engraulis ringens*) was studied using specimens collected from September to November 1987 in Concepcion Bay, Chile. The indices of food preference (α) of Chesson, of diet overlap (D) of Schoener and (L) of Hurlbert, were used. Similar feeding patterns were found in the larvae of the four species. The diet included several developmental stages of copepods: eggs, nauplii and copepodites. The larvae of *Engraulis ringens* showed an early euriphagy. There were no significant differences in food preference between the species, except for *Ethmidium maculatum*, which showed a high preference for eggs, even at larger larval sizes. A general trend for preference for larger prey as larvae grow is displayed by the other species. No significant difference was found between sampling periods. A high level of diet overlap was found, regardless of the index used to estimate it.

Résumé : Sélection de nourriture par la taille et similitude des régimes alimentaires chez les larves d'espèces de Clupéiformes (Pisces ; Teleostei) du Chili Central. Le régime alimentaire des larves de quatre espèces de Clupéiformes (*Sardinops sagax*, *Strangomera bentincki*, *Ethmidium maculatum* et *Engraulis ringens*) a été étudié au cours des mois de septembre et novembre dans la Baie de Concepcion, Chili central. Les indices de préférence alimentaire (α) de Chesson et de similitude alimentaire (D) de Schoener et (L) de Hurlbert ont été utilisés. Les quatre espèces présentent des types d'alimentation semblables comprenant différents stades de développement de copépodes : œufs, nauplii et copépodites. Les larves d'*Engraulis ringens* présentent une euriphagie précoce. Il n'y a pas de différences significatives dans les préférences alimentaires des espèces, à l'exception d'*Ethmidium maculatum* qui préfère nettement les œufs aux larves, même chez leurs plus grandes larves. Chez les autres espèces une préférence générale pour les proies plus grandes se manifeste à mesure que les larves grandissent. Aucune différence n'a été observée entre les périodes d'échantillonnages.

Keywords: fish larvae, diet, food selection, diet overlap, Clupeiforms, Chile.

Introduction

The feeding in larval fish depends on environmental variables as well as on species-specific physiological and

behavioural attributes (Theilacker & Dorsey, 1980). The minimum food availability that allows food capture is determined by biological and oceanographic features, whereas attributes such as size at first feeding, perceptive and locomotive capabilities, feeding strategy, are species-specific responses (Hunter, 1981). The differential abilities to capture prey by different species have an impact on the

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composition of the diet and result in species selectivity. It seems that the most important factor in the selection of food by fish larvae is the availability of prey in the environment (Rajasilta & Vourinen, 1983), which is always variable in time and space. Examples of effects of changes in food availability on the food preferences have been documented for larvae of *Sebastes* spp. (Anderson, 1994) and *Trachurus declivis* (Young & Davis, 1992).

The feeding strategy of fish larvae has received a special attention, particularly in groups of species that coexist in a given geographical area. In general, there is evidence suggesting that larvae can use their food resources differentially, thus avoiding competition (Arthur, 1976; Govoni et al., 1983; Houde & Lovdal, 1984). The scenario of coexisting closely related species would be particularly interesting to study, as their larvae share morphological and functional features (Jenkins, 1987).

Four clupeiform species co-occur in Central Chile (Orellana & Balbontin, 1983): *Sardinops sagax* (Jenyns, 1842), *Strangomera bentincki* (Norman, 1936), *Ethmidium maculatum* (Valenciennes, 1847), and *Engraulis ringens* Jenyns, 1842. All of them are pelagic and two of them, *S. bentincki* and *E. ringens*, support the second most important fishery in the area. As adults, *S. sagax* and *E. maculatum* feed mostly on zooplankton, whereas *S. bentincki* and *E. ringens* are phytoplankton filter feeders (Arrizaga et al., 1993).

These Clupeiform species are partial spawners that reproduce during the same period of the year, winter and spring (e.g. Aguilera et al., 1986; Cubillos et al., 1999). In particular, the Concepcion Bay area has been reported as a spawning ground for many fish species, including the four above mentioned (e.g. Orellana & Balbontin, 1983; Llanos, 1990). As a consequence, larvae of these four species are consistently found coexisting in the plankton.

The larvae of the species under study share different features. At the start of exogenous feeding they measure (mouth width in parenthesis): 5.0 mm (230 μ m) for *S. sagax*; 5.1 mm (220 μ m) for *S. bentincki*; 6.4 mm (315 μ m) for *E. maculatum*, and 3.8 mm (170 μ m) for *E. ringens* (Orellana & Balbontin, 1983; Herrera et al., 1987; Llanos et al., 1996). The comparatively larger size of body and mouth in larvae of *Ethmidium maculatum* can be explained by the existence of larger eggs (Herrera et al., 1987). Previous studies on the same species have shown that the larvae of all of them feed on similar types of prey (Llanos et al., 1996), but the ecological aspects involving selection have received little attention. The aims of this study were to establish the composition of the diet in the larvae of four species, to determine selectivity, and to assess the degree of differentiation (or overlap) in the use of food resources (food size) during different periods of the spawning season.

Materials and methods

Samples were collected three times during the spawning period of the species (see Llanos et al., 1996) in Concepcion Bay (36°40'S, 73°02'W) (Fig. 1), from September to November 1987. Sampling sites and depths were chosen where exploratory samples indicated high abundances of clupeiform larvae (Fig. 1). Discrete samples were collected at a depth of 8 m with a 60 cm diameter, 330 μ m mesh, plankton net provided with an opening-closing system, and towed at approximately 2 knots. Samples were collected during the day, as clupeiform larvae are diurnal feeders (Hunter, 1981). To determine food availability, water samples were taken simultaneously from the same depth with 4 liter Niskin bottles and screened through 25 μ m mesh filters to collect the microzooplankton. All samples were preserved in a solution of filtered seawater with 5% buffered formalin.

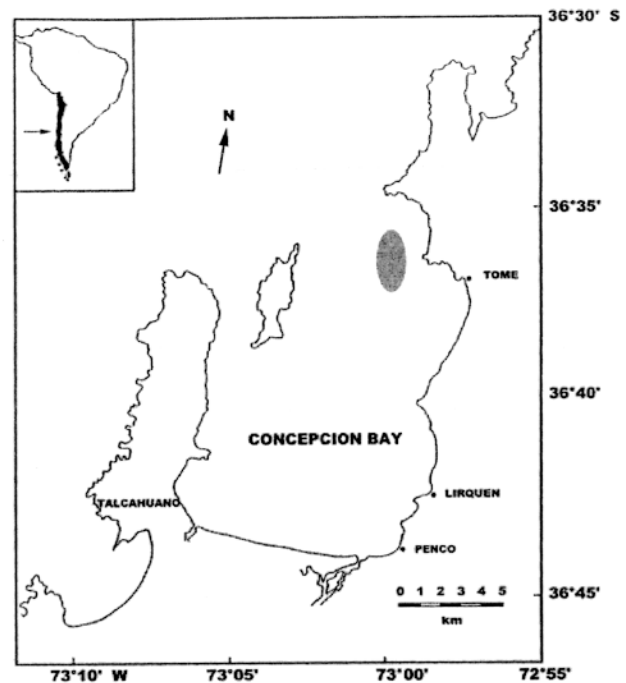


Figure 1. Map of Concepcion Bay with location of sampling area.

Figure 1. Carte de la Baie Concepcion avec emplacement des zones d'échantillonnage.

Larvae were sorted, identified (Orellana & Balbontin, 1983), and processed under a dissecting microscope. All Clupeiform larvae, from post yolk-sac stages up to 20 mm standard length (SL), were considered in the analysis. Larvae were grouped in five size intervals according to Arthur (1976). The first interval ranged from 3.9 to 6.0 mm in length, and included the larvae at the start of the exogenous feeding, except *E. maculatum*, which reaches the

exogenous feeding stage at 6.5 mm (Herrera et al., 1987). The next size intervals were 6.1 - 8.0 mm, 8.1 - 10.0 mm, 10.1 - 12.0 mm, and > 12.0 mm.

Following the gut dissection of each larva, the food items were identified, measured, and counted. In the case of nauplii and copepodites, the maximum width of the cephalothorax was measured, since it has been shown to be the critical dimension for food ingestion of those kinds of prey (Hunter, 1981). Microzooplankton samples were analysed using an inverted microscope. Food particles considered to be potential prey for the larvae were also measured and counted. Microzooplankton items present in both the diet and the gut contents, were grouped into several size categories.

The numeric frequency was used to measure prey abundance of an item in the diet and in the environment. The categories of prey size were established arbitrarily considering the range of variation within each prey type. Food preference was examined using the α_i index of Chesson (1978): $\alpha_i = [r_i/p_i] / \sum (r_i/p_i)$ for $i = 1, \dots, n$, where, r_i : proportion of item i in the diet, p_i : proportion of item i in the environment, n : number of food items. It is considered that there is selection for a food item if $\alpha_i > 1/n$.

To estimate diet overlap, two similarity indices were used: the index D of Schoener (1968), which only considers similarity among gut contents, and the index L of Hurlbert (1978), which includes similarity among gut contents and the food availability in the environment. The index D is obtained from $D = 1 - 0.5 [\sum (p_i - q_i)]$ for $i = 1, \dots, n$, where p_i is the proportion of item i in the diet of species p , and q_i is the proportion of the item i in the diet of species q . The index ranges from 0 to 1, with values > 0.6 indicating a significant overlap (Brodeur & Percy, 1990). The index L of Hurlbert (1978) is determined as $L = (\sum a_i / \sum p_i * \sum q_i) / \sum (p_i * q_i / a_i)$, where p_i and q_i have the same meaning as before, and a_i is the proportion of item i in the environment. $L = 0$ when there is no overlap in the use of food resources, $L = 1$ when both species use all food items in the same proportion as they occur in the environment, and $L > 1$ when both species tend to preferentially select the same item(s). In order to detect possible ontogenetic variations, the estimation of D and L was performed considering each pair of species and five larval size intervals. In order to evaluate differences between pairs of species, the Friedman test was used, and to explore trends of diet overlap with increasing larval size, the Spearman correlation coefficient was calculated (Zar, 1984).

To characterize the diet of each species and size interval, the pooled data (of three months from September to November) of numeric frequency was used. To evaluate differences between sampling periods (using preference index), the samples from each sampling month were treated separately. As no microzooplankton samples were available

for October, the food preference analysis was restricted to the larvae collected in September and November. Due to the absence of one of the species, *E. maculatum*, in the September and October samples, only the ones from November were considered for the diet overlap analyses.

Results

The number of larvae analysed for each species were as follows (percentage of larvae with at least one prey item in parenthesis): 122 *Sardinops sagax* (68%); 178 *Strangomera bentincki* (81%); 89 *Ethmidium maculatum* (40%); and 262 *Engraulis ringens* (80%). Table 1 summarizes the information of number of larvae analysed for each size interval, and of prey items in gut contents of larvae collected during three months. The results of the analysis of the microzooplankton sampled in the environment are given in Table 2. Except for the higher abundances of a dinoflagellate in September and of large copepod eggs in November, the microzooplankton composition is fairly constant with no significant differences between the two sampling dates (Kolmogorov-Smirnov test, $D_{\max} = 0.36$, $p > 0.5$, Table 2).

Diet composition

Typically, most of the diet was composed of developmental stages of copepods, i.e. eggs, nauplii and copepodites. In *Sardinops sagax* and *Engraulis ringens* there is a relatively high proportion of copepod eggs and dinoflagellates in the younger stages, whereas in larger larvae, copepodites and nauplii become numerically more important. In *Strangomera bentincki* there is a larger proportion of large prey (nauplii, copepodites, plus mollusk larvae) compared to the other species. The diet of *Ethmidium maculatum* showed two features not observed in larvae of the other species: only copepod eggs were found in the diet of younger larvae, and they remain the most important food item in larvae of larger sizes.

Food Preference

An obvious feature is the variation in preference between the two months and between different size classes within the same species (Figures 2.1 through 2.4). The larger *Sardinops sagax* larvae show a tendency to select larger prey, especially in November. An unusual finding was the high preference for mollusk larvae observed in the first feeding stages. Although the larvae of *S. sagax* are able to capture larger preys as they grow, nauplii still remain preferred items (Fig. 2.1). The larvae of *Strangomera bentincki* show a general trend to select larger prey as they grow (Fig. 2.2). They display a food preference for eggs in the first feeding stages from September to November. The dinoflagellates are numerically important in the environment and in the diet during November, but they never become selected items. The larvae of *Ethmidium*

Table 1. Numeric frequency (percentage) of food items in the diet of larvae of *Sardinops sagax*, *Strangomera bentincki*, *Ethmidium maculatum* and *Engraulis ringens* at different size intervals, obtained during three months (September through November). Eggs (cop.), eggs of copepods; the prey item "Other" includes pollen grains, ostracods, and unidentified remains. n represents larvae with gut contents.

Tableau 1. Fréquence numérique (pourcentage) des types de proies consommés par les larves de *Sardinops sagax*, *Strangomera bentincki*, *Ethmidium maculatum* et *Engraulis ringens*, de septembre à novembre et selon leur taille. Eggs (cop.), œufs de copépodes ; le type de proies "Other" comprend grains de pollen, ostracodes, et restes non identifiés. n représente le nombre de larves ayant un contenu digestif.

Species / Prey item	Size intervals (mm)				
	3.9 - 6.0	6.1 - 8.0	8.1 - 10.0	10.1 - 12.0	> 12.0
<i>Sardinops sagax</i>					
Eggs (cop.)	56.9	34.4	7.7	6.3	10.7
Nauplii	12.0	53.3	53.8	45.3	42.8
Copepodites		8.9	38.4	48.4	42.8
Dinoflagellates	17.1	1.1			3.6
Mollusk larvae	13.8	2.2			
n	23	26	8	11	15
<i>Strangomera bentincki</i>					
Eggs (cop.)	39.4	28.6	27.1	57.6	25.0
Nauplii	41.5	51.1	52.1	27.3	26.4
Copepodites	4.2	11.3	18.8	15.1	43.1
Dinoflagellates	2.1	1.5			
Mollusk larvae	7.4	0.7			0.7
Other	5.3	6.8	2.0		4.9
n	37	44	16	13	35
<i>Ethmidium maculatum</i>					
Eggs (cop.)		100.0	83.3	53.3	43.5
Nauplii				26.7	17.4
Copepodites			16.7	20.0	39.1
n		1	5	14	16
<i>Engraulis ringens</i>					
Eggs (cop.)	54.0	16.1	23.3		29.2
Nauplii	31.6	65.4	50.0	66.7	8.3
Copepodites	0.4	9.9	26.7	33.3	62.5
Dinoflagellates	8.4	3.7			
Mollusk larvae	4.4	1.2			
Other	1.2	3.7			
n	138	41	13	2	16

maculatum select large eggs (> 130 µm) in all size intervals; copepodites became selected items in larger larvae (Fig. 2.3). The first feeding larvae of *Engraulis ringens* show no food preference in November, but eggs and nauplii are selected in September (Fig. 2.4).

Diet Overlap (index D of Schoener)

Most of the values of D (Table 3) are indicative of a high diet overlap. There are no significant differences between pairs of species ($p > 0.05$). A trend toward a lower diet overlap as larvae grow is observed; this correlation, however, is not significant (Spearman $r = 0.36$, $p = 0.11$). The highest values recorded were in the size interval of 8.1–10.0 mm between two pairs of species: *Engraulis ringens* vs. *Ethmidium maculatum* ($D = 0.99$) and *Sardinops*

sagax vs. *E. maculatum* ($D = 0.97$). In both cases, the overlap is due to the presence of a similar proportion of copepodites in the diet. Among the larvae at first feeding stages, the maximum overlap is found between *S. sagax* and *Strangomera bentincki*; this is due to the presence of high and comparable percentages of mollusk larvae, nauplii and dinoflagellates (see Fig. 2 for reference).

Diet Overlap (index L of Hurlbert)

The results of the analysis of diet similarity using this index are coincident with those obtained using D, showing a high overlap and no significant differences between pairs of species ($p > 0.05$). The same, and non significant, trend toward lower diet overlap in larger larvae is recorded (Spearman $r = 0.24$, $p = 0.28$). The highest values of L were found in the first feeding larvae of *Sardinops sagax* and *Strangomera bentincki* (Table 3). In this case the overlap is explained by the selection of low abundance prey, such as mollusk larvae, dinoflagellates and small nauplii. The next high value of L, 1.58 between *Engraulis ringens* and *S. bentincki* at sizes > 12.0 mm, is explained by the preference of copepodites.

Discussion

With the exception of *Ethmidium maculatum*, an early euriphagy was evident in the remaining three species, mainly due to the presence of dinoflagellates and mollusk larvae, which represented an important portion of the diet. However, the presence of dinoflagellates does not necessarily represent a source of food, as the nutritional value of thecate dinoflagellates has been questioned (e.g. Lasker, 1981). Regardless of nutritional

considerations, the presence of dinoflagellates is useful to evaluate the process of food selection. For example, although thecate dinoflagellates are present in the diet, they are not considered to be a preferred prey at first feeding since they are found in a lower ratio in the diet than in the environment.

The analysis of the diets and comparisons of preferences between the four species studied showed a distinct pattern for *E. maculatum*. An explanation for this pattern could be found in ontogenetic features of the species. The larvae of *E. maculatum* reach the first feeding stage at a large size (6.5 mm vs. 4.0 mm in the other species). Due to this, they are less mature at the same size than the other larvae. The preference of less mobile prey, such as eggs, in early stages

Table 2. Food availability (size and numeric frequency, as percentage) in September and November in Concepción Bay, obtained from microzooplankton analysis.

Tableau 2. Dimensions et disponibilité de la nourriture en septembre et novembre dans la Baie de Concepcion, évaluées à partir de récoltes de microzooplancton.

Item	Maximum width (µm)	September %	November %
Eggs (cop.)	< 30	1.2	2.2
	40-60	1.2	2.2
	70-90	13.2	19.5
	100-120	2.4	4.4
	>130	1.2	15.2
Nauplii	50-80	7.2	8.7
	90-110	6.0	2.2
	120-150	1.2	8.7
	>210	1.2	2.2
Copepodites	80-110	1.2	2.2
	120-150	1.2	4.3
	160-190	1.2	2.2
	>210	1.2	2.2
Dinoflagellates			
<i>Protoperdinium</i> spp.	50-80	53.0	13.0
<i>Diplopsalis minor</i>	50-80	4.8	8.7
Mollusk larvae	130	2.4	2.2

Table 3. Diet overlap values D of Schoener (1968), (bold faced), and L of Hurlbert (1978), between larvae of four clupeiform species, at specified size ranges (mm).

Tableau 3. Variations ontogéniques de l'indice de similitude alimentaire D de Schoener (1968) en gras, et L de Hurlbert (1978), pour les larves des quatre espèces de clupéiformes étudiées.

	Size intervals (mm)				
	3.9 - 6.0	6.1 - 8.0	8.1 - 10.0	10.1-12.0	>12.0
<i>E. ringens</i> vs. <i>S. sagax</i>	0.76	0.59	0.82		0.52
	1.00	1.50	1.01		1.23
<i>E. ringens</i> vs. <i>S. bentincki</i>	0.75	0.80	0.86		0.73
	1.00	1.00	1.00		1.58
<i>S. sagax</i> vs. <i>S. bentincki</i>	0.82	0.88	0.84	0.54	0.77
	2.58	1.46	1.17	1.47	1.52
<i>E. ringens</i> vs. <i>E. maculatum</i>			0.99		0.75
			1.00		1.50
<i>S. sagax</i> vs. <i>E. maculatum</i>			0.97	0.52	0.69
			1.00	0.97	1.22
<i>S. bentincki</i> vs. <i>E. maculatum</i>			0.82	0.76	0.82
			1.38	1.09	1.17

of *E. maculatum* is consistent with less developed sensory and motor capabilities of these early larvae (O'Connell, 1981).

Food preference estimates coincide with the general description of increasing preferences for larger prey that become less abundant as larvae grow (Houde & Lovdal, 1984; Govoni et al., 1986). However, increasing size is also coupled with changes in prey type (e.g. from egg to nauplius or from nauplius to copepodite), which makes difficult to determine the cause for food selectivity (Young & Davis, 1990). Besides, there are important energetic considerations in the change of prey type. For example in the transformation of a nauplius to a copepodite of similar width, there might be an exponential increment in the energetic content (Theilacker & Kimball, 1984). These considerations, however, are beyond the scope of this study.

The most important feature of food preference (see Fig. 2) is the variation between species, size intervals, and sampling dates. The variation in the first two might be associated to species and size specific responses. However, the variation on the third (sampled dates) was recorded even in the absence of a significant change in food availability, as no differences were found in the composition of microzooplankton between the two periods analysed. It seems that the spatial variation in food availability played an important role in the differences recorded.

For the sampling of larvae, a 0.6 m plankton net was used, towed (discrete depth) over a distance of a few hundreds meters, whereas the microzooplankton samples were collected using Niskin bottles that sampled a small volume (4 l) and only at a certain spot. The use of different devices to collect quantitatively fish larvae and their food, zooplankton nets and bottles/pumps, respectively (e.g. Hillgruber et al., 1995; Hillgruber & Kloppmann, 2000), is justified as they belong to different size fractions of the plankton.

Approximately 86% of the values of the index D of Schoener are indicative of significant diet overlap ($D > 0.6$). However, there are two factors that might have led to high values of overlap: i) the index D takes into account only the presence of preys in the gut contents (and not in the environment) of pairs of species; ii) due to anatomical features of the larvae (mouth width) there are few types of prey in the size range where the larvae feed upon, approximately 50 to 100 µm at first feeding (Llanos et al., 1996).

The percentage of cases with significant diet overlap ($L > 1$) using the index of Hurlbert was reduced to 52%. The inclusion of food availability allows to make a further distinction between the items in the gut contents according to its preference. Items that are present in the diet (even abundant) will contribute little to the overlap if they are not selected prey. For example, there were two cases in which

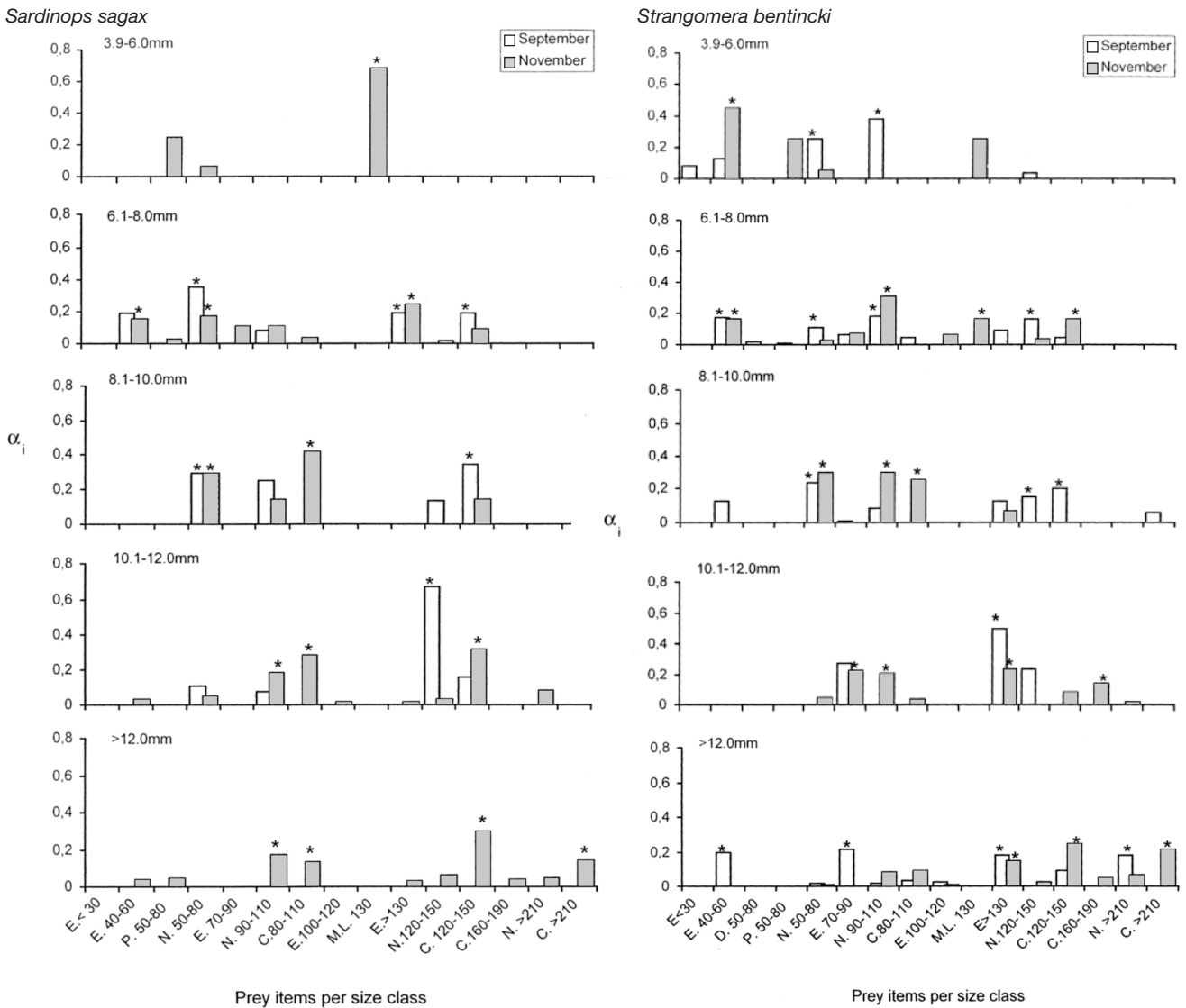


Figure 2. Values of α_i preference index (Chesson, 1978) for the four studied species at the specified size ranges during September and November. Asterisks over the bars indicate selection ($\alpha_i > 1/n$, with n being the number of food items). In food items: C. copepodites; D. *Diplopsalis* sp. (dinoflagellate); E. eggs of copepods; ML. mollusk larvae; N. nauplii; P. *Protoperidinium* spp. (dinoflagellate). Numbers next to food items represent size in μm .

1. *Sardinops sagax*, 2. *Strangomera bentincki*, 3. *Ethmidium maculatum*, 4. *Engraulis ringens*.

Figure 2. Valeurs de l'indice de préférence α_i (Chesson, 1978) pour les quatre espèces étudiées et leur différentes gammes de taille dans les échantillons récoltés en septembre et novembre. Les astérisques sur les barres indiquent la sélection ($\alpha_i > 1/n$, n étant le nombre de types de proies). En abscisse, les types de proies sont suivis de leur taille en μm ; C. copépodites; D. *Diplopsalis* sp. (dinoflagellé); E. œufs de copépodes; ML. larves de mollusques; N. nauplii; P. *Protoperidinium* spp. (dinoflagellé).

1. *Sardinops sagax*, 2. *Strangomera bentincki*, 3. *Ethmidium maculatum*, 4. *Engraulis ringens*.

the presence of comparatively less abundant prey in the gut contents of pairs of species led to contrasting estimations of diet overlap, low D and high L (*Engraulis ringens* vs. *Sardinops sagax* and *S. sagax* vs. *Strangomera bentincki*, see table 2). The tendency to find higher values of diet overlap in larger larvae is consistent with the acquisition of

motor and sensory abilities that appear during development. Larger larvae would be able to respond preferentially to a certain kind of prey, even if they are comparatively scarce, such as copepodites > 210 μm .

Finally, there is another aspect of the larval biology that needs further consideration. If the species grow at different

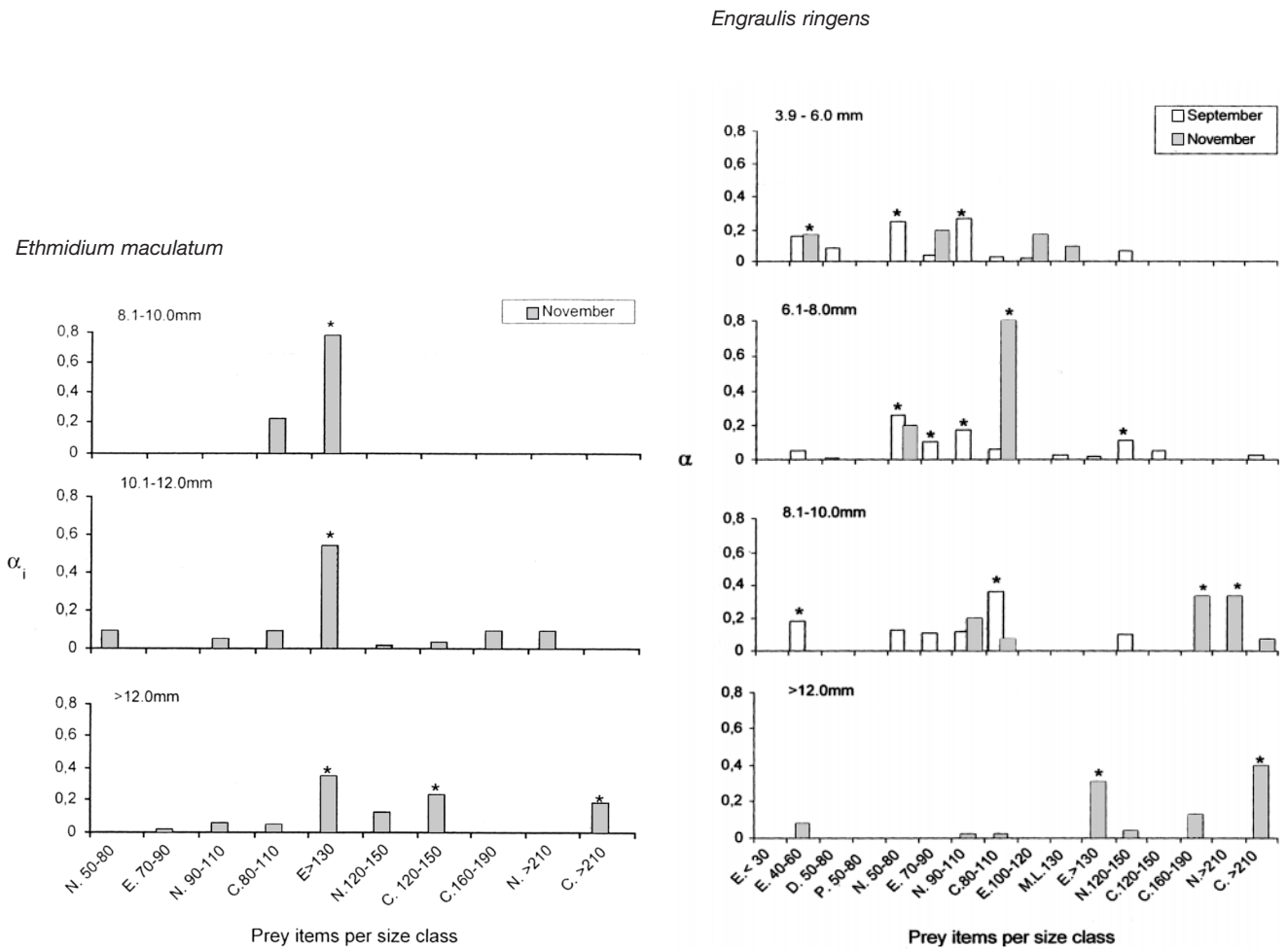


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rates, the recorded diet overlap may only be temporal. However, growth rates (determined using daily growth increment counts in otoliths) are about the same (and low) for larvae of *Sardinops sagax* and *Engraulis ringens* in the studied area (Herrera et al., 1985; Castillo et al., 1985). Due to similar morphological and physiological characters found in all clupeiform larvae, the other two species are expected to show similar growth rate responses. However, in absence of actual data on growth for larvae of *Strangomera bentincki* and *Ethmidium maculatum*, it remains to be determined whether the overlap is permanent or temporal.

Our results for diet composition, food preferences, and diet overlap, clearly indicate a high overlap in the use of food resources, with no significant differences between sampling months. In natural populations the diet overlap is more common when food is abundant and is less evident when food is scarce (Schoener, 1974). Our study was carried out during spring, when primary productivity and zooplankton abundance were high (Pantoja et al., 1987). This led to abundant larval food, which may help to explain in part the high values of diet overlap found.

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