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Food Habits of *Anchovia clupeioides* (Pisces: Engraulidae) in the Ciénaga Grande de Santa Marta, Colombian Caribbean

GUILLERMO DUQUE AND ARTURO ACERO P.

Food habits of the Zabaleta anchovy *Anchovia clupeioides* (Swainson, 1839) in the coastal lagoon Ciénaga Grande de Santa Marta, northeast Colombia, were examined. A total of 4,389 specimens were captured during monthly collections on a 24-hr basis between Oct. 1995 and June 1996. This species is planktophagous, feeding primarily on copepods and detritus. It also feeds on diatoms throughout the year and is a seasonal consumer of crab zoea, rotifers, and fish eggs. Copepod nauplii, larvae of polychaetes, cyanobacteria, and cladocerans comprise a small percentage of the prey. Biomass of large prey did not differ significantly between the high- and low-salinity season but was significantly different during the intermediate salinity season. The ingestion of the main food items was unaffected by seasonal and diel changes. Although the trophic flexibility of *A. clupeioides* allows an opportunistic exploitation of a variety of food items, it feeds preferably on copepods and can be considered as a secondary consumer.

The study of food habits of fish is fundamental for understanding the complex relationship between a species and its environment, as well as interspecific and intraspecific interactions with members of the fish community. Most of the energy exchanges and transformations needed for growth, reproduction, movement, and somatic maintenance depend on these dynamic relationships (Sierra et al., 1994). Hence, important elements of autecology, productivity, and the ecological roles of fish populations are derived from stomach content studies (Windell and Bowen, 1978).

The food habits of engraulid species have been widely studied, indicating that they are planktophagous. Ontogenetic and seasonal shifts in diet have been previously described (Angelescu, 1982; James, 1987; Pauly et al., 1989; Rojas de Mendiola, 1989). Because of their planktophagous habits, these fishes play an important role at lower trophic levels of the food web and are also an important food resource for other marine fishes, birds, and mammals (Murphy, 1978).

The limited research done in the Colombian Caribbean on food habits of the family Engraulidae has been concentrated in the Ciénaga Grande de Santa Marta (CGSM) and adjacent areas. Members of the family Engraulidae are among the most abundant fishes in the region (González, 1981). Castaño (1989), Santos-Martínez and Arboleda (1993), and Duque-Nivia et al. (1996) have shown the ecological importance of engraulids as forage fishes for several commercially valuable fish species. Castaño (1989) determined that *Anchovia clupei-*

oides, the Zabaleta anchovy, feeds primarily on zooplankton (zoea, ostracods, copepods, and polychaete larvae) and to a lesser extent on phytoplankton (diatoms), but this thesis remains unpublished. Gallo-Nieto (1995a) studied age and growth of this species, and Gallo-Nieto (1995b) and Caselles and Acero (1996) described reproductive patterns and concluded that the Zabaleta anchovy is a resident of the CGSM, where it is the most abundant engraulid (Santos-Martínez and Vilorio, 1996). This research determined the food habits of *A. clupeioides*, a key species in the trophic complex of the pelagic zone in the CGSM.

STUDY AREA

The CGSM estuarine lagoon system is part of the Magdalena River exterior delta. The CGSM is located at 10°43'–11°00'N 74°15'–74°32'W on Colombia's Caribbean coast (Fig. 1). The lagoon system is bounded to the east and southeast by the lower hills of the Sierra Nevada de Santa Marta, which rise to 5,800 m above sea level and where the three main rivers that open in the CGSM originate. Isla de Salamanca, a sand barrier, separates the lagoon from the Caribbean Sea in the north except at Boca de la Barra, a 200-m-wide and 10-m-deep man-made opening. On its west and southwest, the lagoon borders the mud plains of the Magdalena River (Cosel, 1986; Botero, 1988; Botero and Mancera-Pineda, 1996).

The area of the CGSM is 450 km², and its mean depth is 1.5 m (IGAC, 1973). Historically, the lagoon has been the main source of seafood (e.g., fish, shrimp, oysters, swimming

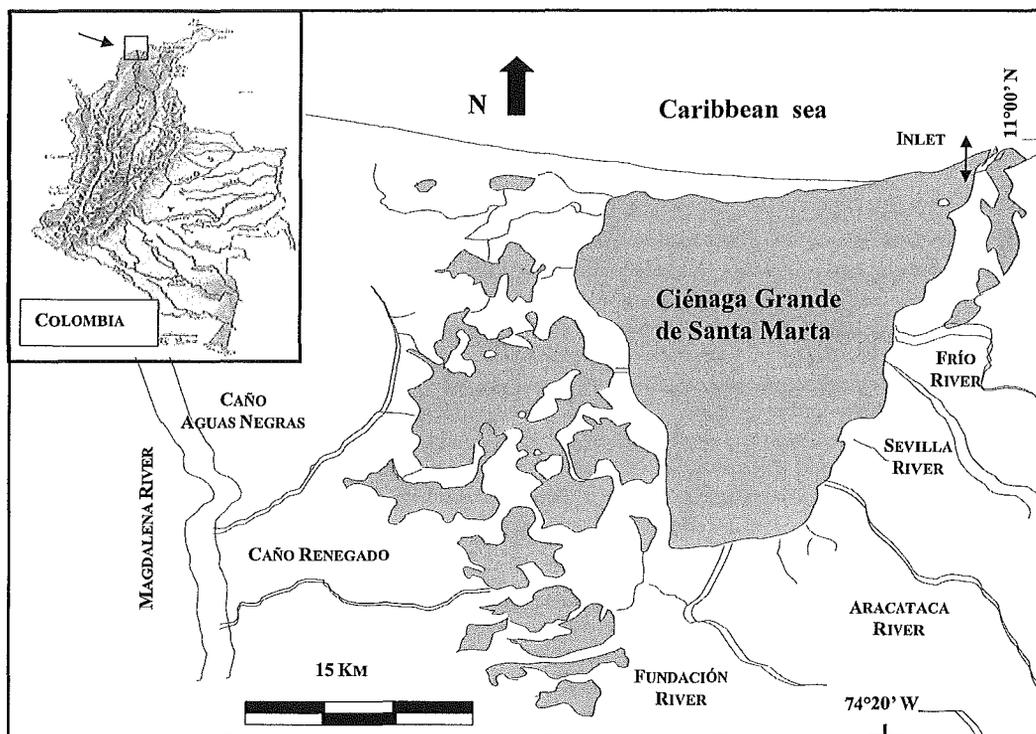


Fig. 1. Map of the Ciénaga Grande de Santa Marta, Colombian Caribbean.

crabs) on the northern coast of Colombia (Santos-Martínez and Acero, 1991). The population of the CGSM, about 20,000, is concentrated in seven towns supported by some 3,200 fishermen (Santos-Martínez and Vilorio, 1996).

MATERIALS AND METHODS

Between Oct. 1995 and June 1996, nine monthly diel sampling surveys were made in the CGSM. The 12-mo sampling was cut short because of lack of funding. During each survey, eight fish collections were taken at 3-hr intervals. The specimens of *A. chupoides* were captured with a monofilament nylon gillnet, with apertures varying between 1.27 and 2.54 cm, following the boliche artisan method (Rueda and Mancera-Pineda, 1995).

Simultaneously, with each sampling, water samples were taken for zooplankton abundance and biomass determination and for seston and chlorophyll *a* analyses. Water temperature and salinity were determined in situ with a portable probe. Water transparency was estimated with a 24-cm-diameter Secchi disc.

Stomach content samples were separated in a water medium using 250-, 125-, and 63- μ m sieves. Each sieve fraction was examined under a microscope to determine the abundance of

prey. Each subsample was dried at 100 C to determine the dry weight.

Total seston and the organic and inorganic fractions were estimated by drying the samples at 100 C from filters of known weights to constant weight and then burning them in an oven at 500 C for 3 hr (Strickland and Parsons, 1972). Chlorophyll *a* concentrations were estimated using the equations described by Lorenzen (1967).

Prey abundance.—A factorial correspondence analysis (FCA) was used to simultaneously observe the hourly and monthly variation in composition and abundance of the stomach contents. Factorial correspondence analysis is used to study contingency or crossed tables or frequency tables obtained after crossing the modalities (modes) of two qualitative variables defined for the same population (samples \times stomach items). Factorial correspondence analysis is used to reduce the number of variables while keeping most of the information (Lebart et al., 1984; Queruz et al., 1992; Everitt, 1994). The results of the 72 samples in the first three axes of correspondence were related to the biotic and abiotic variables using Spearman rank correlation.

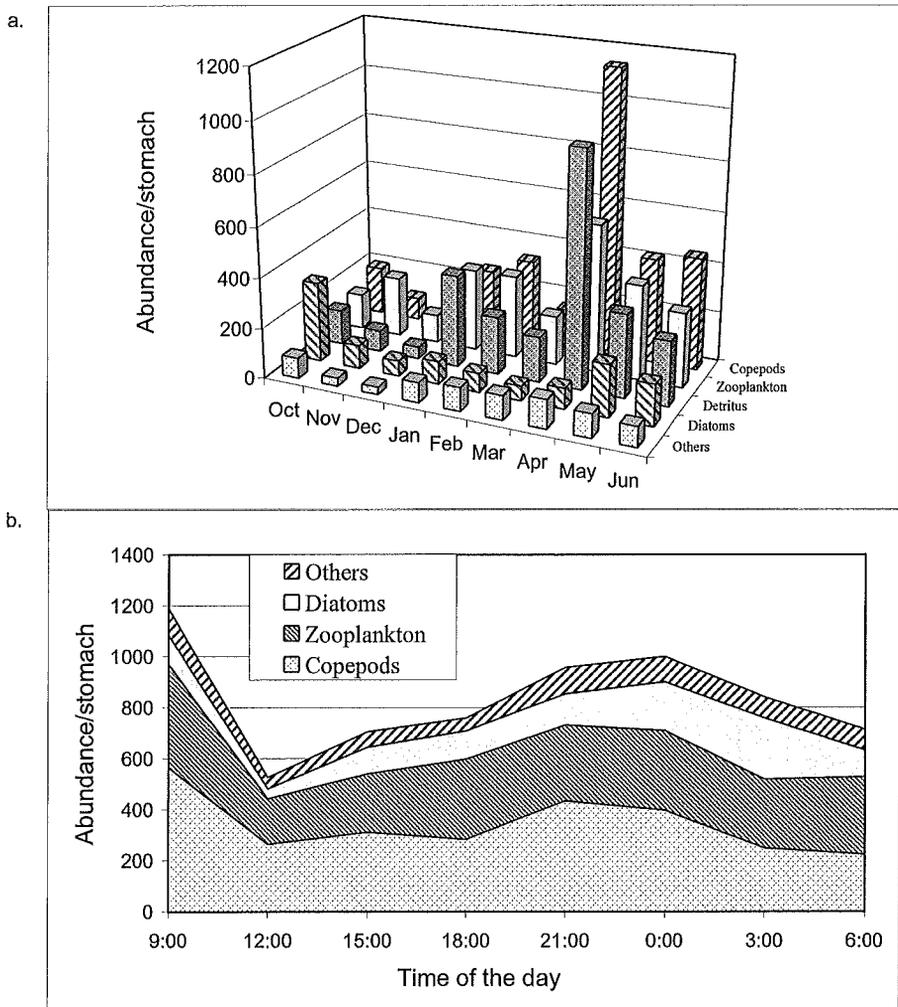


Fig. 2. Average abundance of the food items ingested by *Anchovia clupeioides* during the year (a) and during the day (b).

Prey biomass.—To examine seasonal differences, samples were assigned to one of three seasons on the basis of salinity levels as 1) low salinity (Oct.–Dec.), 2) high salinity (Jan.–March), and 3) intermediate salinity (April–June). Samples were also assigned a time-of-day classification as 1) day (0900, 1200, and 1500), 2) night (1800, 2100, and 0000), 3) early morning (0300 and 0600). A two-way analysis of variance (ANOVA) was fit to determine seasonal and diel differences in prey biomass. When significant differences were detected, posterior testing of means was accomplished using Tukey's adjustment for multiple comparisons. In addition, dry biomass of each prey was related to the biotic and abiotic variables using the Spearman rank correlation.

RESULTS

Abundance.—A total of 11 food items were identified from the stomachs of *A. clupeioides*. By month, the four most abundant items (Fig. 2a), considered the main food of this species, were in decreasing order of copepods (30%), zooplankton remains (apparently mainly highly digested copepods) (26%), detritus (25%), and diatoms (11%). Other food items such as rotifers, fish eggs, crab zoea, copepod nauplii, polychaete larvae, cyanobacteria, and cladocerans appeared sporadically in lower proportions (8% all together). Food consumption reached a peak in April (Fig. 2a), when the abundance of prey was twofold higher than in any other month. Food consumption had two

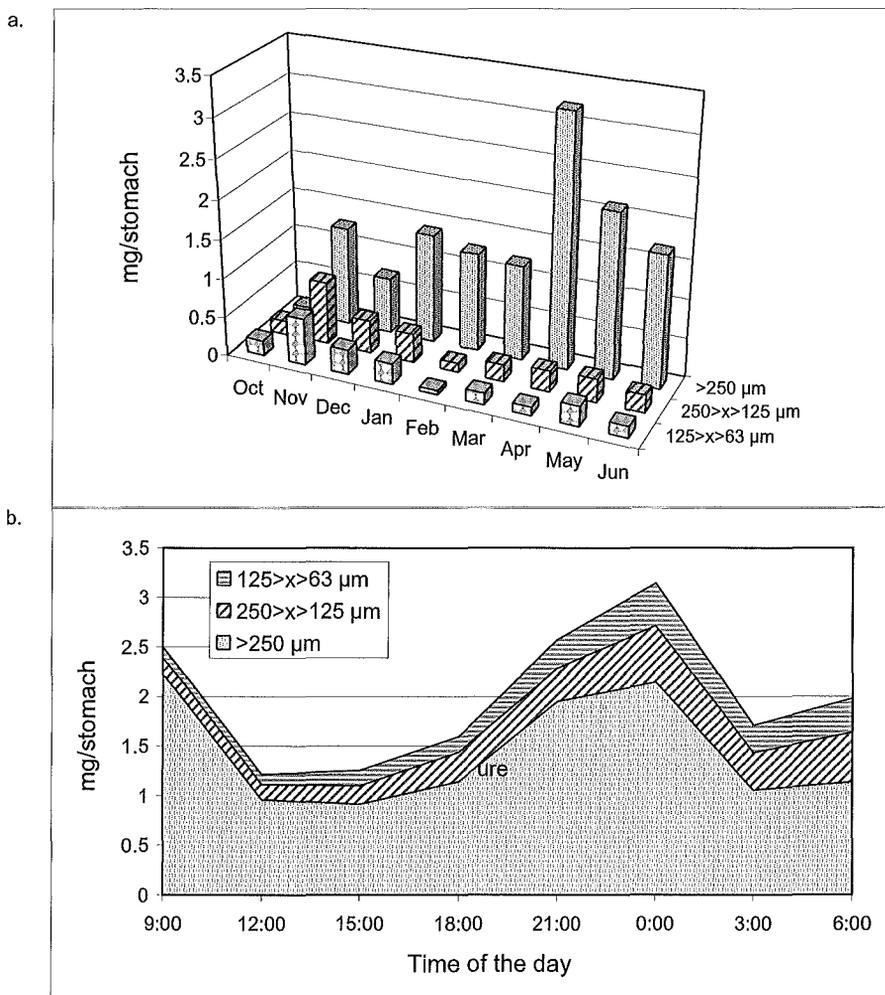


Fig. 3. Variation in food items of *Anchovia clupeioides* in the first and second axes of the factorial correspondence analysis (a) and second and third axes (b). Copepods (Cop), zooplankton remains (Zoo), detritus (Det), diatoms (Dia), rotifers (Rot), fish eggs (Egg), crab zoeas (Zoe), copepod nauplii (Nau), polychaete larvae (Pol), cyanobacteria (Cya), cladocerans (Cla).

peaks during the diel cycle: one during early morning hours and another around midnight (Fig. 2b).

The first three axes of the FCA analysis explained 70% of the total variation (Fig. 3). A larger projected distance indicates a larger variation along a given axis. Diatoms and cyanobacteria varied mainly along the first axis (Fig. 3a), cladoceran and polychaete larvae along the second axis (Fig. 3a,b), and copepod nauplii and cyanobacteria along the third axis (Fig. 3b). Diatoms were the only food item that varied significantly along the first axis. This indicates that other main food items (copepods, zooplankton remains, and detritus) were eaten during all months of sampling. Other prey (diatoms and cyanobacteria in the first axis, cla-

docerans in the second axis, and copepod nauplii and cyanobacteria in the third axis) were highly variable (Fig. 3a,b).

The correlations between the three axes (equivalent to the abundance of the food items) and the biotic and abiotic variables indicated that the changes in magnitude of those variables during the diel cycle were not related to stomach contents. Monthly variations showed several significant correlations (Table 1). The first axis (which mainly explains variation in abundance of diatoms and cyanobacteria) was directly related to salinity and to total, organic, and inorganic seston and inversely related to temperature. The second axis (which mainly explains variation in abundance of cladocerans and polychaetes larvae) was in-

TABLE 1. Monthly correlation between the three axes of the FCA (equivalent to the abundance of the food items ingested by *Anchovia clupeioides*) and biotic and abiotic variables. Significant at $P < 0.01$ (**), $0.01 < P < 0.05$ (*), direct relation (+), and inverse relation (-).

Variables	Axis		
	1	2	3
Biotic			
Zooplankton abundance (ind./liter)		** (-)	
Zooplankton biomass (mg/liter)			* (+)
Chlorophyll <i>a</i> (mg/liter)			
Total seston (mg/liter)	** (+)	* (-)	* (-)
Organic seston (mg/liter)	** (+)	** (-)	
Abiotic			
Transparence (cm)			
Temperature (C)	* (-)		
Salinity (ppt)	** (+)	** (-)	
Inorganic seston (mg/liter)	* (+)	* (-)	* (-)

versely related to zooplankton abundance, salinity, and total, organic, and inorganic seston. The third axis (which mainly explains variation in abundance of cyanobacteria and copepod nauplii) was directly related to zooplankton biomass and inversely related to total and inorganic seston.

Diatoms and cyanobacteria (first axis) were abundant in the stomachs of anchovy collected from waters with low salinity and seston (total, inorganic, and organic) and high temperature (main rainy season) (the signs are inverse because these food items vary in the negative side of the first axis, as is shown in Fig. 3a). Similarly, cladocerans and polychaete larvae (second axis) were positively correlated with high zooplankton abundance, which also occurred during the main rainy season (on the positive side of the second axis). Copepod nauplii were abundant with low zooplankton biomass and high total and inorganic seston (main during the dry season) (this case is similar to the first axis).

To summarize, some of the secondary food items such as cladocerans, polychaete larvae, and cyanobacteria increased during the main rainy season; only the copepod nauplii increased during the main dry season; and fish eggs, rotifers, and crab zoea did not show a clear pattern on any correspondence axis or correlations (probably because of their sporadic and low frequency of occurrence in stomachs). The main food items, except diatoms (i.e., copepods, zooplankton remains, and detritus), were always abundant in stomachs, and their relative temporal variation was low. The food items did not show any significant correlation during the diel cycle, indicating some

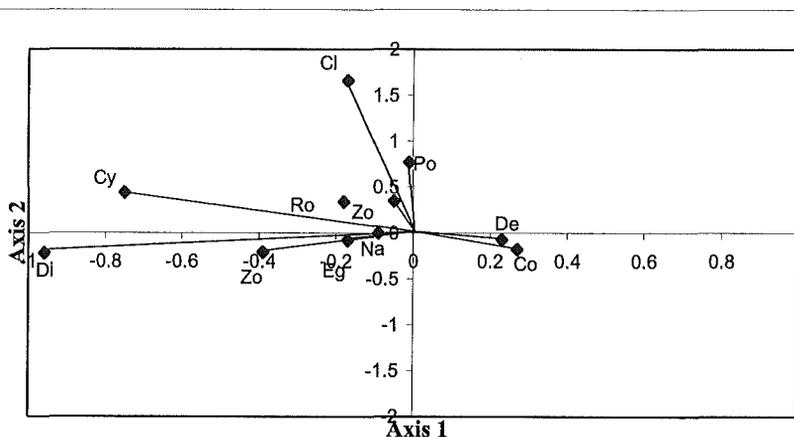
independence between the food consumed during the day and biotic and abiotic variables.

Biomass.—The biomass contribution to the diet of *A. clupeioides* mainly was from food items larger than 250 μm , whereas the contributions of the small- and medium-sized prey were less important (Fig. 4a). This might indicate that the species prefers larger prey. The highest consumption rate per predator biomass showed a major peak in April (high salinity) and a secondary peak in Nov. (low salinity), similar to the pattern found for the prey abundance (Fig. 4a). Diel biomass consumption was highest toward midnight (Fig. 4b).

The ANOVA for prey biomass showed a significant variation among seasons (large salinity variations) in the biomass retained by the 250- μm sieve ($P < 0.01$), but there was no significant difference between daily or monthly variations, or in their interaction (Table 2). The biomass retained in the 125- μm sieve varied significantly in the interaction between season and period ($P > 0.05$), which indicated that variation in biomass among periods (hour of the day) depended on season (large changes in salinity). The biomass retained in the 63- μm sieve varied significantly both among periods ($P < 0.05$) and among seasons ($P < 0.01$), but the interaction was not significant.

Monthly and daily correlation analysis between stomach content biomass and biotic and abiotic variables showed that the biomass of food items larger than 250 μm was directly related to transparency in the diel cycle (Table 3). The biomass of medium-sized food items was directly related to the total weight of zooplankton and inversely related to temperature.

a.



b.

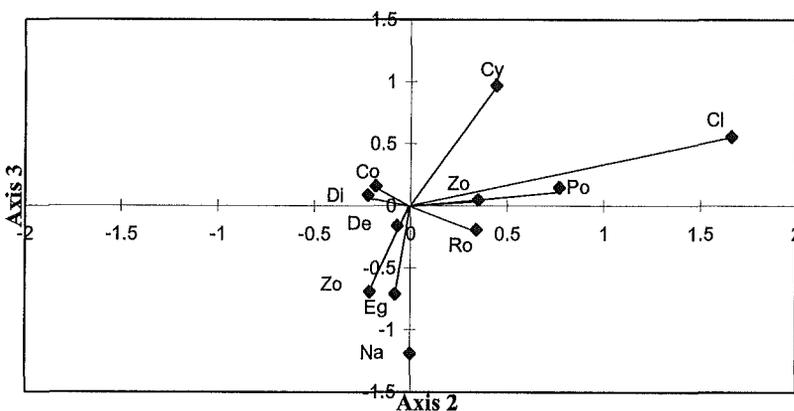


Fig. 4. Average biomass of the food items by size ingested by *Anchovia clupeioides* during the year (a) and during the day (b).

TABLE 2. Seasonal and diel stomach content biomass averages \pm standard error of *Anchovia clupeioides* (retained by 250, 125, and 63 μm sieves). Values with the same letters have the same averages.

Seine size	Daily period	Season			Period average
		Oct.–Dec.	Jan.–March	April–June	
$\geq 250 \mu\text{m}^a$	9–15	0.31 \pm 0.48	1.69 \pm 0.48	2.64 \pm 0.59	1.55 \pm 0.30
	18–00	0.90 \pm 0.48	1.63 \pm 0.59	2.54 \pm 0.48	1.69 \pm 0.30
	03–06	0.96 \pm 0.59	0.66 \pm 0.48	1.94 \pm 0.48	1.19 \pm 0.30
	Season average	0.72 \pm 0.30 A	1.33 \pm 0.30 A	2.37 \pm 0.30 B	1.47 \pm 0.17
250 > x \geq 125 μm^b	9–15	0.19 \pm 0.09	0.32 \pm 0.09	0.26 \pm 0.11	0.26 \pm 0.05
	18–00	0.72 \pm 0.09	0.27 \pm 0.11	0.26 \pm 0.09	0.41 \pm 0.05
	03–06	0.50 \pm 0.11	0.13 \pm 0.09	0.28 \pm 0.09	0.30 \pm 0.05
	Season average	0.47 \pm 0.05	0.24 \pm 0.05	0.26 \pm 0.05	0.32 \pm 0.03
125 > x \geq 63 $\mu\text{m}^{a,c}$	9–15	0.18 \pm 0.08	0.20 \pm 0.08	0.12 \pm 0.10	0.17 \pm 0.05 A
	18–00	0.62 \pm 0.08	0.19 \pm 0.10	0.21 \pm 0.08	0.34 \pm 0.05 B
	03–06	0.28 \pm 0.10	0.09 \pm 0.08	0.16 \pm 0.08	0.18 \pm 0.05 A,B
	Season average	0.36 \pm 0.05 A	0.16 \pm 0.05 B	0.17 \pm 0.05 B	0.23 \pm 0.03

^a Significant variation: season.

^b Significant variation: season–period.

^c Significant variation: period.

TABLE 3. Monthly and daily correlation between the stomach content biomass of *Anchovia clupeioides* (retained by 250, 125, and 63 μm seines) and biotic and abiotic variables. Significant variation: period at $0.01 < P < 0.05$ (+); season at $P < 0.01$ (**); and season at $0.01 < P < 0.05$ (*). Direct relation (+) and inverse relation (-).

Variables	Seine size		
	$\geq 250 \mu\text{m}$	$250 > x \geq 125 \mu\text{m}$	$125 > x \geq 63 \mu\text{m}$
Biotic			
Zooplankton abundance (ind./liter)			
Zooplankton biomass (mg/liter)		† (+) * (+)	
Chlorophyll <i>a</i> (mg/liter)		* (-)	** (-)
Total seston (mg/liter)	* (+)		
Organic seston (mg/liter)			
Abiotic			
Transparency (cm)	† (+) ** (-)		
Temperature (C)		† (-) * (+)	† (-) * (-)
Salinity (ppt)	** (+)		** (-)
Inorganic seston (mg/liter)	** (+)		

Finally, the biomass of the small food items was also inversely related to temperature (Table 3).

Monthly variation in the biomass of larger prey was directly related to salinity and to total and inorganic seston (Table 3). The monthly biomass of larger food items was inversely related to transparency. The biomass of medium-sized food items was directly related to plankton biomass and temperature and inversely related to chlorophyll *a*. The monthly variation in biomass of the smaller food items was inversely related to temperature, salinity, and chlorophyll *a* (Table 3).

To summarize, the biomass of larger food items was higher when salinity, total and inorganic seston, and transparency were high (high-salinity season). The biomass of medium-sized food items was high when plankton biomass and temperature were high and the concentration of chlorophyll *a* was low (June). The biomass of smaller food items was high when temperature was high and when salinity and chlorophyll *a* concentration were low (Dec.). The biomass of larger food items was high during the diel cycle when transparency was low (afternoon and early morning hours). There were more medium-sized food items when zooplankton biomass was high and temperature was low (night). The biomass of smaller food items was high when temperature was low (night).

DISCUSSION

The diet of *A. clupeioides* primarily comprised zooplankton (copepods), agreeing with previous findings for this species (Castaño, 1989)

and for most other engraulids (Blaxter and Hunter, 1982), such as bay anchovy *Anchoa mitchilli* (Vazquez, 1989; Peebles et al., 1996) and striped anchovy *Anchoa hepsetus* (McNeil and Grimes, 1995). As found in this study, the main difference from other engraulid species was the presence of large amounts of detritus, which is abundant in the CGSM (Kuklick, 1987), in the stomachs of *A. clupeioides*.

Phytoplankton is the main item in the diets of Peruvian anchoveta *Engraulis ringens* (Rojas de Mendiola, 1989) and of the South African anchoveta *E. capensis* (King and Macleod, 1976), indicating that filtration is their main feeding mode. The main food item for the northern anchovy *E. mordax* and of the Argentinian anchoveta *E. anchoita* is principally zooplankton (Loukashkin, 1970; Angelescu, 1982); however, phytoplankton appears seasonally in high amounts in the food of those species. Some authors assume that because phytoplankton is an important food source for many engraulid species, they are able to maintain high fish populations in upwelling regions (Rojas de Mendiola, 1989). Nevertheless, Sirotenko and Danilevskiy (1977) suggested that phytoplankton is just an emergency or substitution food item for engraulids when zooplankton prey diminishes. Diatoms constitute only 6% of the diet of the Argentinian anchoveta (Angelescu, 1982). It seems possible that the diatoms ingested by *A. clupeioides* in the CGSM were taken passively when the species was feeding on zooplankton and might not be important energetically for this species.

From the diversity of food items found in the stomachs of *A. clupeioides*, we infer that it has a

wide trophic spectrum (euriphagous or trophic opportunism), feeding on the entire planktonic food chain. Hence, the species appears to be highly adapted to an estuarine life cycle (Whitfield, 1980). Nikolsky (1965) proposed that euriphagy is an adaptation to extremely variable food availability. Even though estuaries are unstable areas with clear planktonic successions (Margalef, 1972), it seems that such variations do not significantly affect the feeding of *A. clupeioides*, which relies on the year-round abundance of copepods. In this aspect, there is a similarity between *A. clupeioides* and *Anchoa mitchilli*, which also rely mostly on copepods (Vazquez, 1989), and even its growth can be zooplankton density dependent (Cowan et al., 1999). Apparently, the abundance of copepods also is adequate, and *A. clupeioides* obtains its energetic needs from this resource. Other engraulids seem to depend more strongly on the kind and concentration of the most abundant prey in the plankton (James, 1987).

The diel feeding rhythm depends on the method used by the fishes to capture their food, on the behavior of the prey, and on the daily dynamics of food composition (Nikolsky, 1965). Nevertheless, we were unable to detect any significant correlation between the composition and the abundance of the food consumed by *A. clupeioides* during the daily cycle and the biotic and abiotic variables (Table 3). The fish seasonal feeding rhythm has been related to their adaptations to the changes in the abiotic conditions (Nikolsky, 1965). Blaxter and Hunter (1982) proposed that salinity is the variable that most strongly affects plankton successions, and then this may affect the feeding habits of planktophagous fishes; however, we found that only the secondary food items of *A. clupeioides* were directly related to salinity. Hence, the proposed relationship may be more applicable to those latitudes where fishes depend more strongly on the seasonal fluctuations of the available prey.

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