

RESUSPENDED INTERTIDAL MICROPHYTOBENTHOS AS MAJOR DIET COMPONENT OF PLANKTIVOROUS ATLANTIC ANCHOVETA *CETENGRAULIS EDENTULUS* (ENGRAULIDAE) FROM EQUATORIAL MANGROVE CREEKS

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Abstract. In the present study we examined the stomach contents of 49 Atlantic anchoveta, *Cetengraulis edentulus* (Engraulidae), caught with a block net from intertidal mangrove creeks at diurnal neap tides between June and September 1997 near Bragança (Pará, northern Brazil). On average the fish had eaten 0.53 % ± 0.35 SD of their wet weight, with fuller stomachs in June/July. *Cetengraulis edentulus* is a phytoplanktivorous filter-feeder. The principal food was composed of about half pelagic and half benthic diatoms, predominantly within a 20 to 200 µm size range. *Coscinodiscus*, other centric diatoms, and *Nitzschia* were abundant in the diet throughout the sample period. Sediment particles and detritus were also ingested. Our observations suggest that foraging occurs close to the substrate and throughout the water column in shallow turbid waters. The study indicates the importance of intertidal microphytobenthos production during low tide being made available to transient planktivorous fish at high tide by tidal resuspension. Atlantic anchoveta may occupy a central position in the food web of many Neotropical mangrove ecosystems along the Atlantic coast. Its close association with mangroves may partially explain its irregular distribution between Mexico and southern Brazil. Accepted 25 November 2008.

Key words: Bacillariophyta, benthic microalgae, Bragança, food analysis, Pará, phytoplankton, tidal resuspension, tropical mangrove creek.

INTRODUCTION

In estuaries, intertidal microphytobenthos resuspended by tidal currents and waves often makes its way into food webs through suspension- and deposit-feeders (de Jonge & van Beusekom 1992, 1995, Middelburg *et al.* 2000, Kang *et al.* 2006). Phytoplanktivorous fish may also use resuspended microphytobenthos and thus transfer benthic production to the pelagic food web. However, the role fish play in linking benthic production to pelagic estuarine food webs has rarely been studied. Melville & Connolly (2005) found that the food webs supporting fish on subtropical mudflats were not based on microphytobenthos. The contribution of microphytobenthos exceeded 50% in only one out of 22 species. If the microphytobenthos production supports fish,

the support is usually indirect via the food web (e.g., Sullivan & Moncreiff 1990). However, benthic microalgae are also directly ingested by certain fish species. Young Mugilidae in particular are known to feed directly on microphytobenthos from the sediment surface and assimilate it (Lin *et al.* 2007).

The Atlantic anchoveta *Cetengraulis edentulus* (Cuvier, 1829) may provide support for the hypothesis that benthic sources of production are transferred to the pelagic food web by filter-feeding fish. *C. edentulus* inhabits inshore, brackish coastal waters of the western Atlantic between 23°N and 28°S (Whitehead *et al.* 1988). Generally *C. edentulus* is associated with muddy substrate in shallow, turbid coastal waters (Simpson 1965, Sergipense & Sazima 1995, Gay *et al.* 2000), thus is often caught adjacent to mangroves. The fish seems to favor the innermost areas of bays and estuaries where phytoplankton densities are highest (Araújo-Silva *et al.* 2003; Scho-

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ries, pers. comm.). Its distribution is irregular between Mexico and southern Brazil (Simpson 1965), though the reason for this has not yet been clarified.

C. edentulus has a brush-like filter apparatus composed of numerous (>100) long and closely adjoining gillrakers (Bornbusch 1988). The well-developed gizzard and grooves lining the inner stomach walls (surface area enhancement) render the genus *Cetengraulis* unique within the family Engraulidae (Harder 1960, Nelson 1984). Simpson (1965) studied the early life history of *C. edentulus* in eastern Venezuela. Several studies, either from southern Brazil or Colombia, concern the estimation of population parameters (Gallo 1993a,b, Clezar *et al.* 1994, Souza-Conceição *et al.* 2005) or changes in spatio-temporal distribution (Clezar *et al.* 1993, Sergipense & Sazima 1995, Gay *et al.* 2000, Araújo-Silva *et al.* 2003). The closely related Pacific anchoveta *C. mysticetus* is distributed along the tropical eastern Pacific coast from Mexico to Peru; the two species are probably descended from one species that was separated after the formation of the Isthmus of Panama (Lowe-McConnell 1987). Currently *C. edentulus* is commercially landed only by Venezuela. Annual catches comprise only 500 t (FAO/FIGIS).

Despite the extended latitudinal distribution of *C. edentulus* along the Atlantic coast, studies on the feeding ecology are restricted to the southern edge of its distribution in subtropical southern Brazil (Goitein 1984, Clezar 1993, Gay 1995, Sergipense *et al.* 1999, Gay *et al.* 2002). Giarrizzo *et al.* (submitted to *Oecologia*) found that *C. edentulus* from another mangrove estuary in northern Brazil was highly $\delta^{13}\text{C}$ -enriched, suggesting a strong dependence on algal carbon sources. To the best of our knowledge, there are no studies on the feeding ecology of *C. edentulus* from the center of its distribution on the tropical coast of South America or the Caribbean. Sergipense *et al.* (1999) concluded that *C. edentulus* from the subtropical Sepetiba Bay, Rio de Janeiro, is a planktivorous filter-feeder. The diet was dominated by centric and pennate diatoms (relative numerical frequency: 73 %); oscillatorial cyanophyta were also abundant (21 %). Dinoflagellates contributed only 3 %. Likewise, the diet of *C. edentulus* from the Itaipu lagoon, Rio de Janeiro, was dominated by diatoms (Gay *et al.* 2002). A high degree of diatoms of benthic origin is a typical feature of the stomach contents of filter-feeding *Cetengraulis* (Bayliff 1963, Sergipense *et al.* 1999). However, it is still unclear

whether benthic diatoms are ingested directly from the substrate or filtered out of the water. Bayliff (1963) regarded adult *C. mysticetus* as iliophagous in view of the similar relative importance of organisms in bottom samples and in their stomachs. Sergipense *et al.* (1999) had no comparative samples and assumed that the food search of *C. edentulus* occurs close to the bottom. Gay *et al.* (2002) found unselective feeding in *C. edentulus* and suggested that the fish exploit the water layers near the sediment. Thus far, there has been no *in situ* observation of the feeding of the genus *Cetengraulis*, likely due to the high turbidity of their foraging grounds (Bayliff 1963). A better understanding of the feeding ecology of *C. edentulus* may help to explain the occurrence of mass mortality events of this species due to harmful algal blooms (Mijares *et al.* 1985; Krumme, unpubl. data).

The aim of the present study is two-fold: (1) to contribute to broadening our knowledge of fish feeding ecology, and in particular to a better understanding of the trophic role of *C. edentulus*, by analyzing the diet of specimens from an equatorial mangrove estuary, and (2) to provide observations on foraging behavior in a dynamic tidal environment.

MATERIAL & METHODS

Study area and study site. The study area is located in the Caeté River estuary near Bragança, about 200 km south-east of the Amazon delta. It is part of the second largest mangrove area in the world, covering about 7000 km² of the north-east coast of South America (Kjerfve & Lacerda 1993). Annual average rainfall is about 2500 mm. There is a wet season (January to June) and a dry season (August to November), when estuarine salinities can fall below 5 psu and exceed 35 psu respectively. Water temperature is high year-round, ranging from 27°C to 30°C.

The sample sites were three intertidal 1st-order mangrove creeks in the muddy upper reaches of the Furo do Meio, located in the central part of the peninsula bordering the western side of the Caeté Bay (see Figure 1 in Barletta-Bergan *et al.* 2002). In the Caeté estuary, intertidal 1st-order creeks (*c.* 25 m wide at the mouth, 3–5 m deep at high water [HW]) that are further ramified upstream, drain the mangrove area into large subtidal main channels (*furos*) that connect to Caeté Bay. According to Barletta-Bergan (1999), creeks 1, 2, and 3 had 6481, 9351, and 1865 m² of inundated area at neap tide HW

respectively. Creek 1 was located upstream of a wooden bridge crossing the Furo do Meio in its upper reaches, while creeks 2 and 3 were located downstream of it. The bridge is *c.* 50 m wide and 6–7 m high, with 1.5–2 m between poles. The tidal range of the semi-diurnal tide is 2–3 m at neap and 3–5 m at spring tides. The tide is asymmetric; flood and ebb tide last 4 and 8 hours respectively. In the last 4 hours, ebb tide is extremely weak with an almost negligible fall in the water level.

Sampling method. *C. edentulus* were caught for stomach analysis during diurnal neap ebb tides of the last quarter moon. Samples were taken monthly between June and September 1997 as part of the one-year study of Barletta-Bergan *et al.* (2002) and Barletta *et al.* (2003). The three creeks were sampled on consecutive days. Each day at slack HW, a creek mouth was blocked with a net (50 m × 5 m, 1 cm stretched mesh size). Fish were collected during ebb tide until the creek was totally drained (*c.* six hours after HW). In the field, specimens were directly fixed in 15 % borax-buffered formalin in sea water. Salinity increased from 22 to 24.7, 28.7, and 31.5 psu between June and September respectively.

Length relationships. Total length (TL), standard length (SL) (both to the lowest 0.5 cm), total wet weight, and wet weight without stomach were taken (Sartorius LC 4200 S ± 0.01 g). The fish were assigned to three size classes: < 9 cm, 9– < 11 cm, ≥ 11 cm SL. The length of the uncoiled digestive tract (DT) was measured from the pylorus to the anus (± 0.5 cm). Relative length of the DT (RLDT) was calculated (DT length × TL⁻¹).

Stomach fullness. The stomach fullness index (SFI) was calculated as $SFI = [(stomach\ content\ weight \times 100) \div total\ fish\ weight]^{-1}$. The intestines were transferred to 8 % buffered formalin, washed, drained on an absorbent paper and wet-weighted (± 0.01 g). The weight of the contents of the intestines (C) was calculated as $C = R - E$; where R is the weight of the removed intestines (g), E is the weight of the empty intestine (g).

A two-way analysis of variance (ANOVA) was calculated to ascertain whether SFI differed by month and size class (Sokal & Rohlf 1995). To fulfill the ANOVA assumptions, SFI raw data (y) were transformed using a logistic transformation [$\log(y/(100-y))$] which transforms SFI values from the 0–100 scale to the range from plus or minus infinity.

To avoid an incomplete design, the months June/July and August/September were pooled. The three creeks were not considered as a source of variance. The Scheffé test was used for *post hoc* analysis.

Stomach content analysis. Stomach contents were diluted in distilled water and stirred to make a homogeneous solution. A defined amount of the solution was transferred with a pi-pette to a microscope slide for identification of food items to the lowest possible taxonomic level (Leitz: Dialux microscope) (Hustedt 1965, Newell & Newell 1970, Drebes 1974, Round 1975, Round *et al.* 1996).

The size categorization of plankton followed Sieburth *et al.* (1978). The presence of food items was recorded as abundant, regular, rare, or sporadic. The origin of the diatom genera ingested was assigned to either benthic or pelagic according to the literature. Genera were omitted that occurred only sporadically or had a vague classification such as *Paralia* sp. and *Frickea* sp. (Round *et al.* 1996). Each abundance category was substituted by a value (abundant: 3, regular: 2, rare: 1) and the monthly percentage of benthic and pelagic diatoms was determined.

After identification, the stomach contents were dried (24 hrs at 60°C) and weighed (dry weight = W_D ; Sauter Typ 404; ± 0.00001 g). The samples were burned (24 hrs at 510°C in a muffle furnace) and weighed (ash free dry weight = W_{AFD}). The difference between W_D and W_{AFD} gave the amount of organic matter (g) that should have been available for the fish and an unknown proportion of organic matter already digested.

RESULTS

We caught 9, 8, 15, and 17 *C. edentulus* in June, July, August, and September 1997 respectively (n = 49; size range: 7.5–12 cm SL). All but three *C. edentulus* were caught in the two creeks downstream of the bridge (creek 2: n = 33, creek 3: n = 13) suggesting that obstacles such as bridge piers standing closely side by side may restrict the daytime passage of schools of *C. edentulus*.

Stomach fullness. The stomach of *C. edentulus* is extremely furled. The mean RLDT was 4.43 ± 0.85 SD (range: 2.63–5.37; n = 17). Only four out of 49 specimens (8 %) had an empty stomach. The others seemed to be well filled. Different stomach fullness stages could not be determined due to the anatomy

of the stomachs and the consistency of the diet. SFI was significantly higher in June/July (late wet season) than in August/September (early dry season) while size class had no significant effect on SFI (two-way ANOVA, month: df: 1, $p < 0.05$; size class: df: 2, $p > 0.30$; interaction: df: 2, $p > 0.08$). On average the fish had eaten $0.53\% \pm 0.35$ SD of their wet weight ($n = 49$; range: 0.07–1.55 %).

Diet composition. The consistency of the stomach contents of *C. edentulus* resembled a clayey compressed matter of low water content. Twenty-one genera were identified. The diet consisted almost

exclusively of phytoplankton, mainly diatoms (Table 1). *Coscinodiscus* sp., other centric diatoms and *Nitzschia* sp. were abundant throughout the sample period. *Skeletonema costatum* and *Navicula* sp. were only abundant in June. In contrast, *Raphoneis surirella* (abundant), *Thalassionema* sp. (regular), *Odontella* sp. (rare), and *Paralia* sp. (rare) occurred mainly from July to September. Dinoflagellates were rare in June/July and sporadic in August/September. The stomachs also contained detritus and sediment particles.

Size composition. The size of most plankton organisms was between 20 μm and 200 μm , i.e., micro-

TABLE 1. Abundance and sizes of food items of *C. edentulus* between June and September 1997 from mangrove creeks near Bragança, Pará, northern Brazil. C: Centrales, Pe: Pennales. Origin: Assignment of taxonomic groups to B: Benthos, P: Plankton. +++++: abundant, +++: regular, ++: rare, +: sporadic, ---: absent.

Taxa, genera or type	Order	Origin	Abundance				Diameter, or length \times width (μm)
			June	July	Aug.	Sept.	
BACILLARIOPHYCEAE							
<i>Coscinodiscus</i> sp.	C	P	+++	+++	++++	+++	261; 221; 208; 186; 166; 102; 97; 69; 50; 14
remaining Centrales	C	P/B	+++	++++	++++	+++	69; 66; 52; 44; 38; 33; 30; 25; 16
<i>Skeletonema costatum</i>	C	P	++++	++	++	+++	Chain: 22 \times 13; 20 \times 12; 16 \times 11; 14 \times 10; 19 \times 8
<i>Odontella</i> sp.	C	P	+	++	++	++	200 \times 91; 111 \times 100; 44 \times 19; 36 \times 25; 33 \times 22; 27 \times 16
<i>Paralia</i> sp.	C	P/B (?)	---	++	++	++	Chain : 13 \times 33; 20 \times 36; 7 \times 10; 7 \times 11
<i>Ditylum</i> cf. <i>brightwellii</i>	C	P	++	+++	++	+	
<i>Chaetoceros</i> sp.	C	P	---	---	---	+	Chain: 8 \times 3
<i>Navicula</i> sp.	Pe	B	++++	+++	++	+++	47 \times 8; 36; 27; 17; 16; 14; 11
<i>Raphoneis</i> aff. <i>surirella</i>	Pe	B	++	++++	++++	++++	Chain: 27 \times 4; 16 \times 3; 14 \times 3; 11 \times 3; 8 \times 4
<i>Nitzschia</i> sp.	Pe	P	++++	+++	++++	++++	220; 158 \times 10; 155; 147; 130; 119; 97; 40; 36; 16
<i>Thalassionema</i> sp.	Pe	B	++	+++	+++	+++	172 \times 6; 169 \times 6; 136 \times 6; 122 \times 6; 113 \times 6; 97 \times 6; 75 \times 4; 44 \times 3
<i>Pleurosigma</i> sp. and <i>Gyrosigma</i> sp.	Pe	B	++	++	++	++	155 \times 14; 91 \times 8; 75 \times 8; 58 \times 8; 50 \times 10; 36 \times 4
<i>Frickea</i> sp.	Pe	?	+	---	+	+	100
<i>Bacillaria</i> sp.	Pe	B	---	---	+	+	Colony: 122 \times 4; 77 \times 4; 72 \times 4
<i>Diploneis</i> sp.	Pe	B	---	++	++	++	60 \times 22; 52 \times 20; 44 \times 19; 36 \times 13; 33 \times 13; 30 \times 11
<i>Delphineis</i> sp.	Pe	B	---	+	+	+	30 \times 3; 20 \times 3
<i>Cymatosiraceae</i> cf. <i>Campylosira</i> sp.	Pe	(B)	---	---	++	++	Chain: 36 \times 6; 25 \times 5; 24 \times 4; 22 \times 4; 20 \times 4
cf. <i>Stenopterobia</i> sp.	Pe	B	---	---	---	+	341; 332; 266; 122
<i>Haslea</i> sp.	Pe	B	++	++	++	+	127 \times 6; 69 \times 4; 38 \times 2
spec. E (cf. <i>Eunotogramma</i> sp.)	(C)	(P)	---	---	+	+	47 \times 52; 44 \times 55; 44 \times 52
spec. A	Pe	?	+	+	+	++	83 \times 41; 58 \times 27
CYANOBACTERIA cf. <i>Oscillatoria</i> sp.	P		---	+	+	+	Chain: 22 \times 33; 3 \times 11
DINOFLAGELLATA	P		++	++	+	+	41 \times 19; 41 \times 22; 36 \times 22
SILICOFLAGELLATA	P		---	---	+	+	27; 4
OTHERS: Veliger larva	P		---	---	+	---	27 \times 36
Nematoda	B		---	+	---	---	

phytoplankton (range: 4–341 μm) (Table 1). Chains usually consisted of only three to six cells. Only *Navicula* sp. and silico-flagellates were assigned to the nanoplankton (< 20 μm). Larger than 100 μm were *Coscinodiscus* sp., *Odontella* sp., *Thalassionema* sp., *Bacillaria* sp., *Gyrosigma* sp., *Nitzschia* sp., *Frickea* sp., *Haslea* sp. and *Stenopterobia* sp. Only *Stenopterobia* sp. and *Coscinodiscus* sp. were > 200 μm and assigned to the mesoplankton (0.2–20 mm).

Benthic vs. pelagic diatoms. Out of a total of 21 genera identified, 12 were assigned to a benthic and nine to a pelagic origin. Diatoms from both the benthic and the pelagic compartment accounted for approximately 50 % of the diet throughout the sample period.

Organic content. The mean organic matter content of the stomach contents was 44.5 ± 10.1 SD (range: 28.6–73.8 %, $n = 44$). The organic matter content did not differ between the four months (Kruskal-Wallis test, $n = 44$, $p > 0.32$).

DISCUSSION

The Atlantic anchoveta *C. edentulus* is a planktivorous primary consumer, filter-feeding on primarily centric and pennate diatoms. A comparison of the diet of *C. edentulus* from the tropics (present study) and the subtropics (Sergipense *et al.* 1999) shows that the fractions of the principal phytoplankton groups in the diet were similar. However the taxonomic composition and the fraction of different species within the phytoplankton groups vary. Such differences in the list of food items may be related to sample size, sampling season, and preciseness of identification. The diet of *C. mysticetus* in the eastern Pacific was also dominated by centric and pennate diatoms, while other organisms were of insignificant importance (Bayliff 1963). The similarities in the diets of *C. edentulus* and *C. mysticetus* suggest that these sister species have similar foraging strategies and occupy similar ecological niches.

Tidal currents disperse benthic diatom mats. It is remarkable that benthic diatoms were just as abundant in the diet of *C. edentulus* as pelagic diatoms. A comparison of the diet composition of *C. edentulus* with the results from surface phytoplankton surveys by Schories (unpubl. data) and Dummermuth (1997) suggests that the relative contribution of benthic and pelagic diatoms was similar in the water column and in the stomachs. Schories (unpubl. data) studied the

tidal and diel dynamics of the phytoplankton community in the Furo do Meio during twelve months in 1996/1997, thus overlapping in time with the present study. Dummermuth (1997) investigated the primary production of the phytoplankton and the microphytobenthos during three dry season months in 1996 in the same area. The species abundant in the two studies (*S. costatum*, *Nitzschia* sp., *Navicula* sp., and *R. surirella*) were also abundant in the stomachs of *C. edentulus*. Despite its low abundance in the Furo do Meio, *Coscinodiscus* was categorized as abundant in the stomachs. This asymmetry could be due to a positive selection by *C. edentulus* or to an abundance overestimation of the large *Coscinodiscus* cells during the stomach content analysis.

Benthic diatoms play a significant role in the pelagic food web of the *furos* (Schories, pers. comm.) because the strong tidal currents disperse the upper sediment layers at each tide (Lucas *et al.* 2000), with current speeds < 0.5 m s^{-1} at neaps and often > 1.2 m s^{-1} at springs in the study area. The ability of the tidal current to displace surface sediments even at weak neap tides was observed in the Furo do Meio, when ADCP measurements were unusable because bedload transport of fine muddy substrate led to missing bottom echoes (Krumme & Hanning 2005). The average Secchi depth is only 0.3 m (Krumme, unpubl. data) and seston content is high, commonly around 0.1 g l^{-1} (Schories, unpubl. data).

Pickney & Zingmark (1991) showed that intertidal benthic diatoms undergo regular vertical migrations to the surface for photosynthesis during the low-tide period. During the low-tide period in the *furos*, extensive mats of benthic diatoms appear on the sediment surface of flat sections and slip-off slopes of exposed intertidal muddy banks, especially in the upper reaches of the *furos* (Dummermuth 1997). Although the majority of the benthic diatoms may slide down sufficiently deep into the sediment prior to inundation at flood tide, the rapid first flood rise (Krumme 2004) regularly flushes away remains of the mats (Dummermuth 1997), together with fine sediment particles. This resuspension of benthic diatoms from the muddy intertidal increases the overall abundance of “pelagic” phytoplankton, making the *furos* the areas with the highest phytoplankton abundance in the Caeté estuary (Schories, pers. comm.). The exceptional nature of this phenomenon in the upper reaches may be the reason for *C. edentulus* foraging in this section of the *furos*.

Foraging habits and sediment particles in the diet. Most *C. edentulus* stomachs from the intertidal creeks contained food and were well filled, suggesting that *C. edentulus* entered the creeks to feed during the daytime HW period. Sergipense *et al.* (1999) also found filled stomachs in daytime samples. However, *C. edentulus* likely feeds continuously. The stomach fullness of *C. edentulus* sampled during consecutive neap tide cycles in the Furo do Meio suggested continuous feeding throughout the tidal cycle, both day and night (Krumme 2004). Algivores/detrivores rarely have empty stomachs because they have relatively short feeding intervals on account of the low energy content, small particle size, and low conversion efficiency of their food (Brett & Groves 1979, Arrington *et al.* 2002).

The great abundance of benthic diatoms in stomachs of *C. edentulus* caught with beach seines in shallow water led Sergipense *et al.* (1999) and Gay *et al.* (2002) to assume that *C. edentulus* filter-feed close to the bottom. However, *C. edentulus* probably feed throughout the water column because strong tides disperse benthic diatoms. During the hydro-acoustic observation of fish movements in the Furo do Meio (Krumme & Saint-Paul 2003), fish schools were seen beneath the water surface (0–2 m), suggesting that *C. edentulus* forage throughout the water column in the relatively shallow furros (< 5 m deep during low tide). In fact, *C. edentulus* seem to feed anytime and everywhere. They were seen filtering with mouths wide open day and night, at flood and ebb tide, and in creeks and channels at water depths ranging from 0.5 m to 5 m (Krumme, pers. obs.).

Bayliff (1963) mentioned that *C. mysticetus* may also stir up the muddy sediment while foraging, probably a behavior used when “natural” phytoplankton concentrations are too low due to lack of organism resuspension by tides or waves. Such an active disturbance of the uppermost sediment may be used by *C. edentulus* at the banks of shallow channels during the stagnant low-tide phase when the phytoplankton falls. During low tide, Krumme *et al.* (2004) caught *C. edentulus* in the Furo in shallow water < 1.5 m deep, where artisanal fishermen often stumble across agglomerations of *C. edentulus* while hand-trawling for penaeid prawns.

The sediment particles in *C. edentulus* are almost inevitably ingested while filter-feeding in turbid waters. The organic matter content of the sediment particles in *C. edentulus* stomachs (44.5 %) was much higher than (e.g.) in iliophagous *Mugil cephalus* (6–

10 %) (Odum 1970). However, though not quantified, the relative contribution of mineral material to the total stomach content was certainly much lower than in *M. cephalus* (40–100 %). The dominance of diatoms in the diet, the foraging habit, and the low proportion of sediment particles in the stomachs render it unlikely that *C. edentulus* is as iliophagous as Bayliff (1963) concluded for adult *C. mysticetus*. The sediment particles in the stomach likely function as an agent to grind diatoms, and may facilitate the function of the gizzard of *C. edentulus* similar to *M. cephalus* (Odum 1970).

Conclusion. The Atlantic anchoveta is a planktivorous filterfeeder, predominantly of diatoms. The study provides evidence for the importance of intertidal microphytobenthos production during low tide being made available to a transient phytoplanktivorous fish at high tide by tidal resuspension. The diet of *C. edentulus* seems to be both unaffected by latitude and similar to the sister species *C. mysticetus*. The foraging activity of *C. edentulus* seems to be restricted to shallow muddy areas close to mangroves (e.g., Clezar *et al.* 1993, Sergipense & Sazima 1995, Araújo-Silva *et al.* 2003) where significant amounts of benthic diatoms are added to the pelagic phytoplankton, either passively by tidal currents and wave action or actively by the fish stirring up the muddy substrate themselves. Therefore the presence of mangroves and occurrence of *C. edentulus* may be closely correlated and may partially explain its irregular distribution between Mexico and southern Brazil (Simpson 1965). This would further highlight the central trophic position the primary consumer *C. edentulus* may have in the food webs of many Neotropical mangrove ecosystems on the Atlantic coast. Given its important trophic role, more information on the spatio-temporal dynamics of foraging, distribution, and autotrophic sources of *C. edentulus* is urgently required.

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