Tidal-Induced Changes in a Copepod-Dominated Zooplankton Community in a Macrotidal Mangrove Channel in Northern Brazil

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Uwe Krumme and Tsui-Hua Liang (2004) Tidal-induced changes in a copepod-dominated zooplankton community in a macrotidal mangrove channel in northern Brazil. *Zoological Studies* **43**(2): 404-414. The zooplankton community of the muddy upper reaches of the Furo do Meio, Caeté system, Pará, Brazil, was studied between March and May 2001 (during the wet season). Zooplankton samples were taken during 2 lunar cycles; during each lunar phase, 4 consecutive tidal cycles were sampled, and for each tidal cycle, 4 hauls were taken (flood, high water (HW), ebb, low water (LW)). Short-term changes in species number, abundance, and biomass were studied. Salinity (mean, 7 ± 3 psu) and water level were positively correlated. Copepods dominated the zooplankton community. Numbers of total zooplankton and copepod species were high at HW and low at LW, irrespective of time of day and tide. In contrast, the abundance and biomass of both total zooplankton and copepods were high at LW and low at HW. Copepod species number and the abundances of total zooplankton and copepods were greater during the spring than the neap tide. The calanoid copepod, *Pseudodiaptomus marshi*, dominated the copepod community in terms of abundance and biomass. Highest abundance occurred at LW, suggesting retention in the cul-de-sac channel. The *P. marshi* population was composed of ovigerous females, adult males, and copepodite stages 4 and 5. Copepod biomass ranged from 0.46 to 6.9 mg dry weight (DW)/m^3, with an overall mean of 2.63 mg DW/m^3. Non-parametric multidimensional scaling revealed that spring tide/neap tide together with HW/LW were important factors structuring the zooplankton community. Time of day had no effect on the community structure. We suggest the occurrence of positive relationships between increased copepod abundances and high sediment loads and decreased salinities during the wet season. Synchronous temporal patterns between zooplankton and fish abundance are discussed.
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Key words: Tropical estuary, Tide, *Pseudodiaptomus marshi*, Fish predation, Amazonia.

Mangrove ecosystems are the predominant type of vegetation still covering about 25 % of tropical and subtropical coastlines worldwide (World Resource Institute 1996) and provide important nursery grounds for fish and shellfish (Robertson and Duke 1987, Little et al. 1988, Chong et al. 1990, Laegdsgaard and Johnson 1995, Louis et al. 1995, Barletta-Bergan et al. 2002). The complex spatial structure of mangrove habitats is an important aspect for small juvenile fish as it apparently provides maximum food availability and minimizes the risk of predation (Laegdsgaard and Johnson 2001), thus optimizing conditions for growth and survival of juvenile fish (Miller et al.

1985). Since mangroves support valuable fisheries in many parts of the world, considerable efforts have been made to elucidate life history patterns of fish and prawns in mangroves (Robertson and Blaber 1992, Sasekumar et al. 1992). However, knowledge of the dynamics of the food preyed upon by juvenile mangrove fish is relatively poor (Robertson et al. 1988).

Zooplankton, particularly copepods, is of paramount importance as prey for many juvenile mangrove fish due to its ubiquitous dominance, the wide range of relatively small-sized organisms, and its ready availability (Turner 1984). In mangrove ecosystems, zooplankton forms a funda-

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mental trophic link in aquatic food webs as well (Godhantaraman 2001). On tidal coasts, the zooplankton community has to cope with continual changes in water level, and current strength and direction. Variations in zooplankton composition and abundance have been correlated to spring/neap tide alterations and to tidal cycles (Wang et al. 1995, Morgan et al. 1997, Villate 1997). These short/medium-term patterns of zooplankton abundance probably determine the availability of food for their predators and may thus have significant implications for the foraging strategies of juvenile fish preying upon zooplankton.

Macrotides characterize the northern and southern coastline of the Amazon estuary. The coast is covered by the 2nd largest mangrove area in the world (Spalding et al. 1997). However, few zooplankton studies have been conducted in this extensive mangrove ecosystem (Magalhães 1998, Peres 1999). Tidal creeks connect the mangrove with adjacent areas and provide well-defined pathways for aquatic organisms and for water and material exchange (Dittmar and Lara 2001). We studied the zooplankton community of a macrotidal mangrove channel in northern Brazil to determine the extent of temporal variability in terms of the number of species, and abundance and biomass on 3 temporal scales: the spring/neap tide alternation, the tidal cycle (flood, high water (HW), ebb, low water (LW)), and the light/dark cycle.

MATERIALS AND METHODS

Sampling site

The sampling site is located in the upper reaches of the macrotidal cul-de-sac mangrove channel, the Furo do Meio, in the Caeté River estuary (Caeté Bay) (Fig. 1). At the sampling site, the width and depth of the Furo do Meio are 30 and 4 m at LW, and 50 and 8 m at HW, respectively. The area is located about 200 km east of Belém on the southeastern margins of the Amazon estuary.

The tidal regime is semidiurnal, with a range at neap and spring tides of 2.5 and 5 m, respectively. The tide is asymmetric, with flood and ebb tides lasting 4 and 8 h, respectively. In the last 4 h, the ebb tide is extremely weak with an almost negligible fall in the water level. However, due to higher velocities at flood than at ebb tides the Furo do Meio is clearly flood-dominated with a net upstream longitudinal current. The mean net

upstream drift is about 0.5 km in a neap (Krumme 2004) and about 1.5 km in a spring tide cycle. Salinities can fall below 5 psu and exceed 30 psu in the wet and dry season, respectively. Secchi depth is low (range, 5 to 100 cm). For a more-detailed description of the study area, refer to Krause et al. (2001).

Field methods and data analysis

Mesozooplankton samples were taken in the Furo do Meio (Fig. 1) during 2 consecutive lunar cycles between Mar. and May 2001, using a conical plankton net (mouth diameter, 0.32 m; mesh opening, 300 µm), provided with a flow meter. Each lunar phase sampling started at LW and covered 4 consecutive tidal cycles. Spring tide hauls were taken at 03:00, 05:00, 07:00, and 10:00; and 15:00, 17:00, 19:00, and 22:00 (corresponding to LW, flood, HW, and ebb). Neap tide hauls were taken at 01:00, 04:00, 08:00, and 11:00; and 13:00, 16:00, 20:00, and 23:00 (corresponding to HW, ebb, LW, and flood). Thus, at each lunar phase, 17 surface hauls were made against the
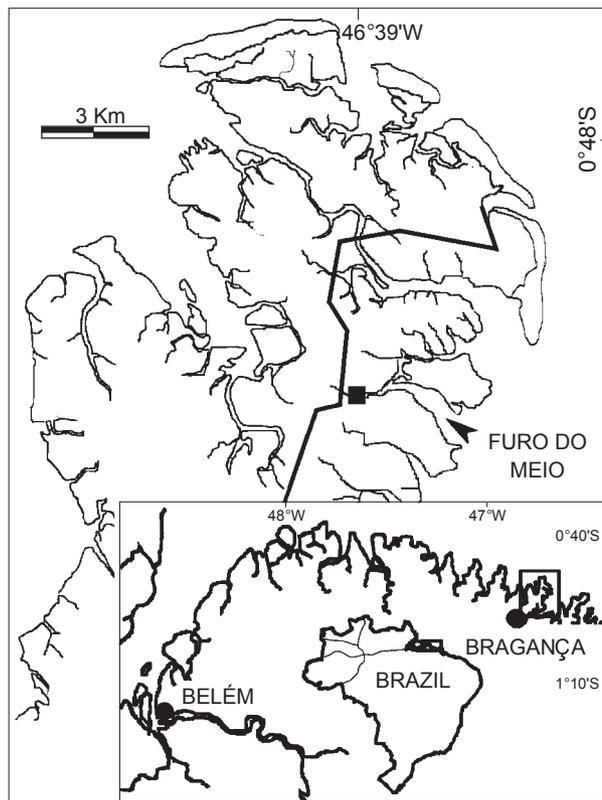
Fig. 1. Location of the study site (square) in the upper reaches of the mangrove channel "Furo do Meio" near Braganca, northern Brazil.

tidal current. In 1 spring tide cycle, 6 hauls could not be taken due to technical problems, yielding a total of 130 hauls. Net samples were immediately preserved in a 5% buffered formalin seawater solution.

For each sampling time, surface temperature and salinity were recorded using a conductivity-measuring instrument (WTW LF197) equipped with a sonde (WTW Tetracon 325). Water level was recorded with a tide gauge.

Zooplankton was identified and counted; copepod species were sorted, counted, and staged. Prosome lengths of copepodite stages were measured with an eyepiece micrometer. Groups of 20-100 individuals of comparable lengths were weighed on a microbalance (± 0.1 µg) after drying in an electric oven at 60°C for 48 h and cooled in a desiccator. Each weighing was repeated 3-6 times until a constant weight was obtained. All measurements were made on material preserved for at least 3 mo, but not exceeding 1 yr. Biomass was estimated by the product of the mean dry weight of each individual belonging to a certain size/maturity class and the abundance of the class.

We used three-way analysis of variance (ANOVA) to test for the separate and interactive effects of tide (spring tide and neap tide), time of day, and tidal cycle (LW, flood, HW, and ebb) using log(x+1)-transformed values of abundance and the number of copepod species. When the multifactor ANOVA detected significant effects, the least significant differences (LSD) test (α = 0.05) was applied to determine which means differed from the others. If the transformed abundance values did not conform to the ANOVA assumptions, (as was the case with biomass values), we used the non-parametrical Kolmogorov-Smirnoff two-sample test (KS test) (Sokal and Rohlf 1995).
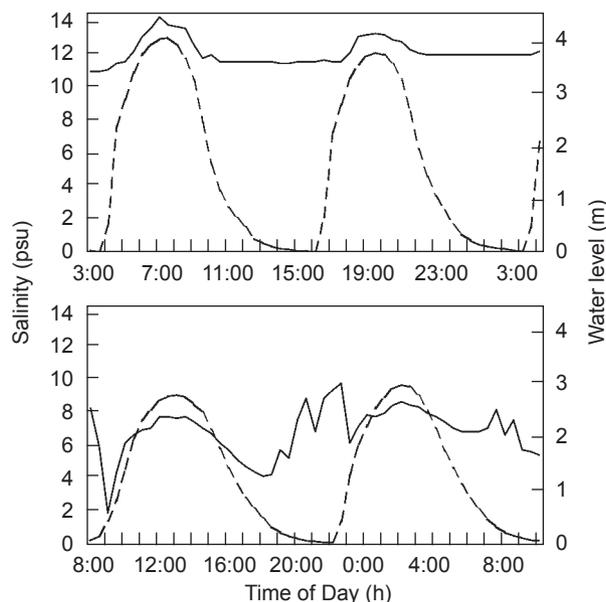
Relationships between salinity and water level, and species numbers and abundances were tested using Spearman's rank correlation. Similarity of species composition between samples was determined by non-parametric multi-dimensional scaling (MDS) using the program package Primer 5 (Clarke and Warwick 1994). We used square-root transformation to generate the Bray-Curtis similarity matrix. A stress value of the MDS representation of 0.1 indicated a fairly accurate and useful 2-dimensional representation of the inter-haul similarities (Clarke and Warwick 1994).

RESULTS

Environmental parameters

During the sampling period, temperature varied from 27.5 to 28.3°C. All salinities were below 10 psu (mean, 7 ± 3 psu; range, 1-14 psu), except in the last sampling campaign in May. Salinity was positively correlated to water level (Fig. 2; Spearman rank correlation, spring tide, R = 0.679, $p < 0.001$; neap tide, R = 0.285, $p < 0.01$). Salinity changes during a tidal cycle ranged between 3.5 ± 2.0 and 1.8 ± 1.1 psu at the neap and spring tides, respectively. Especially at neap tide-LW, measurement variability of salinity was high. Lowest salinities occurred during the 1st sample campaign (neap tide, 16-18 March).

Zooplankton composition

Copepods, appendicularia, chaetognaths, ostracods, and hydromedusa as well as zoea of the Brachyura, fish larvae, and larvae of polychaetes comprised the zooplankton community of the Furo do Meio during the wet season 2001 (Table 1).

Copepods dominated the zooplankton community contributing an average of 85% to the total abundance. Twelve species of copepods were observed: *Pseudodiaptomus marshi*, *P. richardi*,

Fig. 2. 26 h series of salinity (solid line) and water level (dashed line) at spring tide (upper, May 7-8) and neap tide (lower, Apr. 30 to May 1) at the Furo do Meio in the wet season 2001.

Acartia tonsa, *A. lilljeborgi*, *Eucalanus pileatus*, *Paracalanus aculeatus*, *Centropages furcatus*, *Temora turbinata*, *Oithona hebes*, *Caligus* sp., *Hemicyclops* sp. and unidentified Harpacticoida.

Tidal and diel variations

The total number of zooplankton species at HW was always greater than at all other tidal phases, with the lowest numbers at LW (KS-test, $p <$ 0.001). The positive correlation between species number and water level recurred each tidal cycle irrespective of the time of day, and the spring-neap tide alternation (KS-test, $p > 0.1$; Fig. 3, Table 2).

At spring tides, copepods dominated the zooplankton species collected, except for daytime-HW and ebb when other taxa were abundant in the plankton samples. At neap tides, an average of only 3 copepod species was present throughout the tidal cycle (Fig. 3). The number of copepod species was significantly lower at LW than that at HW (three-way ANOVA, $p < 0.01$).

Abundances of zooplankton and copepods were highly variable, ranging from 0.5 to 5434 (mean, 335 ± 55 SE) individuals/m^3 and 0.2 to 5434 (mean, 317 ± 5) individuals/m^3, respectively. Zooplankton and copepod abundances were greater at LW than at all other tidal phases (Table 2). The correlation of tides and tidal cycles on mean copepod biomass is shown in fig. 4. Zooplankton and copepods occurred at significantly greater abundances at spring than at neap tides

Table 1. Mean, maximum (individuals/m^3) and relative abundance and percent presence of the zooplankton taxa found in the mangrove channel Furo do Meio in the wet season 2001. +: present, but < 0.1% of the total abundance

TAXON			Abundane (individuals/m^3)			Presence
			Mean	Max.	%	%
CRUSTACEA	Copepoda	*Pseudodiaptomus marshi*	198.04	3621.50	56.9	92.31
		Pseudodiaptomus richardi	236.03	1983.70	22.8	32.31
		Acartia tonsa	40.93	1397.50	11.6	86.15
		Acartia lilljeborgi	15.22	283.00	3.3	71.54
		Eucalanus pileatus	0.05	0.05	+	0.77
		Paracalanus aculeatus	1.17	2.97	+	4.62
		Centropages furcatus	0.24	0.24	+	0.77
		Temora turbinata	7.65	7.65	+	0.77
		Oithona hebes	0.04	0.10	+	1.54
		Hemicyclops sp.	0.21	0.47	+	6.14
		Caligus sp.	0.01	0.01	+	0.77
		Harpacticoida	1.67	3.32	+	2.31
	Decapoda					
	Brachyura, Ocypodidae	Zoea	8.25	276.87	1.4	55.38
	Brachyura, Ocypodidae	Megalopa	1.97	17.69	0.1	23.08
	Penaeidae		0.49	3.82	+	16.15
	Mysidacea		0.48	1.72	+	3.08
	Ostracoda		5.97	76.53	1.1	63.85
	Cirripedia	Nauplii	2.83	35.37	0.3	35.38
	Isopoda		0.31	0.95	+	5.38
	Amphipoda		0.04	0.06	+	2.31
	Unidentified		0.02	0.02	+	0.77
POLYCHAETA			1.12	5.31	+	12.31
MOLLUSCA	Bivalve	Larvae	5.15	88.45	0.4	25.38
	Gastropoda	Larvae	4.49	23.88	0.3	20.00
CHAETOGNATA		*Sagitta friderici*	2.11	17.69	0.1	23.07
CHIDARIA	Hydromedusae	*Ciytia* sp.	2.44	25.27	0.3	36.15
UROCHORDATA	Apendicularia	*Oikopleura dioica*	0.65	4.54	+	18.46
CHORDATA	Pisces	Eggs and larvae	27.17	566.06	1.3	16.15
PROTOZOA	Foraminifera		0.08	0.17	+	1.54
INSECTA			0.01	0.01	+	0.77

(three-way ANOVA, $p < 0.001$; Fig. 4). Further-more, abundances of zooplankton and copepods were significantly correlated with the tidal cycle (three-way ANOVA, $p < 0.001$), whereas the time of day was not significantly correlated with abundances (three-way ANOVA, $p > 0.05$; Fig. 4). Finally, the interaction of tide versus time of day showed a significant correlation, since neap tide-day abundances were clearly lower than for the 3 other factor combinations (three-way ANOVA, $p < 0.05$).

The calanoid copepod, *P. marshi*, dominated the zooplankton community throughout the wet season. The highest abundance of *P. marshi* was recorded on 25 Mar. at new moon-night-LW (3622 individuals/m³). On average, *P. marshi* accounted for approximately 50% of the total copepod abundance. Total abundances of *P. marshi* were significantly higher during spring than neap tides and higher at night than in the day (KS-test, $p < 0.05$). The tidal cycle variation in abundance was reflective of the patterns revealed for total copepods (Table 2).

The *P. marshi* population was mainly composed of ovigerous females and adult males (Fig. 5). Adult females were present during the entire study period. Unlike the total abundance of *P.*
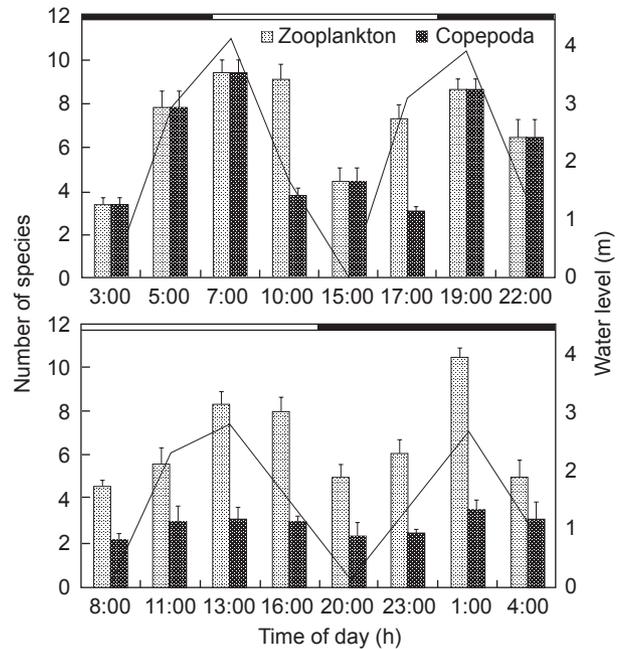
Fig. 3. Mean number of zooplankton and copepod species (± SE) at low water, flood, high water, ebb tide etc. during 25 h at spring tide (upper) and neap tide (lower), wet season 2001, Furo do Meio (*n* = 130). The line indicates the tidal water level. Horizontal bars on top indicate night (06:00 - 18:00).

Table 2. Kolmogorov-Smirnov two-sample test results: differences in the distributions of spring and neap tide (S and N), night and day (N and D) and all combinations of the tidal stages high water (HW), low water (LW), ebb tide (ebb) and flood tide (flood) in terms of abundance (individuals/m³) and the number of species (two bottom rows). C5, C4 and C3/C2/C1 are copepodite stages of *P. marshi*. Significant levels: (*) $0.01 < p < 0.05$; (**) $0.001 < p < 0.01$; (***) $p < 0.001$

Variable	Tide	Time of day	Tidal cycle					
			HW vs LW	HW vs ebb	HW vs flood	LW vs ebb	LW vs flood	ebb vs flood
Zooplankton	**S		**LW	*ebb	**flood	**LW	*LW	
Copepoda	**S		**LW	*ebb	**flood	*LW	*LW	
Total. *P. marshi*	*S	*N	**LW	**ebb	**flood	*LW	**LW	
Females		*N	**LW	**ebb	**flood	*LW	*LW	
Males	*S		**LW	**ebb	**flood		*LW	
C5	*S		**LW	**ebb	**flood	**LW	**LW	
C4	*S		**LW	**ebb	**flood	**LW	**LW	
C3/C2/C1	*S		**LW	**ebb	**flood	**LW	**LW	
P. richardi			*LW					
A. tonsa	**S		*LW	**ebb		*ebb	*flood	*ebb
A. lilljeborgi	**S		**LW	*ebb		**ebb	**flood	
Zooplankton			**HW	**HW	**HW	**ebb	**flood	
Copepoda	*S		*HW					

marshi, the abundance of female *P. marshi* was not correlated with the tide (KS-test, *p* > 0.1), whereas time of day (KS-test, *p* < 0.05) and tidal cycle had a significant correlation with abundances (KS-test, *p* < 0.05). In contrast to female *P. marshi*, abundances of male *P. marshi* and C5, C4, and C3-C1 copepodite stages were correlated
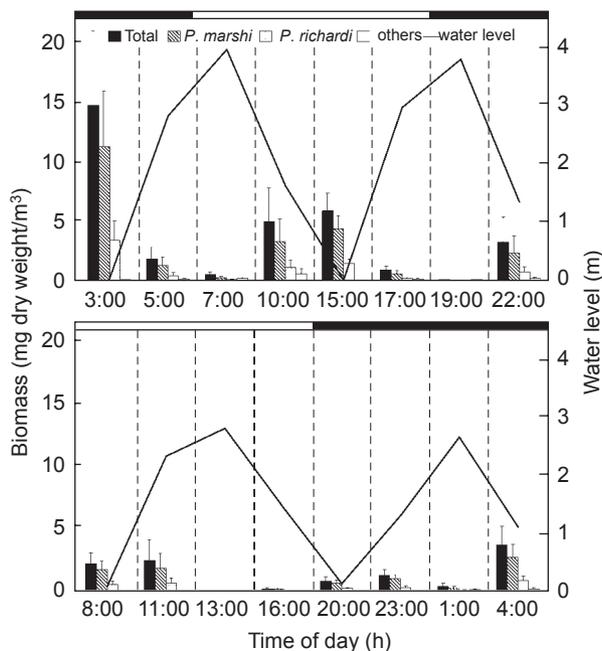
Fig. 4. Mean biomass of total zooplankton, *P. marshi*, *P. richardi*, and the remaining other species (± SE) at low water, flood, high water, ebb tider etc. for spring tide (upper) and neap tide (lower), wet season 2001, Furo do Meio (*n* = 130). Horizontal bars on top indicate night (06:00 - 18:00).
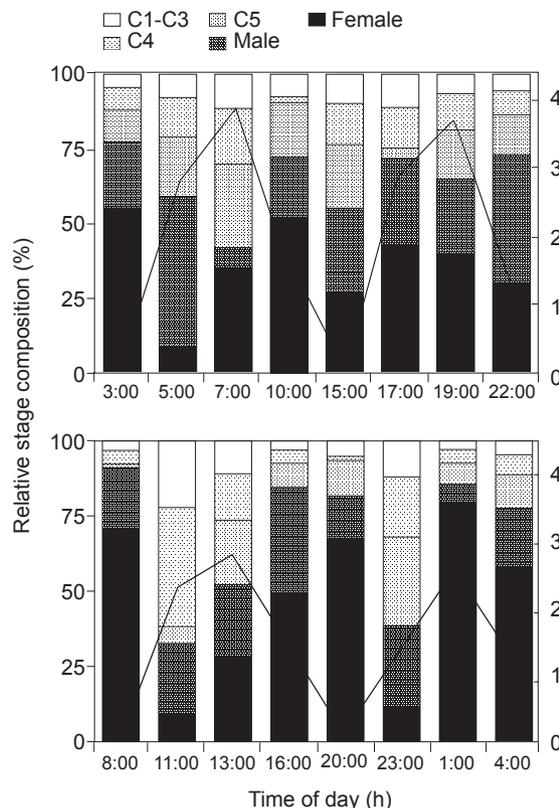
Fig. 5. Proportions of mean abundance (individuals m⁻³) of adult females, males, copepodites C5, C4 and C1-C3 of the copepod *Pseudodiaptomus marshi* during a complete tidal cycle at spring tide (upper) and neap tide (lower), Furo do Meio, wet season 2001 (*n* = 130). The time axis corresponds to the tidal phases (from left to right) low water, flood, high water, ebb tide etc. in both graphs. Night was between 18:00 and 06:00.

Table 3. Mean squares and significance levels for three-way ANOVAs of log(x+1)-abundance of five zooplankton community variables of surface hauls in the macrotidal mangrove channel Furo do Meio during the wet season 2001. S: Spring tide; N: Neap tide. LW: Low water; E: Ebb tide; F: Flood tide; HW: High water. SD: Spring tide-Day; SN: Spring tide-Night; NN: Neap tide-Night; ND: Neap tide-Day. Three-way interactions are not considered due to high complexity. The interactions are listed from highest mean (left) to lowest mean (right) in the *post hoc* LSD test. Significant levels: (*) 0.01 < *p* < 0.05; (**) 0.001 < *p* < 0.01; (***) *p* < 0.001. d.f. = degree of freedom. # Cop. spec.: Number of copepod species

	Main Effects			3-way interaction			LSD			
Variables	Tide(1) (1 d.f.)	Tiime of day(2) (1 d.f.)	Tidal cycle(3) (3 d.f.)	(1)x(2) (1 d.f.)	(1)x(2)x(3) (3 d.f.)	Residual (d.f. 114)	-1	-3	(1)x(2)	(1)x(2)x(3)
Zooplankton	8.54***		4.91***	2.56*	1.60*	0.41	S N	LW E F HW	SD SN NN ND	···
Copepoda	9.11***		5.51***	2.20*	1.99**	0.45	S N	LW E F HW	SD SN NN ND	···
P. richardi	4.10*		2.98*			0.81	S N	LW E F HW		
A. tonsa	9.07***					0.41	S N			
#Cop. spec.	0.08**		0.03*			0.01	S N	LW E F HW		

with tides and tidal cycles, but lacked correlation with time of day (Table 2).

During the spring tide, the proportions between adults and copepodite stages of *P. marshi* were fairly homogenous throughout the tidal cycle. During the neap tide, copepodite stages C1-C5 occurred in increased proportions at flood tides, whereas females were more numerous at LW (Fig. 5).

Abundances of *P. richardi* were greater during spring than neap tides (three-way ANOVA, $p < 0.05$). Within a tidal cycle, the lowest abundance of *P. richardi* occurred at HW compared to all other tidal phases (three-way ANOVA, $p < 0.05$).

Abundances of A. tonsa and *A. lilljeborgi* were greater at spring tides (Tables 2, 3). In contrast to all other species, ebb tide abundances of *A. tonsa* were greater than those at flood tide (KS-test, $p < 0.05$); and ebb and flood tide abundances of *A. tonsa* and *A. lilljeborgi* were greater than those at LW (KS-test, *A. tonsa*: $p < 0.05$, *A. lilljeborgi*: $p < 0.001$).

Salinity was negatively correlated to zooplankton and copepod abundances ($p < 0.05$), and to abundances of *P. marshi* females ($p < 0.05$) and males ($p < 0.01$) (Table 4).

Copepod biomass varied from 0.46 to 6.91 mg DW/m^3 with a mean of 2.63 mg DW/m^3. *Pseudodiaptomus marshi* accounted for 66% of the mesozooplanktonic copepod biomass (range, 0.46-6.82 mg DW/m^3). *Pseudodiaptomus richardi*,

Table 4. Spearman rank correlation analysis between salinity (psu) and several zooplankton community variables, Furo do Meio, wet season 2001; R = Spearman's coefficient, *n* = 129 for all variables; significant levels: (*) $0.01 < p < 0.05$; (**) $0.001 < p < 0.01$

Factor	Variable	R	*p*
	Zooplankton abundance	-0.182	*
	Copepod abundance	-0.197	*
	Number of zooplankton species	0.089	
	Number of copepod species	-0.018	
	Abundance of total *P. marshi*	-0.217	*
	Abundance of *P. marshi* females	-0.226	*
	Abundance of *P. marshi* males	-0.230	**
	Abundance of *P. marshi* C5	-0.124	
	Abundance of *P. marshi* C4	-0.108	
	Abundance of *P. marshi* C1-C3	-0.090	
	Abundance of *P. richardi*	-0.114	
	Abundance of *A. tonsa*	-0.019	
	Abundance of *A. lilljeborgi*	-0.022	

A. tonsa, and *A. lilljeborgi* on average comprised 22%, 19%, and 9% of the biomass in the channel, respectively.

Temporal variations in copepod assemblage structure

Multi-dimensional scaling (Fig. 6) revealed that spring tide/neap tide together with HW/LW were important factors determining changes in the structure of the copepod community (biomass of copepod species for *n* = 129; exclusive of 1 outlier which was a nearly empty haul). Combining the ordination and clustering analysis revealed 4 distinct groups of copepod assemblages (frames in Fig. 6). The S-LW group (upper left) contains hauls taken at spring tide-LW; the S-HW group (upper right) contains hauls at spring tide-HW. The 1st N group (lower left) is comprised mainly of hauls from the 1st neap tide sampling (16-18, March); while the N-HW group (lower left) contains hauls at neap tide-HW. The broken horizontal axis separates the copepod assemblages at spring tide (above) from the neap tide (below). The broken vertical axis divides HW assemblages (on the right) from the remaining assemblages. Diel variations were not significantly associated with changes in the community structure. Separation between the 2 spring tide groups was more marked than between the 2 neap tide groups. At spring tide, the hauls at HW (high number of species, low biomass) markedly differed from those at LW (low number of species, high biomass) (Figs. 3, 4). At neap tide, few copepod species and generally low biomass caused neap tide hauls to be rather uniform. Only the neap tide-HW hauls were distinctly grouped together, and no clear neap tide-LW group was formed (Fig. 6). However, similar hauls taken during the 1st neap tide sampling when the tidal range was small (2.2 m) and salinity extremely low (5 ± 2 psu) were grouped together irrespective of the tidal stage (1st N).

DISCUSSION

Zooplankton composition

The use of a coarse mesh size undoubtedly influenced the composition of zooplankton and copepod species and stages caught. The small copepodite stages C1-C3 of *P. marshi* probably occurred in the samples only because high sedi-

ment loads partially plugged the net and, hence, held back even these smaller stages. Moreover, very small species of the families Oncaeidae and Oithonidae could also have been undersampled. Lopes (1994), collecting zooplankton in the Guaraú estuary with a bottle and filter with a 75-μm mesh net, showed that copepodites and nauplii of *P. richardi* were almost the only species in the inner estuary, whereas in the middle estuary this species coexisted with *A. lilljeborgi* and *O. hebes*. Thus, we believe that the composition patterns found in the Furo do Meio with a 300 μm mesh are representative of the mesozooplankton community except for the younger copepodite stages C1-C3 of *P. marshi*.

In the wet season, the mesozooplankton community of the macrotidal mangrove channel of Furo do Meio was characterized by low numbers of species and was dominated by copepods, particularly *P. marshi*. Björnberg (1981) characterized *P. marshi* as a typical species of estuaries and mangrove systems off the northern and northeastern coasts of Brazil, with high abundances at low tide. Seasonal changes in the zooplankton composition in the Furo do Meio are apparently not severe,

since the wet season community generally resembled the one found during a dry season study (Peres 1999).

The zooplankton composition of the semi-enclosed Furo do Meio differed from the communities found in the open mangrove channel of Furo Grande (located further towards the coast) and in samples taken at the lower reaches of the Caeté estuary system (Liang, unpubl. data). The dominant species in the Caeté estuary are *A. tonsa* and *A. lilljeborgi* (Liang, unpubl. data). In the Furo do Meio, these 2 species exhibited typical features of estuarine copepod species that are imported on strong rising tides and exported with the receding tide in that higher abundances of *A. tonsa* and *A. lilljeborgi* were seen at flood and ebb tides than at LW.

Our wet-season copepod abundances were higher than those found by Peres (1999) during the dry season (0.2 - 1382 individuals/m^3, mean, 91 individuals/m^3), suggesting seasonal fluctuations in abundance related to rainfall and hence to alterations in salinity. A marked seasonality with higher wet season zooplankton densities is apparently a general pattern of tropical mangrove estu-

Fig. 6. Multidimensional scaling plot of the copepod community (biomass, mg DW/m^3) in the Furo do Meio, wet season 2001 (*n* = 129 hauls). Three-letter abbreviations: 1st letter N: Neap tide, S: Spring tide; 2nd letter: D: Daytime, N: Night; 3rd letter: L: Low water, F: Flood, H: High water, E: Ebb tide. Broken horizontal axis divides between copepod hauls at spring (upper) and neap tide (lower). Broken vertical axis separates HW hauls (on the right) from the rest. Frames show distinct groups at spring tide-LW, spring tide-HW, first neap tide sample campaign (March 16-18; lowest salinities) and neap tide-HW.

aries (Robertson et al. 1988).

Tidal variations in abundance and biomass

On a medium time scale, temporal variations within the zooplankton community were related to the spring/neap tidal pulse that is the key factor determining weekly differences in the zooplankton composition. At spring tides, current velocities in the Caeté estuary system can exceed 1.5 m/s. At neap tides, estuarine copepod species are apparently not carried into the channel, most likely because of the weak neap tide current speeds that may not be sufficient to suspend and then transport them to the upper reaches of the mangrove channel (at least 4 km from the estuary). The copepod assemblages at neap tide exhibited a rather uniform structure. We assume that the similarity of the copepod community during the 1st sample campaign was related to the combined effects of a fairly weak neap tide cycle, very low salinities throughout the tidal cycle, and extraordinarily high sediment loads.

On the short term, the tidal cycle additionally determines changes in the zooplankton composition. It remains unclear, however, if water level or salinity determines the short-term changes in the zooplankton community, and whether high abundance of *P. marshi* is more related to low salinities or to the tidal situation at LW per se. Peres (1999) surprisingly found no significant tidally related correlation during the dry season, when in contrast to the wet season, salinity is lower at HW and higher at LW (Lara and Dittmar 1999).

Abundance and biomass were greatest at LW when the number of species was lowest, and was conversely lowest at HW ("highest dilution") when the number of species was greatest. This is in contrast to Robertson et al. (1988) and Wang et al. (1995) who found higher densities and total abundances at high tide than at low tide, respectively. Unlike open estuarine environments, the semi-enclosed Furo do Meio with a net upstream drift due to higher flood tide velocities apparently promotes the retention of copepods from 1 tide to the next. Since the retention is species-specific (dominance of *P. marshi* at LW), a simple mechanism similar to tidal pumping (Pethick 1984) must, however, be ruled out.

Our data lack direct evidence for a pattern of a tidal-related vertical migration since the sampling dealt with surface hauls only. Selective tidal stream transport in layers of different salinities is unlikely to occur in a well-mixed shallow estuary exposed to macrotides. It is rather likely that the weight of *P. marshi*, the net upstream longitudinal current, and hydrodynamic processes that trap fine particulate matter (Castel and Veiga 1990) in the upper reaches of the mangrove channels work together to ensure its population maintenance in the Furo do Meio. Adult and late copepodite stages of *P. richardi* (Lopes 1994) and *P. hessei* (Wooldridge and Erasmus 1980, Kouassi et al. 2001) were found in higher abundances near the bottom at ebb tides, showing that selective avoidance of stronger surface currents during the receding tide also occurs in other species of the Pseudodiaptomidae.

We hypothesize a retention mechanism for copepods resident in the Furo do Meio which are imported into the intertidal area during flood tides: at HW they may tend to sink to ground level preventing horizontal export out of the intertidal creeks within the upper strata during the strong ebb tide current, and then to later return to the main channel during the weak receding tide to resurface at LW. Determination of whether such a mechanism of accumulation operates for copepods in mangrove channels awaits further work on the vertical migratory behavior of individual copepod species.

Retention in lateral, high-turbidity appendices of the estuary during LW may be advantageous when considering the detritivorous feeding habits of estuarine copepods, especially of the family Pseudodiaptomidae. In the wet season, the lowest water clarity was found in the upper reaches of the Furo do Meio. High turbidity is not only linked to reduced visual ranges in predators (Grecay and Targett 1996), but also to high concentrations of detritus and associated microbes that provide an important source of energy for copepods, as suggested for *P. inopinus*, which apparently maintains its population over time in the estuarine turbidity maximum of the Columbia River, USA (Morgan et al. 1997).

Synchronous pattern between zooplankton and fish

At present, we cannot assess the predatory impact of fish on the zooplankton community due to a lack of studies that simultaneously address temporal changes in zooplankton, fish larvae abundances, and larval predation. It is, however, striking that the short- to medium-term changes in abundances of zooplankton (spring > neap; LW > HW) mirror those of tidally migrating fish, including

copepod-feeding species and age groups (Krumme and Saint-Paul 2004; Krumme et al. 2004), suggesting that the tidal pulse synchronizes their temporal patterns and most likely tightly couples their interplay. The stomachs of several fish species so far studied in the Caeté system, especially in the Furo do Meio, contained copepods. Specimens of the 7-9 cm standard length size class of the predatory anchovy *Pterengraulis atherinoides* were specialized consumers of copepods, particularly *P. marshi*, which contributed 40% to the dry weight and 85% to the abundances of the stomach contents (Keuthen 1998). Furthermore, adult *Anchovia clupeoides* (Brenner 2002), *Cathorops* sp. (< 12 cm) (Leal-Flórez 2001), *C. spixii* (Espirito-Santo and Isaac 1999), *Stellifer naso* (4 cm), and *S. rastrifer* (1-3 cm) (Camargo-Zorro 1999) have been recorded as being copepod feeders. All these species, except *C. spixii*, occur at all ages in the Furo do Meio throughout the year (Barletta et al. 2003, Krumme et al. /2004).

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