

## Contribution to the feeding ecology of the banded puffer fish *Colomesus psittacus* (Tetraodontidae) in north Brazilian mangrove creeks

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(With 4 figures)

### Abstract

Stomach contents were examined from 102 banded puffer, *Colomesus psittacus* (Tetraodontidae), caught from intertidal mangrove creeks at diurnal neap tides between June and September, 1997 (early dry season) near Bragança (north Brazil). The study found that *C. psittacus* were specialized predators of Cirripedia (*Balanus* spp.) and Brachyuran crabs (*Uca* spp., *Pachygrapsus gracilis*) (mean: 58 and 38% by dry weight, respectively), emphasizing a short food chain in the mangrove system. Cirripedia and Brachyura dominated the diet in all size classes, however, the prey spectrum narrowed with fish size. The mean daily consumption of Cirripedia and Brachyura was 6.2% body weight of *C. psittacus*. On average *C. psittacus* consumed 100.3 g.ha<sup>-1</sup>.d<sup>-1</sup> of Cirripedia and 178.7 g.ha<sup>-1</sup>.d<sup>-1</sup> of Brachyura (wet weight). The predation on Brachyuran crabs – a significant driver of fluxes of organic matter and energy in the system – provides *C. psittacus* with an important ecological function in the mangrove food web. A plant-animal interaction is proposed where *C. psittacus* exerts a mutually beneficial cleaning function on the Aufwuchs (Cirripedia and associated epibiota) of *Rhizophora mangle* stilt roots. Our results and those of other studies suggest that *C. psittacus* encounter optimum foraging conditions in the mangrove at high inundations at daylight (spring tide-day) whereas darkness and low inundations are linked to poor foraging conditions (neap tide-night). The *C. psittacus* resource could be used as an alternative income in the region in terms of i) sustainable catch and filet processing for exports to East Asia, ii) developing certified aquaculture methods for breeding puffers for the aquarium trade.

**Keywords:** Brachyura, Cirripedia, fish diets, ontogeny, plant-animal interaction.

### Contribuição à ecologia alimentar do baiacu *Colomesus psittacus* (Tetraodontidae) em canais de maré com vegetação de mangue no norte do Brasil

### Resumo

Conteúdos estomacais de 102 baiacus *Colomesus psittacus* (Tetraodontidae) foram examinados. A amostragem foi realizada em canais de maré com vegetação de mangue, durante as marés de quadratura de dia, entre junho e setembro de 1997 (no início do período seco), nas proximidades de Bragança (norte do Brasil). O estudo constatou que *C. psittacus* era um predador especializado em Cirripedia (*Balanus* spp.) e Brachyura (*Uca* spp., *Pachygrapsus gracilis*), com médias de 58 e 38% em peso seco, respectivamente, caracterizando uma curta cadeia alimentar no sistema de manguezal. Cirripedia e Brachyura dominaram a dieta em todos os tamanhos, entretanto, o espectro alimentar diminuiu de acordo com o tamanho do peixe. O consumo diário médio de Cirripedia e Brachyura foi de 6,2% em peso corporal de *C. psittacus*. *C. psittacus* consumiu uma média de 100,3 g.ha<sup>-1</sup>.d<sup>-1</sup> de Cirripedia e 178,7 g.ha<sup>-1</sup>.d<sup>-1</sup> de Brachyura (peso úmido). A intensa predação de Brachyura por *C. psittacus* enfatiza a importante função ecológica desta espécie na cadeia alimentar do manguezal, contribuindo significativamente no fluxo de matéria orgânica. Uma interação planta-animal é indicada no fato que *C. psittacus* exerce uma função limpadora mutuamente beneficiável ao se alimentar do Aufwuchs (Cirripedia e epibiota associada) que cresce nas raízes aéreas de *Rhizophora mangle*. Nossos resultados e os de outros estudos sugerem que *C. psittacus* encontra no manguezal as melhores condições para se alimentar no período diurno durante as maiores inundações (marés de sizigia - de dia), enquanto que períodos noturnos e de pequenas inundações determinam as piores condições para forragear (maré de quadratura - de noite). *C. psittacus* poderia ser usado como alternativa de renda na região com respeito a: i) pesca sustentável e processamento de filés para exportação ao leste da Ásia, ii) desenvolvimento de métodos de aquíicultura certificada para a criação de baiacu para o comércio de peixes ornamentais.

**Palavras-chave:** Brachyura, Cirripedia, dieta de peixes, ontogenia, interação planta-animal.

## 1. Introduction

In the western Pacific, tetraodontids are commercially valuable and highly regarded as fish food, even though the presence of the family-specific tetraodotoxin still causes the death of gastronomers each year (Fiedler, 1991). Furthermore, there is an increasing demand for tetraodontids in the aquarium trade. Although tetraodontids are used commercially, basic ecological knowledge of natural populations is usually scarce.

In tropical and subtropical mangroves, tetraodontids are often amongst the most common fish species sampled (Bell et al., 1984; Hindell and Jenkins, 2004). The banded puffer *Colomesus psittacus* (Bloch and Schneider, 1801) is distributed along the coast from east Venezuela to north Brazil but also occurs in freshwater, e.g. several 100 km upstream in the Amazon and its tributary river systems (Barthem, 1985; Cervigon et al., 1992). In freshwater, *C. psittacus* is carnivorous, feeding mainly on mollusks (Keith et al., 2000) but little is known about marine environments.

In mangroves along the north Brazilian coast *C. psittacus* is one of the dominant fish species of tidal channels year-round (Castro, 2001; Barletta et al., 2003; Krumme, 2004; Krumme et al., 2004). The intestines of tidally migrating *C. psittacus* were empty at flood tide and well-filled at ebb tide when the fish returned from the intertidal zone (Krumme, 2004). *C. psittacus* is usually the only tetraodontid species in these mangroves. Juvenile *Spheroides testudineus* occur as accidental visitors.

The toxicity of pufferfish is well-known among fishermen and only very few seem to have really ever eaten puffer filet (pers. comm. with fishermen). Therefore, *C. psittacus* is usually discarded from the semi-commercial tapagem and curral catches (Barletta et al., 1998) and is of no commercial importance and not marketed.

Puffers have three defense mechanisms against predators: being poisonous, inflation (with water or air) and aposematism (dorsal transverse black bars as warning coloration; Krebs and Davies, 1993). Puffers have a beak-like, terminal mouth with a bony plate in both jaws that can crush hard-shelled organisms. In mangroves, these adaptations enable them to prey on the ubiquitous fiddler crabs, which are unapproachable by many other fish species. Given the important functional role that these crabs have, puffers may have a significant impact on the ecological functioning of the system.

So far, detailed quantitative assessment of the food habits of *C. psittacus*, including the effect of ontogeny, is lacking and its ecological role in the mangroves is still unknown. Trophic modeling relies on a predator-prey matrix and the consumption per unit of biomass (e.g. Wolff et al., 2000). Therefore, the objectives of this study were to describe the diet of mangrove-dwelling *C. psittacus* quantitatively and determine ontogenetic patterns in their diet.

## 2. Materials and Methods

### 2.1. Study area

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 of the world, covering about 7,000 km<sup>2</sup> on the north-east coast of South America (Kjerfve and Lacerda, 1993). Vast forests of *Rhizophora mangle* and *Avicennia germinans* dominate the coastal vegetation in the region.

The sample sites were three intertidal 1<sup>st</sup> 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). Approximately 110 km<sup>2</sup> of the peninsula are covered by mangrove. In the Caeté estuary, intertidal 1st order creeks (about 25 m width at the mouth) that are further ramified upstream, drain the mangrove area into a large subtidal main channel ("Furo", 50 m width and larger) that are connected to the Caeté bay. According to Barletta-Bergan (1999), creeks 1, 2 and 3 had 6,481, 9,351 and 1,865 m<sup>2</sup> of inundated areas at neap tide high water (HW), respectively. The vegetation of the studied creeks is dominated by *R. mangle* and *A. germinans* and can therefore be considered representative for a large part of the mangrove area.

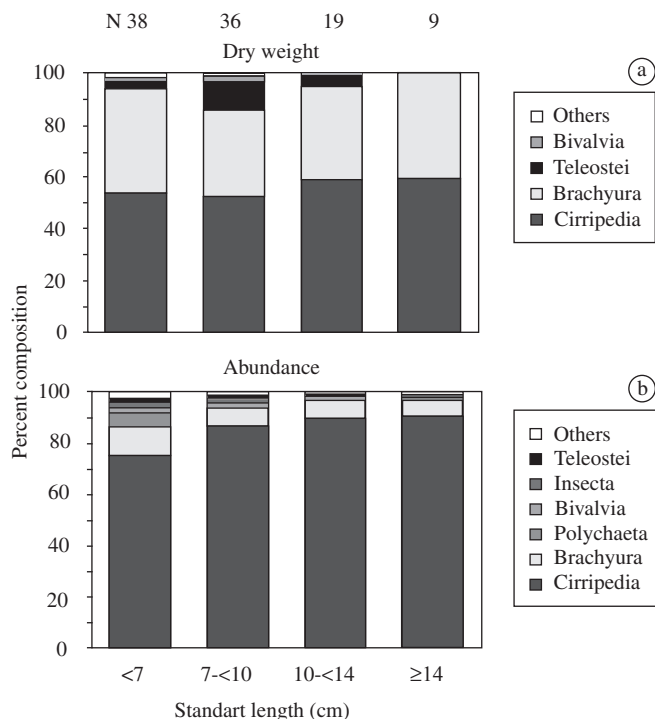
The semidiurnal macrotide has a tidal range of 2-3 m at neap and 3-4 m at spring tides. The tide is asymmetric; the flood and ebb tides last 4 and 8 hours, respectively. In the last 4 hours, the ebb tide is extremely weak with an almost negligible fall in the water level. The annual average rainfall is about 2,500 mm, with a significant dry season between August and November when estuarine salinities can exceed 35 psu. The air and water temperatures are high year-round, ranging from 25 to 33 °C and 27 to 30 °C, respectively. The secchi depth is usually low (on average 30 cm).

### 2.2. Sampling method

*C. psittacus* were caught for stomach analysis during diurnal neap ebb tides of the last quarter moon. Samples were taken monthly between June and September 1997 (early dry season) as part of the one-year study of Barletta et al. (2003) and Barletta-Bergan et al. (2002). The three creeks were sampled on consecutive days. Each day at slack HW, a creek mouth was blocked with a net (50 x 5 m, 1 cm stretched mesh size). Fish were collected during the ebb tide until the creek was totally drained (ca. 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.

### 2.3. Morphometrics

The total length (TL), standard length (SL) (both to the lowest 0.5 cm), total wet weight and wet weight without stomachs were taken (Sartorius LC 4200 S ± 0.01 g). The length-weight relationship ( $W = a \times L^b$ ) of *C. psittacus* was determined, using  $n = 122, 417$  and  $260$



**Figure 1.** Ontogenetic changes in diet composition of *C. psittacus* from intertidal mangrove creeks (north Brazil) caught at diurnal neap tides in the early dry season of 1997. Histogram for each size class shows relative proportions of a) percent dry weight and; b) percent abundance of the food items. Number collected per size class (N) is given on top.

specimens from the present study, from Krumme et al. (2004) and of samples taken in the Furo do Meio in the dry season 2002, respectively. The parameters  $a$  [W in gram; L in cm TL (Xiao, 1998)] and  $b$ , and the condition factor c.f. [c.f. =  $((\sum(W \times 100) \times (L^{-3})) \times n^{-1})$ ] were calculated (Cinco, 1982).

The length of the uncoiled digestive tract (DT) was measured from the pylorus to the anus ( $\pm 0.5$  cm). The relative length of the DT (RLDT) was calculated (DT length  $\times$  TL $^{-1}$ ). The feeding habit was classified according to Odum (1970) who suggested a relative GIT length of <1, 1-3 and >3 for carnivorous, omnivorous and herbivorous fish, respectively.

#### 2.4. Stomach fullness

All but three stomachs were empty. 'Puffers have an inflatable abdominal sac, a ventral diverticulum continuous with the stomach' (Targett, 1978). *C. psittacus* inflated when captured and could thus have drawn extraneous material into the stomach (Targett, 1978). 'Puffer stomachs have poorly developed digestive glands with most digestion taking place in the intestine' (Breder and Clark, 1947). Therefore, only the intestinal contents were analyzed. The intestines were transferred to 8% buffered formalin, washed, drained on absorbent paper and wet-weighed ( $\pm 0.01$  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). Intestines were opened and in-

testine fullness was assigned to five categories, adapted from Pillay (1953): empty; filled to 25%; filled >25-50%; filled >50-75%; filled >75-100% full. Alternatively, the intestine fullness index (IFI) following Hureau (1970) was calculated as  $IFI = ((\text{intestine content weight} \times 100) \times \text{total fish weight}^{-1})$ . The fish were assigned to four size classes: <7 cm; 7-10 cm; 10-14 cm;  $\geq 14$  cm SL.

A three-way analysis of variance (ANOVA) type II was calculated to ascertain whether IFI differed by month, size class and creek (Sokal and Rohlf, 1995). The creek was the unplanned factor. The IFI raw data were  $\log_{10}(x + 1)$ -transformed to fulfil the ANOVA assumptions. To avoid an incomplete design, the two largest size classes and the months June/July and August/September were pooled.

#### 2.5. Stomach content analysis

Intestine contents were washed in distilled water to substitute formol before the contents were observed under a ZEISS-STEMI SV-11 stereo magnifying glass or microscope and separated into prey categories (e.g. Cirripedia, Brachyura) while prey items were identified as precisely as possible according to the literature (Kaestner, 1963; Chace and Hobbs 1969; Riedl, 1970; Abbott, 1974; Rodriguez, 1980; Laguna, 1985; Cervigon et al., 1992; D'Incao, 1995; Hayward and Ryland, 1995). Most prey items, unless very small, are broken once they reach the intestine. Therefore, unique body parts of the prey items were identified and counted, e.g. entire bod-

ies of barnacles, crab eyes or bivalve shells with hinge teeth. The items of each category were counted and transferred to 4% formalin. After freeze-drying, the dry weight of the categories was taken (Sartorius Analytica 200a,  $\pm 0.0001$  g).

### 2.6. Standardization of content weights

The effect of fish size within the different size classes was accounted for by standardizing intestine content weights to the geometrical mean weight of all investigated fish of a single size class according to Brenner et al. (2001). A linear regression between the fish weight (FW) and weight of the empty intestine (E) was established:

$$E = a + b \times WF \quad (1)$$

Subsequently, number ( $NP_{j,i}$ ) and weight ( $WP_{j,i}$ ) of each prey item  $j$  found in the intestine of a fish  $i$  of weight  $WF_i$  was standardized (SF). Standardization used the geometrical mean weight (GM) for the size class where the fish  $WF_i$  was stated as:

$$WP(SF)_{j,i} = (WP_{j,i} \times (a + b \times GM)) \times \quad (2)$$

$$(a + b \times WF_i)^{-1}$$

Using  $y = 0.025x - 0.016$  ( $r^2 = 0.95$ ;  $n = 101$ ) we converted the original stomach content weights into standardized stomach content weights for each size class (Brenner et al., 2001).

### 2.7. Patterns in diet composition and feeding strategy

The similarities in diet composition between size class and month were displayed using non-parametric multi-dimensional scaling (MDS) (Clarke and Warwick, 1994). In the original species-sample table, each cell contained the standardized mean weight of food item (g) per size class and month (e.g. Jun1 = smallest size class in June). We used square-root transformation to generate the Bray-Curtis similarity matrix. The stress of the MDS representation - a measure of how well the ordination represents the similarities between the samples - was assessed using the classification of Clarke and Warwick (1994) where a stress value  $<0.1$  corresponds to a good ordination with no real prospect of a misleading interpretation.

The feeding strategy of *C. psittacus* was assessed using the feeding strategy plot of Costello (1990). The prey-specific abundance was based on dry weight.

### 2.8. Index of predation impact

An index of predation impact was measured as the weight of the prey (Cirripedia or Brachyura) eaten by *C. psittacus* per hectare and day. The index was calculated according to Brewer et al. (1991) and Salini et al. (1998) as the product of predator biomass per tide ( $g \cdot ha^{-1}$ ), the mean proportion of prey in the diet per tide and a factor 2 to account for the semidiurnal tide. We used the sum of the submerged surface area of the three creeks that Barletta-Bergan (1999) estimated for a common neap tide inundation ( $17688 \text{ m}^2$ ) to calculate the surface relationship in the predator biomass. Neap tide inundations are restricted to the network of creeks and therefore, surface area measurements taken once at slack neap high tide can be used as a coarse approximation for the general neap tide inundation area, despite variability in the submerged area between tides (Krumme et al., 2004). We do not provide a conventional evacuation measure. Krumme (2004) found a significant difference between empty flood and well-filled ebb tide intestines of tidally migrating *C. psittacus* at diurnal neap tides in the study area. Hence, we assume that the stomach contents at the end of the ebb tide are the minimum of what the fish have eaten, thus it is a conservative measure. Factor 2 assumes that each intertidal inundation, both in the daytime and at night, is a feeding period for *C. psittacus* while the low water period is not. The dry weight proportion of the prey in each individual predator intestine was used to assess the wet weight proportion and was multiplied by the individual predator wet weight and monthly averages were calculated.

## 3. Results

We caught 28, 24, 25 and 25 *C. psittacus* in June, July, August, and September, respectively, which were used for quantitative assessments of feeding habits ( $n = 102$ ; size range: 4-20.5 cm SL). 73% of the intestines were more than 50% filled. There was no empty intestine and only 6% were filled to less than 25%.

Morphometric relationships of *C. psittacus* are shown in Table 1. *C. psittacus* displayed a slightly negative weight increase ( $b < 3$ ). The condition factor was 3.2. The intestine lies in the posterior section of the abdominal cavity where it forms two or three loops. The mean RLDT ( $1.0 \pm 0.2$  SD; range: 0.7-1.4;  $n = 56$ ) indicated a carnivorous feeding habit of *C. psittacus*.

**Table 1.** Length relationships of *C. psittacus* from mangrove creeks near Bragança, north Brazil. N is the sample size;  $r^2$  is the coefficient of determination.

Relationship	Formula	Variables	Size range	N	$r^2$
Length-weight	$Y = 0.059 X^{2.7}$	$Y = \text{Weight (g)}; X = \text{TL}$	1-31 cm TL	799	0.99
Length-length	$Y = 0.834 X - 0.315$	$Y = \text{TL}; X = \text{SL}$	4-20.5 cm SL	105	0.99
Length-length	$Y = 1.192 X + 0.443$	$Y = \text{SL}; X = \text{TL}$	5-25 cm TL	105	0.99
Stomach length	$Y = 0.886 X + 1.365$	$Y = \text{stomach length}; X = \text{TL}$	5-25 cm TL	56	0.84

### 3.1. Stomach fullness

IFI was significantly higher in the two larger creeks 1 and 2 than in the small creek 3 (three-way ANOVA,  $F = 12.68$ ,  $P < 0.001$ ). The IFI was significantly higher in June/July than in August/September (three-way ANOVA,  $F = 68.65$ ,  $P < 0.05$ ). Although the IFI did not differ between size classes, there was a trend to decreasing IFI with increasing fish size. On average, the fish had eaten  $7\% \pm 3.3$  SD of their wet weight ( $n = 102$ ; range: 0.4-15.4%).

### 3.2. Diet composition

Cirripedia (*Balanus amphitrite*, *B. eburneus*, and probably some other species) and Brachyuran mangrove crabs dominated the diet with on average 58 and 38% of the dry weight, respectively (Figure 1). *Uca* spp. and *Pachygrapsus gracilis* were the most abundant Brachyuran crabs in the diet (Table 2). Other important food items in terms of weight were Teleostei (usually only muscle tissue and scales) and Bivalvia (*Mytella strigata*, *M. guyanensis*, *Crassostrea* aff. *rizophorae*). Less important were Polychaeta (*Isolda* aff. *pulchella*, Nereididae, Capitellidae, Phyllodocidae), insects (Blattodea, Hemiptera, Diptera, Hymenoptera), filamentous red and green algae (lacking any indication of digestion), Gnathiidae (praniza stage), Natantia (*Troglocubanus* sp.), Gastropoda (c.f. *Littorina angulifera*), Amphipoda (Corophiidae), Bryozoa (Membraniporidae), Mysidacea, and seeds. The number of prey categories decreased with increasing fish size (14, 12, 8 and 6 prey categories from the smallest to the largest size class) (Figure 1). Only the largest size class had no Teleostei in the intestines.

Cirripedia dominated the diet in June/July (77 and 83% of the total dry weight, respectively) but decreased in August (43%) down to 16% in September. Contrarily, Brachyura were less important in June/July (14 and 15% respectively), but increased in August (51%) and dominated the diet in September (79%) (Figure 2). The other food items were too rare to detect a temporal trend.

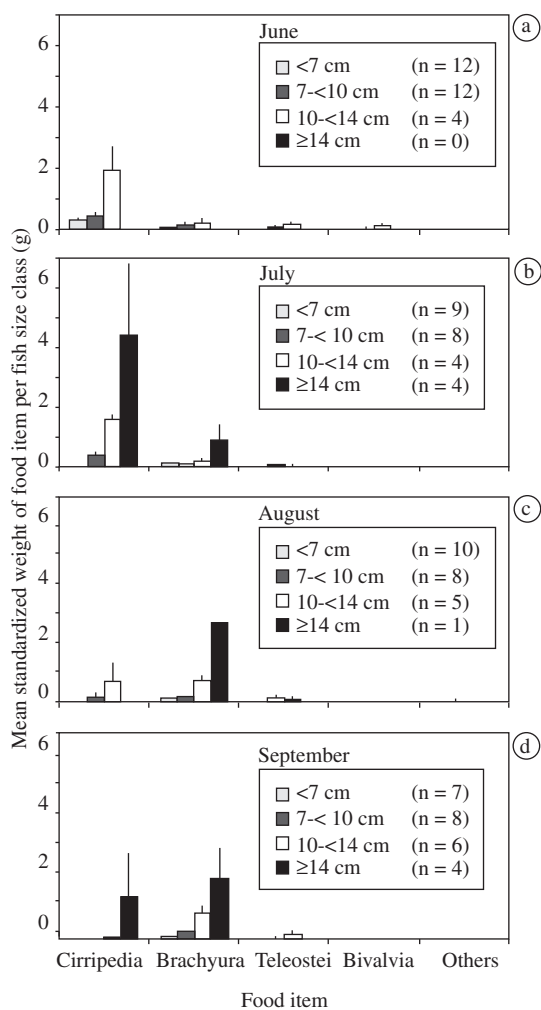
**Table 2.** Relative abundance of taxa within the food category “Brachyura” of  $n = 102$  *C. psittacus* from intertidal mangrove creeks in north Brazil, June-September 1997.

Brachyuran crab species	%
<i>Uca</i> spp. (Ocypodidae) <sup>a</sup>	41
<i>Pachygrapsus gracilis</i> (Grapsidae)	14
<i>Aratus pisonii</i> (Grapsidae)	8
Xanthidae	7
<i>Sesarma</i> sp. (Grapsidae) <sup>b</sup>	4
<i>Goniopsis cruentata</i> (Grapsidae)	1
<i>Callinectes</i> sp. (Portunidae)	1
Unidentified	22

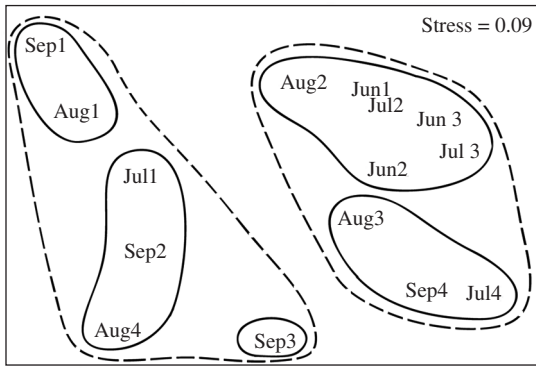
<sup>a</sup>*U. cumulanta*, *U. maracoani*, *U. vocator*; and <sup>b</sup>*S. rectum*, *S. curacaoense*

Classification of the diet composition of *C. psittacus* showed that the grouping patterns were primarily determined by changes in the proportions between Cirripedia and Brachyura (Figure 3). Ordination by non-metric multidimensional scaling (MDS) revealed a “horizontal Cirripedia axis” and a “vertical Brachyura axis”: These samples without or poor in Cirripedia, mainly taken in August and September (left group), were separated from samples containing Cirripedia, mainly taken in June and July (right group). Samples with the highest proportions of Brachyura coinciding with the largest size classes in August and September were located at the bottom (see also Figure 2).

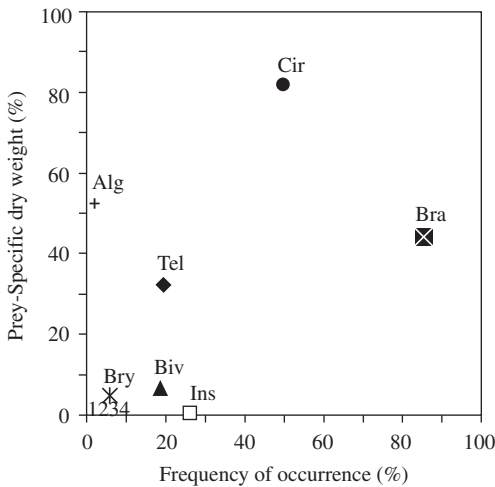
The feeding plot in Figure 4 shows that *C. psittacus* is a specialized feeder of Cirripedia and Brachyura. Cirripedia and Brachyura were found in 50 and 85% of



**Figure 2.** Food composition in monthly samples (June - September) of four size classes of *C. psittacus* in grams dry weight ( $\pm$ SD). Dry weights of food items were standardized per fish size class. Specimens were caught in three intertidal 1st order mangrove creeks of the Furo do Meio (north Brazil) at diurnal neap tides in the early dry season of 1997.



**Figure 3.** MDS plot of the similarities in food composition of *C. psittacus* caught at high water at diurnal neap tides in 1st order mangrove creeks of the Furo do Meio (north Brazil) in four months in the early dry season 1997. Identification codes indicate month of capture and size class (1: <7 cm SL; 2: 7-<10 cm; 3: 10-<14 cm; 4: ≥14 cm). Groups are circled according to 53% (dashed line) and 63% (continuous line) similarity of the cluster dendrogram (not shown).



**Figure 4.** Feeding strategy plot (Costello 1990) based on prey-specific dry weight of *C. psittacus* (n = 102) caught in the mangrove channel Furo do Meio (north Brazil) in the early dry season 1997. The points represent the food items Bra: Brachyura; Cir: Cirripedia; Tel: Teleostei (artefact in the diet); Alg: Red and green algae; Bry: Bryozoa; Biv: Bivalvia; Ins: Insecta; 1: Gastropoda; 2: Amphipoda; 3: Nantantia 4: Polychaeta.

the intestines, respectively, and the average contribution to the intestine weight was 82 and 44%, respectively. Teleostei were only consumed by 20% of the *C. psittacus* but contributed 32% to the intestine weight. Two specimens consumed considerable amounts of algae. There was neither a high within- nor between phenotype component, thus indicating a relatively narrow feeding niche. The other prey categories were occasionally included in the diet of some individuals, but had an insignificant contribution to the intestine weight.

### 3.3. Predation impact

The measure of predation impact on Cirripedia and Brachyura is shown in Table 3. Monthly changes in the predation impact reflect the monthly differences in food consumption (Figures 2, 3). On average 100.27 g.ha<sup>-1</sup>.d<sup>-1</sup> Cirripedia and 178.66 g.ha<sup>-1</sup>.d<sup>-1</sup> Brachyura (wet weight) were eaten by *C. psittacus* during the sample period. The mean daily consumption of Cirripedia and Brachyura was 6.2% per body weight of *C. psittacus*.

## 4. Discussion

This study provides first hand information on the feeding ecology of mangrove-inhabiting *C. psittacus*. A general shortcoming of our study is the limited sample period and the low sample sizes in some month-size class combinations. Nevertheless, some general patterns emerged that contribute to our understanding of the feeding ecology of *C. psittacus*.

### 4.1. Food composition

Cirripedia and Brachyura dominated the diet in all size classes. An ontogenetic feeding shift in *C. psittacus* was only apparent in terms of narrowing the prey spectrum with size. The weight proportion of the wider range of prey items in the smallest size class was too small to be translated quantitatively. In contrast, Targett (1978) found both qualitative and quantitative changes with growth in the diets of *S. spengleri* and *S. testudineus*. The lack of a significant quantitative change in the food habit of *C. psittacus* may reflect the overall abundance and availability of Brachyura and Cirripedia and the minor abundance of bivalves or gastropods in appropriate size ranges in the macrotidal Caeté estuary (Wolff et al., 2000). The considerable amount of hard-shelled items in the diet may explain the relatively long RLDT of *C. psittacus*. According to Al-Hussaini (1947) mollusk feeders have RLDT between 0.6 and 1.4.

Several examples of similar diet spectra have been observed for the Tetraodontidae family. The diet of the milk-spotted puffer *Chelonodon patoca* near Townsville (Australia) (Beumer, 1978) and of the puffers *S. spengleri* and *S. testudineus* (Targett, 1978) in Florida are also dominated by hard-shelled crustaceans and mollusks. However, Cirripedia and Brachyura are less dominant while other food items such as copepods or hermit crabs occurred more frequently. *S. rosenblatti* prey upon mangrove periwinkles up to 13 cm above the water surface in Puerto Rico (Duncan and Szelistowski, 1998). *S. spengleri* breaks the shells of gastropods and only swallowed the soft portions (Targett, 1978). The few gastropods in the diet of *C. psittacus* were consumed including the shell suggesting that gastropods are too rare to induce a specialization in prey handling.

The gradual replacement of Cirripedia by Brachyuran crabs between June and September in the diet of *C. psittacus* paralleled the gradual monthly salinity increase. Unpublished data of Giarrizzo suggest that the wet season diet of *C. psittacus* is dominated

**Table 3.** Predation impact on Cirripedia and Brachyuran crabs by *C. psittacus* expressed in grams of prey wet-weight eaten per hectare per day. Fish were caught at diurnal neap ebb tides in intertidal mangrove creeks (north Brazil) with block nets in the early dry season 1997. The predation impact is the product of the abundance of *C. psittacus* ( $\text{g}\cdot\text{ha}^{-1}\cdot\text{tide}^{-1}$ ), the mean proportion of Cirripedia or Brachyura in the diet per tide and multiplied by 2 to account for the semidiurnal tide. Daily consumption of Cirripedia and Brachyura is given in % body weight of *C. psittacus*.

Month	Predator abundance ( $\text{g}\cdot\text{ha}^{-1}\cdot\text{tide}^{-1}$ )	Cirripedia		Brachyura		Consumption (% BW.d <sup>-1</sup> )
		Proportion in the diet tide <sup>-1</sup>	Predation ( $\text{g}\cdot\text{ha}^{-1}\cdot\text{d}^{-1}$ )	Proportion in the diet tide <sup>-1</sup>	Predation ( $\text{g}\cdot\text{ha}^{-1}\cdot\text{d}^{-1}$ )	
June	1048.65	0.059	123.67	0.019	39.34	7.77
July	1856.09	0.032	118.74	0.030	112.79	6.24
August	5329.36	0.014	152.55	0.043	458.38	5.73
Sept.	1062.91	0.003	6.12	0.049	104.12	5.19
Average	2324.25		100.27		178.66	6.23

by Cirripedia while Brachyuran crabs are common in the dry season diet. The Brachyuran crab resource is abundant in the mangrove throughout the year (Koch, 1999) and unlikely to be subject to strong monthly fluctuations in abundance. In contrast, Cirripedia are known to show high fluctuations in recruitment and survival related to changes in salinity (Sandison, 1966; Bacon, 1971). However, neither monthly changes in abundance of Cirripedia nor Brachyura were investigated during the study period in the mangrove. The IFI were significantly higher in June/July when Cirripedia dominated the diet of puffers. Assuming that Cirripedia really became less abundant in the mangrove and that Brachyura were constant, *C. psittacus* would prefer Cirripedia over Brachyura, hence prey more intensely on Brachyura only when the Cirripedia density decreases. This preference may be due to either greater forage efficiency for sessile Cirripedia or to the fact that Cirripedia are a food resource of higher quality.

The presence of teleostei in the diet of *C. psittacus* is most likely an artefact related to the fishing method. During the receding tide, the fish became physically concentrated on the upstream side of the block net. Such an artificial proximity enabled *C. psittacus* to bite off muscle tissue and scales of other fish. However, entire fish were never found in the intestines.

#### 4.2. Energy flow

*C. psittacus* can be classified as a carnivorous second order consumer. Therefore, one of the dominant fish species of tidal mangrove channels along the north Brazilian coast lives on prey of low trophic levels. This emphasizes the conclusion of Sheaves and Molony (2000) that food chains leading from mangroves to top predators are likely to be shorter than previously thought. *C. psittacus* have a key function in a short intertidal mangrove food web. The energy of the mangrove detritus fuels the microbial production that is consumed by detritivorous mangrove crabs who are the prey of high-level piscine predators such as *C. psittacus*, but also *Sciades herzbergii*, *Batrachoides surinamensis* and some Sciaenidae. According to our current knowledge of the Caeté system, *C. psittacus* is the principal predator of filter feeding Cirripedia.

The mangrove productivity is, however, not exported due to offshore migration by the fish as Sheaves and Molony (2000) assumed for a system in tropical East Australia. South of the Amazon delta, where mangroves cover more than 400 km of continuous coastline (Lacerda et al., 2000, p. 9), other complex shallow water environments such as coral reefs or sea grass beds that could motivate offshore movements of the fish are absent. Therefore, considerable amounts of mangrove productivity, for instance taken by Brachyuran crabs and Cirripedia, are likely to remain in the mangrove ecosystem as *C. psittacus* and other dominant fish species spend their entire life in the mangrove environment (Barletta et al., 2003; Krumme et al., 2004).

#### 4.3. Patterns in feeding

The diurnal neap tide submergence was a major feeding period for *C. psittacus*. Catches at neap and spring tides in intertidal mangrove creeks showed that *C. psittacus* is clearly diurnal at neap tides whereas at spring tide, *C. psittacus* forage both during the morning and the evening submergence (Krumme et al., 2004). In the study area, fiddler crabs are diurnal and cease to feed in the evening (Koch, 1999). Probably, *C. psittacus* rely mainly on visual cues to search for its prey. Targett (1978) also inferred that the two *Sphoeroides* species studied in Florida feed primarily during the day.

The overall foraging pattern of *C. psittacus* may resemble the one that Brenner and Krumme (2007) determined for another, also a visual intertidal forager in the study area, the four-eyed fish *Anableps anableps*: The combination of high inundation during daylight hours (spring tide-day) provided optimum foraging conditions whereas darkness and low inundation were linked to poor foraging conditions (neap tide-night); neap tide-day and spring tide-night were intermediate.

Our assumption - "no feeding at low water" - used in calculating the consumption rates is supported by the diet composition of *C. psittacus*. The specialization on Cirripedia and Brachyura suggests that *C. psittacus*, similar to *A. anableps*, primarily rely on prey located in the intertidal zone. Feeding activity is probably highest during inundation while low-water periods may be

devoted to other activities (e.g. resting or digesting). Hence, tidally migrating *C. psittacus* may transfer mangrove productivity from the intertidal to the subtidal zone.

Given the likely low foraging activity during a nightly neap tide, our daily consumption rates of Cirripedia and Brachyura based on simply doubling the daytime consumption may be overestimates for neap tides (Table 3). However, it may provide a reasonable first estimate for average daily consumption, but a conservative estimate is likely given the increased foraging area under spring tide conditions.

*C. psittacus* caught in the small creek 3 had significantly emptier intestines than those of the two larger creeks 1 and 2 suggesting that smaller creeks are poorer feeding grounds for *C. psittacus*. However, *C. psittacus* also swim against the tide (Krumme, 2004) and possibly would have continued to forage in neighbouring creeks if they had not been blocked by the net.

#### 4.4. Plant-animal interaction

In soft bottom environments of the mangrove, Cirripedia occur as part of the epibiota on permanent hard structures; mainly on stilt roots of *R. mangle* in the intertidal zone. The negligible amounts of gastropods, algae and bivalves in the diet of *C. psittacus* were likely consumed as part of the Aufwuchs (epibiota in the fouling community) associated with Cirripedia living on the stilt roots of *R. mangle*. The extensive predation of *C. psittacus* on Cirripedia suggests the existence of an important plant-animal interaction: The predation of *C. psittacus* decreases the coverage with Aufwuchs of mangrove stilt roots and hence increases mangrove growth as clean roots facilitate oxygen uptake by the root system (Perry, 1988). A similar mutually beneficial cleaning function is likely executed by the four-eyed fish *A. anableps* that primarily forage for epiphytic red algae on the stilt roots (Brenner and Krumme 2007). Likewise, Koch and Wolff (1996) assumed a cleaning function for a mangrove snail in Costa Rica. However, the positive effect of root cleaning fish on mangrove growth still awaits quantification.

#### 4.5. Brachyuran crabs

The other principal food category of *C. psittacus* was semi-terrestrial Brachyuran crabs which have a considerable influence on the fluxes of organic matter and energy of the mangrove ecosystem (Koch, 1999; Koch and Wolff, 2002). Therefore, *C. psittacus* has a quantitatively important predatory function in the mangrove food web (Wolff et al., 2000). In the Caeté estuary, Koch and Wolff (2002) found the highest number of epibenthic species in intertidal mangrove creeks. In this mangrove habitat, *U. maracoani*, *P. gracilis* and *U. cumulanta* contributed most to the total biomass. The latter two crabs were by far the most abundant species (Koch and Wolff, 2002) and their abundance in the diet of *C. psittacus* likely reflected their numerical and weight dominance and availability in the creeks (Table 2).

The distribution of epibenthos species in the Caeté estuary follows a vertical zonation (Koch et al., 2005). Crab species that are abundant in the high intertidal zone on the mangrove plateau such as *Ucides cordatus* and *U. rapax* were absent from the neap tide diet of *C. psittacus* but may occur at spring tides when the mangrove forest is accessible.

Fiddler crabs stay in their burrows during the inundation period and actively forage on the mud only when the intertidal zone is exposed to air (Koch, 1999). Therefore, *C. psittacus* must apparently be able to detect fiddler crabs beneath the mud surface or catch individuals that are somehow active on the mud during submergence.

The relative abundance of Brachyuran crabs in the diet did not change with the fish size (Figure 1). However, especially large *C. psittacus* ate considerable amounts of Brachyuran crabs (Figures 2, 3). Targett (1978) also found that the largest puffers consumed substantial amounts of Brachyuran crabs. This is likely related to the spherical body form of puffers that allows an increase in the intestine volume closer to the power of 3 than in other fish species. The high condition factor of 3.2 highlighted this relationship. Fish with "normal" shapes have condition factors between 0.5 and 1.5 (Cinco, 1982).

#### 4.6. Swimming behaviour and foraging movements

*C. psittacus* produce point wakes (Hanke and Bleckmann, 2004). In the study area, *C. psittacus* have to minutely maneuver in strong tidal currents close to the substrate in a complex mangrove environment in order to focus on both sessile and moving benthic prey. Here, point wakes may be an adaptation to prey on balanids and mangrove crabs with a minimum of turbulent disturbance as behavioral responses to chemical and visual cues are involved in predator avoidance of fiddler crabs (Chiussi and Diaz, 2002) and the mangrove tree crab *Aratus pisonii* (Chiussi, 2003).

In contrast to other mangrove fish, foraging *C. psittacus* often swim close to the water surface. In the center of the larger mangrove channels, they patrol for prey especially at the ebb tide by maintaining a position while swimming against the current (Krumme and Saint-Paul, 2003). In the shallower mangrove creeks *C. psittacus* maneuver close to the creek levees. At spring tides, juvenile *C. psittacus* can be observed on the flooded mangrove plateau in water less than 0.1 m deep foraging for Brachyuran crabs and Insecta (pers. obs.). During these near-surface excursions, the warning coloration in the dorsal aspect may serve against terrestrial predators such as egrets (*Casmerodius albus*, *Egretta thula*), the raccoon *Procyon cancrivorus* or the ape *Cebus apella*. Rapid inflation of the abdominal cavity may serve against the nocturnal fishing bat *Noctilio leporinus* but is primarily a defense against piscine predators.

#### 4.7. Potential resource

The *C. psittacus* resource in north Brazil is currently unused due to the known toxicity of the fish. However, considering the current labor situation of the "mangrove



civilizations” in the region (Glaser, 2003), two possible income alternatives using *C. psittacus* may emerge: i) sustainable catch and filet processing for exports to east Asia; and ii) developing certified aquaculture methods for sustainable breeding of puffers for the aquarium trade (Duncan and de la Parra, 2002; Gasparini et al., 2005).

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