

## THE DIET OF CUBOMEDUSAE (CNIDARIA, CUBOZOA) IN SOUTHERN BRAZIL

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### ABSTRACT

The diet of cubomedusae *Tamoya haplonema* Müller, 1859 (Carybdeidae) and *Chiropsalmus quadrumanus* (Müller, 1859) (Chiropodidae) was examined in specimens collected on the Southern Brazilian coast (25°20' - 25°55' S; 48°10' - 48°35' W), between December 1998 and December 2004. This is the first study to analyze this biological aspect in cubomedusae from the South Atlantic. The gastrovascular cavities of most (55%; n = 29) specimens of *T. haplonema* were empty while the remainder had teleostean parts such as scales, vertebrae and otoliths. In *C. quadrumanus* (n = 726), the most important items were the pelagic sergestid shrimp *Peisos petrunkevitchi* Burkenroad, 1945 and Brachyura larvae, mainly megalops. Small crabs, isopods, fish, fish eggs and nematodes were less common. A dietary shift was clearly observed during *C. quadrumanus* growth. Smaller individuals consumed a greater variety of prey, mostly Brachyura larvae, and they also had higher frequencies of empty stomachs. As their size increased, megalopas decreased and *P. petrunkevitchi* became the most important item in their diet.

### RESUMO

A dieta das cubomedusas *Tamoya haplonema* Müller, 1859 (Carybdeidae) e *Chiropsalmus quadrumanus* (Müller, 1859) (Chiropodidae) foi analisada em espécimes coletados no litoral do Paraná (25°20' - 25°55' S; 48°10' - 48°35' W), sul do Brasil, entre dezembro de 1998 e dezembro de 2004, e é o primeiro estudo a abordar este aspecto da biologia de Cubozoa no Atlântico Sul. A cavidade gastrovascular da maioria (55%) dos 29 exemplares de *T. haplonema* mostrou-se vazia, e dos demais continha partes corporais de peixes teleosteos, como escamas, vértebras e otólitos. Em 726 exemplares de *C. quadrumanus* os itens alimentares mais importantes foram o camarão sergestídeo *Peisos petrunkevitchi* Burkenroad, 1945 e larvas de Brachyura, principalmente megalopas. Pequenos caranguejos, isópodes, peixes, ovos de peixes e nematóides foram menos comuns. Mudanças na dieta evidenciaram-se durante o crescimento de *C. quadrumanus*. Indivíduos menores alimentaram-se de maior variedade de presas, principalmente de larvas de Brachyura, e também apresentaram frequência mais alta de estômagos vazios. À medida que cresciam, a ingestão de larvas diminuía de importância enquanto a do camarão *P. petrunkevitchi* aumentava, até este se tornar o principal item na dieta da espécie.

Descriptors: *Chiropsalmus quadrumanus*, Feeding biology, Jellyfish, Medusae, Ontogenetic dietary shift, *Tamoya haplonema*.

Descritores: Água-viva, Biologia alimentar, *Chiropsalmus quadrumanus*, Medusa, Mudança ontogenética, *Tamoya haplonema*.

### INTRODUCTION

Cubozoans are found in all oceans, typically in tropical and subtropical regions, mostly in shallow coastal waters (MAYER, 1910; GUEST, 1959; FRANC, 1994; COATES, 2003). Cubomedusae are usually large and conspicuous, while their polyps are small and rarely found in the field. Because

cubomedusans are highly dangerous to humans they are popularly known as “sea wasps” (MAYER, 1910; VANNUCCI, 1954; LARSON, 1976).

Diet studies provide important information on the biology of the species, which helps to explain co-existence and species relationships in food webs and may also provide support for the construction of trophic models. Despite the widespread consensus that cubozoans are voracious predators, few data are

available on this subject: Guest (1959), Phillips et al. (1969) and Phillips and Burke (1970) briefly commented on stomach contents of *Chiropsalmus quadrumanus* (Müller, 1859) from the North Atlantic, Larson (1976) described the feeding behavior of *Carybdea marsupialis* (Linnaeus, 1758), Arneson and Cutress (1976), the predation by *Carybdea sivickisi* Stiasny, 1926 on crustaceans, and Hamner et al. (1995) studied ingestion, digestion and food circulation in the poisonous *Chironex fleckeri* Southcott, 1956. In this latter species diet changes with growth, from shrimps to fishes, and this shift was associated with changes in the cnidome (CARRETTE et al., 2002). Buskey (2003) showed behavioral adaptations of *Tripedalia cystophora* Conant 1898 for feeding on copepods [*Dioithona oculata* (Farran, 1913)].

Studies on South Atlantic cubomedusae deal with morphological descriptions and taxonomic surveys (MÜLLER, 1859 in CORRÊA, 1966; VANNUCCI 1954, 1957; KRAMP, 1955; GOY, 1979; PAGÈS et al., 1992; MIANZAN; CORNELIUS, 1999; PASTORINO, 2001; HADDAD, 2002; MORANDINI, 2003; MORANDINI et al., 2005, 2006; NOGUEIRA JÚNIOR; HADDAD, 2006a, b) or records of stings (HADDAD JÚNIOR et al., 2002), while their biology remains unknown.

The present study analyzes the natural diet of the Carybdeidae *Tamoya haplonema* Müller, 1859 and the Chirodromidae *Chiropsalmus quadrumanus* (Müller, 1859), the two cubozoan species found in southern Brazil and widespread along the Brazilian coast (MIANZAN; CORNELIUS, 1999; MORANDINI et al., 2005; NOGUEIRA JÚNIOR; HADDAD, 2006a).

## MATERIAL AND METHODS

Morning collections were carried out at two locations on the inner coast of the state of Paraná (25°20' - 25°57' S; 48°10' - 48°35' W), Southern Brazil, in total, 172 bottom trawls of shrimp fishing boats (Table 1). The first location was at Shangrilá (25°37'S; 48°25'W), in the municipality of Pontal do Paraná, where collections were made from December 1998 to January 2000, with an 8 m wide net, with 3 cm mesh size, at approximately 8 m depth. The second collection site was at Guaratuba (25°54' - 25° 57' S; 48°33' - 48°34' W), made from April 2001 to March 2002, at a depth of 8 m and from February to July 2003, at depths of 8 -12 m, with a 2 cm mesh size net; and from August 2003 to December 2004, also at depths of 8 - 12 m, using two simultaneous nets, with mesh sizes of 1 and 2 cm. Table 1 shows an outline of the sampling program.

The medusae sampled were separated on the boat, taken to the laboratory in plastic bags filled with seawater, ice and menthol crystals and then fixed in 4% saline formalin. Identification followed Mayer (1910), Kramp (1961) and Mianzan and Cornelius (1999). Voucher specimens were deposited at the Zoology Museum of São Paulo University (MZUSP - 926 and 927 - *Tamoya haplonema*; MZUSP - 928 and 929 - *Chiropsalmus quadrumanus*).

In the laboratory, diagonal bell width (DBW - across diagonally opposite pedalia) and height (from umbrellar margin to top, excluding velarium) were measured in fixed material. Dissected animals had their stomachs and gastrovascular cavities (GVC) exposed and observed under the stereomicroscope. Ingested items were separated and identified to the lowest possible taxonomic level.

Table 1. Sketch of the sampling program realized.

<i>Period</i>	<i>Place</i>	<i>Depth (m)</i>	<i>Mesh size (cm)</i>	<i>Number of trawls</i>	<i>Time of each trawl (min.)</i>
December/1998 - January/2000	Shangrilá	~8	2	14	40
April/2001 - March/2002	Guaratuba	~8	3	50	10
February/2003 - December/2003	Guaratuba	~8-12	1 and 2	44	10
January/2004 - December/2004	Guaratuba	~8-12	1 and 2	66	10
Total				172	

RESULTS

The size of the Carybdeidae *Tamoya haplonema* varied between 14-79 mm in DBW and from 20 to 90 mm in height. The height of this jellyfish corresponded to ~136.7% of its DBW. The size class distribution (Fig. 1a) is clearly bimodal. Individuals of 21-30 and 41-50 mm in DBW predominated and together represented more than 50%

of the 29 examined specimens. In bell height, 51% measured 21-50 mm and 41%, 61-90 mm. The size of *Chiropsalmus quadrumanus* varied from 12-122 mm in DBW and between 6-100 mm in height. The height in this species represented ~81.2% of the DBW. Nearly 80% of the specimens were smaller than 40 mm in bell height and smaller than 50 mm in DBW (Fig. 1b).

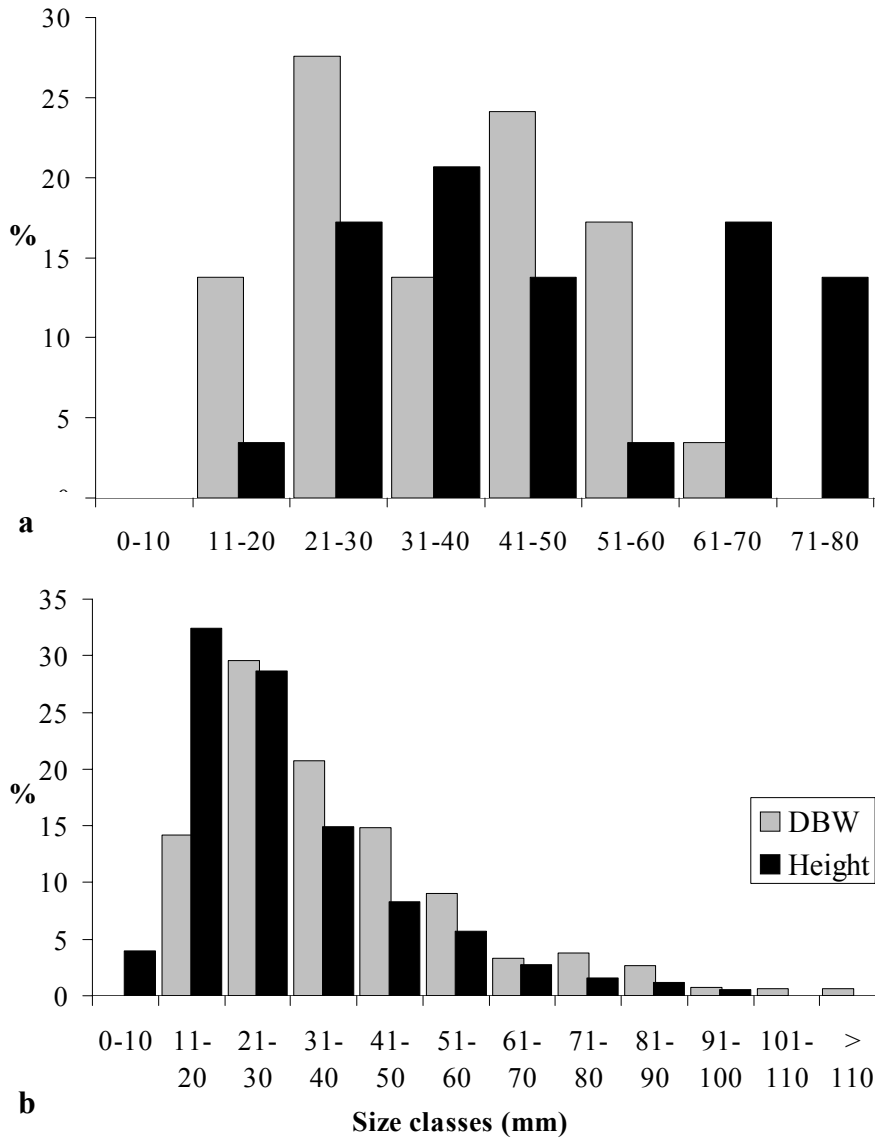


Fig. 1. Diagonal bell width (DBW) and height size class distribution of (a) *T. haplonema* (n = 29) and (b) *C. quadrumanus* (n = 726) from Paraná coast.

The gastric cavity of most of the 29 specimens of *T. haplonema* analyzed (55%) was empty and the remaining ones ( $n = 13$ ) had only fish (Teleostei) parts, such as scales, vertebrae, spines, otoliths, eyes, etc., in their stomachs. In most of the specimens the gastric contents were already partially digested.

Almost half (45%) of the *C. quadrumanus* individuals had empty GVC (Fig. 2a). The frequency of individuals with empty guts differed among size classes, reaching ~57% in smaller individuals (<30 mm in DBW) and only ~9% in the bigger ones (>90 mm) (Fig. 2b).

The diet of *C. quadrumanus* was more variable, yet only a few items were common or abundant. Crustaceans comprised the majority of the diet (Fig. 2a), mostly the sergestid pelagic shrimp *Peisos petrunkevitchi* Burkenroad, 1945 (identified following Costa et al., 2003). This prey, which sometimes could be easily seen through the exumbrellar wall of the stomach (Fig. 3), was found in 21% of the specimens analyzed. The remainder of the crustaceans were Brachyura larvae, mainly megalopas, found in 17% of the GVCs, followed by Penaeoidea shrimps (5%), isopods (3%) and small crabs (0.6%). Fish, nematodes and fish eggs appeared in frequencies always below 5% (Fig. 2a).

*C. quadrumanus*, like *T. haplonema*, had the gastric contents very fragmented and in different stages of digestion, but in many cases it was possible to identify and count the individuals of *P. petrunkevitchi*. Almost 70% of *C. quadrumanus*

contained one to four shrimps, about 10% had more than 13, and 20 shrimps were found in only one medusa (Fig. 4). Only medusae larger than 60 mm in DBW had ten or more sergestid shrimps in their GVC (Fig. 5) and even though some outliers were present, a significant positive correlation (Pearson,  $r = 0.54$ ;  $p < 0.05$ ;  $n = 78$ ; Fig. 5) was verified between the size of *C. quadrumanus* and the number of *P. petrunkevitchi*.

An ontogenetic dietary shift was clearly observed in *C. quadrumanus*. Smaller animals consumed a greater variety of prey: eight prey types appeared in the two first size classes (< 60 mm in DBW), five in the third class (61-90 mm) and only two (Sergestidae and Penaeoidea shrimps) in animals larger than 90 mm (Fig. 2b). Not only has the diversity of food items changed with age, but also their relative frequencies. In smaller animals (< 30 mm), Brachyura larvae were the most common prey. They were found in 23.97% of the GVC examined, while sergestid shrimps were in 6.94%, and other items in less than 5%. In the second smaller class, *P. petrunkevitchi* shrimps were the most frequent prey found in 26.39% of the GVCs, while that with megalopas decreased to 11.8%. Finally, around 82% of the largest individuals (> 90 mm in DBW) contained sergestid shrimps in their GVC. The importance of Penaeoidean shrimps in the *C. quadrumanus* diet also increased with medusae growth, with frequencies increasing from 2.5% in the smallest animals to 27% in specimens larger than 90 mm in DBW (Fig. 2b).

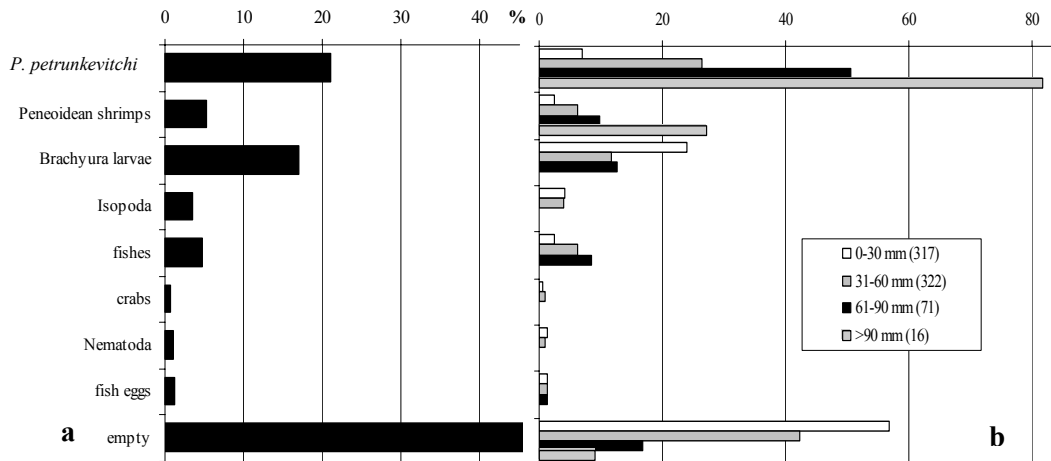


Fig. 2. Stomach contents of *Chiropsalmus quadrumanus*: a) All sizes combined,  $n = 726$ ; b) divided by DBW size class (the numbers in parenthesis represent the number of analyzed exemplars in each size class).

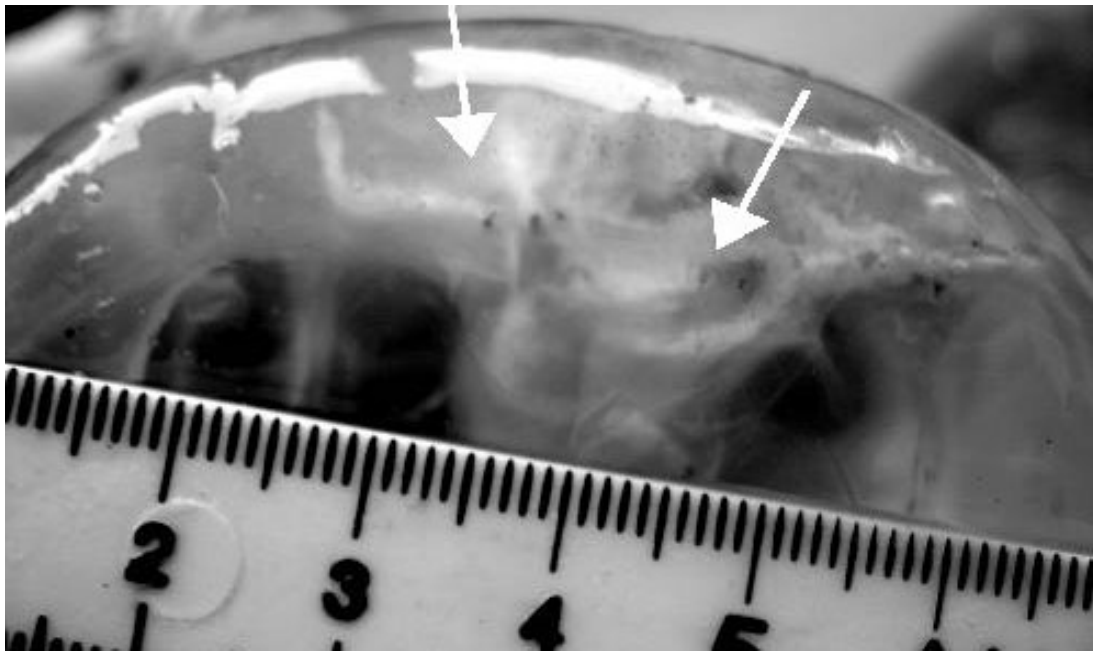


Fig. 3. Aboral view of *Chiropsalmus quadrumanus*, showing some shrimps *Peisos petrunkevitchi* inside its stomach (arrows). Photo by Maurício de Castro Robert.

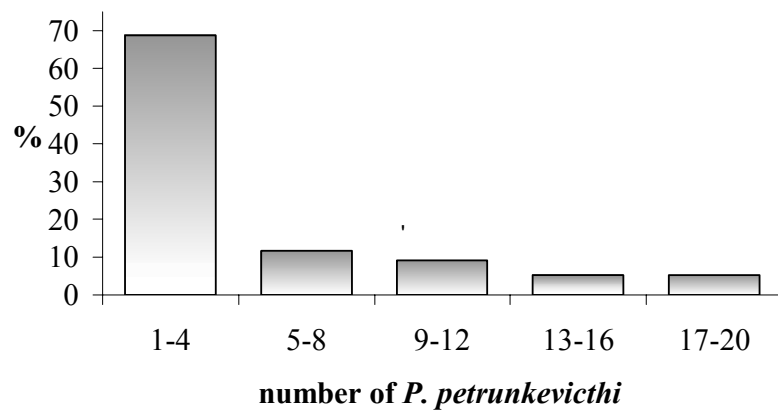


Fig. 4. Abundance class distribution of *P. petrunkevitchi* found inside the gastrovascular cavity of *C. quadrumanus* (n = 78).

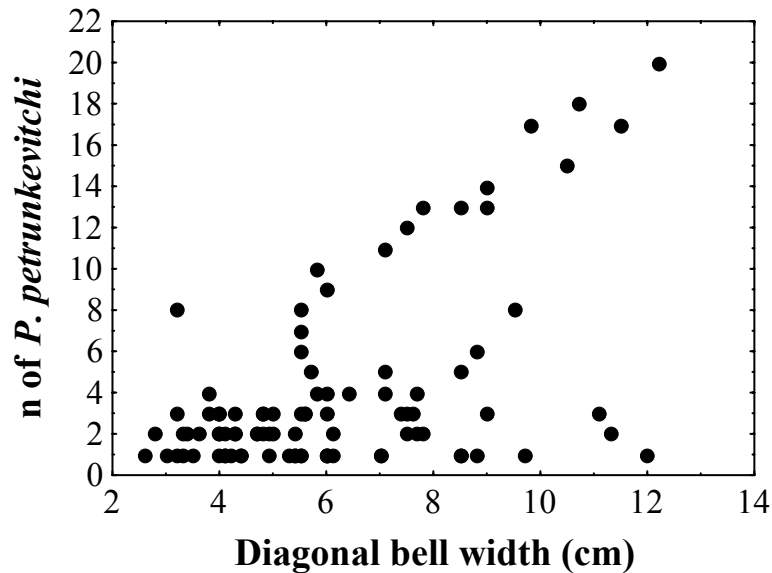


Fig. 5. Dispersion graphic between *C. quadrumanus* size and the number of *P. petrunkevitchi* found inside its GVC. Both variables present a positive significant correlation (Perason,  $r=0.54$ ;  $p < 0.05$ ;  $n=78$ ).

## DISCUSSION

Many individuals of *C. quadrumanus* and *T. haplonema* were found with empty guts, which could be caused by several factors. Although the feeding cycles of the species studied are unknown, it can be presumed that both feed at night. Indeed, the medusae collected in the morning trawls had their prey partially digested already. As cubomedusa produce strong digestive enzymes (LARSON, 1976), in a few hours the ingested prey would be in an advanced state of digestion, indicating they caught their prey during the preceding night-time. Nocturnal patterns of feeding have already been observed in some cubomedusas such as the carybdeids *Carybdea alata*, *C. marsupialis* and *C. sivickisi* (respectively by Arneson and Cutress, 1976; Larson, 1976 and Hartwick, 1991a). However, in some other species, feeding is diurnal as in *C. fleckeri* (SEYMOUR et al., 2003) and *T. cystophora* (BUSKEY, 2003). Other hypothesis for empty GVC is that the animals eliminated the contents during capture due to stress or that the populations were in a period of food shortage. This latter hypothesis, which seems to be relatively common in medusae populations (BAMSTEDT, 1990; OLESEN et al., 1994) is supported by the much higher frequency of empty guts observed among smaller individuals; as they were more numerous, competition for food was probably greater for them than for the few larger ones.

Type and size of prey varied between *C. quadrumanus* and *T. haplonema*. Although both may

share fishes as food items, they explore the available resources differently, thus avoiding competition. The diets of medusae species are conditioned by their swimming and feeding behavior, which are dependent on morphology such as body size, shape of umbrella, number and kind of tentacles and cnidome (see MILLS, 1981; ARAI, 1997; COLIN; COSTELLO, 2002; COSTELLO; COLIN, 2002; COLIN et al., 2003). Neither swimming nor feeding behavior of the two species studied are known, but some of their morphological attributes are remarkably different and can be related to their prey variations. While body size in terms of individual weight is similar for both species (NOGUEIRA JÚNIOR; HADDAD, 2006b), the umbrella of *T. haplonema* is much higher than wide (height corresponding to ~136.7% of its DBW) and it has only four thick tentacles, strong enough to capture large prey. In contrast, the umbrella of *C. quadrumanus* is wider than high (~81.2% of DBW) and this species has up to 44 fine and very extensible tentacles, which hang like a curtain, forming a net to capture small organisms.

The Carybdeidae *T. haplonema* fed exclusively on fish, which were also the most important food item found in the gut of *C. marsupialis*, a species of the same family and similar size (LARSON, 1976). Contrastingly, smaller carybdeids feed on copepods, gammarid amphipods and other small crustaceans (LARSON, 1976; HARTWICK, 1991a; BUSKEY, 2003); yet diet is

very poorly studied in this group, especially in the larger species such as *T. haplonema*.

Differently from our results, North Atlantic populations of *C. quadrumanus* feed primarily on benthic microcrustaceans or detritus (GUEST, 1959; PHILLIPS et al., 1969; PHILLIPS; BURKE, 1970), although it seems that pelagic sergestid shrimps are of fundamental importance in the diet of other Chiropsodidae medusae. Sergestid shrimps are among the most important food items for most Chiropsodidae studied to date (*Chiropsalmus* spp. and *Chironex fleckeri*), but other shrimps, fishes and crab larvae are also important (BARNES, 1966 in LARSON, 1976; PHILLIPS et al., 1969; PHILLIPS; BURKE, 1970; LARSON, 1976; HARTWICK, 1991b; CARRETTE et al., 2002; this study).

Only 1-4 sergestid shrimps found in most *C. quadrumanus* analyzed seems to be an underestimation due to the high degree of digestion of several GVC contents and to the minor size of the majority of the individuals analyzed, since bigger individuals tend to have more shrimps in their GVC (e.g. only specimens >60 mm in BDW had 10 or more *P. petrunkevitchi*, Fig. 5) and they represented the minority in our samples (~11.7%).

The change in the diet of *C. quadrumanus*, an interesting find that has never been reported for this genus, may be a strategy to avoid competition between large and small individuals. A similar ontogenetic shift in prey quality also occurs in *Chironex fleckeri* which was associated with changes in the cnidome (CARRETTE et al., 2002). In that species, nonetheless, the main prey changed from shrimps to fishes. For *Chiropsalmus quadrigatus* Haeckel, 1880, which feed primarily on the sergestid *Acetes* (LARSON, 1976), the change in the cnidome was also verified but the dietary shift was only suggested by the authors (OBA et al. 2004). For the Australian *Chiropsalmus* sp. both the cnidome and diet kept constant (CARRETTE et al., 2002), but GVCs were examined by visual inspections, possibly missing small preys such as brachiuran larvae. Ontogenetic dietary shift in the family Chiropsodidae was demonstrated for two species up to now (CARRETE et al., 2002 and this study), was suggested, through the analysis of the cnidome, for a third one (OBA et al., 2004) and rejected for another one (CARRETE et al., 2002). Consistent analysis of more species and populations will reveal whether or not this is the regular pattern of the feeding habits of these venomous jellyfish.

#### FINAL CONSIDERATIONS

Some medusa, such as the Scyphozoa Coronatae *Periphylla periphylla* (PÉRON &

LESUEUR, 1809) may feed in the cod end of the net, thus feeding data based on net collections had been thought to be unreliable for this species and others (YOUNGBLUTH; BAMSTEDT, 2001). However, this seems not to be the case for the cubomedusans studied, since several items were fragmented and partially digested in the GVC of both species, suggesting that these prey were not captured inside the nets. Moreover, of the two items most frequently preyed on by *C. quadrumanus*, megalopas were never found in the nets and *P. petrunkevitchi* shrimps were only occasionally caught.

#### ACKNOWLEDGEMENTS

Thanks to Drs. Arno Blankstein and Iracema Gomes for donating part of the material that was studied; to Dr. Rogério C. Costa who made bibliography available and confirmed shrimp identification; to Dr. Maurício de Castro Robert who provided the photo of Figure 3.

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(Manuscript received 24 October 2005; revised 05 May 2006; accepted 12 December 2007)