A TROPHIC ANALYSIS OF TARGET SPECIES OF MACROBENTHOS IN A SUBTROPICAL COASTAL COMMUNITY: A TAXA RELATIONSHIP ESSAY

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ABSTRACT. – Studies on the feeding habits of aquatic organisms are a requirement for the management and sustainable use of marine ecosystems. The aim of the present research was to analyze the habits and trophic similarities of decapods, starfish and fish in order to propose trophic relationships between taxa, using Hennigian methods of phylogenetic systematics. This new grouping hypothesis, based on shared and exclusive food items and food types, corresponds to the broad taxonomic groups used in the analysis. Our results indicate that algae, Mollusca, Polychaeta, Crustacea, Echinodermata and Actinopterygii are the most exploited common resources among the species studied. Starfish were differentiated from other organisms for being stenophagic, and were grouped for feeding on bivalve mollusks. A larger group of fish and crustaceans shares algae and mainly crustaceans as food items. A third group united all eight species of Actinopterygii. This largest subgroup of fish is typically carnivorous, feeding on Anthozoa and a great quantity of Crustacea. Synodus foetens has a special position among fishes, due to its unique feeding on nematodes. A Euclidean distance dendrogram obtained in a previous publication grouped S. foetens with starfish. That result was based on a few non-exclusive shared similarities in feeding modes, as well as on shared absences of items, which are not an adequate grouping factor. Starfish are stenophagic, eating bivalves almost exclusively. Synodus foetens and Isopisthus parvipinnis have restricted food items, and are thus intermediary in relation to starfish, decapods, and other fish, which are euryphagous. The trophic cladogram displays details of food items, whether or not shared by all species. The resulting trophic analysis is consistent with known historical relationships.

INTRODUCTION

A main goal of ecology is to understand the nature of species’ interactions and to determine the extent to which they can explain observed patterns and dynamic properties of biological communities. Ecological theory has a long history of describing ecosystems in terms of material and energetic flows between multiple components in interaction (Odum 1968, Paine 1988, Jørgensen & Müller 2000). One particular area of research concerns the properties of food webs and how they might explain community dynamics (Hall & Raffaelli 1991). As Cohen (1989) put it, ecology is just proportions in food webs. The understanding of food web patterns in complex ecosystems has become a central issue in ecological research (May 1986, Levin 1992, Montoya & Solé 2002, Berlow et al. 2004). Food webs function as road maps through Darwin’s entangled bank (Pimm et al. 1991).

Studies on food webs are interesting because they ‘cut’ across habitat versus taxonomical dichotomy which is still a powerful, sometimes even a restricting force in the development of ecological theories (Lawton 1995). In the food web concept, nodes may represent species or functional groups. Food webs do correlate with niche space (Cohen 1978).


Feeding analyses exist only for a small fraction of known invertebrates. Detailed trophic studies on invertebrate species, as well as generalizations by higher taxa such as families and orders, are needed for a better
understanding of food webs. Knowledge about mean path length is important as it quantifies the average number of links necessary for an effect to propagate from one species to another (Froese et al. 2005).

Nearly half of the world’s commercial salt-water fisheries, both marine and estuarine, consist of shellfish and demersal fishes whose main food is benthic (Joydas & Damodaran 2009). The fish species studied herein were on the contrary, Mediterranean fishes are, on average, two trophic links (corresponding to levels 2-4) away from each other (Froese et al. 2004). Benthos represents the main food items of demersal fish (Longhurst & Pauly 1987). Thus fishes which feed on the benthos contribute to energy transfers for higher trophic levels. They thus play a significant role in transferring energy from detritus and other benthic macro- and microvegetation organisms, suspended particulate matter, bacteria, protists, and primary consumers to higher trophic levels (Manickchand-Heileman et al. 1998). A theoretical overview of recent studies of trophic ecology has identified the application of phylogenetic methods as one of the recent breakthroughs in the study of community ecology (Christoffersen et al. 2011).

In this paper we propose a new analysis based on the food items of 15 target species (Lunardon-Branco et al. 2006), and discuss some of the implications of these results for phylogenetic and ecological concepts.

MATERIAL AND METHODS

Information on food content for the 15 target species, representing the most common species captured in commercial trawling activities in the chosen study site, are presented in Appendix I. All references used to analyze the data base are listed in this same appendix.

Monthly collections were carried out at Armação do Itapocoroy (26°40’-26°47’S, 48°36’-48°38’W) in three traditional artisanal shrimp fishing areas: Ponta da Vigia; in the proximity of Feia Island; and between this island and the Itacolomis Islands (Lunardon-Branco et al. 2006). These areas have a predominantly silt-clay sediment. Dredgings were carried out between January and December 1995 on the bottom at depths of 8 to 15 meters between 8:00 and 14:00, during 30 minutes. Two seine nets were dragged by a 10.5 m boat powered by a 40 hp engine that kept a mean constant speed of two knots (Branco et al. 2002).

The Point Method and Frequency of Occurrence (see Hynes 1950, Berg 1979, Williams 1981) was used in the qualitative-quantitative analysis of diets. Food items were used to construct a data matrix and a trophic analysis for 15 target species selected among the most common asteroids, decapods, and fishes from the macrobenthos community in Itapocoroy, southern Brazil (Lunardon-Branco et al. 2006).

The stomach contents were identified to the lowest possible taxonomic level with the aid of appropriate taxonomic guides (see Appendix I). The food items were united in categories that represent organisms at several hierarchical levels. Besides the different analyses of Crustacea items, we grouped all taxa of this subphylum as a special item, because the frequencies of occurrence between the 15 species showed high variation. Whenever the range of frequency variation is very wide, we created another category, indicating the minimum frequency percentual of occurrence of the food item. We considered a species as euryphagous or omnivorous when the stomach items of both vegetal and animal origin are found in significant amounts. In this context, a species is considered stenophagous when it eats practically a single item and only a small percentage of the other items.

Sand is not a food item, as it may have been ingested accidentally by scrapers, diggers or browsing benthic animals. However, as grains of sand were reasonably frequent and occupied a considerable volume of the stomach in some species, this “item” was quantified.

The phylogeny of food items was reconstructed manually following Hennigian principles. Transformation series were hypothesized in an evolutionary context and clustered by congruence with other characters which are expected to share the same evolutionary history and thus to produce congruent hierarchies. Qualitative phylogenetic methods differ from numerical approaches of phylogenetic reconstruction in linking different perceptual character states into extended transformation series. Qualitative methods thus stand a better chance of resolving deep phylogenetic patterns. Numerical methods are more typological because they rely on observational identities and thus will often not be as successful in identifying ancient and extended transformations in evolutionary history.

RESULTS

Analyzing the relations between the items and trophic categories of the 15 species studied by Lunardon-Branco et al. (2006), the starfish, decapods and fish generally ingest other species of mollusks and fish, as well as sand and unidentified organic matter, with the majority of species being carcinophagous. Trophic relations indicate that the groups algae, Polychaeta, Bivalvia, Crustacea, Echinodermata (mainly Ophiuroidea) and Actinopterygii represent the largest contributions to the diet of the studied species (Table I).

In terms of abundance, the main food source exploited by the fish was Crustacea (especially Peracarida). Among the prey that could be identified, the shrimp Acetes americanus Ortmann, 1893 was the most common in terms of frequency of occurrence. Crustaceans represented more than 42 % and up to 73 % of the frequency in the feeding of seven of the eight species of studied fishes. The exception was Synodus foetens (Linnaeus, 1766), which only eats other fish and nematodes. Nematoda were only found in the stomach of fishes, although in small quantities in most of them (see Table I). Among the fish, nematodes
Table I. – Food items (relative frequencies) among 15 target species of macrobenthic predators in Itapocoroy (Santa Catarina, Brazil). The numbers refer to the characters used in the trophic phylogeny (Fig. 1).

<table>
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<th>No</th>
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<th>Hepatus pudibundus</th>
<th>Achelous spinimanus</th>
<th>Callinectes ornatus</th>
<th>Luidia senegalensis</th>
<th>Luidia clathrata</th>
<th>Symodium foetens</th>
<th>Iopisthus parvipinnis</th>
<th>Steller brassilensis</th>
<th>Diplodectrum radiale</th>
<th>Diplodectrum formosum</th>
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were only not found in the stomachs of the sand perch
*Diplectrum formosum* (Linnaeus, 1766) and the bigtooth grunt *Isospisthus parvipinnis* (Cuvier, 1830). The
latter species and *Synodus foetens* are more stenophagic
than the other fish. No cnidarians, echinoderms or sand
were found in the stomachs of the analyzed specimens
of these species. The three species cited above, as well
as *Stellifer brasiliensis* (Schultz, 1945) and *Diplectrum
radiate* (Quoy & Gaimard, 1824), are typically carnivorous,
as shown by the variety of organisms found in their
stomachs, including rare benthic taxa such as Nematoda,
Chaeogonatha and fish (Table I).

*S. foetens* was placed at the base of the remaining fish-
es in our analysis (Fig. 1) while it grouped with the sea-
stars in the Euclidian distance analysis (Lunardon-Branco
et al. 2006). Our clade of all fishes is supported by char-
acters 9.1, 16.1 and 17.1. Another grouping (Fig. 1) is the
clade formed by the two *Diplectrum* species, *Pomada-
sys corrineaformis* (Steinachner, 1868), *Paralochthys
brasiliensis* (Steindachner, 1875), and *Etropus crosso-
tus* Jordan & Gilbert, 1882. In the Euclidian distance analysis
*D. formosum* does not belong to this clade and *E. crosso-
tus* forms a trichotomy with the succeeding species.

List of characters (food items) shown in Fig. 1.
1. Sand: (0) ingests much sand (more than 20 %), (1)
   little or no sand
2. Algae: (0) eats, (1) doesn’t eat
3. Foraminiferida: (0) doesn’t eat, (1) eats, (2) probably
   not registered
4. Anthozoa: (0) doesn’t eat, (1) eats
5. Sipunculida: (0) doesn’t eat, (1) eats
6. Bivalvia: (0) eats, (1) eats a lot (more than 80 %),
   (2) probably not registered
7. Polychaeta: (0) eats, (1) eats a lot (more than 18 %),
   (2) probably not registered
8. Nematoda: (0) doesn’t eat (1) eats, (2) probably not
   registered
9. Crustacea (all taxa): (0) eats, (1) eats a lot (more
   than 40 %)
10. Copepoda: (0) doesn’t eat, (1) eats
11. Stomatopoda: (0) doesn’t eat, (1) eats
12. Cumacea: (0) doesn’t eat, (1) eats
13. Gammaridae: (0) eats, (1) doesn’t eat
14. Isopoda: (0) doesn’t eat, (1) eats
15. Sicynia: (0) doesn’t eat, (1) eats
16. *Acetes americanus*: (0) doesn’t eat, (1) eats, (2)
   probably not registered
17. Caridea: (0) doesn’t eat, (1) eats
18. Paguridae: (0) doesn’t eat, (1) eats
19. Pinnotheridae: (0) doesn’t eat, (1) eats
20. Xanthidae: (0) doesn’t eat, (1) eats
21. *Hepatus pudibundus*: (0) doesn’t eat, (1) eats, (2)
   probably not registered
22. Portunidae: (0) doesn’t eat, (1) eats
23. *L. spinimanus*: (0) doesn’t eat, (1) eats
24. Echinodermata: (0) eats, (1) eats a lot (more than
   18 %), (2) probably not registered
25. *Amphioxus*: (0) doesn’t eat, (1) eats
26. Actinoptygii: (0) eats, (1) eats very little (less
   than 1 %) or probably not registered

Starfish were differentiated from the other studied
organisms for being the most stenophagic species (Table
I). The diets of these two species stood out for the absence
of fish in *Luidia senegalensis* (Lamarck, 1816) and the
absence of crustaceans in *L. clathrata* (Say, 1825), but
were grouped for feeding almost exclusively on bivalve
mollusks.

Foraminiferans were specific items for decapods,
although ingested in low frequencies, with the excep-
tion of the blotched swimming crab *Acheulus spinimanus*
(Latreille, 1819). The ingestion of portunids explains the
decapod cluster, while the presence of xanthids indicates
the importance of true crabs. Several shared food items
are indicated in our proposed analysis (Fig. 1).
The trophic analysis indicates that most species can be characterized as omnivorous, with a clade of five species of fish that are primarily carnivorous – feeding almost exclusively on species of Crustacea. Also, the starfish clade can be distinguished from the decapod and fish clades for being stenophagous in terms of food habits (Fig. 1).

DISCUSSION

Establishing trophic relationships within communities can be a daunting task (Paine 1988, Hobson & Welch 1992). This is particularly true of marine communities. Due to limitations in both temporal and spatial scaling, studies of trophic organization continue to depend, to a large extent, on episodical stomach content analyses (Cortés 1999). There is currently a wide range of methods available for the analysis of the feeding habits of aquatic organisms, the most cited of which are available in the classical reviews by Hynes (1950), Berg (1979) and Hyslop (1980). These authors point out difficulties in standardizing methods and report that the most adequate method is the one that allows the best comparison with the expected results. When dealing with macroinvertebrates, the main problem is with the identification of food items due to the characteristics of the digestive process, especially in crustaceans, which break down food both chemically and mechanically (Williams 1981, Stevens et al. 1982, Haefner 1990, Branco & Verani 1997). Thus, care in the removal, handling and fixation of the digestive apparatus is fundamental to the adequate identification of food items.

In a previous study, Lunardon-Branco et al. (2006) produced a Euclidian distance dendrogram based on food items for all 15 species studied herein. This dendrogram clustered Synodus foetens with the asteroids. According to these authors, only the starfishes were considered stenophagous. In fact, over 95% of the diet of aquatic organisms, the most cited of which are available in the classical reviews by Hynes (1950), Berg (1979) and Hyslop (1980). These authors point out difficulties in standardizing methods and report that the most adequate method is the one that allows the best comparison with the expected results. When dealing with macroinvertebrates, the main problem is with the identification of food items due to the characteristics of the digestive process, especially in crustaceans, which break down food both chemically and mechanically (Williams 1981, Stevens et al. 1982, Haefner 1990, Branco & Verani 1997). Thus, care in the removal, handling and fixation of the digestive apparatus is fundamental to the adequate identification of food items.

In a previous study, Lunardon-Branco et al. (2006) produced a Euclidian distance dendrogram based on food items for all 15 species studied herein. This dendrogram clustered Synodus foetens with the asteroids. According to these authors, only the starfishes were considered stenophagous. In fact, over 95% of the diet of Luidia clathrata is composed of mollusks, while its sister species, L. senegalensis, has a more diversified diet, which includes Polychaeta and Echinodermata, among other organisms (Lunardon-Branco et al. 2006). These results were confirmed by other studies (Brögger & Penchasadeh 2008). Luidia senegalensis uses bivalve mollusks as its main prey-group (Lima-Verde & Matthews 1969), but nevertheless has a vast trophic plasticity (Penchasadeh & Lera 1983).

Echinodermata contains a variety of trophic groups, including detritivorous species, filter-feeders, grazers, scavengers and active predators that compete for food resources with demersal fish (Vázquez-Bader et al. 2008). In our study, sea stars are dominant predators that have an important role in determining the structure of the community, a result also established by Himmelman & Dutil (1991). In our case, the actinopterygians were the most important/dominant predator group, as discussed below. Some asteroids may maintain heterogeneity and biological diversity in their communities (Verling et al. 2003). The preference for large scallops over medium ones by sea stars and crabs has been shown to result in active selection (Barbeau & Scheibling 1994).

Luidia clathrata and L. senegalensis differ in morphology and hence in their ability to capture food. The first species has five additional robust arms when compared to the second, which has nine narrow arms (Hotchkiss 2000). L. clathrata, for example, exhibits negative phototaxis and buries itself in sand to avoid light (Hendler et al. 1995). These characteristics may explain its great ability to capture bivalves. The synapomorphic characteristics of echinoderms (especially Asteroidea), ability of the arms, traction strength of the ambulacrarian feet (hydrovascular system) and extracellular digestion, allow the opening of shells and access to the soft parts of bivalves. In the subtropical community that we have studied, starfish were differentiated from the other organisms for being the most stenophagous and for belonging to the category of sessile invertebrate feeders (Ferreira et al. 2004).

The feeding spectrum of the 15 species varied from 9 food items, in Luidia clathrata, to about 50, in the fish species Diplectrum radiale. If we consider the number of food items, Synodus foetens (14) and Isopisthus parvipinis (12) could be considered as showing the diets with more restrictions within the fish group, whose average number of food items is 33.

For the present analysis, the majority of decapod species were omnivorous. This fact led us to consider them as plesiomorphic when compared to the euryphy and carnivory states, represented, respectively, by Echinodermata and Actinopterygii. These interpretations provide evidence for considering a distinct subgroup of carnivorous fish and for a unique clade of starfish in the trophic analysis, characterized by the apomorphic trait of ingesting small quantities of sand.

In comparison with the Euclidean distance dendrogram, the trophic analysis constructed herein has more consistently related the lizard fish with the remaining group of fishes. Fishes from the genus Synodus play an important role as epibenthic predators in reef communities (Lemberget et al. 2009), as well as on silt-clay sediments in the present study. Due to the fact that they live near the substrate and feed on sessile invertebrates, many of the items in their diets have different macrobenthic species in common with some other species. Nevertheless, Soares et al. (2002, 2003) and Barreiros et al. (2008) showed that Synodus saurus (Linnaeus, 1758) from the Azores (NE Atlantic) are predators of pelagic and even epipelagic fish, a fact probably due to dominant rocky substrates typical of oceanic/volcanic islands.

The eight species of Actinopterygii studied herein were grouped by sharing Nematoda as a food item, and because Crustacea was the most common food item,
with a frequency above 40%, except for *S. foetens*, that ate around 5%. Fish of this species differ from the others for being piscivorous, feeding on *Isopisthus parvipinnis*, *Diplectrum spp.*, *Anchoa spp.*, Engraulidae and other non-identified fishes. These results confirm those from Cruz-Escalona et al. (2005), according to which *S. foetens* feeds on both demersal and pelagic prey, many of which are themselves predators. The particular behavior of the lizardfish, which preys by lurking, resting next to the sandy-muddy bottom, did not exclude active hunting. Individuals of *S. variegatus* (Lacepède, 1803) move frequently over distances of up to 1.5 m among elevated rocks from which they scan the surroundings for prey. They are voracious predators and did not hunt schooling fish (Sweatman 1984). Probably different *Synodus* species select different fish as prey (see Soares et al. 2002, 2003, Barreiros et al. 2008).

In all ecosystems, fish do cover a whole range of trophic levels: from herbivores near 2.0 to top predators above 4.5 (Odum & Heald 1975). Only fish species occupy all trophic levels (Froese 2004). Highest species’ numbers always occur around trophic level 3.2, i.e., with first-level predators feeding mainly on herbivorous organisms. In the Caribbean there are a higher number of herbivorous fishes than in other sites (Froese et al. 2004). Both herbivores and top predators contribute to about (or less than) 5% of total species numbers of the macrobenthic fauna. Fish clearly dominate the predatory levels around 3.0, the level chosen for our study.

Foraging by fish is thought to be a key ecological process shaping the abundances of subtidal organisms (Wellenreuther & Connell 2002). Predation is important in resource limitation (Verity 1998). Fishes have been shown to be important predators of shrimp in Australia and have an impact on prawn stocks (Brewer et al. 1991), as found in this study.

Most tropical fish are trophic opportunists, presenting a broad feeding spectrum, which allows them to adapt rapidly to the availability of abundant resources. This degree of euryphagy in tropical species is due to the high faunistic variety, accompanied by the relatively low biomass of each species. As a consequence, higher energy is consumed as food, in detriment of biomass conversion (Criales-Hernández et al. 2006).

*Diplectrum radiale* and *D. formosum* showed very broad diets similar in composition and frequency, forming a group based on three trophic items: the sharing of *Libinia spinosa* H. Milne Edwards, 1834, *Sicyonia* sp., and Paguridae as food items. On the other hand, in the Euclidian distance based dendrogram, the two species of *Diplectrum* were placed in a distinct group since *D. formosum* was united with *I. parvipinnis* for commonly eating fish from shoals of *Anchoa* (Lunardon-Branco et al. 2006). The two *Diplectrum* species’ are sympatric, have very similar morphological characters and habitat partitions, as well as having a characteristic sea-star following behavior (Gibran 2007). Because sea-stars are stenophagous while both *Diplectrum* are more euryphagous, when related to the other studied species, it is likely that they capture most of the organisms that appear during the act of sea-stars predation on bivalves.

The clade formed by *Pomadasys corvinaeformis* and *Paralonchurus brasilienis* became well determined both in the dendrogram of Lunardon-Branco et al. (2006), as in our analysis proposal. Fish of these species feed basically on crustaceans, echinoderms and polychaetes, as well as three further food items that were exclusive for these two species: Amphioxus, Copepoda, and Sipuncula.

*Paralonchurus brasilienis* has the second position, both in number and biomass, from the ichthyofauna bycatch of Itapocoroy. Stomach contents show diet seasonal fluctuations. This species has a benthic habit and a large trophic spectrum (Branco et al. 2005). On the other hand, *Isopisthus parvipinnis* is a primarily diurnal pelagic feeder (Soares & Vazzoler 2001). *Pomadasys corvinaeformis*, *Paralonchurus brasilienis* and *Etropus crosstos* share a high frequency of Polychaeta (above 18%) in their diets. Flatfish occupy the lowest trophic levels amongst fish groups (Manick-chand-Heileman et al. 2004). *Etropus crosstos* is estuarine-related (Sánchez-Gil et al. 2008) and feeds mostly on polychaetes and small crustaceans (Soares et al. 1993, Lunardon-Branco & Branco 2003, Bornatowski et al. 2004). The most important food source of this species was found to be copepods (Reichert 2003). Records of bivalve shells as part of the diet of *Etropus crosstos* were also reported by Amaral & Migotto (1980) and Lunardon-Branco & Branco (2003). Compared to the remaining seven species of fish studied herein, the characteristics that make the soles nearly sessile animals may explain their habit of feeding on bivalves. Pleuronectiformes have synapomorphies stemming from the cranial twist and are laterally very flat (Yazdani 1969, Gill & Hart 1998), which leads to slow swimming but provides an efficient camouflage effect (Topp & Hoff 1972).

The three species of fish mentioned above, together with the two species of *Diplectrum*, were grouped according to the following common items: eating of Anthozoa and Portunidae. *Stellifer brasilienis* became the outgroup of this clade, sharing three items with some species of decapods: feeding on Stomatopoda, Isopoda, and *Hepatus pudibundus* (Herbst, 1785).

*Hepatus pudibundus* is an opportunistic omnivore (Mantelatto & Petracco 1997) or a carnivore (Santos & Pires-Vanin 2004). Lunardon-Branco et al. (2006) report cannibalism for this species. Cannibalism has also been recorded in *Callinectes ornatus* Ordway, 1863 at this same locality (Branco et al. 2002) as well as in *C. danae* Smith, 1869 from Conceição Lagoon, Florianópolis (Branco & Verani 1997).

*Callinectes ornatus* is a generalist, with a diversified trophic spectrum (Branco et al. 2002), characterized by an
opportunist omnivore predation on macroinvertebrates (Amâncio 2000). Seven of the 17 food categories, besides sand, were present in the stomachs of this species. However, ontogenetic variations associated with molt stages on natural feeding (Mantellato & Christoffoleti 2001), have also been reported for Callinectes danae (Branco 1996a, 1996b, Branco & Verani 1997).

The feeding of Foraminifera has been interpreted as a decapod specialization that apparently occurred in Ache- lous spinimanus. The presence of substrate grains in the crab diet suggests a deposit feeding behavior (Branco & Verani 1997). The ingestion of sand dwelling prey may be considered accidental (Lunardon-Branco et al. 2006). However, the possibility that this prey ingestion is voluntary remains, considering the variety of microorganisms that inhabit the marine sediment such as Polychaeta, Mysidacea, Amphipoda, other Crustacea, Ophiuroidea, Ostracoda, and Foraminifera (Branco & Verani 1997).

Although starfish ingest sand and mud, the quantity is very low when compared to the ingestion in decapods. The ingestion of a large quantity of sand and foraminifera is a feeding condition of the five studied decapod species. The remarkably high quantity of sand ingested by Brachyura (more than 20 % of the stomach content) may be considered a source of carbonate, together with the sediment (Haefner 1990). When a shrimp has a benthic mode of life it feeds on detritus (bacteria, fungi and protozoans) (Stoner & Zimmerman 1988).

Decapods also feed on Echinodermata, other crustaceans (mainly Brachyura), and Polychaeta, although in varied frequencies. The trophic affinities indicate the known taxonomic relationships (De Grave et al. 2009). The trophic relationships of Ferreira et al. (2004) and the results of Lunardon-Branco et al. (2006) illustrate the diversity of the group. The only representative of Peneai- dae, Farfantepeneus paulensis Pérez-Farfante 1967, became the sister group to the remaining studied de- capods, and was considered omnivorous for eating crustaceans and algae. The crab Hepatus padibundus feeds on mobile and sessile invertebrates. The hermit-crab Dardanus insignis (De Saussure, 1858) and the blotched swimming-crab Achelous spinimanus were considered omnivorous, while the shelling-crab Callinectes ornatus is a carnivore that preferably eats crustaceans, fish, and mollusks, but may also feed on small quantities of algae. According to our analysis, only decapods share the feeding of Portunidae in their diet while brachyurans feed on Xanthidae.

Decapod crustaceans are usually opportunistic omni- vores (Albertoni et al. 2003). Crabs represent a signifi- cant proportion of the diets of demersal fish groups (Manickchand-Heileman et al. 2004). Brachyuran crabs are present in most aquatic food chains, occupying differ- ent trophic levels (Gouvêa & Queiroz 1988, Rocha et al. 1998, Barros et al. 2008). They have a key role in energy transfer, linking sediment communities to the higher trophic levels. Some groups of polychaetes, such as Ser- pulidae and Sabellariidae, were common in crabs’ diets, but absent in fishes’ (Petti et al. 1996). Dardanus insignis was the most abundant hermit crab found in Ubatuba, São Paulo, by Fransozo et al. (2008), where it exerts an important role in this marine trophic web (Fransozo et al. 2007).

Penaeid shrimps have been broadly classified as omnivorous and detritus feeders (Dall 1968). Overfishing of other species by trawlers is known to impact the continental shelf community structure of shrimp in Mexico and thus significantly change the existing trophic relations (Abarca-Arenas et al. 2007). There is also field evidence that shrimp predation regulates the meiofauna (Bell & Coull 1978). The main problem in quantifying shrimp diet consists in the trituration of food in penaeid shrimp stomachs, a problem referred to as the “feeding-mill-effect” (Dall & Moriarty 1983). Therefore, most studies have been limited to the observation of the frequency of occurrence of food items (Schwamborn & Criales-Hernández 2000).

Capitoli et al. (1994) studied trophic relations stemming from the fishing of the shrimp Artemesia longinaris Spence Baite 1888 and found that Farfantepeneus brasiliensis (Lateille, 1817) has a preference for feeding on Polychaeta and Hemichordarta. These authors state that, although the species has a broad feeding spectrum, there is a strong tendency toward predation on Polychaeta; the same was reported by Vazzoler (1975), Amaral and Migo-otto (1980), Rodrigues & Meira (1988) and Soares et al. (1993).

According to Capitoli et al. (1994), Penaeidae transfer a caloric content of 850 KJ, which nearly doubles that of polychaetes (482 KJ) and fish (442KJ). The importance of crustaceans as a food source for fish is well documented, including Sciaenidae species’ (Micheletti & Uieda 1996) such as P. brasiliensis, S. brasiliensis and I. parvipinnis, which were also studied by Lunardon (1990). Farfantepeneus paulensis has a similar trophic level as predatory fish. It is mainly carnivorous, with a high trophic level (Jørgensen et al. 2009) or maybe omnivorous (Soares et al. 2005a, 2005b).

Our study area stands out in southeastern Brazil due to its bivalve farming activities as well as traditional fisheries. The ecosystems of this site are home to a diversified marine fauna that use the area for feeding, breeding and development (McLaughlin & Hebard 1961, Chao & Musick 1977, Williams 1981, Haefner 1990, Wooton 1992, 1998, Gasalla & Soares 2001, Soares & Vazzoler 2001). According to Branco & Verani (2006), intensive fishery activity in the area targets the shrimp Xiphope- nes kroyeri (Heller, 1862). Although the shrimp ana-lyzed here was F. paulensis, the importance of Penaeidae as a food source for fish and crustaceans was demonstrat- ed in the present study and has been reported previously by Capitoli et al. (1994) for this same region. We hypoth-
esize that *X. kroyeri* and *P. paulensis* represent the same trophospecies in the Itapocoroy community.

From a phylogenetic perspective, groups that dominate upper trophic levels, like fishes, tend to be highly derived predatory representatives of their classes or phyla, while organisms abundant at the lowest trophic levels (< 3) tend to belong to stem groups (Froese et al. 2004). Dietary groupings do not always reflect taxonomic relationships. There was evidence of convergence in feeding modes and diet between phylogenetically distinct taxa and divergence within particular lineages (Choat et al. 2002). The trophic cladogram displays details of food items, whether or not shared by all species. The resulting trophic analysis is consistent with known historical relationships.

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REFERENCES


TROPHIC ANALYSIS OF MACROBENTHIC SPECIES


Vie Milieu, 2014, 64


Vie Milieu, 2014, 64
Soares R, Peixoto S, Wasielesky W, D’Incao F. 2006. Effect of... 


APPENDIX I. - REFERENCES ON FOOD ITEMS OF STUDIED SPECIES.


Diplectrum radiale (Quoy & Gaimard, 1824): Lunardon-Branco et al. 2006.

Diplectrum formosum (Linnaeus, 1766): Lunardon-Branco et al. 2006.

Pomadasys corvinaeformis (Steindachner, 1868): Lunardon-Branco et al. 2006.


Stellifer brasiliensis (Schultz, 1945): Lunardon-Branco et al. 2006.