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

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CLADOGRAM
COMMON FOOD ITEMS
TROPHIC RELATIONS

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).

Studies on the feeding habits of aquatic organisms provide a description of ontogenic, ecological and other aspects (Wooton 1992, 1998, Blaber 2000), thereby allowing the theoretical discussion on the biological mechanisms of species substitution (Rondineli *et al*. 2007). Such studies are currently a requirement for the management and sustainable use of marine ecosystems (Olaso 1992, Gasalla & Soares 2001).

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 only one trophic level away from each other. In contrast, 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).

No Char.	Food items	*Farfantepenaeus paulensis*	*Dardanus insignis*	*Hepatus pudibundus*	*Achelous spinimanus*	*Callinectes ornatus*	*Luidia senegalensis*	*Luidia clathrata*	*Synodus foetens*	*Isopisthus parvipinnis*	*Stellifer brasiliensis*	*Diplectrum radiale*	*Diplectrum formosum*	*Pomadasys corvinaeformis*	*Paralonchurus brasiliensis*	*Etropus crossotus*
1	Sand*	20.94	29.46	27.5	21.33	26.23	4.2	0	0	0	1.47	0.26	0.98	0.41	0.5	0.43
2	Algae	12.06	11.63	1.67	13.91	3.28	0	0	2.82	1.37	1.47	0.79	0.98	1.23	0.75	0.43
3	Foraminifera	0.52	0.25	0.83	0	0.27	0	0	0	0	0	0	0	0	0	0
4	Anthozoa	0	0	0	0	0	0	0	0	0	0	0.26	0.98	0.2	0.5	0.85
5	Sipunculida	0	0	0	0	0	0	0	0	0	0	0	0	0.2	0.25	0
6	Bivalvia	6.81	2.97	3.33	10.58	11.2	81.51	89.81	0	0	2.94	1.57	0.98	1.02	1.01	0
7	Polychaeta	4.71	6.44	7.5	5.94	4.1	4.2	0	2.82	1.37	7.35	3.94	5.88	23.1	22.61	18.2
8	Nematoda	0	0	0	0	0	0	0	11.27	0	1.47	0.26	0	0.61	3.27	0.43
9	Crustacea (all *taxa*)	37.15	11.39	37.48	22.86	31.43	2.52	2.44	5.64	69.87	66.47	71.32	71.55	46.39	42.45	69.98
10	Copepoda	0	0	0	0	0	0	0	0	0	0	0	0	0.41	0.25	0
11	Stomatopoda	0	0	0.83	0	0	0	0	0	0	1.47	1.57	0.98	0.82	0.25	0.21
12	Cumacea	0	0	0	0.19	0	0	0	0	0	0	0	0.98	1.43	1.76	9.42
13	Gammaridea	6.28	2.23	0.83	0.56	1.37	0	0	0	0	13.24	1.57	0.98	13.7	8.79	17.77
14	Isopoda	0.52	0	0	0.19	0.55	0	0	0	0	1.47	0.26	2.94	0.41	0.25	1.28
15	Sicyonia	0	0	0	0	0	0	0	0	0	0	1.84	0.98	0	0	0
16	*Acetes americanus*	0	0	0	0	0.27	0	0	0	9.59	1.47	1.05	0	0.82	0.5	0.43
17	Caridea	0	0	0.83	0.19	0	0	0	0	0	1.47	0.52	0.98	0.41	0.5	0.43
18	Paguridae	0	0	0	0	0	0	0	0	0	0	1.05	0.98	0	0	0
19	Pinnotheridae	0	0	0	0	0	0	0	0	0	0	4.72	1.96	0.2	0.25	1.28
20	Xanthidae	0	0	0.83	0.19	0.27	0	0	0	0	0	0	3.93	0	0	0
21	*Hepatus pudibundus*	0	0	0.83	0.37	0	0	0	0	0	0	3.41	0.98	0.2	0	0.21
22	Portunidae	0	0.5	2.5	2.79	3.83	0	0	0	0	1.47	8.13	5.88	0.41	0.25	0.64
23	*Libinia spinosa*	0	0	0	0	0	0	0	0	0	0	0.26	0.98	0	0	0
24	Echinodermata	9.95	23.08	5.83	7.05	4.37	4.2	0	0	0	1.47	8.14	7.84	18.4	20.35	0.43
25	Amphioxus	0	0	0	0	0	0	0	0	0	0	0	0	1.02	0.75	0
26	Actinopterygii	4.71	5.94	6.67	12.62	13.39	0.84	0	47.9	21.92	8.82	12.32	8.82	4.09	4.04	7.28

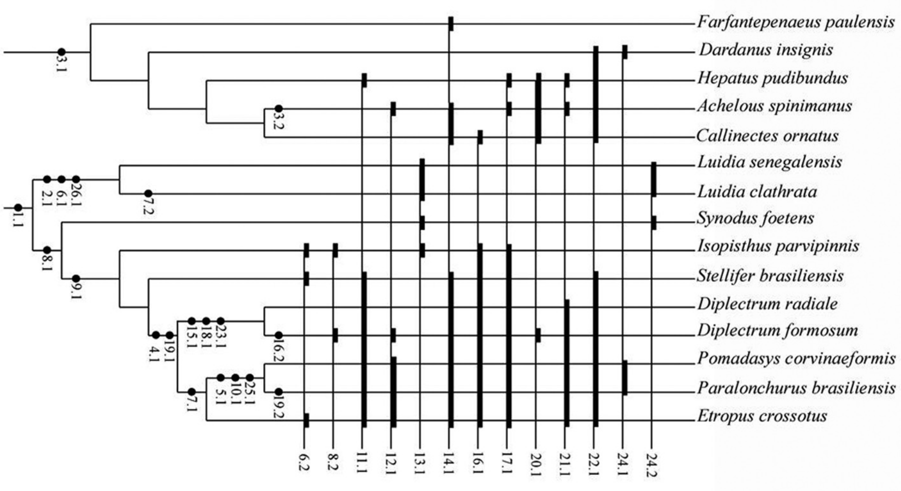

Fig. 1. – Trophic phylogeny, based on food items, among 15 target species of macrobenthic predators in Itapocoroy (Santa Catarina, Brazil).

were only not found in the stomachs of the sand perch *Diplectrum formosum* (Linnaeus, 1766) and the bigtooth grunt *Isopisthus 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 radiale* (Quoy & Gaimard, 1824), are typically carnivorous, as shown by the variety of organisms found in their stomachs, including rare benthic taxa such as Nematoda, Chaetognatha and fish (Table I).

S. foetens was placed at the base of the remaining fishes in our analysis (Fig. 1) while it grouped with the seastars in the Euclidian distance analysis (Lunardon-Branco *et al.* 2006). Our clade of all fishes is supported by characters 9.1, 16.1 and 17.1. Another grouping (Fig. 1) is the clade formed by the two *Diplectrum* species, *Pomadasys corvinaeformis* (Steindachner, 1868), *Paralonchurus brasiliensis* (Steindachner, 1875), and *Etropus crossotus* Jordan & Gilbert, 1882. In the Euclidian distance analysis *D. formosum* does not belong to this clade and *E. crossotus* 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. Libinia spinosa: (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. Actinopterygii: (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 exception of the blotched swimming crab *Achelous 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 *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 & Penchaszadeh 2008). *Luidia senegalensis* uses bivalve mollusks as its main prey-group (Lima-Verde & Matthews 1969), but nevertheless has a vast trophic plasticity (Penchaszadeh & 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 stenophagic 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 parvipinnis* (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 euryphagy 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 *et al.* 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, *Sicynia* 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 brasiliensis* 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 brasiliensis 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 brasiliensis and *Etropus crossotus* share a high frequency of Polychaeta (above 18 %) in their diets. Flatfish occupy the lowest trophic levels amongst fish groups (Manickchand-Heileman *et al.* 2004). *Etropus crossotus* 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 crossotus* 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 brasiliensis* 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 & Petrarco 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 opportunistic 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 *Achelous 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 Penaeidae, *Farfantepeneus paulensis* Pérez-Farfante, 1967, became the sister group to the remaining studied decapods, and was considered omnivorous for eating crustaceans and algae. The crab *Hepatus pudibundus* feeds on mobile and sessile invertebrates. The hermit-crab *Dardanus insignis* (De Sausure, 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 omnivores (Albertoni *et al.* 2003). Crabs represent a significant proportion of the diets of demersal fish groups (Manickchand-Heileman *et al.* 2004). Brachyuran crabs are present in most aquatic food chains, occupying different 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 Serpulidae and Sabellariidae, were common in crabs' diets, but absent in fishes' (Petti *et al.* 1996). *Dardanus insignis* was the most abundant hermit crabfound 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 *Farfantepenaeus brasiliensis* (Latreille, 1817) has a preference for feeding on Polychaeta and Hemichordata. 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 Migotto (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). *Farfantepenaeus 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 *Xiphopenaeus kroyeri* (Heller, 1862). Although the shrimp analyzed here was *F. paulensis*, the importance of Penaeidae as a food source for fish and crustaceans was demonstrated in the present study and has been reported previously by Capitoli *et al.* (1994) for this same region. We hypothesize that *X. kroyeri* and *F. 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 phylae, 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

Abarca-Arenas LG, Franco-Lopez J, Peterson MS, Brown-Peterson NJ, Valero-Pacheco E 2007. Sociometric analysis of the role of penaeids in the continental shelf food web off Veracruz, Mexico based on by-catch. *Fish Res* 87(1): 46-57. doi: 10.1016/j.fishres.2007.06.019.

Abreu PC, Ballester ELC, Odebrecht C, Wasielesky W, Cavalli RO, Graneli W, Anesio AM 2007. Importance of biofilm as food source for shrimp (*Farfantepenaeus paulensis*) evaluated by stable isotopes (delta c-13 and delta n-15). *J Exp Mar Biol Ecol* 347(1-2): 88-96. doi: 10.1016/j.jembe.2007.03.012.

Albertoni EF, Palma-Silva C, Esteves FD 2003. Natural diet of three species of shrimp in a tropical coastal lagoon. *Braz Arch Biol Technol* 46(3): 395-403.

Amâncio IM 2000. Hábitos alimentares dos crustáceos decápodos braquiúros da plataforma interna de São Sebastião, SP. MSc dissertation, Instit Oceanog Univ São Paulo, Brazil.

Amaral ACZ, Migotto A 1980. Importância dos anelídeos poliquetas na alimentação da macrofauna demersal e epibentônica da região de Ubatuba. *Braz J Oceanogr* 29(2): 31-35.

Barbeau MA, Scheibling RE 1994. Behavioral mechanisms of prey size selection by sea stars (*Asterias vulgaris* Verrill) and crabs (*Cancer irroratus* Say) preying on juvenile sea scallops (*Placopecten magellanicus* (Gmelin)). *J Exp Mar Biol Ecol* 180(1): 103-136. doi: 10.1016/0022-0981(94)90082-5.

Barreiros JP, Cardigos F, Soares MSC, Machado LF 2008. Juvenile *Sphyraena viridensis*, preyed by the lizard fish *Synodus saurus*. A new predatory association from the Azores. *Cybium* 32(3): 273-274.

Barros SP, Cobo VJ, Fransozo A 2008. Feeding habits of the spider crab *Libinia spinosa* H. Milne Edwards, 1834 (Decapoda, Brachyura) in Ubatuba Bay, São Paulo, Brazil. *Braz Arch Biol Technol* 51(2): 413-417.

Bell SS, Coull BC 1978. Field evidence that shrimp predation regulates meiofauna. *Oecologia* 35(2): 141-148. doi: 10.1007/BF00344727.

Berg J 1979. Discussion of methods of investigating the food fishes with reference to a preliminary study of prey of *Gobiusculus flavescens* (Gobiidae). *Mar Biol* 50(3): 263-273. doi: 10.1007/BF00394208.

Berlow EL, Neutel AM, Cohen JE, De Ruiter PC, Ebenman B, Emmerson M, Fox JW, Jansen VAA, Jones JI, Kokkoris GD, Logofet DO, Mckane AJ, Montoya JM, Petchey O 2004. Interaction strengths in food webs: issues and opportunities. *J Anim Ecol* 73(3): 585-598. doi: 10.1111/j.0021-8790.2004.00833.x.

Blaber SJM 2000. Tropical Estuarine Fishes: Ecology, Exploitation and Conservation. Blackwell Science, Queensland.

Bornatowski H, Abilhoa V, Brogim RA 2004. A alimentação do linguado *Etropus crossotus* (Pleuronectiformes, Paralichthyidae) em um banco areno-lodoso na ilha do Mel, Paraná, Brasil. *Rev Estudos Biol* 26(57): 11-15.

Braga FM, Braga MA, Goiten R 1985. Fator de condição e alimentação de *Paralonchurus brasiliensis* (Osteichthyes, Sciaenidae) na região da Ilha Anchieta (lat. 23°33'S, long. 45°05'W), Ubatuba, Estado de São Paulo. *Naturalia* 10: 1-11.

Branco JO 1996a. Feeding cycle and rhythm of *Callinectes danae* Smith, 1869 (Decapoda, Portunidae) from Lagoa da Conceição, Florianópolis, SC, Brazil. *Arch Biol Technol* 39: 987-998.

Branco JO 1996b. Seasonal and ontogenetic variations on the feeding natural of *Callinectes danae* Smith, 1869 (Decapoda, Portunidae) from Lagoa da Conceição, Florianópolis, SC, Brazil. *Arch Biol Technol* 39: 999-1012.

Branco JO, Verani JR 1997. Dinâmica da alimentação natural de *Callinectes danae* Smith (Decapoda, Portunidae) na Lagoa da Conceição, Florianópolis, SC, Brasil. *Rev Bras Zool* 14(4): 1003-1018.

Branco JO, Verani JR 2006. Análise quali-quantitativa da ictiofauna acompanhante na pesca do camarão sete-barbas, na Armação do Itapocoroy, Penha, Santa Catarina. *Rev Bras Zool* 23(2): 381-391.

Branco JO, Lunardon-Branco MJ, Verani JR, Schveitzer FX, Vale WG 2002. Natural diet of *Callinectes ornatus* Ordway, 1863 (Decapoda, Portunidae) in the Itapocoroy inlet, Penha, SC, Brazil. *Braz Arch Biol Technol* 45(1): 35-40.

Branco JO, Lunardon-Branco MJ, Verani JR 2005. Biological and fishing aspects of *Paralonchurus brasiliensis* Steindachner (Pisces, Sciaenidae), in the Armação do Itapocoroy, Penha, Santa Catarina, Brazil. *Rev Bras Zool* 22(4): 1063-1071.

Brewer DT, Blaber SJM, Salini JP 1991. Predation on penaeid prawns by fishes in Albatross Bay, Gulf of Carpentaria. *Mar Biol* 109(2): 231-240. doi: 10.1007/BF01319391.

Brögger MI, Penchaszadeh PE 2008. Infaunal mollusks as main prey for two sand bottoms sea stars off Puerto Quequen (Argentina). *Rev Biol Trop* 56(3): 329-34.

Capitoli RR, Bager A, Ruffino ML 1994. Contribuição ao conhecimento das relações tróficas bentônico-demersais nos fundos de pesca do camarão *Artemesia longinaris* Bate, na região da Barra da Lagoa dos Patos, RS, Brasil. *Nauplius* 2: 53-74.

Chao LN, Musick JA 1977. Life history, feeding habits, and functional morphology of juvenile sciaenid fishes in the York River, Virginia. *Fish Bull* 75: 657-702.

Chávez-López R, Rocha-Ramirez A, Álvarez F, Wetzer R 2005. *Elthusa alvaradoensis* Rocha-Ramírez, Chávez-López and Bruce, 2005 (Isopoda, Cymothoidae) parasitizing the inshore lizardfish, *Synodus foetens* (Linnaeus, 1766) on the continental shelf off central Veracruz, Mexico. *Crustaceana* 78(7): 865-872.

Choat JH, Clements KD, Robbins WD 2002. The trophic status of herbivorous fishes on coral reefs - 1: dietary analyses. *Mar Biol* 140(3): 613-623. doi: 10.1007/s00227-001-0715-3.

Christoffersen ML, Araújo ME, Branco JO 2011. An overview of studies on trophic ecology in the marine environment: Achievements and perspectives. *Neotrop Biol Cons* 6(3):143-155.

Cohen JE 1978. Food Webs and Niche Space. Princeton University Press, Princeton.

Cohen JE 1989. Ecology – just proportions in food webs. *Nature* 341: 104-105.

Cortés E 1999. Standardized diet compositions and trophic levels of sharks. *ICES J Mar Sci* 56: 707-717.

Criales-Hernández MI, Garcia CB, Wolff M 2006. Flujos de biomasa y estructura de un ecosistema de surgencia tropical en la Guajira, Caribe Colombiano. *Rev Biol Trop* 54(4): 1257-1282.

Cruz-Escalona VH, Peterson MS, Campos-Dávila L, Zetina-Rejón M 2005. Feeding habits and trophic morphology of inshore lizardfish (*Synodus foetens*) on the central continental shelf off Veracruz, Gulf of Mexico. *J Appl Ichthyol* 21: 525-530. doi: 10.1111/j.1439-0426.2005.00651.x.

Dall W 1968. Food and feeding of some Australian penaeid shrimp. *FAO Fish Rep* 57: 251-258.

Dall W, Moriarty D 1983. Functional aspects of nutrition and digestion. *In* Mantel LH (ed), The Biology of Crustacea: internal anatomy and physiological regulations. Academic Press, New York: 215-261.

De Grave S, Pentcheff ND, Ahyong ST, Chan T-Y, Crandall KA, Dworschak PC, Felder DL, Feldmann RM, Fransen CHJM, Goulding LYD, Lemaitre R, Low MEY, Martin JW, Ng PKL, Schweitzer CE, Tan SH, Tshudy D, Wetzer R 2009. A classification of living and fossil genera of decapod crustaceans. *Raffles Bull Zool* 21: 1-109.

Ferreira CEL, Floeter SR, Gasparini JL, Ferreira BP, Joyeux JC 2004. Trophic structure patterns of Brazilian reef fishes: a latitudinal comparison. *J Biogeogr* 31: 1093-1106.

Fransozo V, Fernandes-Goés LC, Goés JM 2007. Composition and abundance of anomuran (Crustacea, Decapoda) from non-consolidated sublittoral, on the northern coast of São Paulo State, Brazil. *In* Anais do Congresso de Ecologia do Brasil. Caxambu MG, Brazil: 8: 1-2.

Fransozo A, Bertini G, Braga AA, Negreiros-Fransozo ML 2008. Ecological aspects of hermit crabs (Crustacea, Anomura, Paguroidea) off the northern coast of São Paulo State, Brazil. *Aquat Ecol* 42 (3): 437-448. doi: 10.1007/s10452-007-9103-5.

Froese R, Garthe S, Piatkowski U, Pauly D 2004. Trophic signatures of marine organisms in the Mediterranean as compared with other ecosystems. *Belg J Zool* 134: 31-36.

Froese R, Garthe S, Piatkowski U, Pauly D 2005. Trophic signatures of marine organisms in the Mediterranean as compared with other ecosystems. *Belg J Zool* 135: 139-143.

Gasalla MA, Soares LSH 2001. Comentários sobre os estudos tróficos de peixes marinhos no processo histórico da ciência pesqueira e modelagem ecológica. *Bol Instit Pesca* 27(2): 243-259.

Gibran FZ 2007. Activity, habitat use, feeding behavior, and diet of four sympatric species of Serranidae (Actinopterygii: Perciformes) in southeastern Brazil. *Neotrop Ichthyol* 5(3): 387-398. doi: dx.doi.org/10.1590/S1679-62252007000300018.

Gill AB, Hart PJB 1998. Stomach capacity as a directing factor in prey size selection of three-spined stickleback. *J Fish Biol* 53(4): 897-900. doi: 10.1111/j.1095-8649.1998.tb01844.x.

Gouvêa EP, Queiroz EL 1988. Braquiúros (Crustacea, Decapoda) utilizados na alimentação de peixes Rajidae no litoral sul do Brasil. *Cienc Cult* 40: 276-279.

Haefner Jr. PA 1990. Natural diet of *Callinectes ornatus* (Brachyura: Portunidae) in Bermuda. *J Crust Biol* 10(2): 236-246.

Hall SJ, Raffaelli D 1991. Food-web patterns – lessons from a species-rich web. *J Anim Ecol* 60(3): 823-842.

Halpern JA 1970. Growth rate of the tropical sea star *Luidia senegalensis* (Lamarck). *Bull Mar Sci* 20(3): 626-633.

Hendler G, Miller JE, Pawson DL, Kier PM 1995. Sea Stars, Sea Urchins, and Allies. Smith. Institut. Press, Washington DC.

Himmelman JH, Dutil C 1991. Distribution, population-structure and feeding of subtidal seastars in the northern Gulf of St. Lawrence. *Mar Ecol Progr Ser* 76(1): 61-72.

Hobson KA, Welch HE 1992. Determination of trophic relationships within a high Arctic marine food web using delta-13 C and delta-15 N analysis. *Mar Ecol Progr Ser* 84(1): 9-18.

Hotchkiss FHC 2000. On the number of rays in starfish. *Am Zool* 40(3): 340-354.

Hynes HBN 1950. The food of fresh-water sticklebacks (*Gasterosteus aculeatus* and *Pygosteus pungitius*), with a review of methods used in studies os the food of fishes. *J Anim Ecol* 19(1): 36-51.

Hyslop EJ 1980. Stomach contents analysis – a review of methods and their application. *J Fish Biol* 17: 411-429.

Jørgensen P, Bemvenuti CE, Hereu CM 2009. Feeding of *Farfantepenaeus paulensis* (Pérez-Farfante, 1967) (Crustacea: Penaeidae) inside and outside experimental pen-culture in southern Brazil. *Panamjas* 4(1): 39-51.

Jørgensen S, Müller F 2000. Handbook of Ecosystem Theories and Management. Lewis Publishers, Washington DC.

Joydas TV, Damodaran R 2009. Infaunal macrobenthos along the shelf waters of the west coast of India, Arabian Sea. *Indian J Mar Sci* 38(2): 191-204.

Kagiwara F, Abilhoa V 2000. A alimentação do peixe-lagarto *Synodus foetens* Linnaeus, 1766 em um banco areno-lodoso na Ilha do Mel, Paraná. *Arq Ciênc Vet Zool UNIPAR* 3(1): 9-17.

Lawrence J, Dehn PF 1979. Biological characteristics of *Luidia clathrata* (Echinodermata, Asteroidea) from Tampa Bay, shallow Gulf of Mexico. *Flor Sci* 42: 9-12.

Lawton, JH 1995. Ecological experiments with model systems. *Science* 269(5222): 328-331.

Lemberget T, McCormick MI, Wilson DT 2009. Environmental influences on the replenishment of lizardfish (family Synodontidae) in Caribbean Panama. *Coral Reefs* 28(3): 737-750. doi: 10.1007/s00338-009-0489-5.

Lemos D, Navarrete del Toro A, Córdova-Murueta JH, Garcia-Carreño F 2004. Testing feeds and feed ingredients for juvenile pink shrimp *Farfantepenaeus paulensis*: in vitro determination of protein digestibility and proteinase inhibition. *Aquacult* 239(1-4): 307-321. doi: 10.1016/j.aquaculture.2004.05.032.

Levin SA 1992. The problem of pattern and scale in ecology: the Robert H. MacArthur Award Lecture. *Ecology* 73: 1943-1967. doi: http://dx.doi.org/10.2307/1941447.

Lima-Verde JS, Matthews HR 1969. On the feeding habits of the sea star *Luidia senegalensis* (Lamarck) in the Sate of Ceará, Brazil. *Arquiv Ciênc Mar* 9(2): 173-175.

Longhurst AR, Pauly D 1987. Ecology of Tropical Oceans. Academic Press, San Diego.

Lunardon MJ 1990. Hábitos alimentares de *Menticirrhus littoralis* (Holbrook, 1860) (Perciformes - Sciaenidae) na Baía de Paranaguá e adjacências – Paraná – Brasil. *Arquiv Biol Tecnol* 33: 717-725.

Lunardon-Branco MJ, Branco JO 2003. Alimentação natural de *Etropus crossotus* Jordan & Gilbert (Teleostei, Pleuronectiformes: Paralichthyidae), na Armação do Itapocoroy, Penha, SC, Brasil. *Rev Bras Zool* 20: 631-635. doi: http://dx.doi.org/10.1590/S0101-81752003000400012.

Lunardon-Branco MJ, Branco JO, Verani JR 2006. Relações tróficas entre macroinvertebrados e peixes, na Armação do Itapocoroy, Penha, SC. *In* Branco JO & Marenzi AWC (eds), O Cultivo do Mexilhão *Perna perna* no Município de Penha, SC. Itajaí. Ed. Univ. Vale do Itajaí, Itajaí: 183-196.

Manickchand-Heileman S, Mendoza-Hill J, Kong AL, Arocha F 2004. A trophic model for exploring possible ecosystem impacts of fishing in the Gulf of Paria, between Venezuela and Trinidad. *Ecol Modell* 172(2-4): 307-322. doi: 10.1016/j.ecolmodel.2003.09.013.

Manickchand-Heileman S, Soto LA, Escobar E 1998. A preliminary trophic model of the continental shelf, south-western Gulf of Mexico. *Estuar Coast Shelf Sci* 46(1): 885-899. doi: 10.1016/0272-7714(86)90084-3.

Mantelatto FLM, Christofoletti RA 2001. Natural feeding activity of the crab *Callinectes ornatus* (Portunidae) in Ubatuba Bay (São Paulo, Brazil): influence of season, sex, size and molt stage. *Mar Biol* 138(3): 585-594. doi: 10.1007/s002270000474.

Mantelatto FLM, Petracco M 1997. Natural diet of the crab *Hepatus pudibundus* (Brachyura: Calappidae) in Fortaleza Bay, Ubatuba (SP), Brazil. *J Crust Biol* 17(3): 440-446.

May RM 1986. The search for patterns in the balance of nature: advances and retreats. *Ecology* 67(5): 1115-1126. doi: dx.doi.org/10.2307/1938668.

McClintock JB, Lawrence JM 1981. An optimization study on the feeding-behavior of *Luidia clathrata* Say (Echinodermata, Asteroidea). *Mar Behav Physiol* 7(4): 263-275. doi: 10.1080/10236248109386987.

McClintock JB, Lawrence JM 1984. Ingestive conditioning in *Luidia clathrata* (Say) (Echinodermata: Asteroidea): Effect of nutritional condition on selectivity, teloreception, and rates of ingestion. *Mar Behav Physiol* 10(3): 167-181. doi: 10.1080/10236248409378616.

McClintock JB, Lawrence JM 1985. Characteristics of foraging in the soft-bottom benthic starfish *Luidia clathrata* (Echinodermata, Asteroidea) – prey selectivity, switching behavior, functional-responses and movement patterns. *Oecologia* 66(2): 291-298.

McLaughlin PA, Hebard FJ 1961. Stomach contents of the Bering Sea king crab. *Int N Pac Fish Comm Bull* 5: 5-8.

Micheletti CV, Uieda VS 1996. Food resources partitioning among Sciaenidae fishes (Perciformes - Sciaenidae) of the Flamengo Bay, Ubatuba, southeastern Brazil. *Arch Biol Technol* 39(3): 639-649.

Montoya JM, Solé RV 2002. Small world patterns in food webs. *J Theor Biol* 214(3): 405-412. doi: http://dx.doi.org/10.1006/jtbi.2001.2460.

Odum EP 1968. Energy flow in ecosystems: a historical review. *Integ Comp Biol* 8(1): 11-18. doi: 10.1093/icb/8.1.11.

Odum WE, Heald EJ 1975. The detritus-based food web of an estuarine mangrove community. *In* Cronin LE (ed), Estuarine Research. Academic Press, New York: 265-286.

Olaso I 1992. Las interacciones tróficas en la regulación pesquera y en el ecosistema mariño. Informe del Instituto Español de Oceanografía. 5 p.

Paine RT 1988. Food webs – road maps of interactions or grist for theoretical development. *Ecology* 69(6): 1648-1654.

Penchaszadeh PE, Lera ME 1983. Alimentación de tres especies tropicales de *Luidia* (Echinodermata, Asteroidea) en Golfo Trieste, Venezuela. *Carib J Sci* 19: 1-6.

Penchaszadeh PE, Molinet R 1983. Diet of the sea star *Tethyaster vestitus* Say (Astropectinidae) in the Golfo Trieste (Venezuela). *Bull Mar Sci* 33: 187-191.

Petti MAV, Nonato EF, Paiva PC 1996. Trophic relationships between polychaetes and brachyuran crabs on the southeastern Brazilian coast. *Braz J Oceanog* 44(1): 61-67. doi: http://dx.doi.org/10.1590/S1679-87591996000100007.

Phelps GB 1997. Ontogenetic variation in the diet of the inshore lizardfish, *Synodus foetens*. MSc dissertation, Florida Instit. Technol.

Pimm SL, Lawton JH, Cohen JE 1991. Food web patterns and their consequences. *Nature* 350: 669-674. doi:10.1038/350669a0.

Reichert MJM 2003. Diet, consumption, and growth of juvenile fringed flounder (*Etropus crossotus*); a test of the 'maximum growth/optimum food hypothesis' in a subtropical nursery area. *J Sea Res* 50(2-3): 97-116. doi: 10.1016/S1385-1101(03)00081-9.

Rocha GRBA, Gasalla MA, Rossi-Wongtschowski CLDB, Soares LSH, Pires-Vanin AMS, Muto EY, Cergole MC, Aidar E, Mesquita HSL, Gianesella-Galvão SMF, Veja-Perez LA, Jarre-Teichmann A 1998. Quantitative model of trophic interations in the Ubatuba shelf system (southeastern Brazil). *Fishbyte* 21: 25-32.

Rodrigues ES, Meira PTF 1988. Dieta alimentar de peixes presentes na pesca dirigida ao camarão-sete-barbas (*Xiphopenaeus kroyeri*) na Baía de Santos e praia do Perequê, Estado de São Paulo, Brasil. *Bol Inst Pesca* 15 (2): 135-146.

Rondineli GR, Braga FMS, Tutui SLS, Bastos GCC 2007. Dieta de *Menticirrhus americanus* (Linnaeus, 1758) e *Cynoscion jamaicensis* (Vaillant & Bocourt, 1883) (Pisces, Sciaenidae) no sudeste do Brasil, Estado de São Paulo. *Bol Inst Pesca* 33(2): 221-228.

Sánchez-Gil P, Ýanez-Arancibia A, Tapia M, Day JW, Wilson CA, Cowan JH 2008. Ecological and biological strategies of *Etropus crossotus* and *Citharichthys spilopterus* (Pleuronectiformes: Paralichthyidae) related to the estuarine plume, southern Gulf of Mexico. *J Sea Res* 59(3): 173-185. doi: 10.1016/j.seares.2007.12.002.

Santos MFL, Pires-Vanin AMS 2004. Structure and dynamics of the macrobenthic communities of Ubatuba Bay, southeastern Brazilian coast. *Braz J Oceanog* 52(1): 59-73. doi: http://dx.doi.org/10.1590/S1679-87592004000100006.

Schwamborn R, Criales-Hernández MM 2000. Feeding strategy and daily ration of juvenile pink shrimp (*Farfantepenaeus duorarum*) in a South Florida seagrass bed. *Mar Biol* 137(1): 139-147. doi: 10.1007/s002270000317.

Schwartz FJ, Porter HJ 1977. Fishes, macroinvertebrates and their relationships with a calico scallop bed off North Carolina. *Fish Bull* 75(2): 427-446.

Silva DL, D'Incao F 2001. Análise do conteúdo estomacal de *Farfantepenaeus paulensis* (Perez-Farfante, 1967) no estuário da Lagoa dos Patos, Rio Grande do Sul, Brasil (Decapoda, Penaeidae). *In* D'Incao F (ed), Relatório do projeto de avaliação e gerenciamento da pesca de crustáceos no estuário da Lagoa dos Patos, Brasil. Fundação Univ. do Rio Grande, Rio Grande: 89-102.

Soares LSH, Gasalla MA, Rios MAT, Arrasa MV, Rossi-Wongtschowski CLB 1993. Grupos tróficos de onze espécies dominantes de peixes demersais da plataforma continental interna de Ubatuba, Brasil. *Publ Esp Instit Ocean São Paulo* 10(1-2): 189-198.

Soares LSH, Vazzoler AEAM 2001. Diel changes in food and feeding activity of sciaenid fishes from the southwestern Atlantic, Brazil. *Rev Bras Biol* 61(2): 197-216. doi: http://dx.doi.org/10.1590/S0034-71082001000200004.

Soares MSC, Barreiros JP, Sousa L, Santos RS 2002. Agonistic and predatory behaviour of the lizardfish *Synodus saurus* (Linnaeus, 1758) (Actinopterygii: Synodontidae) from the Azores. *Aqua – J Ichthyol Aquat Biol* 6(2) 53-60.

Soares MSC, Sousa L, Barreiros JP 2003. Feeding habits of the lizardfish *Synodus saurus* (Linnaeus, 1758) (Actinopterygii: Synodontidae), from the Azores. *Aqua – J Ichthyol Aquat Biol* 7(1): 29-38.

Soares R, Peixoto S, Bemvenuti C, Wasielesky W, D' Incao F, Murcia N, Suita S 2004. Composition and abundance of invertebrate benthic fauna in *Farfantepenaeus paulensis* culture pens (Patos Lagoon estuary, southern Brazil). *Aquaculture* 239(1-4): 199-215. doi: 10.1016/j.aquaculture.2004.05.041

Soares R, Peixoto S, Bemvenuti C, Wasielesky W, D' Incao F 2005a. Feeding rhythms and diet of *Farfantepenaeus paulensis* under pen culture in Patos Lagoon estuary, Brazil. *J Exp Mar Biol Ecol* 322 (2): 167-176. doi: http://dx.doi.org/10.1016/j.jembe.2005.02.019.

Soares R, Wasielesky W, Peixoto S, D' Incao F 2005b. Food consumption and gastric emptying of *Farfantepenaeus paulensis*. *Aquaculture* 250(1-2): 283-290. doi: 10.1016/j.aquaculture.2005.04.072.

Soares R, Peixoto S, Wasielesky W, D' Incao F 2006. Effect of different food items on the survival and growth of *Farfantepenaeus paulensis* (Pérez-Farfante 1967) postlarvae. *Aquacult Res* 37(14): 1413-1418. doi: 10.1111/j.1365-2109.2006.01574.x

Stevens BJ, Armstrong DA, Cusimano R 1982. Feeding habits of the dungeness crab *Cancer magister* as determined by index of relative importance. *Mar Biol* 72(2):135-145. doi: 10.1007/BF00396914.

Stoner AW, Zimmerman RJ 1988. Food pathways associated with penaeid shrimps in a mangrove-fringed estuary. *Fish Bull* 86(3): 543-551.

Sweatman HPA 1984. A field study of the predatory behavior and feeding rate of a piscivorous coral reef fish, the lizardfish *Synodus englemani*. *Copeia* 1984(1): 187–194.

Topp RW, Hoff Jr. FH 1972. Flatfishes (Pleuronectiformes) - Memoirs of the Hourglass cruises. Florida Dept Natl Resour, Saint Petersburg.

Vázquez-Bader AR, Laguarda-Figueras A, Gracia A, Sólis-Marín FA, Celaya-Hernández EV, Durán-González A 2008. Seasonal changes in the density and species composition of the epifaunal echinoderms recorded from the southwestern Gulf of Mexico. *Rev Biol Trop* 56: 297-310.

Vazzoler G 1975. Distribuição da fauna de peixes demersais e ecologia dos Sciaenidae da plataforma continental brasileira, entre as latitudes 29º21S (Tôrres) e 33º41S (Chuí). *Bol Inst Ocean* 24: 85-169.

Verity PG 1998. Why is relating plankton community structure to pelagic production so problematic? *S Afr J Mar Sci* 19(1): 333-338. doi: 10.2989/025776198784126962.

Verling E, Crook AC, Barnes DKA, Harrison SSC 2003. Structural dynamics of a sea-star (*Marthasterias glacialis*) population. *J Mar Biol Ass UK* 83(3): 583-592. doi: 10.1017/S0025315403007513h.

Wellenreuther M, Connell SD 2002. Response of predators to prey abundance: separating the effects of prey density and patch size. *J Exp Mar Biol Ecol* 273(1): 61-71. doi: 10.1016/S0022-0981(02)00145-4.

Williams MJ 1981. Methods for analysis of natural diet in portunid crabs (Crustacea: Decapoda: Portunidae). *J Exp Mar Biol Ecol* 52(1) 103-113. doi: http://dx.doi.org/10.1016/0022-0981(81)90174-X.

Wootton RJ 1992. Fish Ecology. Chapman & Hall, New York.

Wootton RJ 1998. Ecology of Teleost Fishes. 2nd edit. Kluwer Academic Publishers, Dordrecht.

Yazdani GM 1969. Adaptation in the jaws of flatfish (Pleuronectiformes). *J Zool* 159(2): 181-222. doi: 10.1111/j.1469-7998.1969.tb03078.x.

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

Farfantepenaeus paulensis Pérez-Farfante, 1967: Silva & D'Incao 2001; Albertoni *et al.* 2003; Lemos *et al.* 2004; Soares *et al.* 2004, 2005a, 2005b, 2006; Lunardon-Branco *et al.* 2006; Abreu *et al.* 2007; P. Jørgensen *et al.* 2009.

Dardanus insignis (De Sausure, 1858): Lunardon-Branco *et al.* 2006; V. Fransozo *et al.* 2007; A. Fransozo *et al.* 2008.

Hepatus pudibundus (Herbst, 1785): Petti *et al.* 1996; Mantelatto & Petrarco 1997; Lunardon-Branco *et al.* 2006; Santos & Pires-Vanin 2004.

Callinectes ornatus Ordway, 1863: Petti *et al.* 1996; Amâncio 2000; Mantellato & Christoffoleti 2001; Branco *et al.* 2002; Branco & Verani 2006; Lunardon-Branco *et al.* 2006.

Achelous spinimanus (Latreille, 1819): Petti *et al.* 1996; Lunardon-Branco *et al.* 2006.

Luidia clathrata (Say, 1825): Schwartz & Porter 1977; Lawrence & Dehm 1979; McClintock & Lawrence 1981, 1984, 1985; Penchaszadeh & Lera 1983; Penschaszadeh & Molinet 1983; Lunardon-Branco *et al.* 2006.

Luidia senegalensis (Lamarck, 1816): Lima-Verde & Matthews 1969; Halpern 1970; Penchaszadeh & Lera 1983; Lunardon-Branco *et al.* 2006.

Synodus foetens (Linnaeus, 1766): Phelps 1997; Kagiwara & Abilhoa 2000; Chávez-López *et al.* 2005; Cruz-Escalona *et al.* 2005; Lunardon-Branco *et al.* 2006.

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.

Isopisthus parvipinnis (Cuvier, 1830): Soares & Vazzoler 2001; Lunardon-Branco *et al.* 2006.

Paralonchurus brasiliensis (Steindachner, 1875): Braga *et al.* 1985; Soares & Vazzoler 2001; Branco *et al.* 2005; Lunardon-Branco *et al.* 2006.

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

Etropus crossotus Jordan & Gilbert, 1882: Soares *et al.* 1993; Lunardon-Branco & Branco 2003; Reichert 2003; Bornatowski *et al.* 2004; Lunardon-Branco *et al.* 2006.