Food web characterization based on δ^{15}N and δ^{13}C reveals isotopic niche partitioning between fish and jellyfish in a relatively pristine ecosystem

Renato Mitsuo Nagata[1],*, **Marcelo Zacharias Moreira[2], Caio Ribeiro Pimentel[3],**
André Carrara Morandini[1]

[1]Departamento de Zoologia, Instituto de Biociências, Universidade de São Paulo, Rua do Matão, trav. 14, n. 101, 05508-090, São Paulo, Brazil
[2]Laboratório de Ecologia Isotópica, Centro de Energia Nuclear na Agricultura, Campus Luis de Queiroz, Universidade de São Paulo, Piracicaba, Brazil
[3]Departamento de Oceanografia Biológica, Instituto Oceanográfico, Universidade de São Paulo, Brazil

ABSTRACT: Human-induced stresses on the marine environment seem to favor some jellyfish species to the detriment of other competitors such as planktivorous fishes. In pristine ecosystems, trophic relationships among these consumers are poorly understood. We determined stable carbon and nitrogen isotope signatures of representative consumers in the relatively pristine ecosystem of the Cananéia Estuary, Brazil, in order to understand the food web structure. We described isotopic niche breadth, position, and overlaps between fish and jellyfish (including comb jelly) species. Most of the δ^{13}C values suggest that phytoplankton is the major carbon source, especially for pelagic consumers. Sessile benthic invertebrates had enriched δ^{13}C values, suggesting a contribution of microphytobenthic algae. Seasonal variation of values was significant only for ^{13}C, with different patterns for pelagic and benthic organisms. Isotopic niche breadth of some jellyfishes was wider than those of fish species of the same trophic group, possibly as a consequence of their broad diets. Isotopic niche overlaps of fish and jellyfish species were related to: (1) trophic diversity, since planktivorous species occupied niches distinct from macroinvertebrate/fish feeders; and (2) life stages, since isotopic niche partitioning pattern can change during species ontogeny. Replacement of declining populations of fish by jellyfish competitors probably depends on the pool of other compensatory species, as well as on reproductive, growth, and feeding performance of other consumers. Description of isotopic niches provides a general picture of trophic roles, interactions and the degree of functional redundancy among species, allowing an evaluation of possible directions of community shifts resulting from the removal or proliferation of keystone consumers.

KEY WORDS: Gelatinous zooplankton · Trophic position · Forage fish · Dietary overlap · Stable isotopes

INTRODUCTION

Although some controversies exist concerning changes in the number and extension of jellyfish blooms (Condon et al. 2012, Gibbons & Richardson 2013), historical data from some parts of the world show that jellyfish populations are increasing (Brotz et al. 2012, Purcell 2012). Factors whereby jellyfish may increase have been widely discussed, and it has been speculated that human-induced stresses to the marine environment (eutrophication, species introduction, climate change, overfishing) seem to favor the proliferation of gelatinous zooplankton species (Purcell 2012). Trophic interactions may account for these increases, since evidence suggests that the depletion of fish stocks has shifted some ecosystems

from planktivorous fish- to jellyfish-dominated, such as in the northern Benguela Current (Richardson et al. 2009).

Because many jellyfish feed on fish eggs and larvae, top-down control is a possible explanation for the inverse relationship between these populations, as first stated by Möller (1980). The predation impact of jellyfish species can be high, with some species like *Chrysaora melanaster* in the Bering Sea and *Aurelia* sp. in Japan consuming 33% d^{-1} and 26% d^{-1}, respectively, of standing stock zooplankton (Brodeur et al. 2002, Uye & Shimauchi 2005). Jellyfish species have diverse feeding habits, yet their ecological roles are often oversimplified (Condon et al. 2012). Species occupy a variety of trophic levels, feeding on micro- and mesozooplankton, epibenthic invertebrates, other jellyfish, and fish (Purcell 1997), and potentially use the same resources as many other consumers (such as crustaceans and fishes). Trophic overlap between planktivorous jellyfish and fish populations was demonstrated in studies applying stomach-content methods (Purcell & Grover 1990, Purcell & Sturdevant 2001) and stable-isotope analyses (Brodeur et al. 2002, Brodeur et al. 2008, Shoji et al. 2009). Richardson et al. (2009) argued that in ecosystems dominated by fish, jellyfish populations are kept in check through predation and competition. Nevertheless, jellyfish may overtake fish competitors when overfishing opens a vacant niche for the former, but also under some conditions such as: low oxygen concentrations, when feeding performance of fish decreases (Shoji et al. 2005); and low visibility, when visual foraging of fish is hampered (Eiane et al. 1999).

In order to understand the ecosystem's response to the removal of a consumer, it is important to examine the trophic position of several keystone species, which probably will fill that vacated trophic niche. Stable Isotope Analysis (SIA) has been used over the past ~25 yr to describe food web structures of different ecosystems, leading to huge advances in this field (Layman et al. 2012). SIA data integrate spatial and temporal information and provide long-term evidence of trophic relationships that cannot be gleaned from 'snapshot' dietary analysis (Layman et al. 2012). Although stomach-content analyses provide valuable insights into feeding relationships, they have analytical limitations, since they require many samples and do not always reflect the assimilated food. Studies with SIA can evaluate the trophic structure of many coastal ecosystems, by investigating issues such as the primary sources of organic matter, as well as the energy pathways through a large number of consumers (Sherwood & Rose 2005, Layman et al. 2012). The position of consumers in the isotopic space (δ-space) also illustrates some aspects of the actual ecological niche, such as habitat and resources used, in the concept of the 'isotopic niche' (Newsome et al. 2007). The isotopic values of a given group of community members can be analyzed to quantify aspects of their trophic ecology, such as species niche breadth and niche overlaps (Newsome et al. 2007, Jackson et al. 2011, Newsome et al. 2012).

The productive waters of estuaries are used by different fish species (including coastal and oceanic populations) to feed and as nurseries (Potter et al. 2001). Because larvae and juveniles of most fish species are zooplanktivorous, regardless of what they eat in adulthood (Bond 1996), it is reasonable to suggest that the trophic niche of juveniles of many fish species overlaps with that of zooplanktivorous jellyfish. The South Brazilian Bight (SBB) (23° to 28°S) is a transitional region of mixed climate and faunal components with warm-temperate characteristics (Heileman & Gasalla 2008). The coast of the central SBB receives outflows from large adjacent estuarine systems (Cananéia and Paranaguá) and harbors high zooplankton biomasses and ichthyoplankton densities (Lopes et al. 2006). A relatively high diversity of large jellyfishes (10 species of Cubozoa and Scyphozoa) (Morandini et al. 2005) with distinct trophic roles is present. A historical baseline of field population abundances and seasonality is lacking for jellyfish (but see Nogueira et al. 2010), although a few studies have mentioned episodes of high biomasses in nearby areas (Moreira 1961, Mianzan & Guerrero 2000, Graça-Lopes et al. 2002, Nagata et al. 2009). Because of the good conservation status of the Cananéia Lagoon Estuarine System (CLES) area (MMA 2007), an analysis of its food web structure represents a unique opportunity to understand the trophic role of jellyfish at lower levels of anthropogenic stresses that are presumed to favor their proliferation.

This study, thus, aims to provide a general picture of the food web structure of the CLES based on ^{13}C and ^{15}N isotope signatures of species of mesozooplankton, gelatinous zooplankton, demersal macrofauna, and nekton. We analyzed isotope data in order to answer the following questions: (1) Knowing that the main sources of organic matter in the CLES, phytoplankton, mangrove litterfall, and microphytobenthos (Schaeffer-Novelli et al. 1990), have distinct δ^{13}C values, what is their respective contribution to the consumers of this ecosystem? (2) How much do isotopic signatures vary during an annual cycle? (3) Based on recently developed Bayesian statistical

tools for SIA, do jellyfish and other consumers (mainly fish) occupy similar isotopic niches in this ecosystem? For this last question, we compared isotope data of known dominant pelagic species (jellyfish and fish consumers) to assess isotopic niche breadth, seasonal variability, and possible overlaps. Note that in this article we use the term jellyfish synonymously with the term gelatinous zooplankton, i.e. we include ctenophores as well as cnidarians.

MATERIALS AND METHODS

Study site

The Cananéia Lagoon Estuarine System (CLES) is located in the state of Sao Paulo, Brazil, in a wide coastal plain surrounded by mountains of the Serra do Mar. The CLES is a mangrove-bordered estuary with an area of 100 km^2 of which 52 km^2 are covered by mangroves (Schaeffer-Novelli et al. 1990). Terrestrial organic matter comes from the Ribeira River valley and from several small creeks. Primary production in estuary waters is phytoplankton-based with values ranging from 0.10 to 0.80 g C m^{-2} d^{-1} (Tundisi et al. 1973), but probably also influenced by the export of materials from mangrove forest (Knoppers & Kjerfve 1999). The contribution of the C$_4$ salt-marsh cordgrass *Spartina alterniflora* to the estuary total production is lower because of its limited distribution (Schaeffer-Novelli et al. 1990). Another important source of primary production is the microphytobenthos, based on high values of chlorophyll *a* (870 µg cm^{-2}) found in the sediments (Schaeffer-Novelli et al. 1990). Mesozooplankton densities are high year-round, with summer increases (Ara 2004). Copepods account for ~84.8% (annual mean = 3.33 × 10^4 org m^{-3}) of the mesozooplankton organisms (Ara 2004). The fish fauna in CLES is represented by 68 species, with Carangidae (10 species), Ariidae (7), and Engraulidae (7) the best-represented families (Tundisi & Matsumura-Tundisi 2001). Artisanal fisheries within the estuary target many fish species such as mullet *Mugil platanus*, snook *Centropomus* spp., and whitemouth croaker *Micropogonias furnieri*; and invertebrates such as the mangrove crab *Ucides cordatus*, oysters *Crassostrea brasiliana*, and mussels *Mytella falcata* (Mendonça & Katsuragawa 2001). The CLES is part of the Cananéia, Iguape, and Paranaguá Lagoon Estuarine System, which is surrounded by the largest continuous remnant of Brazil's Atlantic rainforest (MMA 2007). The area has been proclaimed a Biosphere Reserve Biodiversity
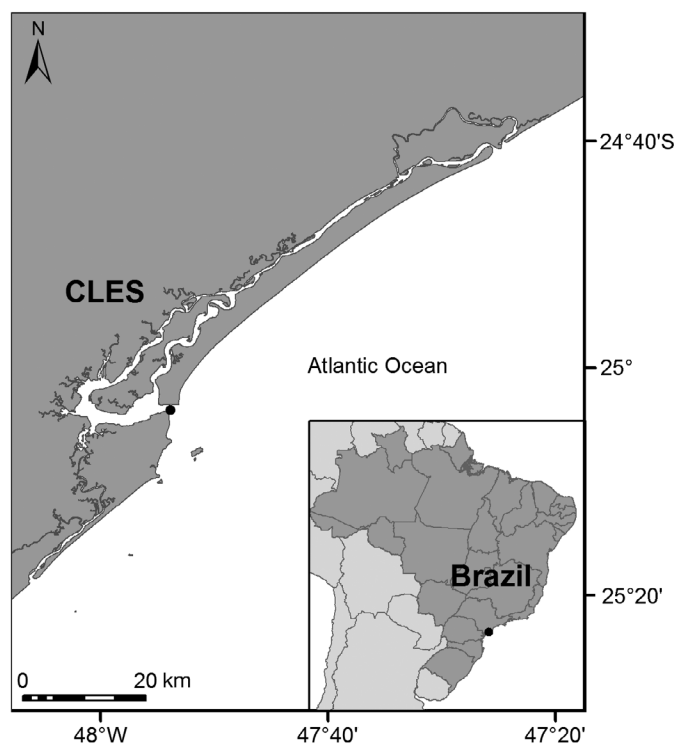
Hotspot, and a Natural World Patrimony Site for scientific knowledge and the conservation of human values and traditional knowledge (UNESCO 1999).

Fig. 1. Study site with sampling station (●) at the mouth of the Cananéia Lagoon Estuarine System (CLES)

Sampling and processing

Sampling was carried out from a small boat in April (autumn), July (winter), October (spring) 2011, and January (summer) 2012, in the Cananéia Sea, between the islands of Cardoso and Comprida, at the mouth of the estuary (Fig. 1) during high tide. We sampled at the mouth of the estuary because we expected to find here a more diverse assemblage of gelatinous species and co-occurring fish species than further up the estuary system, since few large jellyfish species are found in upper estuaries of the SBB (except for *Chrysaora lactea* and *Mnemiopsis leidyi*) (Morandini 2003, Nogueira et al. 2010). Mesozooplankton was collected with a plankton net (200 µm mesh size), and larger organisms with a bottom trawl net (1 cm mesh size). Plankton samples were split into 2 parts: one, with all organisms, was immediately frozen (−10°C) after collection; the other was sorted under the stereomicroscope in the laboratory to obtain ~1 mg per species/taxonomic group,

and then frozen. For fish species, 2 to 3 g of muscle tissue was removed from between the dorsal and caudal fins and stored in plastic tubes and frozen (−10°C), and the total length (nearest cm) was measured for each specimen. For macroinvertebrates, we discarded the guts and collected samples from different tissues depending on the group: leg muscle of crabs, caudal muscle of shrimp, peduncle core of sea pansies *Renilla reniformis*, gonads of echinoderms, tentacle core of squids *Lolliguncula brevis*, whole colony of bryozoans, and pieces of the umbrella for jellyfishes or of the ectoderm of the lobes of comb jellies *Mnemiopsis leidyi*, and then frozen (−10°C). Samples were dried to constant weight in a drying oven at 50°C (96 h for gelatinous zooplankton and 48 h for other animals) and ground to a fine powder using a mortar and pestle. Mesozooplankton samples were also split into 2 parts: one was used to estimate $\delta^{15}N$ and was not acidified, and the other was used to estimate $\delta^{13}C$ and was soaked in 1 N HCl for 3 h in order to remove carbonates and exoskeletons, and the samples then re-dried. Between 0.5 and 2 mg of each powdered sample was stored in tin capsules. The isotope ratios were determined at the Laboratory of Isotope Ecology (Universidade de São Paulo, Brazil). Each sample was oxidized in an elemental analyzer coupled with a mass spectrophotometer, and with the resulting CO_2 and N_2, the ratio of ^{15}N and ^{13}C was measured. The values were expressed in delta notation (δ‰), defined as parts per thousand, and the change in relation to international reference materials as the formula: $\delta^{13}C$ (or $\delta^{15}N$) = $1000 \times [(R_{sample} - R_{reference}) - 1]$, where $R = {}^{13}C/{}^{12}C$ (or $^{15}N/^{14}N$). The reference materials were Peedee Belemnite (PDB) for ^{13}C and atmospheric nitrogen for ^{15}N. The samples (10%) were analyzed in duplicate; the standard mean error was 0.11‰ for $\delta^{13}C$ and 0.12‰ for $\delta^{15}N$ (n = 45).

Trophic level estimation

Several studies have demonstrated that enrichment factors can vary for $\delta^{15}N$, depending on the species, diet, and other factors (see 'Discussion'). However, these factors could not be controlled in our study. In order to provide a broad overview of the trophic structure of CLES, we estimated the trophic level of the organisms relative to the calanoid copepod *Parvocalanus crassirostris*, which we assumed to occupy trophic level (TL) 2 (primary consumer), according to a previous study (Eskinazi-Sant'Anna 2000). We then calculated the relative trophic level of consumers, following Post (2002):

$$TL = \lambda + (\delta^{15}N_{consumer} - \delta^{15}N_{P.\ crassirostris})/\Delta \qquad (1)$$

where λ is the trophic position of *P. crassirostris* (TL: 2); $\delta^{15}N_{consumer}$ is the value of each consumer, which is measured directly; and Δ is the enrichment in $\delta^{15}N$ per trophic level. We assumed a constant enrichment factor (Δ) of 3.4‰, according to Minagawa & Wada (1984).

Distinctive isotopic values of the main primary producers allow an evaluation of the main carbon sources for consumers. It was not possible to directly determine the stable isotope signatures of pelagic phytoplankton and microphytobenthos, and thus models to quantify relative contribution of primary sources (Layman et al. 2012) were not employed. We used $\delta^{13}C$ values of particulate organic matter (POM) (−19.40‰), measured at the same site, from Barcellos et al. (2009), as an indication of phytoplankton. For microphytobenthos, we used the value of −13‰, since benthic algae have enriched $\delta^{13}C$ values (6‰ on average), in relation to phytoplankton (France 1995). Values of mangrove leaves measured here were depleted (−27.86‰) in relation to phytoplankton and microphytobenthos (see Table S1 in the Supplement at www.int-res.com/articles/suppl/m519 p013_supp.pdf for average stable isotope values by taxon). Relative position of consumers and resources on $\delta^{13}C$ and $\delta^{15}N$ biplots were evaluated in order to make general inferences on carbon sources for consumers.

We classified the species into trophic guilds (primary producers, zooplankton, gelatinous zooplankton, sessile benthic invertebrates, vagile benthic invertebrates, benthic fish, demersal fish, bentho-pelagic fish, cephalopods, and cetaceans) according to taxonomy and habitat (following Sherwood & Rose 2005). To identify general patterns of isotopic values of species, a cluster analysis was performed. Mean $\delta^{13}C$ and $\delta^{15}N$ values of species were used to apply a hierarchical cluster analysis, with group average linking over a matrix of Euclidean distances between species. This approach created a cluster that gathers groups of species with similar patterns of isotopic values. We identified the main clusters at <2.5 Euclidian metric distance (EMD); species not clustered within these groups at <7 EMD (Alcyonacea sp., *Penilia avirostris* and *Rhizophora mangle*) were excluded from the analysis. Mean isotopic values of species in each cluster were grouped and plotted in $\delta^{13}C$ and $\delta^{15}N$ biplots. This grouping aimed to provide an overview of consumer groups with similar isotopic values in this ecosystem for general exploratory purposes, such as comparison with the previous classification of trophic guilds.

MANOVA was also used to test seasonal differences in the isotopic signatures of $\delta^{13}C$ and $\delta^{15}N$ for taxa present during the 4 seasons. When significant ($p < 0.05$) differences were found, ANOVA was used to separately test interspecific differences in $\delta^{13}C$ and $\delta^{15}N$. Normal distribution (Shapiro-Wilk's W test) and homogeneity of variances (Bartlett test) were tested before these analyses. Deviations from the normal distribution or homogeneous variances were corrected by log-transforming the data (absolute values were used for $\delta^{13}C$), otherwise Kruskal-Wallis tests were used if necessary.

The position of a certain species in these $\delta^{13}C/\delta^{15}N$ biplots reflects the isotopic niche (δ-space), which can be considered a representation of its ecological niche (Newsome et al. 2007). In order to evaluate the total trophic-niche breadth, we applied quantitative metrics using a Bayesian approach (Jackson et al. 2011). We calculated the Standard Ellipse Area, corrected for small sample sizes (SEA_c), from individual measurements, which are bivariate equivalents to standard deviations in a univariate analysis (Jackson et al. 2011). To evaluate possible niche overlap between jellyfish and other consumers of the same trophic group (classified by cluster analysis), we estimated the trophic-niche overlap as the percent of overlapping SEA_c between these species, applying step size = 5 (Parnell et al. 2008). These analyses were performed using the Stable Isotope Analysis in the R (SIAR) package (Parnell et al. 2008) for the R statistical computing package (R Development Core Team 2011).

RESULTS

We analyzed the isotope values of 62 taxa collected seasonally (see Table S2 in the Supplement). The signatures (mean ± standard deviation) of the most important taxa of each trophic guild are shown in Fig. 2. For the carbon isotope, the largest variation was found for the primary producers, ranging from −27.87‰ in mangrove leaves to −13‰ for macroalgae.

Among mesozooplankton, $\delta^{13}C$ ranged over 11 δ units, with wider variation in values (as indicated by the SD) for the pooled taxa (e.g. brachyuran zoeae, fish eggs) and *Penilia avirostris* than those that were separated at species level (Fig. 2). Among benthic invertebrates, values ranged over 10.88 δ units, with more enriched values for sessile benthic invertebrates (mean: −11.85‰) (Fig. 2). Among gelatinous zooplankton and fish, variation of $\delta^{13}C$ was narrower:

values ranged over 5.84 δ and 7.79 δ units. On one hand, most (~70%) $\delta^{13}C$ data for pelagic groups (mesozooplankton, gelatinous and pelagic fish) varied from −21 to −17‰ (Fig. 2), which suggests a major contribution by phytoplankton to organic production. On the other hand, depleted $\delta^{13}C$ values, indicating a mangrove contribution, were detected in just a few samples of brachyuran zoeae ($\delta^{13}C$: −24 to −27‰).

For the nitrogen isotope, the highest $\delta^{15}N$ variation was observed among mesozooplankton (~13 δ units). Of the 4 trophic levels, most mesozooplankton taxa and vagile and sessile benthic invertebrates were below TL 3. Most gelatinous zooplankton, cephalopods, and fish taxa were placed between TL 3 and 4. The tucuxi dolphin *Sotalia guianensis* had the most enriched $\delta^{15}N$, and was the sole occupant of TL 4 (TL: 4.3) (Fig. 2).

Cluster analysis

The cluster analysis identified distinct groups of consumers using carbon and nitrogen isotopic signatures (Fig. 3), with some similarities to the trophic guilds (Fig. 2). The cetacean *S. guianensis* is the only species of branch A. Sessile benthic invertebrates, which were characterized by enriched $\delta^{13}C$, were grouped into clusters F (species occupying a higher TL) and G (species in a lower TL and also Microphytobenthos) (Fig. 3).

Mesozooplankton species were grouped into clusters E and D. Cluster E occupied the lowest TL among all consumers and grouped herbivorous zooplankton and phytoplankton. Cluster D grouped omnivorous and carnivorous zooplankton, and the ctenophore *Mnemiopsis leidyi*. Cluster C grouped conspicuous benthic (*Xiphopenaeus kroyeri* and *Callinectes danae*) and planktonic (*Lucifer faxoni*) decapods. These species occupied lower trophic levels and were enriched in $\delta^{13}C$ in relation to other large crustaceans (Fig. 2).

Gelatinous zooplankton species (except *Mnemiopsis leidyi*) were grouped with fish species in the large cluster B, which also grouped some consumers in a higher TL (Fig. 3). Cluster B was subdivided into clusters B1, B2, B3, and B4. Gelatinous species occupied distinct positions in B, with at least one species in each subgroup of B. Cluster B1 grouped benthic invertebrate feeders and piscivore species, such as the limnomedusa *Olindias sambaquiensis*, the catfish *Cathropsis spixii*, and the squid *Lolliguncula brevis*. Cluster B2 grouped planktivo-
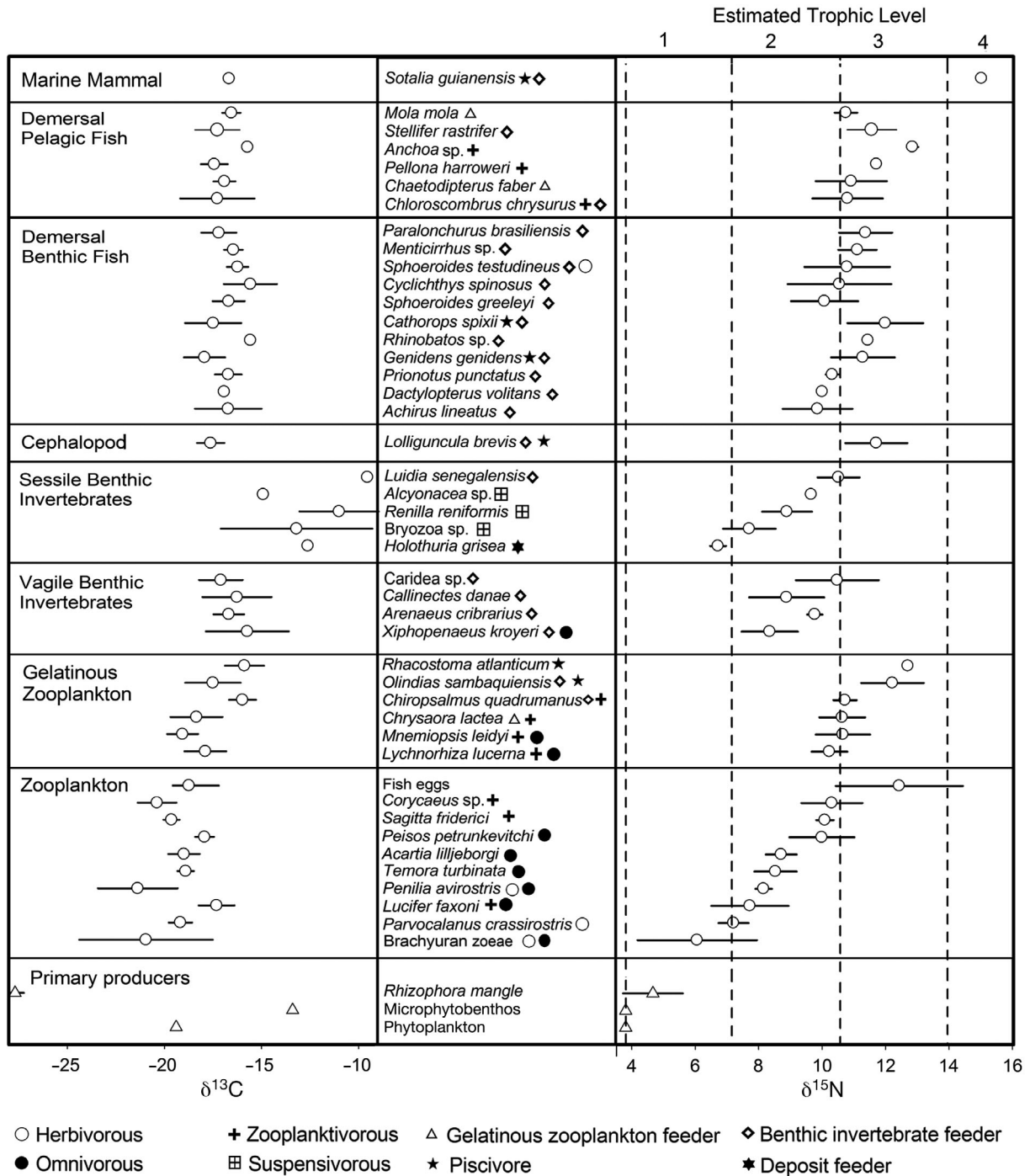
Fig. 2. Isotope signatures (mean ± SD) for the most representative taxa of the Cananéia Lagoon Estuarine System. Data presented for each trophic guild, trophic-level estimates, and feeding habits (symbols) according to the literature

rous species, such as the scyphomedusae *Chrysaora lactea* and *L. lucerna*, and the fish *Chloroscombrus chrysurus*, as well as benthic invertebrate feeders such as the catfish *Genidens genidens* and the lined sole *Achirus lineatus*. Cluster B3 grouped fish and invertebrates of benthic and demersal habits, except for *Mola mola* and *Chaetodipterus faber* which are pelagic fish. Cluster B4 grouped the hydromedusa *Rhacostoma atlanticum* and the fish *Anchoa* spp., which are pelagic species in the highest TL among fish and invertebrate consumers (Fig. 2).
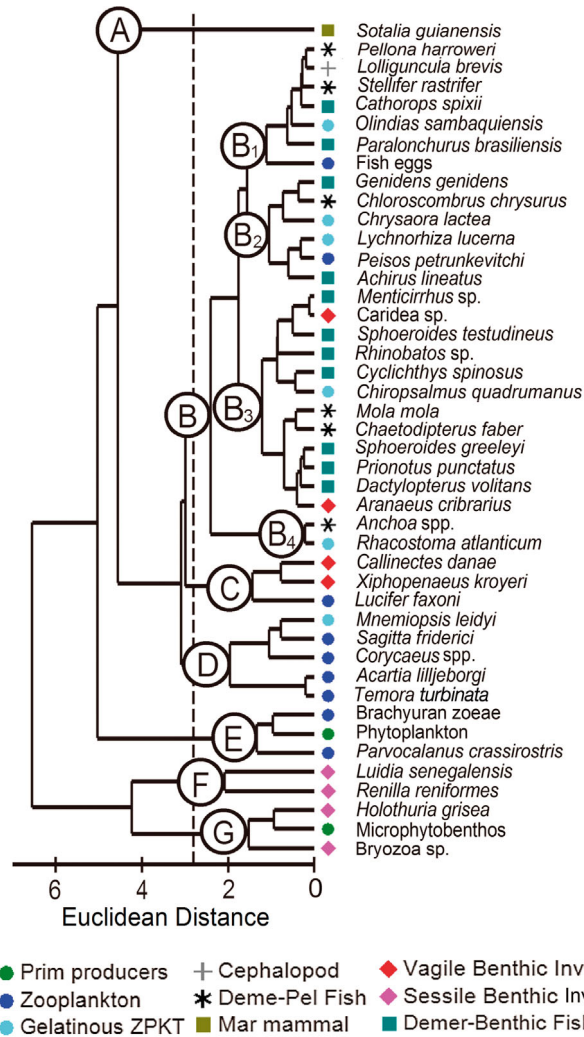
Fig. 3. Hierarchical cluster analysis (group-average method and Euclidean distances) of consumers from the Cananéia Lagoon Estuarine System, Brazil, based on mean values of $\delta^{13}C$ and $\delta^{15}N$. Capital letters indicate the main clusters at 2.5 Euclidean metric distance and symbols indicate the classification by trophic guilds from Fig. 2

Fig. 4. $\delta^{13}C$ and $\delta^{15}N$ (mean ± SD) and trophic-level estimates of trophic groups of consumers from the Cananéia Lagoon Estuarine System, Brazil. The groups (letters in parentheses) were defined by a hierarchical cluster analysis (see Fig. 3)

microphytobenthos (Fig. 4). Herbivorous and carnivorous zooplankton, as well as planktivorous-benthic feeders, piscivorous-macroinvertebrate feeders, and cetaceans were aligned with phytoplankton carbon (Fig. 4). Some groups lying between phytoplankton and microphytobenthos such as decapods occupying a lower trophic level, benthic-demersal consumers, and pelagic consumers of a higher trophic level possibly receive contributions from both carbon sources (Fig. 4).

Seasonal variation

We observed seasonal differences (MANOVA, $F =$ 20.861, $p < 0.001$) in the isotope values of pooled samples of pelagic organisms that occurred in all seasons (*Acartia lilljeborgi*, *Mnemiopsis leidyi*, *Lychnorhiza lucerna*, *Stellifer rastrifer*, *Chloroscombrus chrysurus*) and total mesozooplankton. In the univariate analysis, only $\delta^{13}C$ differed among seasons (ANOVA, $F = 16.13$, $p < 0.001$), with the most depleted values in the spring (Tukey test, $p < 0.001$). In tests for $\delta^{13}C$ of each species, *S. rastrifer* had no seasonal differences, while *A. lilljeborgi* (ANOVA, $F =$ 7.25, $p = 0.003$, Tukey test, $p < 0.05$), total mesozooplankton (Kruskal-Wallis, $H = 17.25$, $p < 0.001$), and

Trophic groups from Cananéia Estuarine system

Mean isotope values ($\delta^{13}C$ and $\delta^{15}N$) of species in each cluster were plotted along with the main primary sources of carbon at the mouth of CLES to provide a general picture of the food web structure (Fig. 4). The main primary producers were separated by ~6 δ units of ^{13}C. Consumers occurred near values of phytoplankton and microphytobenthos. Similarities to mangrove samples were absent. Sessile benthic invertebrates of lower and higher trophic levels clearly rely on benthic carbon of
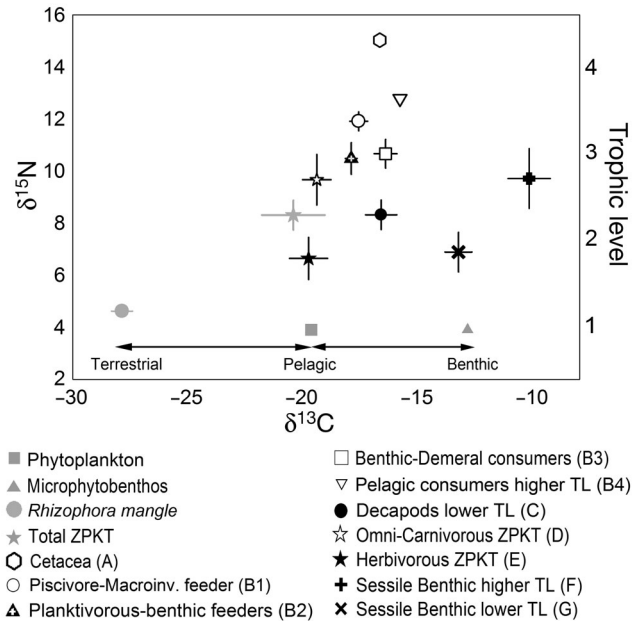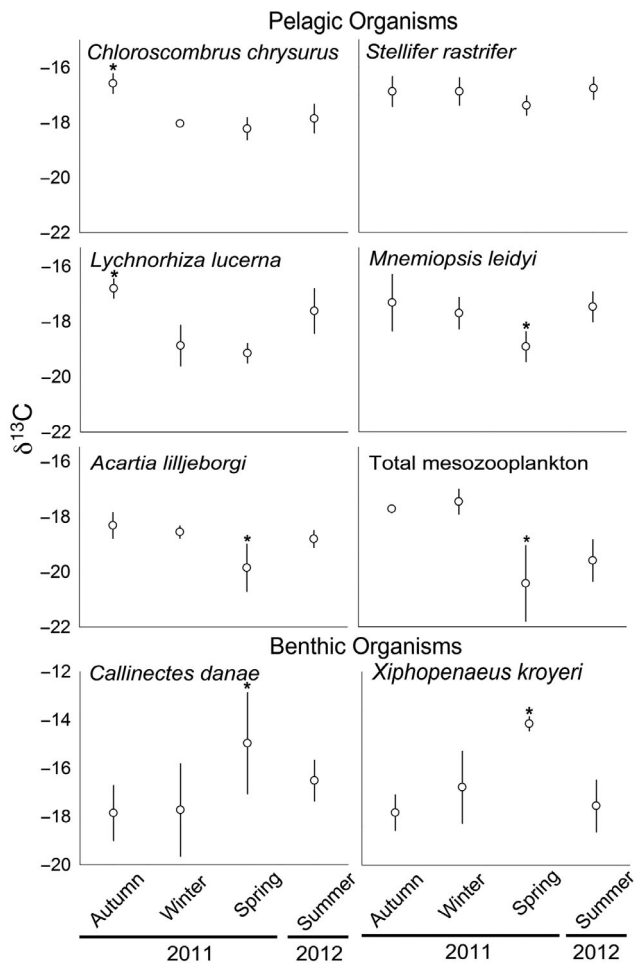
Fig. 5. Seasonal variation of $\delta^{13}C$ in pelagic and benthic organisms. *p < 0.05

$M.\ leidyi$ (ANOVA, $F = 5.12$, p < 0.01, Tukey test, p < 0.05) had more depleted $\delta^{13}C$ in spring, and $L.\ lucerna$ (ANOVA, $F = 38.24$, p < 0.001, Tukey test, p < 0.05) and $C.\ chrysurus$ (ANOVA, $F = 12.60$, p < 0.001; Tukey test, p < 0.05) had enriched values in autumn (Fig. 5). Among the benthic organisms, $Callinectes\ danae$ (ANOVA, $F = 3.36$, p = 0.047) and $Xiphopenaeus\ kroyeri$ (ANOVA, $F = 12.82$, p < 0.001, Tukey test, p = 0.051) showed enriched $\delta^{13}C$ in spring (Fig. 5).

Isotopic niche of jellyfish and potential competitors

The isotopic location of jellyfish species differed substantially. The macroinvertebrate/fish feeder $Olindias\ sambaquiensis$ (see trophic categories in Fig. 2) occupied an upper area of the biplot, whereas planktivorous jellyfishes $Mnemiopsis\ leidyi$, $Lychno$-

$rhiza\ lucerna$, and $Chrysaora\ lactea$ dominated an intermediate-lower area (Fig. 6A,B). The SEA_c of $O.\ sambaquiensis$ and $C.\ lactea$ was wider than most all other consumers in their trophic groups (Table 1, Fig. 6). The SEA_c of $O.\ sambaquiensis$ did not overlap with $L.\ lucerna$ and $M.\ leidyi$, and had a minimal overlap with $C.\ lactea$ comprising 2.5% of its SEA_c (Table 1, Fig. 6A,B). The SEA_c of zooplanktivorous jellyfish had a high degree of overlap. $C.\ lactea$ had overlaps of 61.3 and 46.9% of its SEA_c with $L.\ lucerna$ and $M.\ leidyi$, respectively. The overlaps between $L.\ lucerna$ and $M.\ leidyi$ were relatively low, representing 26.1 and 31% of their SEA_c's (Table 1, Fig. 6A,B). Table S2 presents detailed population metrics of the species mentioned in Fig. 6.

The trophic-niche overlap was high among animals of the same cluster (see Fig. 4), which possibly reflects similarities of their feeding habits. The SEA_c of the jellyfish $O.\ sambaquiensis$ overlapped with 100% of $Pellona\ harroweri$ SEA_c and with most of $S.\ rastrifer$ (63%), $L.\ brevis$ (78.3%), and 'other consumers of cluster B1' (73.2%) SEA_c's (Fig. 6C,D). Species of cluster B2 occupied an intermediate-lower area of the biplot (Fig. 6E,F), which possibly reflects feeding habits on lower trophic levels. The SEA_c of the lined sole $A.\ lineatus$ did not overlap with $G.\ genidens$, but all other pairs of species of B2 had overlaps among themselves (Table 1). The SEA_c of $A.\ lineatus$ had the lowest overlap with other species (11% on average), while the SEA_c of the scyphomedusa $L.\ lucerna$ had the highest overlap (48.5% on average) with other species.

The upper part of the SEA_c of $L.\ brevis$, $S.\ rastrifer$, 'other consumers of Cluster B1', $Genidens\ genidens$, and $Chloroscombrus\ chrysurus$ overlapped with the jellyfish $O.\ sambaquiensis$, whereas the lower part overlapped with the zooplanktivorous jellyfishes $C.\ lactea$ and $L.\ lucerna$ (Table 1). In order to evaluate if this pattern is a consequence of ontogenetic shifts of niche occupancy, we evaluated a possible relationship between body size and $\delta^{15}N$. For most species, a significant relationship was absent (see Fig. S1 in the Supplement). Nevertheless, body size explained a considerable amount of variation in $\delta^{15}N$, with increasing $\delta^{15}N$ as body size increased for $L.\ lucerna$ ($F_{1,29} = 10.22$, p < 0.01, $r^2 = 0.28$), $A.\ lineatus$ ($F_{1,11} = 5.87$, p < 0.05, $r^2 = 0.37$), $C.\ chrysurus$ ($F_{1,15} = 39.24$, p < 0.001, $r^2 = 0.74$), $Sphoeroides$ spp. ($F_{1,9} = 6.70$, p < 0.05, $r^2 = 0.46$), and 'other consumers of cluster B1' ($F_{1,7} = 5.47$, p < 0.05, $r^2 = 0.47$). This pattern demonstrates that some species explore distinct trophic levels and exhibit a pattern of trophic niche overlap dependent on the life cycle stage.
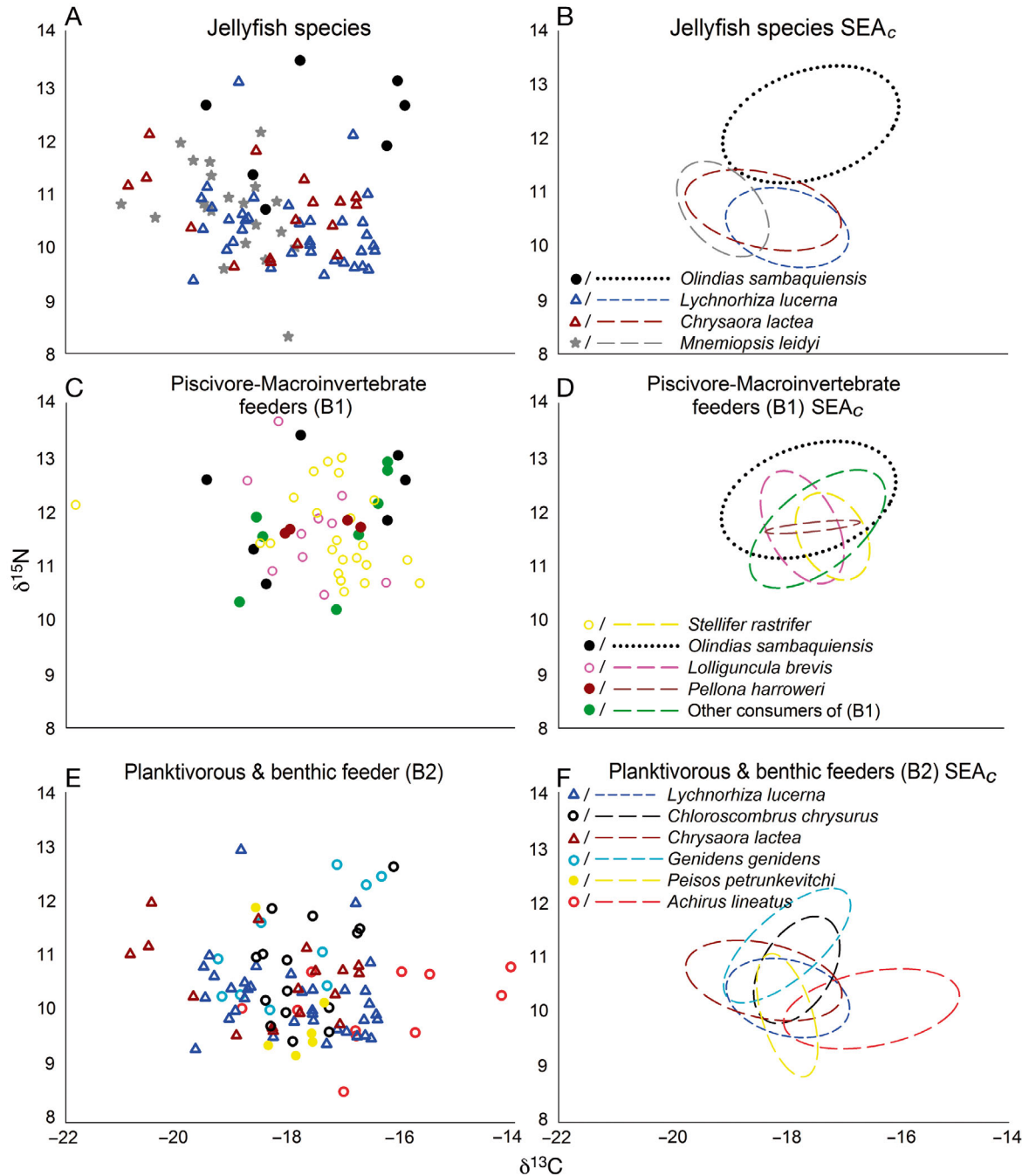
Fig. 6. (A) Biplots of isotope values of jellyfish species, and (B) their isotopic niche (as size-corrected Standard Ellipse Area, SEA$_c$) from the Cananéia Lagoon Estuarine System. Isotope values of jellyfish were plotted along with (C–F) other consumers of the same trophic group, according to the cluster analysis

DISCUSSION

Isotopic signatures of primary producers were similar to others found in subtropical regions (Bouillon et al. 2002). The designation of the value of −19.40‰ (from Barcellos et al. 2009) for phytoplankton $\delta^{13}C$ is indirectly supported by the $\delta^{13}C$ of the herbivore copepod *Parvocalanus crasirostris* (−19.18‰), and within the range expected for phytoplankton from tropical regions (from −22 to −18‰) (Peterson & Fry 1987). Since the carbon fixed by the main primary producers of the region (marine phytoplankton, microphytobenthos, and C_3 plants) have distinct $\delta^{13}C$ values, the carbon source for this ecosystem could be distinguished; $\delta^{13}C$ data of pelagic groups suggest major contribution by phytoplankton to organic pro-

Table 1. Trophic-niche width as the sample size-corrected Standard Ellipse Area (SEA$_c$) as δ units^2 of the main jellyfish species (in bold) and their potential competitors, and the overlap of their SEA$_c$ between pairs of species, as δ units^2

	SEA$_c$ (δ units^2)	Cluster	Overlap on SEA$_c$ (δ units^2)										
			O s	S r	L b	Ot B1	P h	L l	C l	C c	G g	A l	P p
Olindias sambaquiensis (n = 7)	5.07	B1											
Stellifer rastrifer (n = 24)	1.61	B1	1.01										
Lolliguncula brevis (n = 10)	2.20	B1	1.72	0.95									
Other B1 (*Paralonchurus* + *Cathorops*) (n = 8)	3.39	B1	2.48	1.31	1.63								
Pellona harroweri (n = 4)	0.23	B1	0.23	0.16	0.19	0.23							
Lycnorhiza lucerna (n = 30)	2.46	B2	0.00	0.00	0.09	0.40	0.00						
Chrysaora lactea (n = 17)	3.08	B2	0.13	0.00	0.22	0.67	0.00	1.89					
Chloroscombrus chrysurus (n = 16)	2.16	B2	0.59	0.52	0.95	1.27	0.11	1.22	1.40				
Genidens genidens (n = 10)	2.68	B2	1.49	0.87	1.30	2.01	0.20	0.82	1.24	1.25			
Achirus lineatus (n = 12)	3.45	B2	0.00	0.00	0.00	0.00	0.00	0.87	0.46	0.21	0.00		
Peisos petrunkevitchi (n = 6)	1.68	B2	0.00	0.00	0.28	0.00	0.00	1.17	0.92	0.90	0.41	0.39	
Mnemiopsis leidyi (n = 22)	2.07	D	0.00	0.00	0.00	0.03	0.00	0.64	1.44	0.18	0.56	0.00	0.14

duction. Despite the high production of mangrove litterfall (9.02 t ha^{-1} yr^{-1}) in CLES (Tundisi & Mat-sumura-Tundisi 2001), its importance to the total organic production at the mouth of the estuary must be minimal as well as in other similar mangrove-bordered systems (Heithaus et al. 2011). Nevertheless, it is important to mention that our samplings were spatially limited and probably do not represent inner regions of CLES. The contribution of mangrove litter should be higher in the upper estuary and near creeks, whereas in the mouth of the estuary, phytoplankton is considered more important.

Values of δ^{13}C discriminated the benthic vs. pelagic pathway of matter transfer and showed consumers with intermediate values possibly receiving contributions from both sources (Fig. 4). Enriched values of δ^{13}C among benthic consumers, especially sessile animals, are common in coastal ecosystems (Sherwood & Rose 2005, Newsome et al. 2007). An explanation for these values relies on microphytobenthos production, which have enriched δ^{13}C values (6‰ on average) in relation to phytoplankton (France 1995). Decapods occupying a lower trophic level had intermediate δ^{13}C values between phytoplankton and microphytobenthos (Fig. 4). Due to the high abundance of these decapods (Graça-Lopes et al. 2002), they represent an important link coupling pelagic and benthic primary production to higher trophic levels, such as benthic-demersal consumers (Fig. 4).

The seasonal variation of isotopic signatures of pelagic taxa (Fig. 5) showed some similarities, with enriched values of δ^{13}C in autumn and depleted values in spring. These changes may be caused by shifts in the balance of carbon contributions from the major primary producers during the seasonal cycle. Pulses in production of the main primary producers may shift the mean values of consumers. Concerning phytoplankton and mangrove litterfall, in Cananéia Estuary, individual studies have recorded increased production rates in spring and summer; however, seasonal data for microphytobenthos are lacking (Schaeffer-Novelli et al. 1990).

Trophic niches of fish and jellyfish and ecological implications of trophic overlaps

Planktivorous jellyfish species (*Mnemiopsis leidyi*, *Chrysaora lactea*, and *Lychnorhiza lucerna*) had low isotopic niche overlap with the hydromedusa *Olindias sambaquiensis*. *O. sambaquiensis* occupied a high trophic level, which is compatible with its known diet, since the species can feed on larger prey, such as large decapods and fishes, close to its own size (<10 cm), and also on copepods (Zamponi & Mianzan 1985). The planktivorous jellyfishes *M. leidyi* and *L. lucerna* had low isotopic niche partitioning, as a consequence of their distinct prey selectivity patterns. The ctenophore *M. leidyi* feeds on a variable diet ranging from microzooplankton and slowly swimming zooplankton to calanoid copepods (Granhag et al. 2011); whereas, the scyphomedusa *L. lucerna*, like other rhizostome medusae, probably feeds on micro- and mesozooplankton (Larson 1991), and on large and emergent zooplankton (Pitt et al. 2008). The trophic diversity found here illustrates the importance of a more precise characterization of the ecological role of jellyfish species, which are often

pooled into a single trophic category in ecosystem models (Condon et al. 2012).

The jellyfish species *O. sambaquiensis* and *C. lactea* had wider isotopic niches (as SEA$_c$ area) than most fish species of their trophic groups, possibly as a consequence of their broad diets. Species of the genus *Chrysaora* consume a wide range of prey, including other gelatinous species (Purcell 1997), fish eggs and larvae, and holoplanktonic crustacean zooplankton (Riascos et al. 2014). Larger trophic niche areas may be evidence of the versatility of feeding habits of these species, from copepods to fish in the case *O. sambaquiensis* (Zamponi & Mianzan 1985). This feature provides potential advantages to jellyfish over narrow-niched fish species, especially when changes in the trophic structure of pelagic environments switch the biomass dominance to lower trophic levels (Richardson et al. 2009).

Similar to many other estuaries, most fish species were found at young and juvenile stages (e.g. Potter et al. 2001), when they are zooplanktivores and/or benthic invertebrate feeders, which explains why they occupy relatively low trophic levels. Some exceptions to these feeding habits can be noted for the gelatinous zooplankton feeders *Chaetodipterus faber* and *Mola mola*, which showed trophic levels lower than expected, i.e. lower than the zooplanktivore *Anchoa* sp. (Fig. 2). One reason may be that both *C. faber* and *M. mola* possibly feed on prey other than gelatinous zooplankton (e.g. Syväranta et al. 2012). The high TL of the zooplanktivore *Anchoa* sp. is surprising since the species eats mainly calanoid copepods (Din & Gunter 1986). Another reason could be an erroneous trophic classification of *Anchoa* sp., as well as *Pellona harroweri*, as zooplanktivorous fish, since both can also feed on benthic crustaceans and fish (Höfling et al. 2000).

Overlaps of isotopic niches of fish and jellyfish were related to life stage, since the pattern of overlap can change with the animal's growth. Ontogenetic shifts in trophic level were absent for jellyfishes except for *L. lucerna*. Nevertheless, several fish species increased their trophic level with body size. The increase of TL of the fish *Chloroscombrus chrysurus*, resulting in changes in trophic-niche partitioning, must be a pattern of many other fish species. At young stages (<5 cm of body length), the fish feeds on mesozooplankton, mainly copepods (Silva & Lopes 2002), as well as filter-feeding jellyfish. For the medusae *L. lucerna* and *C. lactea*, and the fish *C. chrysurus*, the highest overlap (winter and summer) coincided with the smallest sizes of the fish (Fig. 7). Thereafter, at larger sizes (>5 cm), the fish starts to
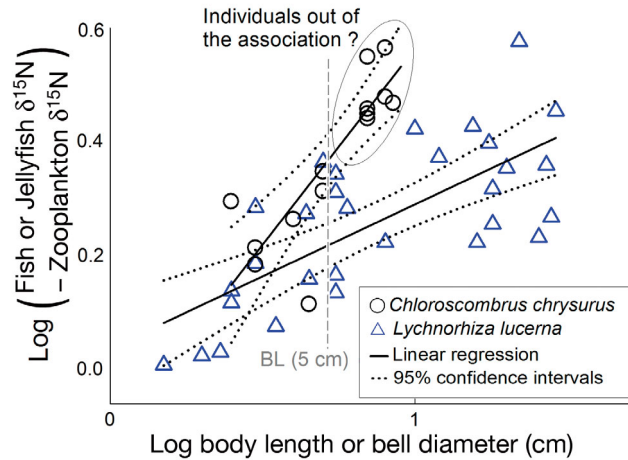

Fig. 7. δ^{15}N vs. size as body length for *Chloroscombrus chrysurus* and as bell diameter for *Lychnorhiza lucerna*. Fish specimens >5 cm body length (inside the ellipse) occupied a higher trophic level and were not observed in association with the medusa

feed on other prey items, such as epibenthic crustaceans and other fish (Silva & Lopes 2002). This explains the rise in its trophic level when large-sized individuals of *C. chrysurus* had overlaps with invertebrate/fish-feeders such as the hydromedusa *O. sambaquiensis* and the fishes *Stellifer rastrifer* and *G. genidens* (Fig. 6, Table 1).

Another possible explanation for the overlap of the isotopic niches of *C. chrysurus* and *L. lucerna* is a symbiosis between them. Up to 5 cm, small individuals of the fish species are commonly found as symbionts of scyphomedusae (Tolley 1987). The ecological importance of symbiosis involving large medusae is scarcely understood, and regarding fish, it is usually classified as phoresy, with the symbionts merely transported by the host (Ohtsuka et al. 2009), possibly gaining some protection against predators (Purcell & Arai 2001). Nevertheless, an alternative explanation, based on the similarities of the trophic niches of *L. lucerna* and young *C. chrysurus*, is that the fish symbionts, besides gaining some protection, steal prey captured by the medusa (Purcell & Arai 2001, Lynam & Brierley 2007). As the fish grows, larger individuals (>5 cm) leave the protection of the host jellyfish and start to exploit new habitats (Tolley 1987). Unlike *C. chrysurus*, the medusa *L. lucerna* showed a slight increase in its trophic level during its growth (Fig. 7, Fig. S1). Similar to other rhizostome medusae, *L. lucerna* has a mouth measured in millimeters, which limits the size of ingested prey (Larson 1991). Therefore, even larger medusae (>25 cm in bell diameter) may feed on mesozooplankton items only a few millimeters long (<2 mm).

The isotopic niche overlap of planktivorous and predatory fish and jellyfish species highlight the ecological significance of possible resource partitioning among these populations. The diet of jellyfish can be similar to co-occurring pelagic fish species (Purcell & Sturdevant 2001, Brodeur et al. 2008), but few studies have demonstrated competition between these consumers (but see Purcell & Grover 1990). Despite the significant advance in understanding possible triggers of jellyfish outbreaks (Condon et al. 2012, Purcell 2012), the reasons why they do not bloom are scarcely understood. It has been suggested that competition for planktonic food and predation (on polyps, ephyrae, and medusae) by fishes may prevent proliferations of jellyfishes (Richardson et al. 2009). In the CLES, a great number of potential predators of gelatinous animals are found, ranging from sessile invertebrate feeders, sea turtles, some specialized jellyfish feeders (e.g. *Mola mola*, stromateoid fishes), amphipods, and other jellyfish (e.g. *Beroe* spp. and *C. lactea*). In addition, a great number of potential competitors, such as the examples shown here (Fig. 6), along with many other species not sampled may use the same planktonic resources as jellyfish. Given the key ecological role of competitors and predators of jellyfish, identifying trophic relationships among these consumers is urgently needed to understand the importance of biological interactions keeping gelatinous populations 'in check' in pristine ecosystems.

Our SIA-based trophic niche characterization identified potential competitors allowing a further examination on the possible consequences of environmental changes, such as the decline of keystone consumers. When a dominant species is removed, the community can respond through compensatory increases in other species (Frank et al. 2007). It has been demonstrated that overexploited planktivorous fish populations (e.g. anchovy, sardine, or herring) were replaced by filter-feeding jellyfish, in highly productive areas such as in the northern Benguela Current, Sea of Japan, and the Bering Sea (Purcell 2012). Richardson et al. (2009) proposed that jellyfish increase after the collapse of an overexploited planktivorous fish, if an alternate fast responding planktivorous species is absent and unable to replace that collapsed fish stock. Subtropical marine regions harbor higher fish species richness than colder regions (Macpherson 2002), and thus have a potentially larger set of species capable of replacing a lost keystone consumer (Frank et al. 2007). In addition, the jellyfish species sampled here (*C. lactea*, *L. lucerna*, *M. leidyi*, and *R. atlanticum*) are taxonomically and functionally similar to the blooming species in other areas, providing significant chances to replace a declining consumer. Since species-rich food webs contained a larger pool of compensatory species (Gonzalez & Loreau 2009), possible responses to species removal or decline may be less predictable. Thus, it is necessary to evaluate other biological features of key members, like reproductive, growth, and feeding performance in order to understand an ecosystem's response to stresses like overfishing.

Conclusions based solely on isotope data must be carefully interpreted, especially when using only isotope data as input to analytical models (Layman et al. 2012). It is essential to understand the species' natural history in order to reach well-founded interpretations of trophic relationships (Layman et al. 2012). Because of the different factors that generate variation in isotope values, our data provide only indirect evidence of the actual trophic structure of CLES and of the isotopic niches of the species studied. Some pre-analytical factors can affect $\delta^{15}N$ and $\delta^{13}C$ values. For jellyfish, processing methods still need to be standardized (Fleming et al. 2011). The widespread preservation method of freezing can increase $\delta^{15}N$ values of jellyfish (Fleming et al. 2011), whereas for fish, octopus, and kelp samples, no effect of freezing was found (Kaehler & Pakhomov 2001).

Tissues rich in lipids are depleted in $\delta^{13}C$ values relative to those rich in proteins (DeNiro & Epstein 1977). Trophic interpretations based on $\delta^{13}C$ may, therefore, be biased by lipid effects (e.g. Wada et al. 1987). In contrast to temperate and higher latitude environments, tropical and subtropical zooplankton is characterized by low lipid contents, and does not accumulate lipid reserves seasonally (Hagen & Auel 2001). Lipids were not chemically extracted from our samples, and the $\delta^{13}C$ values were not mathematically corrected. The carbon-to-nitrogen (C:N) ratio is a proxy of lipid content, indicating the need to apply lipid extraction or correction to $\delta^{13}C$ values, if C:N >3.5 (Post et al. 2007). The lipid bias in our study should be minimal, as the majority of our samples were low-lipid muscle tissues (except for some benthic invertebrates). In our dataset, all fish and medusae samples were <3.5. Most C:N values of the ctenophore *M. leidyi* were >3.5 with $\delta^{13}C$ estimated error up to 5%, using the correction described by Post et al. (2007). For mesozooplankton, 30% of samples (n = 68) were >3.5 and <5, with estimated error between 0.5 and 15% (mean: 4%). Among benthic invertebrates, 31% of samples (n = 23) were >3.5 and <8.6, with estimated error between 0.5 and 51% (mean: 16%).

Estimates of trophic level from ^{15}N require a good knowledge of the variation of baseline values and trophic fractionation factors ($\Delta^{15}N$). We used the globally accepted value of $\Delta^{15}N$: 3.4‰ in coastal studies (Minagawa & Wada 1984). Trophic Enrichment Factors (TEF) for C and N need to be experimentally studied in different taxonomic groups. Recent reviews demonstrated that for ^{15}N this factor may vary (from 2 to 4.5‰) among groups of organisms, and could be related to the consumer's nutritional status, diet quality, size, age, dietary ontogeny, and the biochemical form of nitrogen excretion (Minagawa & Wada 1984, Vander Zanden & Rasmussen 2001, Vanderklift & Ponsard 2003). $\delta^{15}N$ of the planktivorous jellyfishes *L. lucerna* (mean: 10.31), *C. lactea* (10.64), and *M. leidyi* (10.66) were from 1.95 to 2.29‰ higher than total mesozooplankton (8.37), which is probably the main food source for these predators. For jellyfishes, the only experimental study to determine TEF showed much higher values for C (~4‰) in *Aurelia* sp., compared to other animals (~1‰) (Post 2002) and lower than typical for N (<1‰) in *Aurelia* sp. compared to other animals (2–4‰) (D'Ambra et al. 2014).

Because of the wide variation in $\delta^{13}C$ values of the main primary producers, phytoplankton carbon is probably the main source for most consumers, especially for pelagic groups (zooplankton, jellyfish, fish, and cephalopod). For some benthic species (especially sessile invertebrates), the enriched $\delta^{13}C$ suggests a contribution of microphytobenthic carbon. Depleted $\delta^{13}C$, which may characterize terrestrial carbon from mangrove litterfall, was uncommon. Connectivity between primary (zooplankton) and secondary consumers (planktivorous fish and jellyfish) is suggested by their patterns of seasonal variation of ^{13}C. Jellyfish species had high trophic diversity, and their feeding habits (planktivorous, benthic invertebrate feeders) were distinguished in isotopic space. Isotopic niche of jellyfish were often broader than fish at the same trophic category, possibly as a consequence of their broad diets. This study demonstrates an overlap of isotopic niche between jellyfish and fish with similar feeding habits (Figs. 2 & 6), which can change along a species' life history (Fig. 7). Description of isotopic niches provides a general picture of trophic roles, interactions, and the degree of functional redundancy among species, allowing an evaluation of possible directions of community shifts resulting from the removal or proliferation of keystone consumers. Further laboratory and field studies are needed to understand the mechanisms regulating jellyfish outbreaks, and to evaluate the consequences of possible environmental changes to the pelagic community of relatively pristine ecosystems.

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