Aquat Ecol (2019) 53:407–430
https://doi.org/10.1007/s10452-019-09698-0

Food web structure of a subtropical coastal lagoon

V. M. Muro-Torres · M. F. Soto-Jiménez · L. Green · J. Quintero ·
F. Amezcua

Received: 11 February 2019 / Accepted: 13 May 2019 / Published online: 31 May 2019

Abstract The food webs of a coastal lagoon ecosystem in the southeastern Gulf of California were investigated through the use of stomach contents analyses and carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotopes of fish and macroinvertebrates. Food sources and species representative of primary producers and primary-to-tertiary consumers were examined. Macroinvertebrates (47.5%) and fish (45%) assemblages represented over 90% of the total biomass. The most representative groups were fish (45%), crustaceans (24%), mollusks (16%), and echinoderms (8.5%). Based on the results from stomach content analysis, stable isotope analysis, and mixing models using Bayesian statistics, the estuarine food web was reconstructed from food chain bases to tertiary consumers, including the most representative species in the ecosystem. Four food webs were identified according to the primary producers, and five trophic levels were identified. However, in the higher trophic levels, these food webs are indistinguishable due to the high degree of omnivory and the complexity of the system which allows the predation in different environments.

Keywords Estuarine food webs · Trophodynamic model · Stomach contents · Stable isotopes · Demersal fish · Benthic invertebrates

Handling Editor: Télesphore Sime-Ngando.

V. M. Muro-Torres
Conacyt-Centro de Investigaciones Biológicas del
Noroeste, La Paz, BCS, Mexico

M. F. Soto-Jiménez · F. Amezcua (✉)
Instituto de Ciencias del Mar y Limnología, Universidad
Nacional Autónoma de México, Joel Montes Camarena
s/n, 82040 Mazatlán, Sinaloa, Mexico
e-mail: famezcua@ola.icmyl.unam.mx

L. Green
International Master in Marine Biological Resources,
Ghent University, Campus De Sterre, S8, Krijgslaan 281,
9000 Ghent, Belgium

J. Quintero
Instituto de Ciencias del Mar y Limnología, Posgrado en
Ciencias del Mar y Limnología, Circuito Exterior s/n
Ciudad Universitaria, C.P. 04510, México D.F., Mexico

Introduction

Coastal lagoons are among the most productive systems at various levels (Costanza et al. 1997), as they are characterised by a large variety of primary producers, the existence of a large quantity of detritus, and high biodiversity (Doi et al. 2005). The nutritional value, digestibility, and abundance of primary producers are important factors that determine their availability to consumer production and therefore the structure of the food web (Newell et al. 1995; Wainright et al. 2000).

Previous studies have shown that the trophic base of an estuarine ecosystem is usually a suite of primary producers and therefore cannot be simply generalised. The existence of diverse primary producers (such as phytoplankton, sea grasses, macroalgae, benthic/epiphytic microalgae, and vascular plants), together with the transportation of organic matter from adjacent rivers, seas, and other sources, nourishes the estuarine food webs (Page 1997; Little 2000; Doi et al. 2005), although the importance of every one of them can be different for a given system, or in fact, they may be the basis of different food webs within a system. For example, the importance of marsh macrophyte and organic detritus production for benthic consumers has already been demonstrated (Doi et al. 2005). In some cases, the main base of the food web is river-borne terrestrial organic matter, marsh detritus, and sea grass (Wainright et al. 2000; Doi et al. 2005; Wissel and Fry 2005), whilst other studies point at the importance of benthic and pelagic microalgal productions to primary consumers (Page 1997; Wainright et al. 2000; Doi et al. 2005; Choy et al. 2008, 2009), or a combination of macroalgae, sea grass epiphytes, microphytobenthos, and phytoplankton as the preferred diets of primary producers (Kwak and Zedler 1997; Page 1997; Moncreiff and Sullivan 2001; Doi et al. 2005; Yokoyama et al. 2005); others have signalled the relative importance of algal versus marsh production in the estuarine food web which may vary between estuarine types (Deegan and Garritt 1997).

If the estuarine system is large, with inputs from different sources (rivers, sea, etc.), more than one food web may be present because of the different mixes of several organic matter sources rather than by the exclusive contribution of a particular source (Deegan and Garritt 1997; Wainright et al. 2000; Doi et al. 2005). Previous studies in such estuarine environments have demonstrated that carbon sources for consumers change considerably over the length of estuarine and coastal systems (Doi et al. 2005; Choy et al. 2008, 2009), especially if there is a highly diverse primary producer community and the estuarine system has inputs from both marine and freshwater sources.

One of the largest estuarine systems in the southeast (SE) Gulf of California is the subtropical coastal lagoon of Santa Maria la Reforma (SMR). It is characterised by high floral and faunal diversity and a large watered area of about 51,172 ha. One hundred and ninety-one fish species have been recorded, and it is one of the most important fishing grounds in the region, as more than 2000 metric tonnes is landed every year (Amezcua and Amezcua-Linares 2014). This system has been severely modified by human activities: agricultural activities are commonplace, and the main freshwater input comes from irrigation channels used for agricultural purposes; the lower basin of this system has an adjacent human population of almost 170,000 inhabitants, and at the margins of the system, there is approximately 7700 ha of shrimp ponds that also discharge into this system (Páez Osuna et al. 2007). This system is connected to the sea by two inlets which allow a permanent communication with the adjacent sea. However, despite its high biotic diversity, ecological and economical importance, and all the human alterations it has suffered, studies on its food sources and the structure of the food webs are nonexistent for this or any other estuarine system in the region.

Although the understanding of carbon/energy flow in estuarine systems is extensive, this is usually true for temperate systems, but for the particular case of the Gulf of California such studies are scarce or nonexistent; moreover, considering the significance of the above-mentioned human modifications to estuarine food webs, there are surely consequences that are as yet unclear. The knowledge of the food sources and the structure of food webs in estuarine ecosystems is crucial for the understanding of the way these ecosystems function; by assessing dietary sources of consumers in estuarine habitats, it would be possible to understand the role of the primary producers in consumer production and allow the evaluation of the potential consequences of the loss or modification of the primary producers in estuarine environments. However, these kinds of studies have seldom been undertaken in tropical estuarine systems, and for the Gulf of California similar studies are nonexistent.

In this study, we employed the combined application of stomach content analysis (SCA), stable isotope analysis (SIA), and mixing models to provide a powerful tool for obtaining information on the trophic structure of this estuarine system (Christensen and Pauly 1992; Kline and Pauly 1998; Pauly et al. 2000; Polunin and Pinnegar 2000). Studies attempting to use the combination of these three methods (SIA, SCA, and mixing models) at the scale of the entire food web in an estuarine environment are nonexistent for this region, or for any tropical or subtropical ecosystem as far as we know.

In this context, the aim of this work was to identify the relative contribution of main primary producers to consumer production to elucidate the trophic interactions among consumers and thus establish the structure and number of food webs on the subtropical coastal lagoon of Santa Maria la Reforma (SE Gulf of California), which is the largest estuarine system in the region and has inputs from marine and freshwater sources. The working hypothesis is that the different inputs in the system allow the existence of different primary producers and that these are the source of more than one food web in the system.

Materials and methods

Study area

SMR coastal lagoon is located in the southern part of the central Gulf of California. It is an arid climatic zone, but with large agriculture fields thanks to highly technified agriculture activities, with more than 7000 ha of shrimp farm ponds installed around this system, producing approximately 10,000 tons of shrimp per year (Toscano and Ochoa 2003). This is a transition zone between the Gulf of California and the Pacific Ocean. It is a coastal lagoon with a barrier island and permanent communication to the sea through two inlets, or a Type III5 estuary according to Roy et al. (2001). The area of this system is 53,140 m^2, populated mainly by mangrove forests (18,700 ha), which are the primary producers in terms of vegetal biomass (Flores-Verdugo et al. 1993).

Sample collection

A network of 29 sampling stations was established at SMR and aimed to catch the most representative biota in the system in order to identify the food webs. The stations included the coastal lagon and the inlets (Fig. 1). Specimens were sampled for five consecutive days at monthly intervals during two shrimp fishing seasons (September 2014–March 2015, September 2015–March 2016); the shrimp closed season is from April to August each year, and no fishing operations were undertaken during that period. A total of ten boats of 7.5 metres of length with 115 hp outboard motors were used to sample these stations.

At each station and sampling event, triplicated superficial water samples were collected in order to sample for suspended particulate matter (SPM) in HCl-cleaned polyethylene 2-L bottles and transported to the laboratory for analysis. Surficial sediments were also collected in triplicate at each site using a Van Veen bottom drag. The upper layers (5 cm) were re-sampled from surface sediments. Polychaeta and other benthic macrofauna were separated from sediment samples obtained with a 0.1 m^2 grab and sieved through 0.5-mm mesh. The organic matter in surface sediments considered as detritus, benthic microalgae, and meiofauna (< 0.5 mm) was not separated, but was analysed as a single category of detritus.

At the same stations, plankton samples were collected with 30- and 200-μm-mesh conical nets towed at two knots for approximately 10 min for phytoplankton and zooplankton, respectively. Macroalgae were collected from each site (three replicates). Mangrove, saltwort, and cattail were also collected by hand with replicates of 15–20 of the second-youngest leaves from three to five plants at the stations where these were present.

In order to catch fish and macroinvertebrates, at every station three types of fishing gear were used in order to collect bentic, demersal, and pelagic organisms from a suite of lengths: (1) a shrimp trawl net fitted with a footrope of 24 m and a 50-mm liner at the cod end, (2) a gill net 300 m long and fitted with a 75-mm liner, and (3) a suripera net fitted with a 3.5-cm liner (detailed description of this gear: Amezcua et al. (2006). Each fishing process lasted for 20 min, the catch was sorted, and the fish were stored separately from the macroinvertebrates in plastic bags. Additionally, species of macroinvertebrates associated with mangrove roots were collected by hand in the mangrove zones close to the sampling stations.

Sample processing and laboratory work

SPM was separated by filtering 500–2000 ml from water samples through a pre-combusted (500 °C, 4 h) glass fibre filter (GF/F) with a plastic syringe. Total SPM was determined by weight differences (before and after filtration) and was considered as 'seston' in this study, which principally comprises the living or dead phytoplankton and plant detritus.

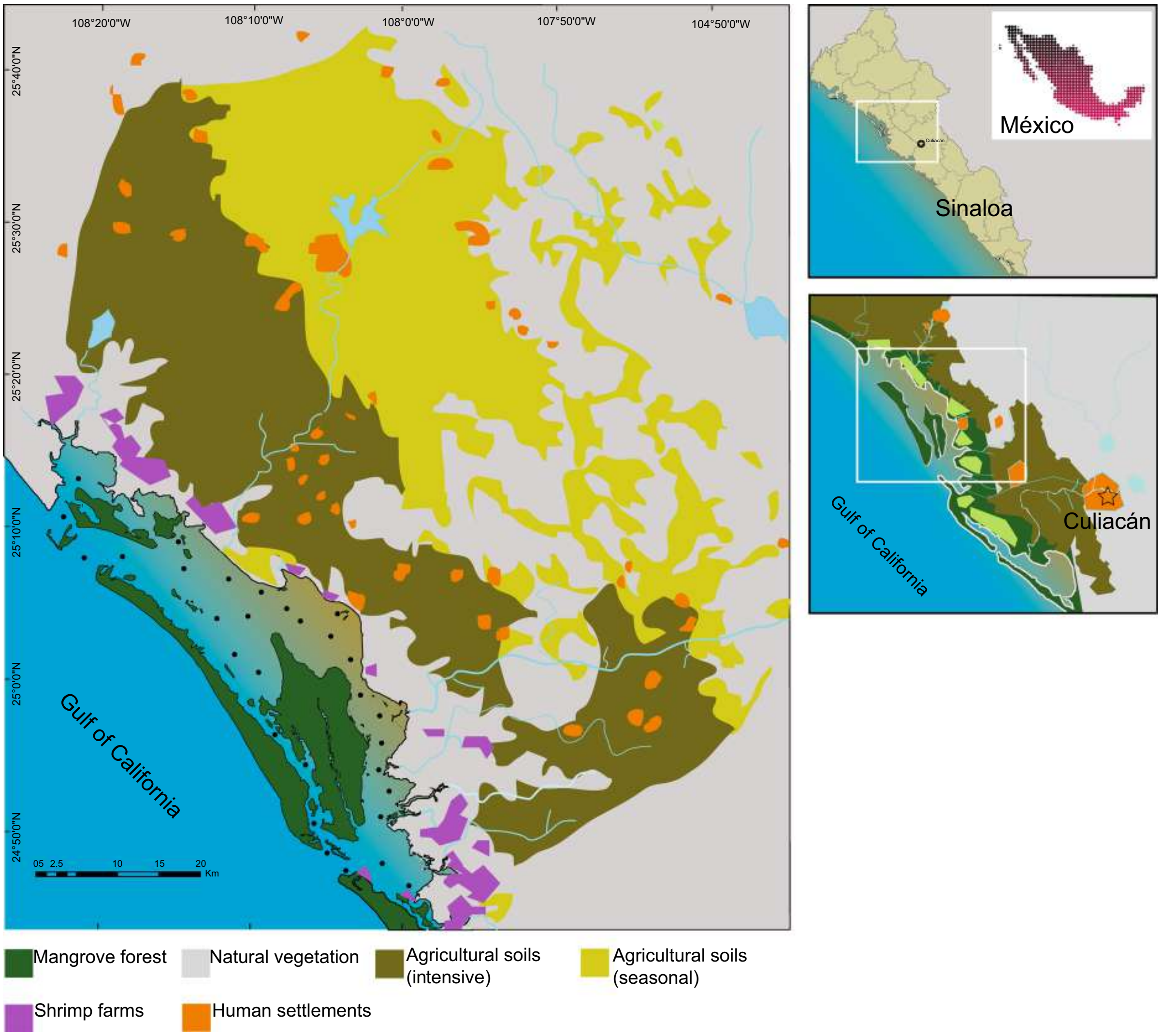


Fig. 1 Studied area and sampling sites in the SMR system (black dots)

Macroalgae and angiosperm samples were first rinsed with potable water to remove sediments and salt particles, and then rinsed with MilliQ water. Phytoplankton samples collected in the nets were cleansed with MilliQ water and filtered through GF/F filters with a 0.45-µm pore with the aid of a vacuum pump. Organic matter particles that could not be removed from phytoplankton samples were considered seston. Detritus and seston samples were pre-filtered through 75- and 30-µm mesh, respectively, and visually inspected to remove large particulate contaminants and large invertebrates from detritus samples. The rest of the organic matter was considered as detritus. The zooplankton samples were identified and separated. Over 90% of the samples corresponded to copepods and fish larvae.

Macroinvertebrates and fish were identified to species level, weighted, and the total length was recorded. Posteriorly, they were dissected and the stomach extracted and partially dried with blotting paper. Subsamples of fish species from a wide range of lengths and squids, star fish, and macrocrustaceans (shrimps, crabs, stomatopods) were used for stomach content analysis. The stomachs were stored in plastic bottles at 70% ethanol for later analysis. Also, low-lipid muscle tissue from all fish and macroinvertebrate species was extracted for the isotope analysis in order to minimise the lipid effects [depleted δ^{13}C values; DeNiro and Epstein (1977); Bodin et al. (2007)].

All biota and environmental samples used for the isotopic analyses were stored frozen at − 20 °C, lyophilised at − 45 °C for 3 days, and pulverised to a homogeneous powder with an agate mortar. The samples were then transferred to plastic containers and stored until analysis.

The catch for every fishing operation was standardised by dividing the total catch in every tow by the CPUA; thus, the biomass and abundance of organisms per hectare were calculated. This standardised number was used for all further analyses. The detailed methods used to estimate CPU, relative abundance, and relative biomass can be found in Amezcua and Amezcua-Linares (2014).

Stomach contents analysis (SCA)

Stomach contents of fish and macroinvertebrates were identified under a stereoscopic microscope; when possible, prey items were identified to species. However, they were typically identified to family or the lowest taxonomic level possible due to partial digestion. They were counted and weighed to the nearest milligram after removal of surface water. For analyses, prey items were divided into groups following the methods of Langton and Watling (1990) which consider the taxonomy of the different prey items, as well as their life history traits (e.g. mobility, size, and morphological relationships). Items that were too digested to be counted, but still recognisable as belonging to a large taxonomic group, were described as 'remains' of that group. The number of incomplete prey items was determined by counting their parts, such as claws and legs for crustaceans, otoliths for fishes, and beaks for cephalopods.

To quantitatively express the importance of various prey items in the diet of each predator, we used the frequency of occurrence (%F) that provides the most robust and interpretable measure of diet composition (Baker et al. 2014): $\%F = (\text{number of stomachs containing prey}/\text{total number of stomachs}) \times 100$. With this information, a matrix was constructed that included all the fish species in the rows and the prey items as columns. The data were fourth-root transformed to reduce the effect of very abundant prey on the analysis whilst retaining the quantitative nature of the data, and transformed to a resemblance matrix. In order to statistically check whether the different fish species of the system could be grouped according to their feeding habits, a single factor was assigned to group the prey items according to their habitat (plankton, benthos, pelagic, algae feeders). A permutational MANOVA (PERMANOVA) (Anderson et al. 2008) was undertaken in order to test the H_0 that the diet of the different fish species is not different according to the factor utilised. A pairwise test was performed to determine the specific differences between the groups of fish eating on different habitats of prey. If results were significative, a Canonical Analysis of Principal Coordinates (CAP) was performed in order to visualise the differences. The purpose of CAP is to find axis through the multivariate cloud of data in order to find the accommodation that best discriminates between a priori groups (the factor in this case). This analysis is done specifically to emphasise differences among the habitats of the prey in this case. This is valid if the permanova indicates that statistical differences exist according to that factor. If statistical differences are found, vectors of the fish predators were added in order to visualise which fish species are preying on the different prey items according to the defined habitat, and therefore form groups of species according to a feeding habit. A correlation > 0.6 was added in order to reduce the number of fish predators in the plot.

Sample preparation and stable isotope analysis

Isotopic analyses included seston, detritus, phytoplankton/zooplankton, macroalgae, angiosperms, macrofaunal benthic organisms, and the most abundant species of macroinvertebrates and fish in the system. Samples for δ^{13}C analysis were treated with acid prior to isotopic analysis (HCl vapours for 4 h within a glass desiccator). Aliquots were weighed, pressed into tin capsules, and sent to the Stable Isotope Facility at the University of California, Davis, for determination of stable isotope ratios (^{13}C/^{12}C and ^{15}N/^{14}N). Analyses of stable isotope composition used a PDZ Europa ANCA-GSL elemental analyser interfaced to a PDZ Europa 20–20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK). Results are reported as parts per thousand differences from a corresponding standard: $\delta_X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 10^3$, where $R = {}^{15}\text{N}/{}^{14}\text{N}$ or ${}^{13}\text{C}/{}^{12}\text{C}$. The standards were carbon in the PeeDee Belemnite and nitrogen in the air. The analytical precision of these measurements was 0.2% for δ ^{13}C and 0.3% for δ^{15}N.

Statistical analysis of isotopic signals

In order to determine whether differences exist in the isotopic signals according to season and feeding guild, a two-way ANOVA was performed (JMP 11.0) using season and feeding guild as the factors. Two seasons were identified, the hot and rainy season (September to November), and the dry and cold season (December through March). The feeding guilds were based on Livingston (1982) and Robertson and Allen (2006). A total of six feeding guilds were identified: primary producers, herbivores, planktivores, omnivores, detritivores, and carnivores. The carnivores were also divided according to the TP of the prey there were feeding on: Carnivores 0 preyed on first-order predators, Carnivores 1 preyed on Carnivores 0 and so on. A Cochran's C test was performed to determine whether the variances were homoscedastic, and if differences were found, a Tukey HSD test was performed (Zar 1999).

Estimation of trophic position

We estimated the trophic position (TP) of consumers using both values of N and C isotopes according to the equation (Post 2002):

$$\mathrm{TP}_{\mathrm{SIANC}} = \lambda + \left(\delta^{15}\mathrm{N}_{SC} - \left[\delta^{15}\mathrm{N}_{\mathrm{base1}} x\alpha + \delta^{15}\mathrm{N}_{\mathrm{base2}} x\left(1-\alpha\right)\right]\right)/\Delta^{15}\mathrm{N} \quad (1)$$

where λ is the trophic level of the base of the food web, $\delta^{15}\mathrm{N}_{\mathrm{SC}}$ is the nitrogen signature in secondary consumer, $\delta^{15}\mathrm{N}_{\mathrm{base1}}$ and $\delta^{15}\mathrm{N}_{\mathrm{base2}}$ are mean δ^{15}N signatures of food web 1 (pelagic) and 2 (benthonic) baselines, respectively, for this system according to Amezcua et al. (2015), Δ^{15}N is the fractionation of N between each trophic level, and α was estimated following a two-end member-mixing model that distinguishes both sources of carbon or energy:

$$\alpha = \delta^{13}\mathrm{C}_{\mathrm{SC}} - \delta^{13}\mathrm{C}_{\mathrm{base2}} / \delta^{13}\mathrm{C}_{\mathrm{Base1}} - \delta^{13}\mathrm{C}_{\mathrm{Base2}} \quad (2)$$

In this study, four primary sources were considered: (1) phytoplankton, (2) seston (defined as a mix of phytoplankton and suspended organic matter) and detritus (comprised of living organisms and plants present in the sediment), (3) benthic macroalgae, and (4) mangroves (Amezcua et al. 2015). The constant α used in Eq. 1 was 0.67 considering the different carbon sources. The average values used for the pelagic base were − 22.03 and 7.37 for δ^{13}C and δ^{15}N, respectively, and − 20.85 and 7.63 for δ^{13}C and δ^{15}N for the benthic base.

Several authors have suggested that the value of trophic fractionation varied between 2.5 and 3.5‰ (Minagawa and Wada 1984; Post 2002; Vanderklift and Ponsard 2003). An assumed value of $F = 3.4$‰ was used in this study as this value is the only one known for a system similar to this (Minagawa and Wada 1984).

Food web structure

With the aim of building a detailed quantitative flow for the SMR food webs and determining the primary producers nourishing them, we followed an approach that combines data from SCA and SIA: (1) We began with a simple connectivity web by identifying the presence or absence of food items through stomach content analysis; (2) we converted the connectivity web into a diet proportion web based on the fraction of each food found in the SCA (%F); and (3) based on SIA results, we estimated the proportion of each prey in the diet of each predator by using a Bayesian mixing model Stable Isotope Analysis in R (SIAR) v. 4.2 (Parnell, et al. 2010). The algorithm takes into account isotopic error by using as inputs all predator δ^{13}C and δ^{15}N values and mean (± SD) δ^{13}C and δ^{15}N values of each prey.

Results

Over 12,000 samples of seston, detritus, phytoplankton/zooplankton, macroalgae, angiosperms, macrofaunal benthic organisms, macroinvertebrates, and fish species were collected and examined (Tables 1, 2). Primary producers included phytoplankton, three species of macroalgae (*Ulva lactuca*, *Gracilaria vermiculophylla*, and *Caulerpa sertularioides*), and four angiosperm species: mangroves (*Rhizophora mangle* and *Conocarpus erectus*), saltwort (*Batis maritima*), and cattail (*Typha angustifolia*). Primary consumers were constituted by zooplankton, polychaetes (*Streblospio benedicti*), bivalves (*Mytella strigata*), and snails (*Littoraria aberrans* and *L.*

Table 1 Relative contribution (abundance A % and biomass B %), feeding guild, primary food items, mean value of isotopic composition of C and N (δ^{13}C and δ^{15}N), and trophic position (TP) of primary producers and invertebrates collected at SMR

Species	Common name	*N*	A %	B %	Feeding guild	Food item	δ^{13}C (± SD)	$\delta 1^{5}$N (± SD)	TP (± SD)
Phytoplankton detritus	Seston	19			Primary producer	Autotroph	− 24.7 ± 3.10	7.6 ± 1.75	1.0
Detritus	Detritus	15			Primary producer	Autotroph	− 23.9 ± 2.4	8.2 ± 1.36	1.0
Phytoplankton	Phytoplankton	20			Primary producer	Autotroph	− 20.1 ± 1.9	8.1 ± 1.21	1.0
Typha angustifolia	Salt marsh plant	16			Primary producer	Autotroph	− 23.6 ± 0.57	6.7 ± 0.89	1.0
Batis maritima	Salt marsh plant	17			Primary producer	Autotroph	− 25.6 ± 0.9	6.6 ± 0.5	1.0
Rhizophora mangle	Red mangrove	15			Primary producer	Autotroph	− 26.1 ± 3.2	8.1 ± 2.0	1.0
Conocarpus erectus	Button mangrove	3			Primary producer	Autotroph	− 26.9 ± 1.68	9.08 ± 0.88	1.0
Gracilaria vermiculophyla	Macroalgae	18			Primary producer	Autotroph	− 20.7 ± 2.3	6.50 ± 1.76	1.0
Caulerpa sertularioides	Macroalgae	14			Primary producer	Autotroph	− 20.9 ± 1.9	7.06 ± 2.01	1.0
Ulva lactuca	Macroalgae	10			Primary producer	Autotroph	− 20.2 ± 3.4	6.74 ± 1.34	1.0
Zooplanktonic copepods	Copepods	17			Planktivores	Phytoplankton	− 21.1 ± 1.9	8.46 ± 1.28	1.3 ± 0.26
Zooplanktonic fish larvae	Fish larvae	13			Carnivores	Zooplankton	− 20.0 ± 1.19	9.39 ± 0.78	1.6 ± 0.11
Nematodes	Infaunal worm	13			Omnivore	Detritus, zoobenthos	− 23.1 ± 1.10	8.81 ± 1.4	1.4 ± 0.30
Crassostrea corteziensis	Oyster	24			Herbivore	Phytoplankton, detritus.	− 20.9 ± 1.93	10.98 ± 2.12	2.1 ± 0.51
Mytella strigata	Mussel	22			Herbivore	Phytoplankton, detritus.	− 21.2 ± 2.22	11.06 ± 1.64	2.1 ± 0.37
Littoraria pintado	Snail	18			Herbivore	Macroalgae	− 23.6 ± 0.57	9.45 ± 3.86	1.6 ± 1.03
Littoraria aberrans	Snail	20			Omnivores	Macroalgae, detritus, polychaetes	− 22.9 ± 1.71	8.35 ± 2.10	1.3 ± 0.51
Fistulobalanus dentivarians	Barnacles	16			Filter feeding	Phytoplankton, detritus, zooplankton	− 21.1 ± 1.35	9.26 ± 0.54	1.6 ± 0.04
Streblospio benedicti	Polychaetes	14			Omnivore	Detritus, infaunal crustaceans	− 20.6 ± 0.53	10.92 ± 0.51	2.1 ± 0.03
Callinectes sapidus	Crab	14			Omnivore	Macroalgae, crustaceans, detritus	− 14.7 ± 0.10	12.08 ± 0.20	2.4 ± 0.06
Callinectes arcuatus	Blue crab	18		3.7	Omnivore	Macroalgae, crustaceans, detritus, fish	− 17.5 ± 0.53	13.85 ± 0.43	2.9 ± 0.01
Uca sp.	Fiddler crab	15			Omnivore	Macroalgae, detritus, fish, crustaceans	− 15.3 ± 0.4	12.2 ± 0.2	2.4 ± 0.06
Grapsus sp.	Mangrove crab	13			Omnivore	Macroalgae, mussels, barnacles, crabs, fish	− 24.3 ± 0.3	12.3 ± 0.1	2.5 ± 0.09

Table 1 continued

Species	Common name	*N*	A %	B %	Feeding guild	Food item	δ^{13}C (± SD)	δ^{15}N (± SD)	TP (± SD)
Portunus asper	Crab	13		11.3	Omnivore	Polychaetes, infaunal crustaceans, bivalves	− 18.3 ± 0.3	12.30 ± 1.21	2.5 ± 0.24
Petrochirus californiensis	Hermit crab	13		0.1	Omnivore	Fish, detritus	− 21.2 ± 0.2	16.50 ± 0.21	3.7 ± 0.05
Luidia brevispina	Star fish	13		2.1	Carnivore	Sea urchins, bivalves	− 23.2 ± 0.8	11.45 ± 3.86	1.6 ± 0.03
Loligo sp.	Squid	13			Carnivore	Fish, crustaceans, cephalopods	− 16.6 ± 0.1	14.71 ± 0.60	3.2 ± 0.06
Squilla mantis	Mantis	13			Carnivore	Infaunal crustaceans	− 17.3 ± 0.24	15.10 ± 2.19	3.3 ± 0.53
Litopenaeus vannamei	White shrimp	11		2.5	Omnivore	Detritus, worms, bivalves, crustaceans	− 16.3 ± 0.89	14.11 ± 1.44	3.1 ± 0.31
Farfantepenaeus californiensis	Brown shrimp	13		0.5	Omnivore	Detritus, worms, bivalves, crustaceans	− 15.7 ± 0.9	14.6 ± 0.63	3.2 ± 0.07
Farfantepenaeus brevirostris	Crystal shrimp	16		0.1	Omnivore	Detritus, worms, bivalves, crustaceans	− 16.6 ± 0.9	15.7 ± 0.96	3.4 ± 0.79

N number of samples used in the isotopic analysis (sample is equivalent to individual except for all classes of plankton, seston, detritus, algae and vascular plants), *SD* standard deviation

pintado). The main components of the zooplankton were copepods, fish larvae, and decapods, but it also contained herbivorous cladocerans, rotifers, foraminifera, and chaetognatha. However, the copepods were the dominant group of zooplankton (80–90% in all analysed samples).

The macroinvertebrate community included shrimps (*Litopenaeus vannamei*, *L. stylirostris*, *Farfantepenaeus brevirostris*, *F. californiensis*), crabs (*Portunus asper*, *Callinectes sapidus*, *C. arcuatus*, *and Petrochirus californiensis*), herbivore gastropod mollusks (*Littoraria aberrans and Littoraria pintado*), filter-feeding mollusks (*Crassostrea corteziensis* and *Mytella strigatta*), a cephalopod (*Loligo* sp.), and a polychaete (*Streblospio benedicti*). Crustaceans and filter-feeding mollusk specimens and their potential food sources were mostly collected in macroalgal beds, mudflats, and mangrove root habitats. The most important species of macroinvertebrates in terms of biomass were *P. asper* (11.3%), *C. arcuatus* (3.7%), and *F. californiensis* (2.5%). From these, 11% were herbivores, 15% planktivores, 21% filter feeding and carnivores, and 18% detritivores and omnivores (Table 1).

A total of 84 fish species belonging to 48 families were collected (Table 2). The most abundant families were Gerreidae (mojarras, nine species), Carangidae (jacks and pompanos, 16 species), Haemulidae (grunts, 14 species), Urolophidae (round rays, seven species), Tetraodontidae (puffers, four species), and Engraulidae (anchovies, eight species). The five species having the highest abundance were the Pacific moonfish (*Selene peruviana*), the Peruvian mojarra (*Diapterus peruvianus*), the fringed flounder (*Etropus crossotus*), the shining grunt (*Haemulopsis nitidus*), and the bull eye puffer (*Sphoeroides annulatus*). The five most important species in terms of biomass were the bullseye puffer (*S. annulatus*, 10.5%), the speckled guitarfish (*Rhinobatos glaucostigma*, 5.11%), the Chilean round ray (*Urotrygon chilensis*, 5.04%), the Peruvian mojarra (*D. peruvianus*, 3.62%), and the Pacific moonfish (*S. peruviana*, 1.7%). Carnivorous fish represented 46% of the fish samples, detritivores/omnivores 29%, and planktivores 25%. Carnivores were mostly comprised of grunts (*Orthopristis chalceus*, *Pomadasys panamensis*, *P. branickii*, and *H. nitidus*), moonfishes (*S. peruviana* and *S. brevoortii*), puffers (*Sphoeroides annulatus* and *S. lobatus*), flatfishes (*Etropus crossotus*, *Syacium ovale*, *Achirus*

Table 2 Relative contribution (abundance A % and biomass B %), feeding guild, primary food items, mean value of isotopic composition of C and N (δ^{13}C and δ^{15}N), and trophic position (TP) of the main fish species in SMR

Species	Common name	*n*	A %	B %	Feeding guild	Prey item	δ ^{13}C (± SD)	δ^{15}N (± SD)	TP (± SD)
Achirus mazatlanus	Mazatlan sole	13	1	0.41	Carnivores	Fish, polychaetes, crustaceans	− 16.3 ± 0.95	15.21 ± 0.3	3.3 ± 0.03
Albula nemoptera	Shafted bonefish	11	0.01	0.01	Carnivores	Polychaetes, infaunal crustacean, bivalves, snails	− 18.32	13.22	2.7 ± 0.12
Anchoa mundeola	Panama anchovy	14	1	0.15	Planktivores	Copepods, ostracods, fish larvae	− 15.3 ± 0.76	15.99 ± 1.2	3.5 ± 0.24
Anchoa nasus	Bignose anchovy	11	0.01	0.01	Planktivores	Copepods, ostracods, fish larvae	− 15.40	14.99	3.2 ± 0.32
Anchoa walkeri	Walker’s anchovy	14	1.5	0.38	Planktivores	Copepods, ostracods	− 15.4 ± 1.05	15.47 ± 1.2	3.4 ± 0.24
Anchovia macrolepidota	Big-scale anchovy	14	3	0.36	Planktivores	Copepods, eggs and larvae of fish	− 15.6 ± 1.16	15.81 ± 1.8	3.5 ± 0.43
Balistes polylepis	Fine-scale triggerfish	14	0.4	0.32	Carnivores	Decapods. gastropods bivalves, echinoderms, polychaetes	− 14.5 ± 0.54	14.0 ± 0.91	3.0 ± 0.35
Caranx hippos	Crevalle jack	13	2.5	0.06	Carnivores	Fish	− 15.8 ± 0.1	14.9 ± 1.1	3.2 ± 0.23
Cathorops fuerthii	Congo sea catfish	11	0.04	0.04	Carnivores	Infaunal crustaceans, fish, bivalves, polychaetes	− 16.05	15.7	3.5 ± 0.27
Centropomus robalito	Yellowfin snook	14	0.06	0.04	Carnivores	Fish, shrimps, crabs, bivalves	− 15.98 ± 1.8	15.21 ± 2.2	3.3 ± 0.53
Chaetodipterus zonatus	Pacific spadefish	13	3.4	0.76	Omnivores	Jelly fish, polychaetes, crustaceans, mollusks	− 15.79 ± 0.2	12.66 ± 0.2	2.5 ± 0.06
Cyclopsetta panamensis	Panamic flounder	18	3.3	0.43	Carnivores	Benthic crustaceans	− 16.28	17.2	3.9 ± 0.47
Cyclopsetta querna	Toothed flounder	15	0.2	0.3	Carnivores	Fish, polychaetes, shrimps, crabs, cephalopods.	− 16.17 ± 1.1	16.98 ± 1.9	3.8 ± 0.44
Cynoscion reticulatus	Striped corvina	13	0.3	0.39	Carnivores	Fish, shrimp, cephalopods.	− 15.08 ± 0.6	17.47 ± 1.2	4.0 ± 0.24
Dasyatis longa	Longtail stingray	13	0.08	0.44	Carnivores	Crabs, fish, shrimps, mantis, snails.	− 17.1 ± 1.8	17.5 ± 2.1	4.0 ± 0.50
Diapterus aureolus	Golden mojarra	15	0.3	0.03	Omnivores	Polychaetes, bivalves	− 16.08 ± 0.1	14.7 ± 0.6	3.2 ± 0.06
Diapterus peruvianus	Peruvian mojarra	17	3.7	2.29	Omnivores	Polychaetes, shrimps, crabs, snails, bivalves	− 11.25 ± 1.0	11.91 ± 0.9	2.3 ± 0.35
Diplectrum eumelum	Orange-spotted sand perch	12	0.01	0.01	Carnivores	Shrimp, crabs, fish	− 17.18 ± 1.6	16.49 ± 0.1	3.7 ± 0.33
Diplectrum rostrum	Barsnout sand perch	16	0.02	0.03	Carnivores	Shrimp, crabs, fish	− 14.93 ± 0.9	17.57 ± 0.1	4.0 ± 0.06
Engraulis mordax	Northern anchovy	11	0.01	0.01	Planktivores	Copepods, ostracods, crustaceans’ larvae, fish larvae	− 16.19	16.29	3.6 ± 0.33
Etropus crossotus	Fringed flounder	12	3.5	3.08	Carnivores	Infaunal crustaceans, polychaetes, squids, fish	− 14.51	13.9	2.9 ± 0.38
Eucinostomus argenteus	Spotfin mojarra	14	0.01	0.01	Omnivores	Polychaetes, copepods, infaunal crustacean, bivalves, anfipods	− 14.70 ± 0.1	16.99 ± 0.1	3.8 ± 0.41

Table 2 continued

Species	Common name	*n*	A %	B %	Feeding guild	Prey item	δ ^{13}C (± SD)	δ^{15}N (± SD)	TP (± SD)
Eucinostomus currani	Pacific flagfin mojarra	15	0.8	0.39	Omnivores	Benthic crustaceans and mollusks, polychaetes, bivalves, snails,	− 13.99 ± 1.8	16.71 ± 1.2	3.8 ± 0.24
Eucinostomus entomelas	Dark-spot mojarra	15	28.4	58.1	Omnivores	Polychaetes, benthic crustaceans	− 16.1	15.6	3.4 ± 0.18
Fistularia corneta	Pacific cornetfish	12	0.02	0.03	Carnivores	Fish	− 19.27 ± 1.1	13.4 ± 0.9	2.8 ± 0.15
Gerres cinereus	Yellowfin mojarra	12	0.07	0.04	Omnivores	Cirripedia, polychaetes, gastropods, shrimps, crabs	− 13.7	17.9	4.1 ± 0.02
Gymnothorax panamensis	Masked moray	12	0.3	0.33	Carnivores	Fish, crabs, shrimps, lobsters	− 14.89 ± 0.5	17.1 ± 0.8	3.9 ± 0.12
Haemulopsis axillaris	Yellowstripe grunt	13	0.09	0.03	Carnivores	Polychaetes, shrimp, crabs, bivalves, squids	− 13.93 ± 0.3	18.2 ± 0.5	4.2 ± 0.03
Haemulopsis elongatus	Elongate grunt	13	0.01	0.01	Carnivores	Mysids, shrimps, stomatopods, snails, cephalopods.	− 15.53 ± 0.7	17.09 ± 1	3.9 ± 0.47
Haemulopsis leuciscus	White grunt	11	0.3	0.37	Carnivores	Decapods, polychaetes, bivalves, cephalopods.	− 15.49	17.7	4.1 ± 0.08
Haemulopsis nitidus	Shining grunt	11	3.4	3.59	Carnivores	Benthic mollusks, crabs, polychaetes, shrimp	− 15.42 ± 0.7	16.7 ± 1.0	3.8 ± 0.18
Isopisthus remifer	Silver weakfish	18	0.3	0.38	Carnivores	Shrimp, fish, crabs, squillas.	− 15.41 ± 0.7	17.11 ± 1.7	3.9 ± 0.39
Larimus acclivis	Steeplined drum	16	0.49	0.38	Carnivores	Decapods, infaunal crustaceans, juvenile fish	− 16.17 ± 0.5	15.99(1.1)	3.5 ± 0.86
Larimus effulgens	Shining drum	13	0.7	0.43	Carnivores	Decapods, infaunal crustaceans	− 16.46 ± 1.1	17.05 ± 0.5	3.9 ± 0.03
Lepophidium prorates	Spine-snout cusk-eel	11	0.03	0.03	Carnivores	Shrimp, crabs, fish, bivalves, polychaetes	− 16.78	16.12	3.6 ± 0.17
Lutjanus argentiventris	Yellow snapper	13	0.01	0.01	Carnivores	Fish, benthic crustaceans, stomatopods, crabs, shrimps	− 15.41 ± 0.13	16.99 ± 0.06	3.8 ± 0.10
Lutjanus guttatus	Spotted snapper	13	0.3	0.33	Carnivores	Fish, benthic crustaceans	− 16.44 ± 1.1	17.6 ± 0.9	4.0 ± 0.15
Lutjanus novemfasciatus	Pacific dog snapper	14	0.01	0.01	Carnivores	Fish, benthic crustaceans, stomatopods, crabs, shrimps	17.16	16.73	3.8 ± 0.12
Menticirrhus elongates	Slender kingfish	11	0.01	0.01	Carnivores	Benthic mollusks, shrimps, crabs, snails, polychaetes, fish.	− 15.06	15.48	3.4 ± 0.12
Menticirrhus nasus	Highfin king-croaker	14	0.3	0.35	Carnivores	Benthic mollusks, shrimps, crabs, snails, polychaetes, fish.	− 17.1 ± 0.7	16.15 ± 0.5	3.6 ± 0.03
Microlepidotus brevipinnis	Brassy grunt	11	0.01	0.01	Carnivores	Benthic shelled mollusks, polychaetes, shrimp, crabs	− 14.38	18.58	4.3 ± 0.12
Mugil cephalus	Striped mullet	17	0.3	0.06	Omnivores	Zooplankton, phytoplankton	− 16.15 ± 1.1	16.3 ± 0.3	3.6 ± 0.03
Mulloidichthys dentatus	Mexican goatfish	11	0.05	0.03	Carnivores	Fish, benthic crustaceans and mollusks, polychaetes	− 14.32	18.3	4.2 ± 0.56

Table 2 continued

Species	Common name	*n*	A %	B %	Feeding guild	Prey item	δ ^{13}C (± SD)	δ^{15}N (± SD)	TP (± SD)
Ophichthus zophochir	Yellow snake-eel	10	0.03	0.03	Carnivores	Clams, fish, snails.	− 14.35	17.7	4.1 ± 0.47
Ophioscion imiceps	Blinkard croaker	18	0.3	0.06	Carnivores	Shrimps, crabs, polychaetes small fish, snails.	− 14.33	18.0	4.1 ± 0.50
Opisthonema medirastre	Middling thread herring	11	0.01	0.01	Planktivores	Copepods, ostracods, crustaceans' larvae, fish larvae, phytoplankton	− 15.33	14.21	3.0 ± 0.12
Orthopristis chalceus	Brassy grunt	15	0.07	0.03	Carnivores	Decapods, bivalves, polychaetes, snails	− 16.24 ± 0.8	15.79 ± 1.4	3.5 ± 0.30
Paralabrax maculatofasciatus	Spotted sand-bass	14	0.3	0.33	Carnivores	Fish, crabs, bivalves	− 16.01 ± 0.3	15.91 ± 0.7	3.5 ± 0.09
Peprilus medius	Long-finned butterfish,	13	0.3	0.38	Omnivores	Ctenophore, zooplankton polychaetes, shrimps, squids	− 15.66 ± 0.5	15.24 ± 0.5	3.3 ± 0.03
Peprilus snyderi	Short-finned butterfish	11	0.3	0.09	Omnivores	Ctenophore, zooplankton, anchoas, crabs, shrimps, polychaetes.	− 16.14 ± 1.5	16.54 ± 0.4	3.7
Pliosteostoma lutipinnis	Yellowfin herring	16	3.3	0.83	Planktivores	Zooplankton	− 15.82 ± 2.6	16.31 ± 2.2	3.6 ± 0.53
Pomadasysbranickii	Sand grunt	16	0.4	0.46	Carnivores	Mysids, polychaetes, squillas, shrimps, snails, bivalves, cephalopods	− 14.87 ± 0.7	18.78 ± 0.3	4.4 ± 0.03
Pomadasys panamensis	Panama grunt	17	0.3	0.38	Carnivores	Shrimp, mysids	− 14.54 ± 1.2	18.3 ± 0.8	4.2 ± 0.12
Porichthys analis	Gulf saddled toadfish	13	0.6	0.43	Carnivores	Benthic decapods, snails, bivalves, fish	− 14.33 ± 0.11	18.1 ± 0.4	4.2
Prionotus ruscarius	Rough sea robin	15	0.3	0.38	Carnivores	Shrimp, infaunal crustaceans, fish, polychaetes	− 15.98 ± 0.6	16.76 ± 0.4	3.8
Prionotus stephanophrys	Blackfin sea robin	15	0.5	0.3	Carnivores	Shrimp, infaunal crustaceans, fish, polychaetes, snails, squids.	− 16.1 ± 0.2	17.1 ± 0.5	3.9 ± 0.03
Pseudupeneus grandisquamis	Big-scale goatfish	14	3.3	0.4	Carnivores	Polychaetes, shrimp, crabs, bivalves, fish, squids	− 15.29 ± 1.5	17.16 ± 2.2	3.9 ± 0.53
Rhinobatos glaucostigma	Speckled guitarfish	13	3.3	3.33	Carnivores	Benthic crustaceans, bivalves, polychaetes.	− 16.37 ± 0.2	16.12 ± 1.2	3.6 ± 0.34
Roncado rstearnsii	Spotfin croaker	13	0.01	0.01	Carnivores	Bivalves, crabs, polychaetes, fish	− 15.11 ± 0.8	16.5 ± 0.5	3.7 ± 0.03
Sciades platypogon	Cominate sea catfish	13	0.3	0.37	Carnivores	Crabs, shrimp, fish, snails	− 14.78 ± 0.1	18.9 ± 0.4	4.4
Sciades seemanni	Sea catfish	14	0.3	0.33	Carnivores	Decapods, fish, snails, polychaetes, bivalves	− 15.56 ± 0.4	15.8 ± 0.4	3.6
Scomberomorus sierra	Pacific sierra	17	0.3	0.39	Carnivores	Fish	− 15.59 ± 1.3	18.3 ± 1	4.2 ± 0.18
Scorpaena mystes	Stone scorpionfish	12	0.03	0.01	Carnivores	Decapods, fish, squids	− 16.23 ± 1.8	17.3 ± 1.1	3.9 ± 0.21

Table 2 continued

Species	Common name	*n*	A %	B %	Feeding guild	Prey item	δ ^{13}C (± SD)	δ^{15}N (± SD)	TP (± SD)
Selene brevoortii	Pacific lookdown	16	3.5	0.66	Carnivores	Shrimp, stomatopoda, fish, crabs, squids, polychaetes	− 16.44 ± 1.1	16.02 ± 1.7	3.6 ± 0.39
Selene peruviana	Pacific moonfish	11	3.3	0.83	Carnivores	Fish, shrimp	− 16.67 ± 0.9	16.05 ± 0.7	3.6 ± 0.09
Sphoeroides annulatus	Bullseye puffer	14	3.3	6.63	Carnivores	Benthic crustaceans, benthic mollusks, snails, squids	− 16.07 ± 0.9	15.80 ± 1.4	3.5 ± 0.59
Sphoeroides lobatus	Longnose puffer	12	3.3	0.53	Carnivores	Decapods, infaunal crustacean, mollusks	− 15.15 ± 1.4	18.4 ± 0.8	4.3 ± 0.12
Sphyraena ensis	Mexican barracuda	11	0.03	0.01	Carnivores	Fish, squid, shrimps, crabs, cephalopods	− 15.4	15.0	3.3 ± 0.31
Stellifer furthii	White stardrum	11	3.5	0.7	Carnivores	Decapods, polychaetes, zooplankton, shrimps, crabs	− 14.82	16.9	3.8 ± 0.50
Syacium ovale	Oval flounder	11	3.5	0.7	Carnivores	Shrimp, fish, crabs, stomatopods	− 16.10 ± 0.4	15.40 ± 0.5	3.4 ± 0.33
Symphurus atramentatus	Ink-spot tonguefish	11	0.01	0.03	Carnivores	Infaunal crustacean	− 16.1	16.5	3.7 ± 0.40
Symphurus elongatus	Elongate tonguefish	11	0.3	0.08	Carnivores	Polychaetes, infaunal crustacean, bivalve, snails	− 16.7	16.3	3.6 ± 0.47
Symphurus melanurus	Drab tonguefish	12	0.3	0.04	Carnivores	Polychaetes, infaunal crustacean, bivalve, snails	− 17.32 ± 1.5	17.22 ± 1.3	3.9 ± 0.27
Synodus scituliceps	Lance lizardfish	16	0.9	3.37	Carnivores	Fish, decapods, polychaetes, squilla, crabs, bivalves and squids	− 16.14 ± 0.5	16.31 ± 1.5	3.6 ± 0.33
Trinectes fonsecensis	Spotted-fin sole	13	0.01	0.01	Omnivores	Bivalve, polychaeta, smalls crustaceans	− 17.54 ± 2.1	13.38 ± 2.0	2.8 ± 0.47
Umbrina xanti	Surf croaker	11	0.01	0.01	Carnivores	Decapods, infaunal crustacean, zooplankton, fish	− 15.11	16.47	3.7 ± 0.12
Urotrygon chilensis	Chilean round ray	17	3.5	3.38	Carnivores	Polychaetes, infaunal crustaceans, crabs, shrimps, bivalves, snails, squids	− 14.03	15.8	3.5 ± 0.44
Urotrygon reticulata	Reticulate round ray	11	0.03	0.03	Carnivores	Infaunal crustaceans, polychaetes	− 13.98	15.3	3.3 ± 0.37
Urotrygon rogersi	Thorny stingray	11	0.01	0.01	Carnivores	Polychaetes, infaunal crustaceans, crabs, shrimps, bivalves, snails, squids	− 16.24	18.51	4.3 ± 0.12

N number of individuals used in the isotopic analysis, *SD* standard deviation *mazatlanus*, and *Cyclopsetta panamensis*), and rays (*U. chilensis*). Planktivorous fish species were represented by anchovies (*Anchoa walker* and *A. macrolepidota*) and sardines (*Pliosteostoma lutipinnis*). Detritivores and omnivores were represented mainly by mojarras (*D. aureoles*, *D. peruvianus*, *Gerres cinereus*, *Eucinostomus currani*, and *E. argentus*), mullets (*Mugilcephalus*, *M. curema*), and the Pacific spadefish (*Chaetodipterus zonatus*).

Stomach content analyses (SCA)

Filter-feeding mollusks (snails) consumed suspended organic matter (detritus), phyto and zooplankton, whilst squids were predators from the water column preying on fish, shrimps, and other decapods.

Stomatopods ate infaunal crustaceans; all shrimp species preyed on detritus, polychaetes, bivalves, and benthic crustaceans. All crabs fed on macroalgae; swimming crabs fed also on smaller decapods, amphipods, juvenile fish, and detritus. Their diet was similar to that of the fiddler crab, but the proportions changed, as the former ate mainly detritus and macroalgae instead of other animals. Mangrove crabs fed on mangroves, detritus, crabs, polychaetes, and fish. The common crab preyed on mussels and other bivalves, infaunal crustaceans, and polychaetes. The hermit crab preyed predominantly on fish, but also detritus was found in its stomach. Finally, star fish ate sea urchins and bivalves.

For the fish, three groups were identified according to their main prey items. The first group was planktivorous fishes preying on phyto and zooplankton, but also on detritus and macroalgae. This group included anchovies (e.g. *Anchovia macrolepidota*, *A. walkeri*, *Anchoa mundeola*) and mullets (*Mugil* sp.). The second group was benthic feeders preying on all kinds of invertebrates inhabiting the benthos, such as polychaetes, snails, bivalves, and benthic crustaceans. Most of the fish species captured pertain to this group, which included species such as rays (Myliobatiformes and Rajiformes), croakers (*Menticirrhus* sp.), puffers (*Sphoeroides* sp.), and soles (*Achirus mazatlanus*) among others. The third group fed predominantly in the water column on fish and squids, and it included pelagic species such as the pacific sierra (*Scomberomorus sierra*) and the barracuda (*Sphyraena ensis*), but also typical demersal species such as the striped corvina (*Cynoscion reticulatus*) and the toothed flounder (*Cyclopsetta* sp.) (Fig. 2).

Isotopic composition of the estuarine biota

A total of 1522 samples were isotopically analysed, representing species from all the trophic levels; these accounted for more than 90% of the total biomass captured.

Primary producers

According to the carbon isotopic composition, the primary producers in SMR are a combination of marine C3 type (phytoplankton and benthic macroalgae), marine C4 type (salt marsh plants), estuarine-freshwater C3 type (*Typha*sp. and mangrove), plants, seston, and detritus. The δ^{13}C values in the primary producers ranged from − 26.2 ± 0.9‰ (*T. angustifolia*) to − 20.1 ± 1.9‰ for phytoplankton. Values of δ^{13}C for the organic matter in seston (− 22.5 ± 2.7‰) suggested that the origin is mostly phytoplankton, and to a lesser extent decomposed angiosperm leaves and macroalgae. The isotopic C signal in detritus revealed mixed sources with a predominance of terrestrial material (e.g. mangrove detritus) and also marine organisms (mainly phytoplankton and macroalgaes). The δ^{15}N values of the primary producers ranged between 6.50 ± 1.76‰ and 9.08 ± 0.88‰ (macroalgae in both cases) (Table 1; Fig. 3).

Consumers

The values of δ^{13}C for primary consumers varied between − 23.55 ± 0.57 (*Littoraria pintado*) and − 20.65 ± 0.53‰ (*Streblospio benedecti*), and their δ^{15}N values varied between 8.71 ± 2.94 (zooplankton) and 11.06 ± 1.64 (*Mytella strigata*). The δ^{13}C values in secondary consumers ranged from − 24.30 ± 0.30‰ to − 14.70 ± 0.10‰, the lowest value corresponded to mangrove crab (*Grapsus* sp), and the highest to the crab *Callinectes sapidus.* The lowest δ^{15}N was recorded in the swimming crab *Callinectes sapidus* (12.08 ± 0.20‰), and the highest was found in the hermit crab *Petrochirus californiensis* (16.50 ± 0.21‰). Concerning fish, most of the organisms showed δ^{13}C values in the range of − 19.27 to − 13.22‰ and δ^{15}N between 11.36 and 18.9 ‰

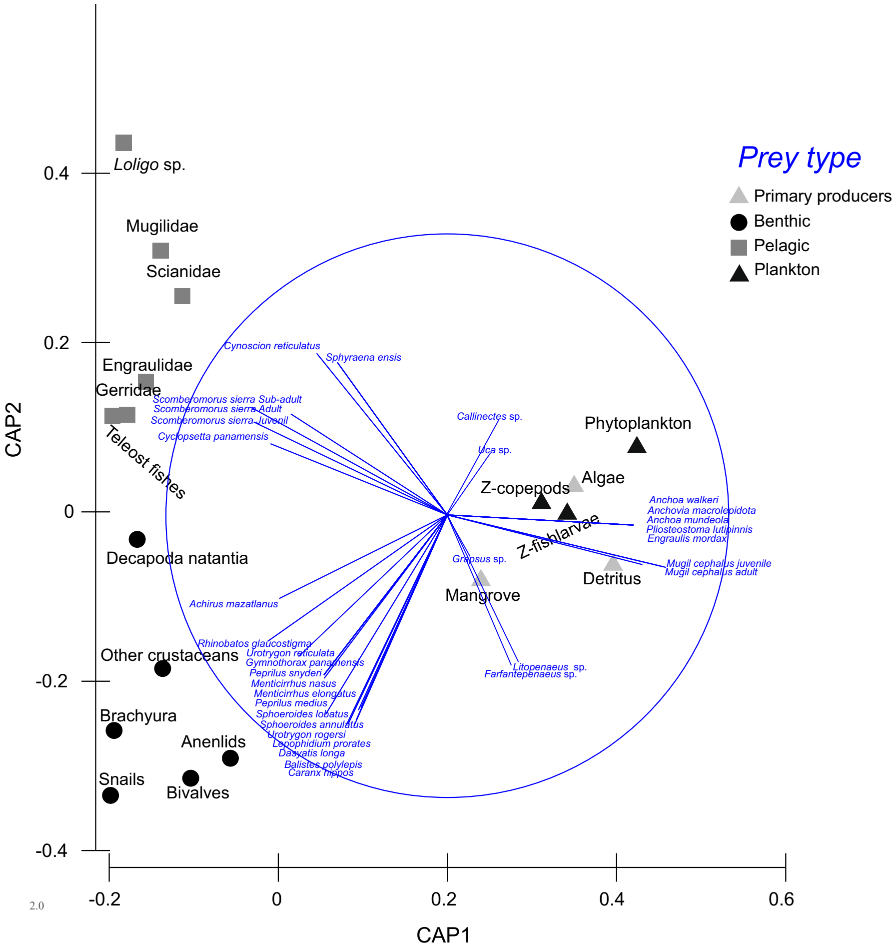


Fig. 2 Canonical analysis of principal coordinates showing the main prey items of the fish species collected at SMR. The vectors indicate the fish predators preying on the different groups of prey items. The *Z* at the beginning of some groups stands for zooplankton

(Table 2; Fig. 3). The highest δ^{13}C was found in *Diapterus peruvianus* (− 13.25 ± 1.0‰) and lowest in *Mugil cephalus* (− 19.18 ± 0.40‰), whereas the highest δ^{15}N was recorded in *Pomadasys branickii* (18.78 ± 0.30‰) and lowest in *Chaetodipterus zonatus* (11.36 ± 0.20‰). According to the type of feeding guild, the omnivores had the wider range of δ^{13}C signatures (− 24.3 to − 13.25‰), whilst planktivores had the most consistent values (− 15.82 to − 15.3‰).

ANOVA results indicated that there were no statistical differences in the mean signals of δ^{13}C and δ^{15}N according to season ($F_{\delta 13C(1,338)} = 0.158$, $F_{\delta 15N(1,338)} = 0.491$; $p > 0.05$) or the interaction of season/feeding guild ($F_{\delta 13C(8,338)} = 1.368$, $F_{\delta 15N(8,338)} = 1.392$; $p > 0.05$). However, differences were found according to feeding guild ($F_{\delta 13C(8,338)} = 20.826$, $F_{\delta 15N(8,338)} = 77.409$; $p < 0.05$). The Tukey HSD test for the δ^{13}C values allowed the determination that there were no differences in the mean δ^{13}C values of primary producers, herbivores, planktivores, and detritivores, but the mean δ^{13}C signal of the first three guilds was different for carnivores and omnivores. Differences were not found between the values of detritivores with carnivores and omnivores, but differences were found with all the other carnivores and the detritivores. All the carnivores 0 and the omnivores had similar mean δ^{13}C values, as no differences were found between them (Fig. 4a; Table 3).

Regarding the mean value of δ^{15}N, Fig. 4b shows an almost linear relationship according to the way the guilds were accommodated. In this way, the mean δ15 N signal of every guild is not statistically different to the immediate superior or inferior guild; for example, primary producers were not different to the mean δ^{15}N value of herbivores, but this value was different to all the others. The mean δ^{15}N value of

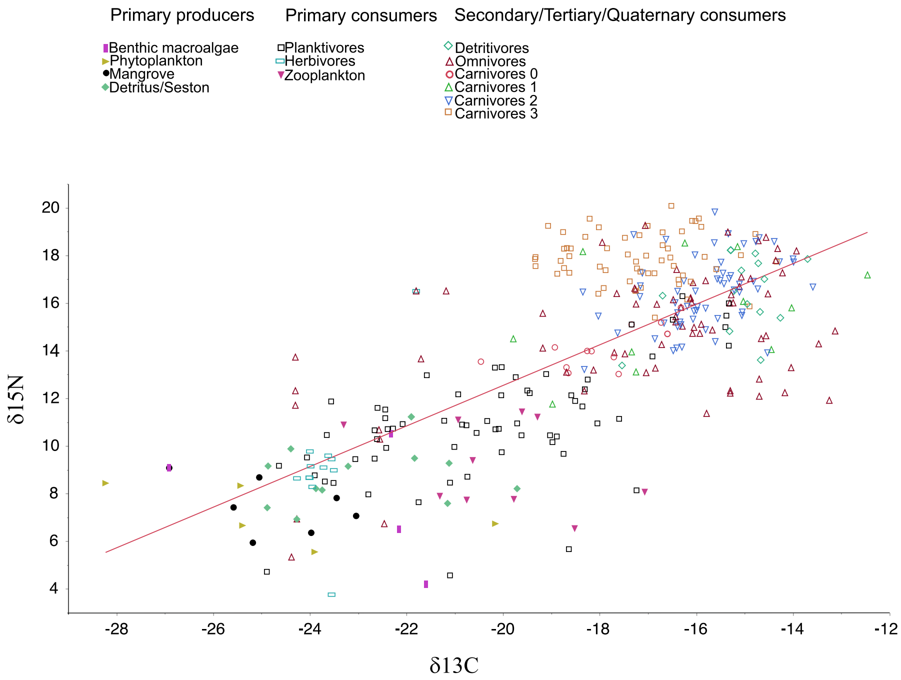


Fig. 3 Relationships between mean $\delta^{13}C$ (‰) versus mean $\delta^{15}N$ (‰) in food sources (primary producers) and predators (zooplankton, macroinvertebrates and fish) collected at SMR, representing > 70% of the biomass and abundance in the system

herbivores was not different to planktivores and primary producers, but it was different to all the others and so on until carnivores 3 whose mean $\delta^{15}N$ value was different to all the other guilds (Table 3).

Trophic position (TP)

The estimated TP based on values of $\delta^{13}C$ and $\delta^{15}N$ allowed the definition of five trophic levels. The community presented 70% of the fish species located as intermediate consumers (TP between 3 and 4), 10% as lower consumers (TP < 3), and 20% as higher consumers (TP > 4) (Fig. 5). From a total of 110 species analysed, ten species were primary producers, eight were planktivores, four herbivores, 23 omnivores and the rest carnivores (65). For primary consumers (e.g. bivalves, zooplankton, gastropods, and polychaetes), the TP values varied from 1.3 to 2.65, whilst for secondary (e.g. bivalves, zooplankton, gastropods, and polychaetes), tertiary, and quaternary consumers (e.g. crabs, squids, shrimps, stomatopods, and fishes) the values were between 2.4 and 4.96.

For fish groups, planktivorous species such as anchovies (*Anchoa* sp.) and the butterfish (*Peprilus medius*) occupied the lower trophic positions, whilst grunts (*Pomadasys branickii*, *Microlepidotus brevipinnis*, and *Pomadasys panamensis*), puffer (*Sphoeroides lobatus*), sea catfish (*Occidentarius platypogon*), and Pacific sierra (*Scomberomorus sierra*), among others, were the top trophic predators (Fig. 5).

Statistical differences were found in the trophic position according to the feeding guilds designated a priori ($F_{(7,348)} = 211.08$, $p \leq 0.01$). The mean TP of the primary producers was different from all the others. The TP of herbivorous and planktivorous organisms showed no significant differences between them, but they were significantly different to the primary producers, omnivores, detritivores, and carnivores. The mean TP of detritivores and omnivores was not different between them either; however, it was different to the primary producers, herbivores, planktivores, and all the carnivores. The mean TP of carnivores 1 and carnivores 2 was not different, but their mean TP differed to all the others. Finally, the mean TP of carnivores 3 was different to the mean TP of all the other feeding guilds (Fig. 5).

Food webs structure

Although the food webs in this system are intricate and complex, due to the large number of species and their abundance, and primary consumers usually preying on more than one food source or primary producer, four

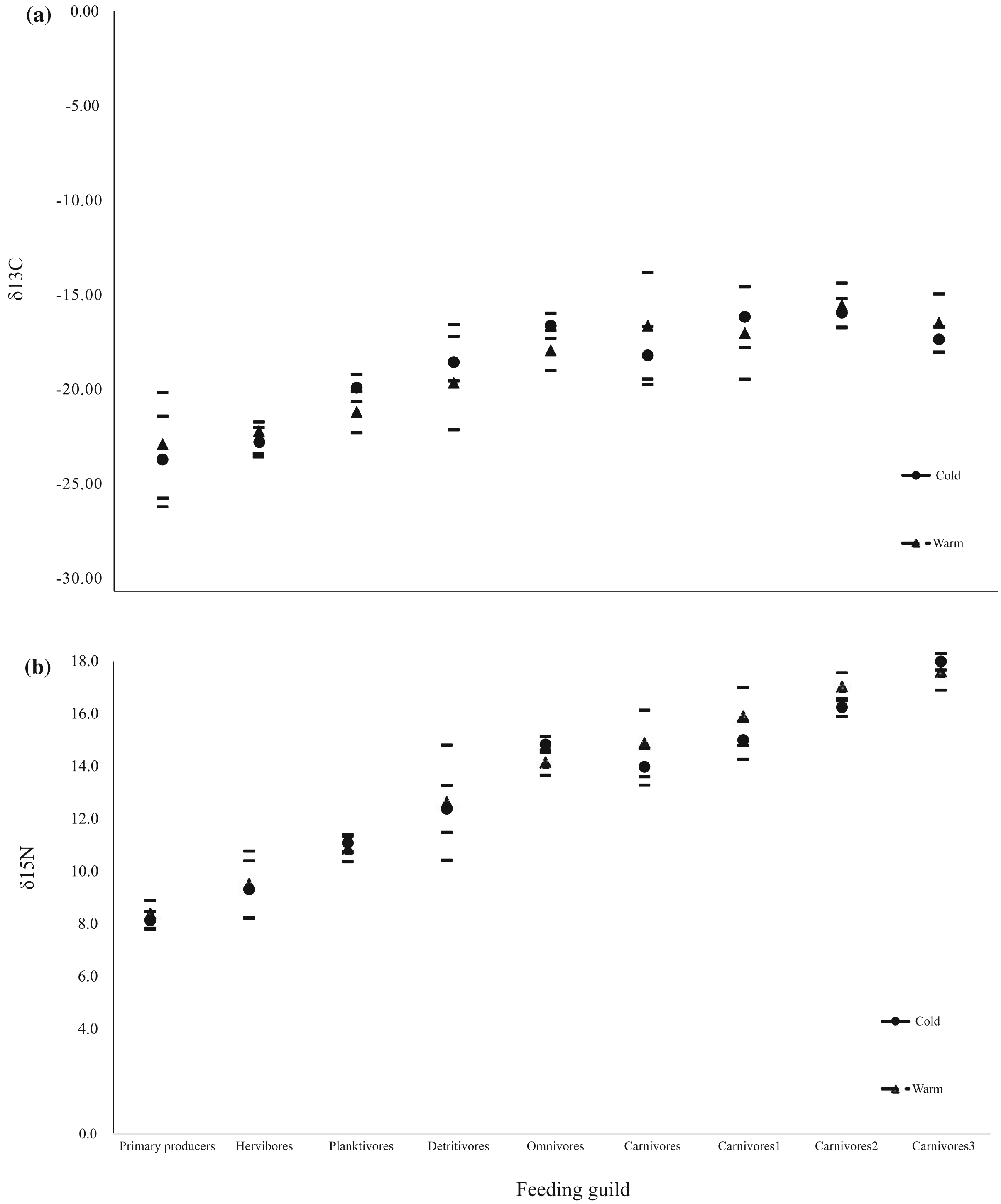


Fig. 4 Mean values of $\delta^{13}C$ (**a**) and $\delta^{15}N$ (**b**) of the different feeding guilds of SMR during the two studied seasons. Horizontal bars denote SD

Table 3 Tukey HSD test for pairwise comparisons between the mean δ^{13}C and δ^{15}N values for the different feeding guilds

δ^{13}C	Carnivores0							
Carnivores1		Carnivores1						
Carnivores2			Carnivores2					
Carnivores3				Carnivores3				
Detritivores					Detritivores			
Herbivores	*	*	*	*	*	Herbivores		
Omnivores						*	Omnivores	
Planktivores		*	*	*	*		*	Planktivores
Primary producers		*	*	*			*	
$\delta1^{5}$N	Carnivores0							
Carnivores1		Carnivores1						
Carnivores2	*		Carnivores2					
Carnivores3	*	*	*	Carnivores3				
Detritivores					Detritivores			
Herbivores	*	*	*	*	*	Herbivores		
Omnivores			*	*		*	Omnivores	
Planktivores	*	*	*	*	*		*	Planktivores
Primary producers	*	*	*	*	*		*	

*Significant differences were found

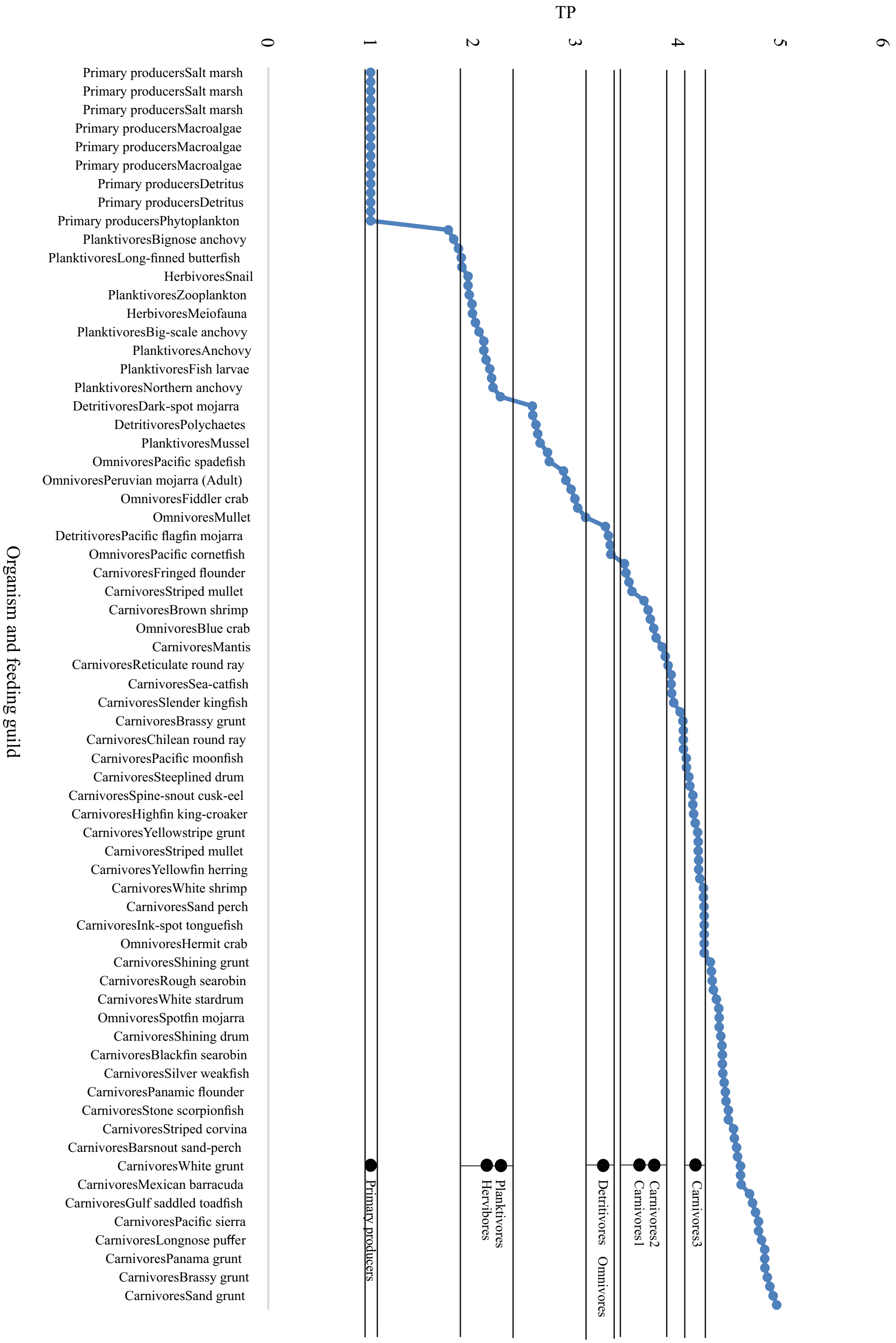
major potential food sources for this system were identified: (1) phytoplankton, (2) detritus and seston, (3) benthic macroalgae, and (4) mangrove forest (Fig. 6).

The first identified food web is based on phytoplankton, which is preyed upon by zooplankton, bivalves, anchovies, and sardines. A second food web is supported by detritus and seston as the food web base, with a suite of primary consumers. This food web is mainly established in the sediments associated with mangrove forests, but receives other autochthonous (e.g. phytoplankton and macroalgae) and allochthonous (agriculture, sewage, and shrimp farm) inputs of organic matter. Detritus and seston constitute the main food sources in the sediments for polychaetes, zooplankton, crabs, and snails, but are also quite important to bivalves and some demersal fish species. A third food web is supported by benthic macroalgae, which are principally preyed upon by snails and mullets. The fourth food web is supported by mangroves that are eaten only by some crabs, and not as their main food source.

Primary consumers have a TP of less than two to around three, because some of them prey only on primary producers (i.e. zooplankton, polychaetes, bivalves, and snails), whilst others eat at higher trophic levels as well (fish and decapoda).

After the primary consumers, the food web complicates, as there are many links and connections, because the secondary and tertiary consumers preyed on a wide range of organisms from different TPs. All the primary consumers are in turn the main component in the diet of several species of macroinvertebrates and fish species; polychaetes and zooplankton are preyed upon by both crustaceans and fish, bivalves and snails are preyed upon only by fish, whilst species of fish and crustaceans which are primary consumers are preyed upon by squids and fish. Some second-order consumers (fish, crabs, shrimps) preyed not only on first-order consumers, but also on primary producers (phytoplankton, detritus, and macroalgae). Decapod crustaceans did not exhibit a predominant food source, but for this group primary producers had a significant contribution.

In the upper trophic levels (third- and fourth-order consumers), it is not possible to distinguish the four previously identified food webs, as the predators from trophic levels 3 and 4 preyed on a large diversity of


TP
0
1
2
3
4
5
6
Organism and feeding guild
Primary producersSalt marsh
Primary producersSalt marsh
Primary producersSalt marsh
Primary producersMacroalgae
Primary producersMacroalgae
Primary producersMacroalgae
Primary producersDetritus
Primary producersDetritus
Primary producersPhytoplankton
PlanktivoresBignose anchovy
PlanktivoresLong-finned butterfish
HerbivoresSnail
PlanktivoresZooplankton
HerbivoresMeiofauna
PlanktivoresBig-scale anchovy
PlanktivoresAnchovy
PlanktivoresFish larvae
PlanktivoresNorthern anchovy
DetritivoresDark-spot mojarra
DetritivoresPolychaetes
PlanktivoresMussel
OmnivoresPacific spadefish
OmnivoresPeruvian mojarra (Adult)
OmnivoresFiddler crab
OmnivoresMullet
DetritivoresPacific flagfin mojarra
OmnivoresPacific cornetfish
CarnivoresFringed flounder
CarnivoresStriped mullet
CarnivoresBrown shrimp
OmnivoresBlue crab
CarnivoresMantis
CarnivoresReticulate round ray
CarnivoresSea-catfish
CarnivoresSlender kingfish
CarnivoresBrassy grunt
CarnivoresChilean round ray
CarnivoresPacific moonfish
CarnivoresSteeplined drum
CarnivoresSpine-snout cusk-eel
CarnivoresHighfin king-croaker
CarnivoresYellowstripe grunt
CarnivoresStriped mullet
CarnivoresYellowfin herring
CarnivoresWhite shrimp
CarnivoresSand perch
CarnivoresInk-spot tonguefish
OmnivoresHermit crab
CarnivoresShining grunt
CarnivoresRough searobin
CarnivoresWhite stardrum
OmnivoresSpotfin mojarra
CarnivoresShining drum
CarnivoresBlackfin searobin
CarnivoresSilver weakfish
CarnivoresPanamic flounder
CarnivoresStone scorpionfish
CarnivoresStriped corvina
CarnivoresBarsnout sand-perch
CarnivoresWhite grunt
CarnivoresMexican barracuda
CarnivoresGulf saddled toadfish
CarnivoresPacific sierra
CarnivoresLongnose puffer
CarnivoresPanama grunt
CarnivoresBrassy grunt
CarnivoresSand grunt
Primary producers
Planktivores
Hervibores
Detritivores
Omnivores
Carnivores2
Carnivores1
Carnivores3

◀**Fig. 5** Trophic position of the different organisms analysed. The black dots to the far right denote the mean TP for the indicated feeding guild. The horizontal bars denote the standard deviation of the dots

organisms. For the upper part, it is easier to separate groups according to their strategy of feeding and TP. The first group represents the lower levels of the food web which includes decapods, mullets, spadefish, and mojarras. The second group is a myriad of secondary consumers separated into two subgroups that consist of: (1) fish planktivores, such as sardines and anchovies, and (2) a mixture of demersal fish with a wide range of feeding. The third group corresponded to the species located in the upper levels of the food web that feed on fish and macroinvertebrates. These predators were identified according to their prey: (1) pelagic predators such as anchovies and sardines linked to plankton, (2) benthic predators (e.g. macroinvertebrates and rays), and (3) omnivore predators (e.g. decapod crustaceans, and several species of fish).

Discussion

Our results show that the trophic structure of tropical and subtropical estuarine ecosystems is, in general, very complex. The estuarine system of SMR is a large ecosystem with an important extension of mangrove forests, and it is also one of the most important fishing grounds in the region. It is characterised by a variety of potential sources of organic matter due to the input of subsidies by the surrounding environment and its high in situ production. Human activities in the system cause different sources of organic matter (Páez Osuna et al. 2007), which vary temporally in terms of quantity and quality, making the analysis of trophic studies very difficult because it complicates the direct use of $\delta^{13}C_{base}$ and $\delta^{15}N_{base}$ as indicators to estimate the TP for consumers.

Previous studies have outlined that anthropogenic alteration has an effect on primary producers (Choy et al. 2008); therefore, it is likely that all the human activities occurring in this system have had an effect on these organisms. However, no similar studies exist

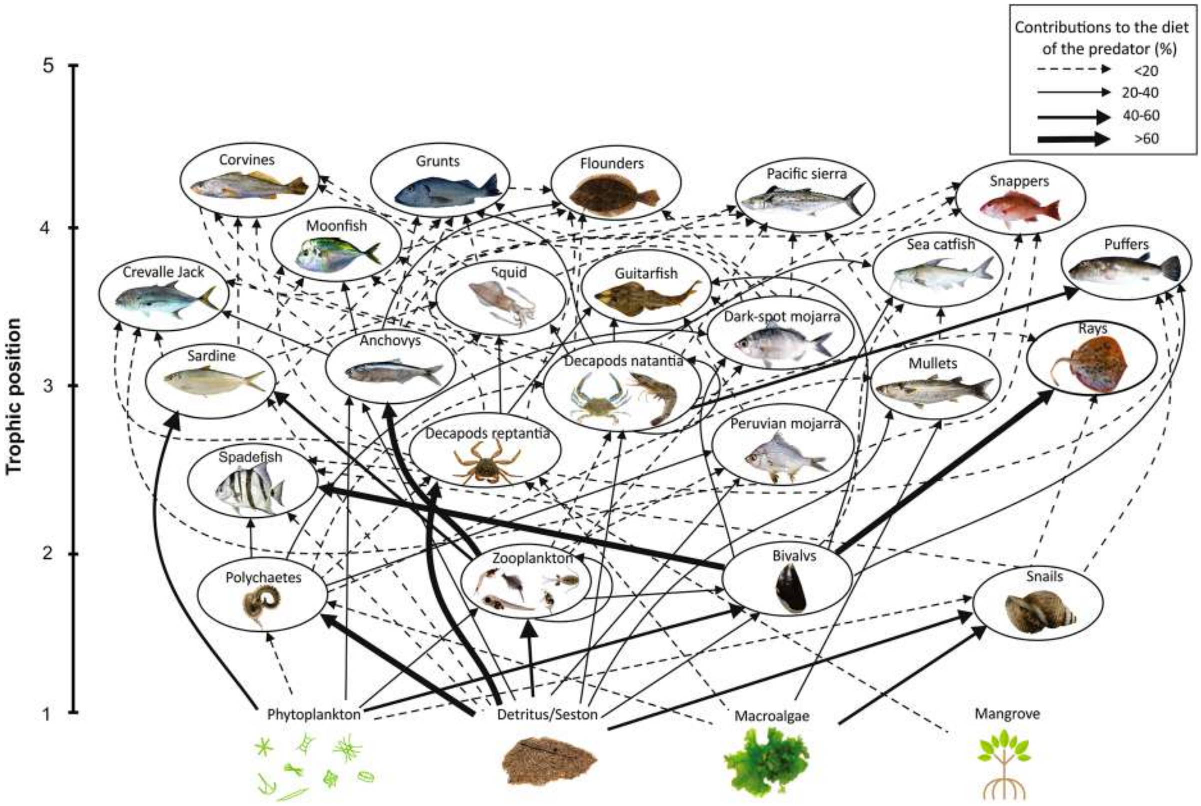


Fig. 6 Trophic structure and food linkages of the food web at SMR

in the past, therefore precluding any comparison to determine the extent or the way in which these alterations affected primary producers and their distribution. Nevertheless, preceding studies have signalled that variations in the inputs of organic matter, together with ontogenetic changes in diet of the organisms inhabiting the system, migratory patterns, and the different use of the habitat by all the inhabitants, could result in significant spatiotemporal modifications of the food web structure in this system (Polis et al. 1997; Marczak et al. 2007), thus complicating its description. In this sense, the present study is useful as a basis for any further studies undertaken in this system.

The suite of organisms analysed represented approximately 70% of the total species captured during the course of this work, representing all the TP, from primary producers to top predators. The most important organisms in the system, both in terms of diversity and abundance, were the fish.

The SCA permitted an initial glimpse of the food web in the system, allowing us to identify groups of predators. The CAP on SCA shows three different groups: one group preying on organisms from the water column composed of fish and squid, another group composed mostly of fish preying on benthic fauna (macrobenthos), and a third group including planktivorous fish and decapods that also ate primary producers. Within this group, the planktivorous fishes form a well-defined group, whilst the decapods remain between this and the other two groups; surely, this result is related to the fact that they can feed on a wide range of prey from different trophic levels. The three groups could be defined as predators of demersal fauna, predators of benthic fauna, and planktonic predators, with decapod organisms moving between these groups.

SIA results allowed us to analyse the isotopic values of both carbon and nitrogen, determine the number of primary producers, as well as to classify all the organisms into feeding guilds. In general, there was enrichment in both δ^{13} C and δ^{15}N signals as trophic levels increased, being lower for both isotopes in the primary producers, and then increasing towards the top predators. However, some values within the same feeding guild varied considerably, with the exception of the herbivores that all had similar values.

The high variation on isotope signatures of δ^{13}C may be attributable to the temporal and spatial changes in the organic carbon sources through food webs in the system in which a gradual mixing of fluvial (light δ^{13}C) and marine (heavy δ^{13}C) organic matter sources may occur (Fontugne and Jouanneau 1987), or due to a variation in the primary energy source, such as benthic versus pelagic photosynthesis (O'Reilly et al. 2002). The results suggest that the diet of these species is mixed between benthic and pelagic sources, so for example, predators with lighter δ^{13}C values (i.e. *Loligo* sp., *Scomberomorus sierra*, and *Selene peruviana*.) were characterised by a pelagic diet, whilst the highest values in δ^{13}C isotopic signals were recorded for species that consume benthic prey such as rays, puffers, and some species of grunts.

Besides these variations in sources, it is necessary to consider that the variations in both carbon and nitrogen isotopes for predators within the same feeding guild might be reflecting the complexity of the food web. The feeding habits of many predators have a degree of omnivority by feeding at different trophic levels (Shephard et al. 1989). Thus, the ability of certain species to feed at more than one trophic level can also increase the intraspecific variability in δ^{15}N signals. Omnivorous species (i.e. mullets and mojarras) have the ability to feed on primary producers (algal–plant material, detritus) as well as animals (e.g. polychaetes, annelids, crustaceans, and fish). Such diet flexibility results in variations of the δ^{13}C and/or δ^{15}N composition for these species.

Also, there is the presence of fish that enter the system sporadically, implying that their signal might reflect a marine diet and their main food may be based on dams of the adjacent marine area. Fish in estuaries are often characterised as omnivores that share common resources and are flexible, so they are able to exploit a variety of prey (Ley et al. 1994). This means that we are comparing organisms with different turnover times associated with each trophic level. For example, phytoplankton population growth rates are usually 1.2 d^{-1} or higher (Coulter 1991), and thus their stable isotope signal represents carbon and nitrogen uptake and sources over the last few days. On the other hand, fishes can integrate their diet over a period of several months to even years (Coulter 1991), and if the fish is a migrant species, entering and exiting the estuarine system, its signal might be reflecting the intake of organisms from different environments, so the variations are the effect of this greater temporal integration.

Finally, the high variation in both isotopic signals might also be related to the nitrogen sources into the system, and to eutrophication of some areas of this coastal lagoon due to a high input of nutrients. The inputs from agricultural discharges, shrimp ponds, and sewage from neighbouring human settlements are rich in nitrogen, which can affect the δ^{15}N signal. This in turn can also affect the δ^{13}C signal; under conditions of high nutrient availability, phytoplankton productivity increases and discrimination against the heavier carbon isotope eventually decreases, giving them an enriched carbon signal (Farquhar et al. 1989), and this could be the reason why we observed a large variation in the isotopic carbon signals of the primary producers.

Nevertheless, in spite of the high variations in both isotopic signals, both of them showed enrichment from the basis of the food web towards the top predators. This was more evident in δ^{15}N signals than δ^{13}C ones, because δ^{13}C signatures show an asymptote towards the top predators, and differences were not found, either between primary producers and first-order consumers or between second-order consumers to top predators. The reason for this might be related to the arguments earlier exposed, a high variation in the carbon signals of the primary producers may preclude finding differences with the following trophic chain, and among the predators, the asymptote might be reflecting the fact that most species show certain degree of omnivory.

Another reason for these variations might be related to the isotopic turnover, or the rate at which elemental isotopes in the diet are incorporated into consumer tissues (Tieszen et al. 1983). Most organisms rarely exhibit fixed diets, and spatiotemporal and ontogenetic shifts are common, as our results and other studies have shown (Thomas and Crowther 2015). Therefore, our estimates based on SIA assume that all consumers exhibit limited dietary plasticity and that a constant isotopic steady state exists with their resources (Kaufman et al. 2008). Although it has been pointed out that using muscle tissue adequately provides predictable, long-term dietary information (Thomas and Crowther 2015), considering the diversity of taxa present in this system, it is likely that the turnover rate is causing some of this variation as well.

However, for the δ^{15}N signals, it is clear that these increased from primary producers towards top predators. These differences are surely related to the feeding strategy of the different species, the lowest concentrations were recorded in primary consumers, followed by first-order consumers, and so on, until the highest signals in top predator species.

Results on the trophic position revealed that the food web in SMR system is composed of five trophic levels and that these agree with the feeding guilds established a priori: primary producers; first-order predators (herbivores and planktivores), second-order predators (detritivores and omnivores), second- and third-order predators (carnivores 1 and 2), and top predators (carnivores 3).

Our results indicate the presence of four primary producers that can each be considered the basis of a food web. The most important is detritus, as there are many first-order consumers that depend on this producer (invertebrates and fish). The next one is phytoplankton, as this is the main source for bivalves and sardines, but is also important for zooplankton as well. The macroalgae sustain a short food chain, since they are the main source of food for snails and some fish species such as mullets. Finally, the mangrove is only directly consumed by a species of crab, and although it is not the main source of direct food for organisms, it can be a primary factor in the production of detritus.

These four food chains are not evident as we move towards the top of the food chain, and the trophic relations become more complicated. This might be attributable to ontogenetic changes in the diet of many species, to a large number of omnivore species, and also to the presence of several migrating species that can feed in a wide range of habitats within the system or in the adjacent marine area; organisms feeding inside the lagoon may be preying on abundant invertebrate fauna, whilst species feeding in the adjacent coastal waters might be preying on smaller fishes (Albertini-Berhaut 1974; Tandel et al. 1986; Robertson and Allen 2006). Thus, in those migratory species, isotopic variations between distinct marine zones and inside the coastal lagoon and subsequent changes in TP are expected. In addition, the high variability among fish species occupying different habitats leads to an overlap in TPs that is inclusive when these species are categorised with different feeding strategies. This implies that the trophic ecology of this site needs to be considered not as a static but as a changing food web.

Unfortunately for a large number of the species collected in this study, there is not enough information on their feeding habits and habitat use in order to make more precise conclusions. However, there seems to be a greater diversity of trophic niches for species that usually inhabit the estuarine environment, which causes a complex food web. The success of the omnivorous strategy as opposed to other feeding strategies is possibly due to the advantage of having a broad dietary flexibility that allows it to make food adaptations in the face of possible fluctuations in the environment and therefore in resources. The importance of the omnivory between species means that in a habitat very similar species are found occupying different trophic positions (Doi et al. 2005), as observed in some species of this study. This fact would be favoured by the dominance of species such as decapods, mojarras, and mullets consuming detritus which then is transferred to a large number of predators at higher levels, and also to the open sea and probably to other systems in the case of migratory species. Therefore, a connection and a flow of energy occur from this system to other systems and other food webs.

Nevertheless, three distinct groups were identified, making a clear distinction between pelagic feeders (anchovies, sardines, squid, Pacific sierra, etc.) and those that are strictly benthic (polychaetes, crabs, rays, flatfishes, grunts, etc.), with an intermediate group that feeds in both environments (pelagic and benthic), comprised by demersal fish species as well as decapods and mollusks.

In contrast, the planktivore and herbivore species that only feed on primary producers (e.g. phytoplankton, macroalgae, and/or plants) have δ^{15}N values that are more constrained and a well-defined trophic position in the food web, although the δ^{13}C values for herbivores demonstrated a high level of intraspecific variability.

The strong dependence on detritus in this system implies that species such as shrimps and crabs have a high importance linking the estuarine and marine systems as these species are known to have life cycles that include both environments. In terms of trophic relationships, it means that shrimp and crabs intervene extensively in the energy flows of the food web. This has been observed by different authors such as Hill and Wassenberg (1993). Siqueiros-Beltrones and Argumedo-Hernandez (2006) mention that shrimps and crabs are abundant components in estuarine and coastal ecosystems and that they feed mainly on invertebrates, detritus, and other organisms that are found on the sediment, therefore, they have great importance in the trophic plots of these types of ecosystems.

Comparing the results from the present work to similar studies undertaken in temperate areas, it is possible to say that the food web complexity in this tropical ecosystem is different and higher than that of temperate ones. The number of species found in this study (over 100 species were analysed, and these were only the most representative), and therefore the number of connections, is much higher when compared to the number of species found in temperate systems (i.e. Kwak and Zedler (1997) analysed 38 species for southern California wetlands; Pasquaud et al. (2008); analysed nine fish species from the Gironde estuary; Choy et al. (2008) analysed 18 macroinvertebrates from the Nakdong River estuary; and Doi, Matsumasa, Toya, Satoh, Kikuchi, and others (2005) analysed ten macroinvertebrates from the Kitakami River estuary; etc.), and it seems that the results obtained from temperate ecosystems cannot be extrapolated to tropical ecosystems, as demonstrated here. Therefore, these types of studies are much needed in order to understand and to manage these ecosystems. At present, there is a consensus that most of the world's fish populations are overexploited, depleted, or collapsed, and the ecosystems that sustain them are degraded as an unintended consequence of fishing: habitat destruction, incidental mortality of nontarget species, evolutionary shifts in population demographics, and changes in the function and structure of ecosystems (Pikitch et al. 2004; Pauly 2007; Worm et al. 2009). To date, existing fisheries management practices are failing to protect individual stocks and ecosystems as they tend to focus on maximising the catch of a single target species, often ignoring habitat, predators, and prey of the target species and other ecosystem components and interactions. Data collection on feeding habits and trophic connections combined with ecosystem models could lead to modification of single-species control rules to account for ecosystem understanding.

Acknowledgements A.N. Rojas prepared the samples for isotopic analysis. Financial support was provided by the projects PAPIIT-UNAM IN217408 and IN215206. V. M. Muro-Torres and J. Quintero thank CONACYT for the Ph.D. grant.

References

Albertini-Berhaut J (1974) Biologie des stades juveniles de teleosteens Mugilidae Mugil auratus Risso 1810, Mugil capito Cuvier 1829 et Mugil saliens Risso 1810. Aquaculture 4:13–27

Amezcua F, Amezcua-Linares F (2014) Seasonal changes of fish assemblages in a subtropical lagoon in the SE Gulf of California. Sci World J 2014:16–19

Amezcua F, Madrid-Vera J, Aguirre-Villaseñor H (2006) Effect of the artisanal shrimp fishery on the ichthyofauna in the coastal lagoon of Santa María la Reforma, southeastern Gulf of California. Ciencias Mar [Cienc Mar] 32:97–109

Amezcua F, Muro-Torres V, Soto-Jiménez MF (2015) Stable isotope analysis versus TROPH: a comparison of methods for estimating fish trophic positions in a subtropical estuarine system. Aquat Ecol 49:235–250. https://doi.org/10.1007/s10452-015-9517-4

Anderson MJ, Gorley RN, Clarke KR (2008) PRIMER+ for PERMANOVA: guide to software and statistical methods. 214. Primer-e, Plymouth

Baker R, Buckland A, Sheaves M (2014) Fish gut content analysis: robust measures of diet composition. Fish Fish 15:170–177

Bodin N, Le Loc'h F, Hily C (2007) Effect of lipid removal on carbon and nitrogen stable isotope ratios in crustacean tissues. J Exp Mar Biol Ecol 341:168–175

Choy EJ, An S, Kang CK (2008) Pathways of organic matter through food webs of diverse habitats in the regulated Nakdong River estuary (Korea). Estuar Coast Shelf Sci 78:215–226. https://doi.org/10.1016/j.ecss.2007.11.024

Choy EJ, Richard P, Kim KR, Kang CK (2009) Quantifying the trophic base for benthic secondary production in the Nakdong River estuary of Korea using stable C and N isotopes. J Exp Mar Biol Ecol 382:18–26. https://doi.org/10.1016/j.jembe.2009.10.002

Christensen V, Pauly D (1992) ECOPATH II—a software for balancing steady-state ecosystem models and calculating network characteristics. Ecol Model 61:169–185

Costanza R, Arge R, De Groot R et al (1997) The value of the world' s ecosystem services and natural capital by. Nature 387:253–260. https://doi.org/10.1016/j.ijrobp.2010.07.1349

Coulter GW (1991) Lake Tanganyika and its life, G.W. Coulter (Ed.) with contributions from J.-J. Tiercelin, A. Mondegver, R.E. Hecky and R.H. Spigel, British Museum (Natural History) Publications — Oxford University Press, 1991. 354 pp. Price: £60.00. Aquat Conserv Mar Freshw Ecosyst 1:190–191. https://doi.org/10.1002/aqc.3270010210

Deegan LA, Garritt RH (1997) Evidence for spatial variability in estuarine food webs. Mar Ecol Prog Ser 147:31–47

DeNiro MJ, Epstein S (1977) Mechanism of carbon isotope fractionation associated with lipid synthesis. Science 197(80):261–263

Doi H, Matsumasa M, Toya T et al (2005) Spatial shifts in food sources for macrozoobenthos in an estuarine ecosystem: carbon and nitrogen stable isotope analyses. Estuar Coast Shelf Sci 64:316–322

Farquhar GD, Ehleringer JR, Hubick KT (1989) Carbon isotope discrimination and photosynthesis. Annu Rev Plant Physiol Plant Mol Biol 40:503–537. https://doi.org/10.1146/annurev.pp.40.060189.002443

Flores-Verdugo F, González-Farias F, Zaragoza-Araujo U (1993) Ecological parameters of the mangroves of semi-arid regions of Mexico: important for ecosystem management. In: Lieth H, Al Masoom AA (eds) Towards the rational use of high salinity tolerant plants. Springer, pp 123–132

Fontugne MR, Jouanneau J-M (1987) Modulation of the particulate organic carbon flux to the ocean by a macrotidal estuary: evidence from measurements of carbon isotopes in organic matter from the Gironde system. Estuar Coast Shelf Sci 24:377–387

Hill BJ, Wassenberg TJ (1993) Why are some prawns found in seagrass? An experimental study of brown (*Penaeus esculentus*) and grooved (*P. semisulcatus*) tiger prawns. Mar Freshw Res 44:221–227

Kaufman MR, Gradinger RR, Bluhm BA, O'Brien DM (2008) Using stable isotopes to assess carbon and nitrogen turnover in the Arctic sympagic amphipod Onisimus litoralis. Oecologia 158:11–22

Kline TC, Pauly D (1998) Cross-validation of trophic level estimates from a mass-balance model of Prince William Sound using 15 N/14 N data. In: Alaska Sea Grant College. Citeseer

Kwak TJ, Zedler JB (1997) Food web analysis of southern California coastal wetlands using multiple stable isotopes. Oecologia 110:262–277

Langton RW, Watling L (1990) The fish-benthos connection: a definition of prey groups in the Gulf of Maine. In: Trophic relationships in the marine environment: proceedings 24th European marine biology symposium, pp 424–438

Ley JA, Montague CL, Mclvor CC (1994) Food habits of mangrove fishes: a comparison along estuarine gradients in northeastern Florida Bay. Bull Mar Sci 54:881–899

Little C (2000) The biology of soft shores and estuaries. Oxford University Press, Oxford

Livingston RJ (1982) Trophic organization of fishes in a coastal seagrass system. Mar Ecol Prog Ser 7:1–12

Marczak LB, Thompson RM, Richardson JS (2007) Meta-analysis: trophic level, habitat, and productivity shape the food web effects of resource subsidies. Ecology 88:140–148

Minagawa M, Wada E (1984) Stepwise enrichment of 15 N along food chains: further evidence and the relation between δ^{15}N and animal age. Geochim Cosmochim Acta 48:1135–1140

Moncreiff CA, Sullivan MJ (2001) Trophic importance of epiphytic algae in subtropical seagrass beds: evidence from multiple stable isotope analyses. Mar Ecol Prog Ser 215:93–106. https://doi.org/10.3354/meps215093

Newell RIE, Marshall N, Sasekumar A, Chong VC (1995) Relative importance of benthic microalgae, phytoplankton, and mangroves as sources of nutrition for penaeid prawns and other coastal invertebrates from Malaysia. Mar Biol 123:595–606

O'Reilly CM, Hecky RE, Cohen ASC, Plisnier PD (2002) Interpreting stable isotopes in food webs: recognizing the role of time averaging at different trophic levels. Limnol Oceanogr 47:306–309

Páez Osuna F, Ramírez Reséndiz G, Ruiz Fernández AC, Soto Jiménez MF (2007) La contaminación por nitrógeno y fósfoto en Sinaloa: Flujos, fuentes, efectos y opciones de manejo. Universidad Nacional Autónoma de México, Mazatlán

Page HM (1997) Importance of vascular plant and algal production to macro-invertebrate consumers in a southern California salt marsh. Estuar Coast Shelf Sci 45:823–834

Pasquaud S, Elie P, Jeantet C et al (2008) A preliminary investigation of the fish food web in the Gironde estuary, France, using dietary and stable isotope analyses. Estuar Coast Shelf Sci 78:267–279. https://doi.org/10.1016/j.ecss.2007.12.014

Pauly D (2007) The sea around us project: documenting and communicating global fisheries impacts on marine ecosystems. AMBIO J Hum Environ 36:290–295

Pauly D, Froese R, Rius M (2000) Trophic pyramids. In: Froese R, Pauly D (eds) FishBase. pp 203–204

Pikitch E, Santora C, Babcock EA et al (2004) Ecosystem-based fishery management. Science 305:346–347

Polis GA, Anderson WB, Holt RD (1997) Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. Annu Rev Ecol Syst 28:289–316

Polunin NVC, Pinnegar JK (2000) Trophic-level dynamics inferred from stable isotopes of carbon and nitrogen. Fish Down Mediterr Food Webs 12:69–72

Post DM (2002) Using stable isotopes to estimate trophic position: models, methods, and assumptions. Ecology 83:703–718

Robertson DR, Allen GR (2006) Shorefishes of the tropical eastern Pacific: an information system: an information system. Panama Smithson Trop Res Insitute, Balboa

Roy PS, Williams RJ, Jones AR et al (2001) Structure and function of south-east Australian estuaries. Estuar Coast Shelf Sci 53:351–384. https://doi.org/10.1006/ecss.2001.0796

Shephard SA, McComb AJ, Bulthuis DA et al (1989) Decline of seagrasses. Elsevier Science Pub.

Siqueiros-Beltrones D, Argumedo-Hernandez U (2006) Identificación de Diatomeas en Contenidos Intestinales de Camarones para ubicar su sitio de captura, un caso jurídico. Conversus 53:22–24

Tandel SS, Athalye RP, Gokhale KS (1986) On the seasonal changes in food habit of Mugil cephalus of the Thana Creek. Indian J Fish 33:270–276

Thomas SM, Crowther TW (2015) Predicting rates of isotopic turnover across the animal kingdom: a synthesis of existing data. J Anim Ecol 84:861–870

Tieszen LL, Boutton TW, Tesdahl KG, Slade NA (1983) Fractionation and turnover of stable carbon isotopes in animal tissues: implications for $\delta^{13}C$ analysis of diet. Oecologia 57:32–37

Toscano AL, Ochoa DR (2003) Evaluacion/sistematizacion de la experienca del proceso para establecer una Estrategia de Manejo para la Conservacion y desarrollo de bahia Santa Maria. –Un documento sintetiza de los resultados del estudio. Narragansett

Vanderklift MA, Ponsard S (2003) Sources of variation in consumer-diet $\delta^{15}N$ enrichment: a meta-analysis. Oecologia 136:169–182

Wainright SC, Weinstein MP, Able KW, Currin CA (2000) Relative importance of benthic microalgae, phytoplankton and the detritus of smooth cordgrass *Spartina alterniflora* and the common reed *Phragmites australis* to brackish-marsh food webs. Mar Ecol Prog Ser 200:77–91

Wissel B, Fry B (2005) Tracing Mississippi River influences in estuarine food webs of coastal Louisiana. Oecologia 144:659–672

Worm B, Hilborn R, Baum JK et al (2009) Rebuilding global fisheries. Science 325:578–585. Kapiti Mar Reserv (New Zealand) 89

Yokoyama H, Tamaki A, Koyama K et al (2005) Isotopic evidence for phytoplankton as a major food source for macrobenthos on an intertidal sandflat in Ariake Sound, Japan. Mar Ecol Prog Ser 304:101–116. https://doi.org/10.3354/meps304101

Zar JH (1999) Biological statistics. Prentice Hall, Upper Saddle River