[EN] This article reproduces entirely the chapter I of the dissertation: Efectos del cambio global en la estructura trófica de los humedales a través del uso de isótopos estables, de Lilia Serrano-Grijalva (2015), http://hdl.handle.net/10261/127832

EFECTOS DEL CAMBIO GLOBAL EN LA ESTRUCTURA TRÓFICA DE LOS HUMEDALES A TRAVÉS DEL USO DE ISÓTOPOS ESTABLES

[ES] Este artículo reproduce completamente el capítulo I de la tesis doctoral: Efectos del cambio global en la estructura trófica de los humedales a través del uso de isótopos estables, de Lilia Serrano-Grijalva (2015), http://hdl.handle.net/10261/127832

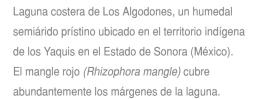
Capítulo I

Efectos de los efluentes de las granjas camaronícolas en la estructura de las redes tróficas en las lagunas costeras subtropicales

Effects of shrimp-farm effluents on the food web structure in subtropical coastal lagoons

Este capítulo corresponde al artículo publicado en la revista "Journal of Experimental Marine Biology and Ecology" (JEMBE) en el año 2011







La laguna de San José es un humedal fuertemente degradado por las descargas de efluentes procedentes de las granjas camaronícolas. Véase que la alteración que presenta el mangle en los márgenes de la laguna.

Resumen

Aunque numerosos estudios han reportado efectos negativos de las granjas camaronícolas en la calidad del agua, poco se sabe sobre los efectos ecológicos de estas actividades en las lagunas costeras y en los hábitats marinos cercanos a la costa. Los impactos de los efluentes de las granjas camaronícolas en las redes tróficas de una laguna costera del Golfo de California fueron evaluados a través de las medidas de las firmas isotópicas (δ¹3C, δ¹5N) en los sedimentos, plantas y animales y se compararon con los resultados de un sitio prístino cercano como referencia. La degradación fue manifestada con una fuerte reducción de la diversidad de peces en el sitio perturbado. Los valores de δ^{13} C proveyeron evidencias ambiguas de la degradación mientras que los valores de δ¹⁵N fueron mejores descriptores de los impactos de los efluentes de las granjas camaronícolas en las redes tróficas de las lagunas costeras. El sitio que recibe descargas ricas en nutrientes mostró un enriquecimiento significativo de $\delta^{15}N$ ($\approx 5\%$) en los sedimentos, macroalgas, algas bentónicas, filtradores y omnívoros, resultando en diferencias cualitativas en la estructura de la red trófica en ambas lagunas. La red trófica en el sitio perturbado estuvo sostenida por el detritus del sedimento y dominada por especies oportunistas. Los niveles tróficos más altos registraron la más baja influencia en los valores de 8¹⁵N por las descargas acuícolas, el cual puede ser explicado por el cambio de la composición de las comunidades bióticas y por las estrategias alimenticias asociadas. Mientras que las alteraciones en la disponibilidad de los recursos no afectan directamente en la longitud de la cadena alimenticia, los vínculos tróficos entre los compartimentos de las redes tróficas pueden ser reducidos como resultados de los impactos de las granjas camaronícolas. Nuestros estudios demuestran que las descargas enriquecidas en nutrientes de las granjas camaronícolas generan cambios en la disponibilidad de las fuentes de alimentos, lo cual reduce la biodiversidad y altera las características estructurales y funcionales de las redes tróficas.

Abstract

Although numerous studies have reported the negative effects of shrimp aquaculture on water quality, little is known about the ecological effects of these practices in coastal lagoons and near-shore marine habitats. The impact of shrimp-farm effluents on the food webs of an impacted subtropical coastal lagoon in the Gulf of California was evaluated through measurements of isotopic $(\delta^{13}C, \delta^{15}N)$ signatures in sediments, plants and animals, and compared with the results of a near-pristine reference site. Degradation was manifested in a strong reduction on fish diversity at the perturbed site. δ^{13} C signatures provided ambiguous evidence of degradation while 8¹⁵N was a better descriptor of shrimp-farm effluent impact on coastal lagoon food webs. The site receiving nutrient-rich discharges showed significant enrichment of $\delta^{15}N$ ($\approx 5\%$) in sediments, macroalgae, benthic algae, filterfeeders and omnivorous feeders, resulting in qualitative differences in foodweb structure between both lagoons. The food web in the perturbed site was sustained by sediment detritus and dominated by opportunistic species. The lowest influence on δ^{15} N signatures by aquaculture discharges recorded in the upper trophic levels could be explained by the shift in the composition of biotic communities, and associated feeding strategies. While alterations in resource availability do not affect directly food chain length, trophic linkages between food web compartments can be reduced as a result of shrimp farm impacts. Our study demonstrates that nutrient-enriched discharges from shrimp-farm aquaculture generate changes in the availability of food sources, which reduce biodiversity and alter structural and functional food web characteristics.

1. Introduction

Despite mangrove wetlands being considered among the most productive ecosystems, they are one of the most threatened ecological systems in the world (Alongi, 2002). Most mangrove wetlands are located in developing countries where anthropogenic activities are growing uncontrollably causing often irreversible environmental degradation. For example, during the last two decades, Mexico experienced the highest loss of mangrove forest around the world (Wilkie and Fortuna, 2004), mostly resulting from shrimp aquaculture development (De La Lanza-Espino et al., 1994).

Aquaculture farms generate high amount of organic wastes and unassimilated inorganic fertilizers (García-Sandoval et al., 1991). Usually, these untreated effluents discharge directly in coastal lagoons and disperse until 500 m away from the point source (Meili et al., 2000; McGhie et al., 2000; Sutherland et al., 2001). The nutrient surplus is such that the annual nutrient loading from shrimp aquaculture into the Gulf of California through coastal lagoons can be 2,900 t N y⁻¹ and 834 t P y⁻¹, considering a scenario of ca. 26,000 ha of shrimp-farms in operation (≈110 kg N ha⁻¹ y⁻¹ and 30 kg P ha⁻¹ y⁻¹) (Páez-Osuna et al., 1999). Although numerous studies have reported the effects of shrimp aguaculture on water quality, eutrophication and biodiversity in both coastal lagoons and near-shore marine habitats (e.g. Penczak et al., 1982; Boaventura et al., 1997; Ruiz et al., 2001; Karakassis et al., 2002; Paez-Osuna, et al., 2003), little attention has been paid on the impact on ecosystem structure. Few studies have reported the effects of aquaculture on coastal food web structure, using either qualitative approaches or focusing on the first trophic level (e.g. Naylor et al. 2000; Schaal et al., 2008). Therefore, there is still a lack of understanding how impact of aquaculture shrimp-farms affects integrally food webs in subtropical coastal lagoons.

During the last decades, ecologists have demonstrated that allochthonous subsidies have strong effects on species interactions and food web dynamics (Polis et al., 1997). Theoretically, subsidies of nutrients can affect all trophic levels of food webs either directly or indirectly (Persson et al., 2001). Because coastal lagoon metabolism is altered by nutrient-rich discharges from shrimp farming over the last 2-3 decades, we expect changes in species composition and diversity, and consequently altered food-web structure and dynamics in these systems. δ^{15} N stable

isotopes have been used successfully to assess food web structure and trophic pathways in coastal wetland ecosystems (Haines and Montague, 1979; Stoner and Zimmerman, 1988; Sullivan and Mocreiff, 1990; Abrantes and Sheaves, 2008; Nyunja et al., 2009). Since shrimp-farms discharge nutrient-rich waters into the coastal lagoons, the impact of aquaculture should also modify the signatures of δ^{13} C and δ^{15} N stable isotopes in the food web. Previous findings demonstrated that anthropogenic disturbances and urban wastewater discharges on near-shore coastal marine habitats increased the δ^{15} N signatures in the benthic food web, modifying the trophic structure and functioning of food webs (Vizzini and Mazzola, 2004; Vizzini and Mazzola, 2006; Schaal et al., 2008); however very little is known about the effects of aquaculture discharges on the structure of coastal lagoon ecosystems (e.g. Ye et al., 1991; Lojen et al., 2005; Salazar-Hermoso, 2007), especially in tropical areas. Some progress has been made to detect the effects of shrimp-farm discharges on δ^{15} N signatures of primary producers (Jones et al., 2001; Costanzo et al., 2004; Lin and Fong, 2008). Although these such changes may help to identify incipient environmental degradation, they may not be representative of large scale changes in ecosystem and community structure.

Since the aquaculture organic effluent is δ^{13} C depleted and δ^{15} N enriched (Jones et al., 2001; Costanzo et al., 2004; Vizzini and Mazzola, 2006; Lin and Fong, 2008; Piñon-Gimate et al., 2009), organisms living in these coastal lagoons should show decreased δ^{13} C and increased δ^{15} N signatures. Therefore, we hypothesize that these isotopic alterations reveal structural changes in the food web of coastal lagoons. To test this hypothesis, we have measured the δ^{13} C and δ^{15} N stable isotope signatures in sediments, plants and animals in two nearby but environmentally contrasting subtropical coastal lagoons in the Gulf of California. Shrimp-farm effluents have impacted one site over the last 25 years, while the other site is near pristine and served as the control site.

2. Material and methods

2.1. Study area

The study was performed in two small coastal lagoons located in the Yaqui River Delta in semi-arid Northwestern Mexico (Fig. 1). Both coastal ecosystems are fringed by mangroves (*Rhizophora mangle* and *Avicennia germinans*) and halophytes (*Batis maritima* and

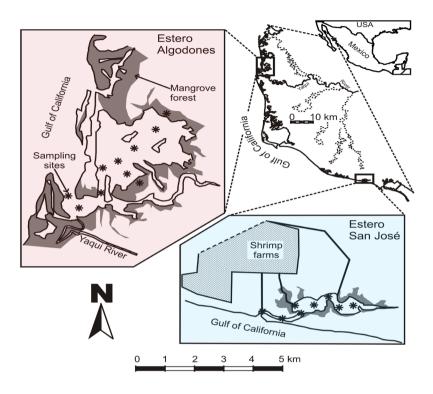


Fig. 1. Location of the studied lagoons at the Gulf of California. Asterisks show sampling sites for isotopic analyses.

Salicornia virginica). Climate in the area is warm and dry, with a mean annual air temperature of 24°C (min. 16 to max. 48°C) and rainfall < 300 mm y⁻¹. The site receiving shrimpfarm discharges was Estero San José (SJ; 2707´N, 11008´W), which is a very shallow (mean depth 0.6 m) lagoon occupying 82 ha.

This lagoon is covered by a large bed of *Ulva clathrata*, *U. lactuca* and *Ulva* spp. The near –pristine lagoon which served as a control was Estero Los Algodones (ALG, 27°41′N, 110°34′W; 165 ha and mean depth 2.3 m) which is located in the native Yaquis Reserve Territory where the economy exclusively depends on the artisanal fishery. The lagoon supports fishery of shrimp, flathead mullet, round ray, squid and blue crab, but under strong control of captures to ensure sustainability and, therefore, maintaining the ecosystem relatively free from overfishing. Neither shrimp-farm effluents discharge into the lagoon

nor is it impacted by other forms of human impacts (e.g., settlements). The mangrove cover to open water area ratio is 2 and 1.6 in SJ and ALG, respectively. Estimated annual nutrient discharges of shrimp-farm effluents into SJ are 168 t N y⁻¹ and 48 t P y⁻¹ (1,592 ha of shrimp farms; Sánchez-Carrillo, unpublished results). Differences in water quality between both ecosystems are summarized in Table 1. SJ registered highest averaged concentrations of total nitrogen and total phosphorus and hence result in high phytoplanktonic chlorophyll-a.

Table 1. Comparison of mean water quality variables and phytoplanktonic net primary productivity (NPP) in Estero San José and Estero Algodones during 2006. DO: dissolved oxygen, Tot-N: total nitrogen, Tot-P: total phosphorus, Chl-a: chlorophyll-a.

		DO (mg l ⁻¹)	Salinity (ppt)	Tot-N (mg l ⁻¹)	Tot-P (mg l ⁻¹)	Chl- <i>a</i> (μ l ⁻¹)	
	San José	10,9±2,0	61,9±2,5	4,02±5,21	0,47±0,15	21,2±6,7	
	Algodones	5,6±0,9	54,3±2,5	0,25±0,09	0,14±0,05	2,5±1,7	

2.2. Field collection and sample processing for isotopic analysis

Sampling was conducted in both lagoons during a one-week period of March 2006 coinciding with the annual cold water period of Gulf of California (Cervantes, 1994). This period was chosen because it is the time when organisms enter the lagoons from the sea for breading and can reach high abundance (Gendron, 1992; Thomson et al., 2000; Sala et al., 2003). All samples were taken randomly from several sites within each ecosystem to account for spatial heterogeneity effects (Fig. 1).

As mangrove litter is the plant fraction entering the coastal lagoon food web as detritus, yellow freshly senescent leaves of mangroves were collected from the forest floor instead of picking them directly from the trees because the mangrove tree have a nutrient reabsorption ranging 45 to 55% prior to senescence (Twilley et al., 1986). Aboveground fractions of pickleweeds were collected by hand. Fish were captured using multiple gears (beach seines and cast nests) to collect representative samples of the fish diversity at each sampling site.

Crustaceans were taken using traps. Mollusks and macroalgae were picked randomly by hand in diverse places of each ecosystem. Microbial benthic algae were scrapped from 15 randomly selected submerged stones from the littoral zone of each lagoon, suspended in water and filtered immediately (65 µm) upon return to the laboratory a few hours after sample collection. Sediment samples were taken along transects from the continent shoreline to the sea (lagoon mouth) using a sediment corer. Phytoplankton was not considered in this study because of the complex interpretation of its isotopic signature resulting from its high spatiotemporal turnover in community composition and its mixing with detritus (Gu et al., 1997; France, 1998; Keough et al., 1998; Bouillon et al., 2000).

All samples were placed on ice for transport to the laboratory where they were stored frozen. Isotopic analysis were carried out on leaves for plant species, macroalgae, approximately 5g of dorsal muscle tissue of fish, claw muscle of crustaceans, and the adductor muscle of molluscs. Consumers were treated with methanol: chloroform (2:1) for 24h to remove lipids. Because of financial constraints we could not analyse each consumer species separately; therefore, fish, crustaceans, and molluscs of each lagoon were gathered into composite samples by species and, after homogenization, were analyzed in triplicate. While the analysis of a composite sample does not allow us for covering spatial heterogeneity in the isotopic signatures of these organisms, we do not expect that such heterogeneity be pronounced because of the high mobility of these organisms. Due to their ability to move throughout the entire ecosystem, we assume that a composite sample may well represent the average values of stable isotopes of each species in each studied ecosystem. Prior to isotopic analysis, all samples were processed following protocols by Lewis et al. (2001), Parkyn et al. (2001), O'Reilly and Hecky (2002), and Demaoupolus (2004). Briefly, sediment samples were washed with 1M HCl for 24 h to eliminate carbonate and plant samples were washed in distilled water, 5% HCl. Finally, samples were rinsed with distilled water, placed on sterile Petri dishes and dried in an oven at 60° C for 48-72h. Dried samples were ground to fine powder and stored in clean glass vials. Stable isotope ratios (13C / 12C and ¹⁵N / ¹⁴N) were calculated after analyses in a stable isotope mass spectrometer (Stable Isotope Laboratory of the University of Arizona). Results are reported as parts per thousand (‰) differences from a corresponding standard: $\delta X = [(R_{sample}/R_{standard}) - 1] \times 103$, where R = ¹⁵N / ¹⁴N or ¹³C / ¹²C. Standards were carbon in the PeeDee Belemnite and nitrogen in air. Analytical precision of δ^{13} C and δ^{15} N replicate analyses were 0.16 % and 0.10 %, respectively.

The habitat and permanence of each species in the coastal lagoons were assessed using the available literature (Yañez-Arancibia, 1978; Meinkoth, 1981; Goodson and Weisgerber, 1988; Buchsbaum et al., 1989; Amezcua-Linares et al., 1992; Ruíz-Durá, 1992; Allen and Robertson, 1994; Ruppert and Barnes, 1994; García-Ortega et al., 2002; López-Peralta and Arcilla, 2002; Santamaría-Miranda et al., 2003; Bester, 2004; Santamaría-Miranda et al., 2005). Briefly, most molluscs and crustacean species can be considered as permanent inhabitants of the studied lagoons. Also juvenile stages of shrimps are well represented in these ecosystems, Some fish (Diapterus peruvianus, Eucinostomus currani, Achirus mazatlanus, Sphoeroides annulatus, Etrophus crossotus, and Cyclopsetta querna) use only the lagoons for breeding while others (Anchoa spp., Selene brevoortii, Lutianus argentiventris. Pomadasys macracanthus) live in the marine coastal environment. Diplectrum pacificum, Scorpaena sonorae, Paralabrax maculatofasciatus and Urobatis halleri can be considered as occasional visitors of these lagoons. Only Mugil cephalus can be considered as permanent inhabitant of these coastal lagoons. Finally, in order to estimate the impact of effluent on existing feeding habits, all species were classified in functional feeding groups using the above-cited literature.

2.3. Data analysis

The organic matter pathway across the food web shows that 13 C increases varying 0-2 ‰ of isotopic signature (DeNiro and Epstein, 1978; Marguillier et al., 1997). Because heavier 15 N accumulates in consumers as it moves up the food web, consumers tend to be δ^{15} N enriched 2.5-3.5 ‰ relative to their food sources (Lewis et al., 2001; and Vanderklift and Ponsard, 2003). Thus, δ^{15} N signatures of consumers relative to those of a base-line value were used to indicate the trophic position of consumers following the equation:

$$TL_i = \lambda + (\delta^{15}N_i - \delta^{15}N_{PC}) / F$$

where TL_i is the average trophic level of the species i, $\delta^{15}N_i$ is the average content of species i, $\delta^{15}N_{PC}$ is the average content of primary consumers, λ is the trophic level of consumers

estimating the base of the food web and F is the per-trophic-level fractionation of nitrogen. In this study, we used the fractionation value of 2.54 suggested by the meta-analysis of Vanderklift and Ponsard (2003).

Scatter plots of $\delta^{15}N$ and $\delta^{13}C$ values were used to evaluate patterns of isotopic variation among trophic levels and lagoons. Sources of organic carbon assimilated by consumers were indicated by relative positions of taxa on the x-axis ($\delta^{13}C$ values), whereas trophic level was indicated by the relative position on the y-axis ($\delta^{15}N$) (Peterson and Fry, 1987) (Fig. 2). An analysis of variance (using type III sum of squares to account for the unbalanced sampling design; Fig. 1) was used to compare $\delta^{13}C$ and $\delta^{15}N$ variation within species and trophic levels among sites within both lagoons. Prior to the statistical analysis data were log transformed when necessary to fulfill the requirements of parametric tests. All statistical analyses were performed using SPSS V17.0.

2.4. Assessment of the food web complexity in coastal lagoons

Primarily, food web structure in both coastal lagoons was assessed through simple food web descriptors. Food chain length was quantified as the modal number of trophic levels (Pimm et al., 1991). Directed connectance was used to get the number of actual links over the number of possible links in each food web $(C = L / S^2)$, where L is the number of undirected links and S is the number of species (Hawkins et al., 1997; Bersier et al., 2002). L was assessed using diet information for each species from the literature (see section 2.2); briefly, if a species occurred in the diet of a predator, they were joined by an undirected link using a food web diagram (Morin, 2005). Afterwards, the number of links was computed by an interaction matrix (Megrey and Aydin, 2009). Linkage density was obtained through the average number of feeding links per species which is a function of connectance and number of species in the web (D = L / S; Morin, 2005). Trophic level proportionality was evaluated through the proportion of top (% T), intermediate (% I) and basal (% I) species (Sugihara et al., 1997; Bersier et al., 2002).

In addition, we used quantitative metrics proposed by Layman et al. (2007), which are appropriate for community-wide analyses of stable isotope data and which can provide

deeper insights into the modifications of food webs affected by anthropogenic disturbances. Descriptor estimations were calculated independently for each lagoon following two approaches: first, considering the whole ecosystem pathways (primary producers, consumers and sediments), and second, taking into account only the biotic compartments (primary producers and consumers). Descriptors used were: (i) δ^{13} C range (CR) and δ^{15} N range (NR), which are distances between the species with the most enriched and most depleted δ^{13} C and δ^{15} N values (NR is one representation of vertical structure within a food web; increased CR would be expected in food webs in which there are multiple basal resources with varying δ^{13} C values. providing for niche diversification at the base of a food - additionally, CR and NR were calculated for consumers only); (ii) total area (TA), which is the convex hull area encompassed by all species in δ^{13} C – δ^{15} N bi-plot space (this represents a measure of the total amount of niche space occupied, and thus a proxy for the total extent of trophic diversity within a food web); (iii) mean distance to centroid (CD), which is the average Euclidean distance of each species to the δ^{13} C – δ^{15} N centroid (this metric provides a measure of the average degree of trophic diversity within a food web); (iv) mean nearest neighbor distance (NND), which is the mean of the Euclidean distances to each species' nearest neighbor in bi-plot space (it is a measure of the overall density of species packing, i.e. resource partitioning or niche partitioning); and (v) standard deviation of the nearest neighbor distance (SDNND), a measure of the evenness of species packing in bi-plot space that is less influenced by sample size than NND (low SDNND values suggest more even distribution of trophic niches). Convex hull areas were computed using the software TraitHull (http://www.pricklysoft.org/software/traithull.html; Cornwell et al., 2006). For further information on these metrics see Layman et al. (2007).

3. Results

3.1. Species richness and isotopic signatures

In the perturbed lagoon (SJ) the number of collected species was slightly lower than those gathered at ALG (26 species versus 30 species, respectively; Table 2). Fish were the most abundant group in ALG, representing around 50% of the total collected species, while in SJ they only accounted 9 %.

Table 2. δ^{13} C, δ^{15} N values and C:N of major primary producers, aquatic animals and sediments collected from Algodones (ALG) and San Jose (SJ). F.H. Feeding habits: F, filter; O, omnivorous; H, herbivorous; C, carnivorous, D, detritivorous, P, planktiovorous. ^a include species *Eriphia squamata*, *Pachygrapsus transverses* and *Petrolisthes nigrunguculatus*; ^b include specie *Pagurus lepidus*.

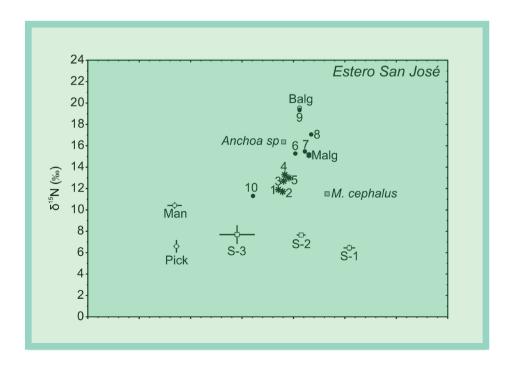
			C/N		δ ¹³ C		δ ¹⁵ N	
		FH	ALG	SJ	ALG	SJ	ALG	SJ
Mangroves	Rhizophora mangle		26.8	27	-26.9	-27.7	10.3	10.7
	Avicennia germinans		21.9	19.8	-25.7	-25.5	8.4	9.8
Herbs	Batis mairitima		21.0	23.1	-24.9	-26.6	8.5	7.2
	Salicornia virginica		20.3	23.6	-25.1	-25.9	10.5	5.6
Macroalgae	Ulva intestinalis		13.3		-17.3		8.7	
	Ulva clathrata			10.2		-13.5		14.5
	Ulva lactuca			10		-13.4		15.7
	Ulva spp.			9.7		-13.6		15.2
Benthic algae	Benthic algae		10.4	5.8	-9.2	-14.4	11.2	19.5
Mollusks	Crassostrea corteziensis	F		3.6		-16.5		11.9
	Semele flavescens	F		3.9		-16		12.7
	Anadara spp.	F		4.3		-16.1		11.7
	Chione californiensis	F		3.8		-15.9		12.6
	Phlyctiderma discrepans	F		3.7		-15.4		13
	Chione spp.	F		3.8		-15.8		13.3
	Agropecten circularis	F	3.3		-17.1		10,9	
	Loliliopsis diomedae	0	3.5		-15.2		16,4	
	Aplysia californica	Н	3.6		-15.3		13	
	Octopus spp.	С	3.5		-14.4		13,4	

Table 2. (Continuación) δ^{13} C, δ^{15} N values and C:N of major primary producers, aquatic animals and sediments collected from Algodones (ALG) and San Jose (SJ). F.H. Feeding habits: F, filter; O, omnivorous; H, herbivorous; C, carnivorous, D, detritivorous, P, planktiovorous. a include species *Eriphia squamata*, *Pachygrapsus transverses* and *Petrolisthes nigrunguculatus*; b include specie *Pagurus lepidus*.

			C/N		δ ¹³ C		δ ¹⁵ N	
		FH	ALG	SJ	ALG	SJ	ALG	SJ
Crustaceans	Geograpsus lividus	Н	3.5	3.3ª	-18.7	-18.9 a	11.2	11.3ª
	Sycionia peniallarte	Ο	3.3		-14.2		13.6	
	Farfantepenaeus californiensis	Ο	3.2		-14.3		12.3	
	Clibanarius panamensis	Ο		3.4 ^b		-13.3 b		17.1 ^b
	Callinectes arcuatus	С	3.4	3.4	-14.5	-13.9	13	15.5
	Callinectes bellicosus	С		3.7		-14.8		15.3
	Ocypode occidentalis	D		3.3		-14.4		19.3
Fish	Anchoa spp.	Н		3.4		-16		16.4
	Eucinostomus currani	0	3.4		-15		14.9	
	Sphoeroides annulatus	0	3.3		-15.2		14.6	
	Mugil cephalus	0	3.4	3,4	-14.3	-11.7	13.9	11.5
	Achirus mazatlanus	0	3.3		-12.6		13.2	
	Diplectrum pacificum	С	3.3		-14.9		15.2	
	Diapterus peruvianus	С	3.4		-13.4		14.2	
	Lutjanus argentiventris	С	3.3		-12.9		13.7	
	Selene brevoortii	С	3.4		-16		17.1	
	Cyclopsetta querna	С	3.3		-13.2		13.1	
	Scorpaena sonorae	С	3.4		-15.3		14.2	
	Pomadasys macracanthus	С	3.3		-12.7		13.7	
	Paralabrax maculatofasciatus	С	3.3		-13.6		14.3	
	Etrophus crossotus	С	3.3		-15.7		14.4	
	Urobatis halleri	С	2.9		-14.6		16.8	
Cnidaria	Stomolophus meleagris	Р		3.9		-18.2		14.3
	Mouth		13.6±1.1	12.5±1.2	-8.5±0.8	-9.6±0.8	7.8±0.3	6.4±0.3
Sediment	Open water		16.3±4.9	10.5±1.2	-12,1±2,3	-14.3±0.9	5.9±0.7	7.6±0.3
	Mangrove zone		11.9±1.4	8,2±3,6	-18,2±1,5	-20.5±3.3	6.5±0.8	7.7±1.8

The most abundant groups in SJ were mollusks and crustaceans comprising 27% and 23% of species found in the lagoons. While vascular plants were represented by the same species in both lagoons, the phylum Chlorophyta was represented by different species of the *genus Ulva: Ulva* sp., *U. clathrata* and *U. lactuca* in SJ, and *U. intestinalis* in ALG. Both sites shared only two crustacean species (*Geograpsus lividus* and *Callinectes arcuatus;* Table 2). *Mugil cephalus* (Chordata) occurred at both sites (Table 2), but with high abundances in SJ (3.67 and 0.13 catch per unit effort in SJ and ALG, respectively).

The isotopic signatures of δ^{13} C and δ^{15} N and atomic carbon to nitrogen ratios of primary producers (vascular plants, macroalgae and benthic algae), aquatic animals (mollusks, crustaceans, fish and cnidaria) and sediments collected at each lagoon are summarized in Table 2 and Fig. 2. At both sites, mangrove leaves showed lower δ^{13} C values (-26.3 ±0.8% ALG, -26.6 ± 1.5 % SJ). In contrast, benthic algae in ALG (-9.2 ± 0 %) and macroalgae in SJ (-13.5 ± 0.1 %) were the most δ^{13} C enriched. The highest δ^{15} N values were found in fish in ALG (14.2 ± 1.2 %) and in microbial benthic algae in SJ (19.5 ± 0 %). The most depleted δ^{15} N signature was found in ALG sediments (6.2 ± 0.9 %), and pickleweed in SJ (6.4 ± 1.1 %) (Table 2, Fig. 3).



Capítulo I

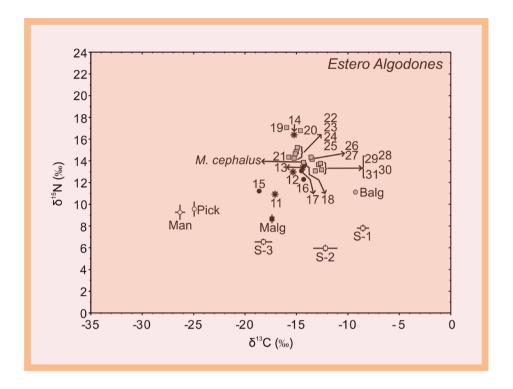
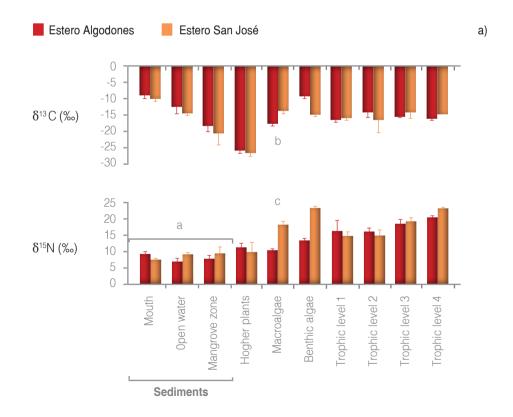


Figure 2. Relationship between $\delta^{13}C$ and $\delta^{15}N$ values obtained of, primary producers, aquatic animals and sediments collected from both studied lagoons. Codes: Sediments (\square) S1: sediment at the lagoon mouth, S2: sediment at the open water area, S3: sediment at the mangrove zone; C3 plants (\bigcirc) Man: mangroves, Pick: pickleweeds; Algae Balg (\bigcirc): benthic algae, Malg (\blacksquare): macroalgae; Molusks (\clubsuit) 1: *C. cortesiensis*, 2: *Anadara sp.*, 3: *C. californiensis*, 4: *S. flavescens*, 5: *P. discrepans*, 11: *A. circularis*, 12: *A. californica*, 13: *Octopus* sp., 14: *L. diomedae*; *Crustaceans* (\bigcirc) 6: *C. bellicosus*, 7: *C. arcuatus*, 8: *P. Lepidus*, 9: *O. occidentalis*, 10: *E. Squamata*, 15: *G. lividus*, 16: *F. californiensis*, 17: *C. arcuatus*, 18: *S. peniallarte*; *Fish* (\square) 19: *S. brevoorti*, 20: *U. halleri*, 21: *E. crossotus*, 22: *D. pacificum*, 23: *E. currani*, 24: *S. annulatus*, 25: *S. sonorae*, 26: *P. maculatofasciatus*, 27: *D. peruvianus*, 28: *P. macracanthus*, 29: *L. argentiventris*, 30: *A. mazatlanus*, 31: *C. querna.*

Sediments from both lagoons showed a gradual enrichment in δ^{13} C signatures from the mangrove zone to the lagoon mouth (Table 2, Fig. 2). Although SJ sediments had a lower δ^{13} C signature (ALG: -12.4 \pm 3.3 %; SJ: -16.3 \pm 0.9 %), these differences were not significant (ANOVA, p > 0.05). On the contrary, δ^{15} N values in SJ sediments showed a significant enrichment (7.5 \pm 1.2 % SJ; 6.2 \pm 0.9 % ALG; ANOVA, F_{1.13} = 5.6, p = 0.03; Table 2, Fig. 3).

 δ^{13} C and δ^{15} N ranges of higher plants (mangrove and pickleweeds) did not differ significantly between coastal lagoons (ANOVA, p > 0.05). In contrast, ALG macroalgae had very low δ^{13} C values (-17.3 % ALG, -13.4 % SJ), whilst SJ macroalgae had elevated δ^{15} N signatures (14.5-15.7 % SJ, 8.7 % ALG). Differences in macroalgae δ^{13} C and δ^{15} N signatures were statistically significant between the two sites (ANOVA, $F_{1,2} = 840.9$, p = 0.001 and $F_{1,2} = 143.5$, p = 0.007; Fig. 3). Although δ^{13} C and δ^{15} N signatures of benthic algae in SJ and ALG (Table 2, Fig. 3) were well separated, no significant differences between sites were detected.



Capítulo I

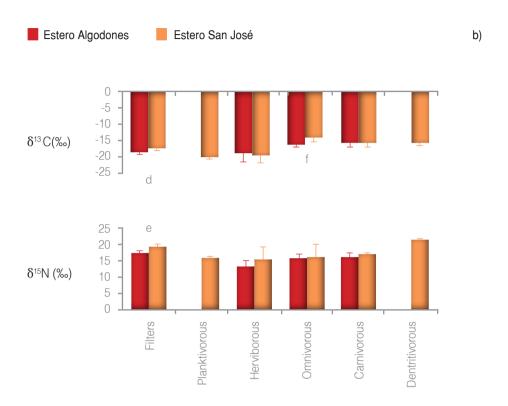


Figure 3. Average (±SD) δ^{15} C and δ^{15} N values for (a) sediments, primary producers and consumer trophic levels, and for (b) different feeding habits, in both lagoons. Lowercase letters denote statistical significant differences (p < 0.05) in ANOVA type-III comparisons between lagoons (a: F=5.6 p=0.03; b: F= 840.9 p=0.007; c: F=143.5 p=0.001; d: F= 8.1 p=0.04; e: F=6.6 p=0.05, f: F=6.7 p= 0.03).

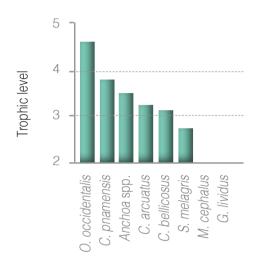
3.2. Effects of nutrient enrichment on the isotopic signatures of trophic levels

Consumers were distributed into 4 trophic levels (TL) in both coatal lagoons (Fig. 4). Trophic level one (TL1) was composed by 6 species of mollusks in SJ (*Crassostrea corteziensis*, *Semele flavescens*, *Anadara* spp., *Chione californiensis*, *Phlyctiderma discrepans* and *Chione* spp.), while only 2 were included in ALG (*Agropecten circularis* and

Aplysia californica). Fish dominated the consumer food web in ALG while mollusks and crustaceans did in SJ (Fig. 4). In ALG, fish dominated TL2 and TL3; crustaceans were restricted to TL2 and no filtering mollusks were located in TL2 and TL3. In SJ, crustaceans were the main group in TL3, with fish being represented by single species in TL2 and TL3. TL3 was the most diverse trophic level at both sites (ALG: 6 species; SJ: 4 species). The top of the food web (TL4) appeared dominated by single species at each site: the fish Selene brevoortii in ALG and the crustacean Ocypode occidentalis in SJ (Fig. 4). All trophic levels showed similar δ^{13} C and δ^{15} N signatures at both sites (ANOVA, p > 0.05; Fig. 3), and C:N ratios at all trophic levels were not significantly different between lagoons (ANOVA, p > 0.05). Food web connectance and linkage density were higher in ALG (0.4 and 5.4 respectively) compared to SJ (0.3 and 2.9 respectively). The fractions of species occupying trophic levels showed great discrepancy between lagoons. Although at the base of the food web both lagoons exhibited the same genera (Rhizophora, Avicennia, Ulva, Salicornia and Batis), SJ displayed a higher proportion in basal species (0.42 vs 0.09), Regarding intermediate species proportions, ALG showed a higher score in TL2 (0.59 ALG; 0.21 SJ) whereas TL3 increased slightly in SJ (0.27 ALG; 0.29 SJ). Intermediate species taxa were greatly separated between lagoons in classes and genera (7, 23 in ALG and 3, 13 in SJ, respectively). Finally, top species showed the lowest proportion at the two lagoons (0.05 ALG; 0.07 SJ), but being represented by different classes in each lagoon.

Metrics based on stable isotope ratios showed more pronounced differences between food webs when only primary producers and consumers rather than the whole ecosystem data were analyzed. In both approaches, the pristine lagoon ALG showed slightly higher CR (ecosystem level CR= 18.4‰ vs 18.1‰; biotic level CR= 17.7‰ vs 16.0‰). By contrast, considering consumers only, CR was higher in SJ (7.2‰ vs 6.1‰). NR showed higher values at the perturbed lagoon SJ (ecosystem level NR= 13.9‰ vs 12.2‰; biotic level NR= 13.9‰ vs 8.7‰; only consumers NR= 8.0‰ vs 6.2‰). SJ also showed a higher index of niche diversification within the food web (ecosystem level CD= 5.6‰ vs 5.2‰; biotic level CD= 5.7‰ vs 4.5‰) and niche space dimensions (ecosystem level TA= 122.7‰ vs 108.81‰; biotic level TA= 90.4‰ vs 50.7‰). Finally, the density of species packing (NND) and unevenness of species packing (ecosystem level NDD= 1.2‰ vs 1.0‰, SDNND= 1.0‰ vs 0.8‰; biotic level NDD= 1.1‰ vs 0.8‰; SDNND= 1.0‰ vs 0.8‰) was greater at SJ.

Estero San José



Estero Algodones

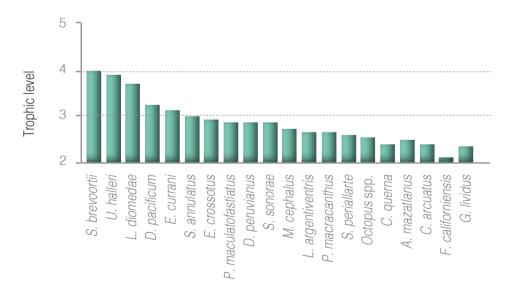


Figure 4. Consumer trophic level estimates of mollusks, crustaceans, cnidaria and fish collected at San José and Algodones lagoons.

Capítulo I

3.3. Effects on functional groups (feeding modes)

Carnivorous species dominated in ALG (54%); these were composed of fish, mollusks and crustaceans. In SJ, carnivory was due to crustaceans only and less important compared to SJ (15%). Carnivores were characterized by similar δ^{13} C and δ^{15} N signatures between lagoons (ANOVA p > 0.05; Fig. 3b). Filterfeeders were the major group in SJ (46% vs 5% in SJ and ALG, respectively; Table 2), displaying enriched δ^{13} C and δ^{15} N signatures in SJ (ANOVA, δ^{13} C F1,5 = 8.1, p = 0.04; δ^{15} N F1,5 = 6.6, p = 0.05; Fig. 3b). Herbivores were poorly represented in both lagoons (8% in SJ and 5% in ALG; Table 2), with similar δ^{13} C and δ^{15} N signatures between lagoons (ANOVA p > 0.05; Fig. 3b). Omnivory, the second abundant feeding category in ALG (36%), showed significant δ^{13} C depletion in ALG (ANOVA, F1,7 = 6.5, p = 0.03), whilst δ^{15} N signatures were similar (ANOVA, p > 0.05). Finally, detritivorous and planktivorous species were only collected in SJ and were composed of single species of crustaceans and cnidaria (Table 2).

4. Discussion

The first consequence of coastal lagoon degradation due to nutrient enrichment is usually a strong reduction of biological diversity (Mouillot et al., 2005). In our study, nutrient-enriched discharges from shrimp-farm aquaculture contributed to a reduced species diversity. As observed in other studies, aquatic ecosystem degradation through water quality deterioration resulted in a strong reduction of fish species diversity (Pombo et al., 2002; Miranda et al., 2005), promoting the dominance of those species that are very resistant to ecosystem perturbations (Martens, 1982), such as *Mugil cephalus* (Loneragan and Potter, 1990). Low biodiversity shortens the food chain and hence the negative effects of the degradation feedback cannot be controlled, and consequently the trophodynamic stability decreases (Neutel et al., 2002).

Usually, the isotopic signatures of the aquaculture effluents as well as sewage domestic effluents are δ^{13} C-depleted compared with average values of coastal and marine particulate matter (Kwak and Zedler, 1997; Mazzola and Sarà, 2001). The effects on macroalgae appear to be linked to this isotopic depletion (e.g. Kwak and Zedler, 1997; Vizzini and Mazola, 2004).

Our results demonstrated that the disturbed lagoon showed a significant increase of macroalgal δ^{13} C signatures (+ 3.8%; Table 2, Fig. 3). Because no other community showed any δ^{13} C increase, that difference could be attributed to the effect of the organic source supplied from shrimp-pond effluents, which might display different stable isotope signatures than those cited in the literature. Organic matter inputs from the sea have also been cited to increase the δ^{13} C signatures of primary producers (Bouillon et al., 2002). Other hypothesis of the enriched macroalgal δ^{13} C signatures in the disturbed lagoon could be related with preferential uptake of the isotopically light dissolved inorganic carbon by the phytoplankton resulting from the bacterial respiration of the large amounts of shrimp-farm wastes (Hellings et al., 1999; Bouillon et al., 2000), which would enrich the water column with the heavier carbon isotope used by macroalgae. Unfortunately, the lack of isotopic signatures of the effluent and other supplementary data does not allow us to clarify this contrasting phenomenon. At the ecosystem level, when all biotic and abiotic compartments were considered (mean δ^{13} C signature of sediments, mangroves, herbs, benthic algae, macroalgae, mollusks, crustacean, fish and cnidaria) the lagoon receiving shrimpfarm effluents showed a slight mean δ^{13} C-depletion * -1.1%. This δ^{13} C depletion at ecosystem level is biased by benthic algae and sediments (mean difference between ecosystems -5.2 and -3.9% in benthic algae and sediments, respectively; Table 2). It seems to indicate that impacts of shrimp-farm discharges on the ecosystem are buffered by the benthic food web. Most δ^{13} C signatures in consumers do not seem to be affected by nutrient-rich aquaculture discharges (Table 2; Fig. 3). Similar findings have been reported by Vizzini and Mazzola (2006).

The observed δ^{13} C shift between higher plants and primary consumers confirms results of previous studies which have shown a low contribution of mangroves to the food-webs in subtropical coastal lagoons (Primavera, 1996; Loneragan et al., 1997, Marguillier et al., 1997; Nyunja et al., 2009), which is opposed to that reported in temperate salt marshes (Abrantes and Sheaves, 2008). Contrasting with the findings of Hsieh et al. (2002), the main organic source to these subtropical coastal ecosystems is not marine phytoplantk-ton. Since marine phytoplankton from tropical regions shows a δ^{13} C signal between -18 and -22‰ (Fontugne and Duplessy 1981; Goericke and Fry 1994), it is unlikely that phytoplankton are the main organic source supporting secondary production of the coastal lagoons of the Gulf of California. Moreover, considering the δ^{13} C signatures reported for shrimp feed wastes (δ^{13} C = -21.9 ± 0.07‰; Kon et al., 2009), the influence of this source

appears to be very limited in the lagoons receiving the shrimp farm effluent. Our data rather suggest that sediment represent the main basis supporting the food web in both ecosystems.

In agreement with the literature (Rogers, 1999; Riera et al., 2000; Piola et al., 2006; Lepoint et al., 2008), δ^{15} N was the best descriptor of the anthropogenic impacts on coastal food webs. The enrichments with $\delta^{15}N$ were significant in the sediments, macroalgae and benthic algae of the lagoon receiving shrimp-farm effluent. Benthic algae and macroalgae species showed the highest $\delta^{15}N$ enrichments, so that these communities can be considered as the best biological indicators of the effects of nutrient enrichment by shrimp-farm discharges on the ecosystem food web. Similar results were found in macroalgae and seagrasses in other coastal ecosystems receiving shrimp pond effluents by Jones et al. (2001), in tidal creeks at Moreton Bay (east Australia), by Costanzo et al. (2004), in a tidal mangrove creek in north-east Australia, and by Lin and Fong (2008), in Opunohu Bay (French Polynesia), although the observed enrichment was quite variable between sites (from 1‰ to 17‰). Also, fish farming discharges enriched the δ^{15} N signatures of macroalgae and seagrasses (Anderson et al., 1999; Savage and Elmgren, 2004; Vizzini and Mazzola, 2006), but the mean δ^{15} N enrichments were lower (*2-3%) compared to shrimp farming effluents. Contrary to our findings, Jones et al. (2001) and Costanzo et al. (2004) found significant ¹⁵N enrichment in mangroves receiving shrimp farm discharges even in areas far from the effluent; however, the highest $\delta^{15}N$ signatures observed by these authors were lower than those recorded in our study (7.3-7.7% vs 9.8-10.7%). The absence of strong ¹⁵N enrichment of mangroves as compared to macroalgae has been associated with the high availability of nutrients in sediments compared to the water column as well as with the preferential take up of isotopically light ^{14}N (Jones et al., 2001). Lower $\delta^{15}N$ signatures of mangroves and macroalgae reflect the lower initial δ^{15} N of the shrimp effluent. because isotopic fractionation by bacteria in shrimp creeks is absent. This can be due to low NH₄⁺ availability for nitrification because NH₄⁺ in shrimp ponds is typically taken up by phytoplankton and bacteria rather than oxidized by nitrifying bacteria (Hargreaves, 1998; Jones et al., 2001). Furthermore, denitrification and NH₄⁺ volatilization are depressed in shrimp ponds (Alongi et al., 2000). δ¹⁵N signatures in shrimp farm effluents ranged 6-7‰ (Jones et al., 2001) as opposed to sewage effluents ~10% (Costanzo et al., 2004), and to open ocean in tropical sites < 3% (Costanzo et al., 2001). This suggests that the availability of nitrogen for mangroves and macroalgae in our sites have higher δ^{15} N values.

The Gulf of California is a system generally enriched in ¹⁵N compared to other marine environments (Altabet et al., 1999): $\delta^{15}N$ of particulate organic matter in the Guaymas basin, which is close to the lagoons studied here, ranged $\sim 9-10\%$; $\delta^{15}NO_3^{-1}$ is also enriched ~ 10-12% due to either marine phytoplankton fractionation during assimilation or dentrification. Observing the δ^{15} N signatures of vascular plants at both lagoons, could reflect the strong influence of organic matter inputs from the Gulf of California to primary producers. Another explanation may be the existence of uncontrolled wastewater discharges in SJ lagoon, a likely fact considering the existence of a small settlement of fishermen located to the southern edge (Sánchez-Carrillo, personal observation). Yet other explanations may be sought in microbial metabolism in the sediments. Microbial processing of nitrogen in sediments of these mangroves can be guite high (Sánchez-Andrés et al., 2010), and it is possible that microbes prefer the lighter ¹⁴N for metabolism, leading to enrichment of ¹⁵N in the free nitrogen pool (Mariotti et al., 1998; Costanzo et al., 2004), which would be quickly taken up by mangroves. Our low- δ^{15} N values in sediments at the mangrove zone in the pristine lagoon could reflect this process. Also NH, + volatilization could contribute partially to ¹⁵N enrichment of mangrove forest sediments, although the retention time in these coastal lagoons is not high enough (Sánchez-Carrillo et al., 2009). Further research is required to assess the relative importance of these processes on stable isotope dynamics in these ecosystems.

The $\delta^{15}N$ enrichment observed in the sediments at both the mangrove and the open water zones in the disturbed lagoon demonstrates the wide distribution range of the discharged effluents as also observed in other studies (e.g. Jones et al., 2001). However, as reflected by the $\delta^{15}N$ signatures at the lagoon mouths, the distribution of nutrients to the adjacent marine habitats in the area is limited by hydrodynamic forcing (i.e. microtides; Sánchez-Carrillo et al., 2009). The shallowness of the lagoon (0.6 ± 0.7 m) probably contributes to enhance the resuspension events after deposition, highlighting the potential role of this process in impacted areas (Cromey et al., 2002).

On the other hand, $\delta^{15}N$ isotopic composition was not able to show any significant change in the consumers due to shrimp-farm discharges. This finding has been also observed systems affected by sewage discharges (Kwak and Zedler, 1997). Unfortunately, there is no similar

study to ours for comparison. This marginal influence of $\delta^{15}N$ signatures on consumers can be attributed to the ability of certain species to move inside and outside the lagoon ecosystems (Vizzini and Mazzola, 2004). For example, fish migration as well the composition of consumer biotic communities can mask the effective sensitivity to pollution of each group (Vizzini and Mazzola, 2006). The $\delta^{15}N$ signatures of consumers show that the same species may occupy different trophic levels (Fig. 4) even in nearby ecosystems indicating that flexible foraging strategy of consumers as a function of food availability (Thimdee et al., 2004). The adaptive capacity of opportunistic organisms to change their feeding modes depending on the availability of the food sources is a well studied topic (e.g. Schaal et al., 2008).

Considering the feeding modes of consumer communities, the influence of discharges from shrimp farms on isotopic composition seems to be limited to filtering (δ^{13} C and δ^{15} N) and omnivorous (δ^{13} C) organisms (Fig. 3b). Both feeding modes would better reflect any change on available food sources caused by shrimp-farm discharges. For example, omnivorous species inhabiting the perturbed lagoon, such as the crustacean *Geograpsus lividus*, displayed a δ^{13} C signature very similar to that of sediment in the mangrove zone. This suggests that sediment organic matter is the main available food source in the perturbed site. Moreover, the small ranges found in δ^{13} C values of distinctive feeding groups at SJ suggest that this ecosystem experiences a potential depletion of available food sources, as a consequence of shrimp-farm discharges. This tendency was also supported by the community-wide isotope metric CR, which indicated lower basal resource pools supporting consumers at the perturbed lagoon. This would also be confirmed by the lower abundance of omnivorous and carnivorous species (Robertson et al., 1992; Whitmore, 1997).

Shrimp-farm effluents can be viewed as external subsidies in these coastal lagoons which influence ecosystem food web structure and dynamics (Polis et al., 1997; Callaway and Hastings, 2002; Melián and Bascompte, 2004). Our primary results would confirm that resource availability and disturbance do not affect directly the food chain lengths (Briand and Cohen, 1987; Post et al., 2000; Post, 2002). However, the NR metric revealed higher length of the food web at the perturbed lagoon. Shrimp farm discharges reduce taxa aggregation at the consumer trophic levels as suggested by the niche space dimensions (TA). As suggested by Sugihara et al. (1997), this pattern should increase the fragility of the food web when one species disappears from the ecosystem. For example, if the species

located at the highest trophic level in SJ (*Anchoa* spp.) is removed, then the overall trophic diversity in the food web would be reduced dramatically. Our results on metrics for community-wide stable isotope data demonstrated that although perturbation caused by the shrimp-farm discharges increases the niche space for trophic diversification (CD), it is limited by the high species dispersion in the ecomorphological space. That is, there are few similar trophic niches (NDD), which reduces food web stability due to this low redundancy in trophic characteristics. Dispersal of consumers and resource heterogeneity desynchronize dynamics at all trophic levels, which is enhanced by the variation through time of the local food web dynamics (migration and extinction–colonization dynamics; Amarasekare, 2008).

Shrimp-farm effluent discharges into coastal lagoons tend to impose sediment detritus-based food webs, promoting opportunistic species (Langdon and Newell, 1990; Whitmore, 1997; Whitledge and Rabeni, 1997). Nutrient-rich effluent discharges cause structural changes to the whole coastal lagoon ecosystem through alterations in top-down and bottom-up regulating forces in food webs (Polis et al., 1997). We acknowledge that the limited replication in our study does not allow for an extrapolation of the results to other coastal environments. However, the results obtained here suggest that further research is warranted. Long-term observations at higher spatial resolution could be useful for assessing generalities in food-web responses to the effects of shrimp-farm effluents. The integrative approach of trophic assessments of coastal lagoons from local (few coastal lagoons) to regional scales (all coastal lagoons of the Gulf of California) could allow increasing our understanding of how ecosystems respond to cumulative impacts through changes in trophic dynamics.

In summary, our results demonstrate that shrimp-farm discharges into coastal lagoons reduce species diversity and change the biotic composition of the food web. Nutrient-rich discharges from shrimp-farms do not seem to affect clearly $\delta^{13}C$ signatures, whilst $\delta^{15}N$ was a better descriptor of effluent impact within coastal lagoon food webs. Aquaculture discharges have severely altered the structure of coastal lagoon ecosystems around the world for many years. Despite the economic support of aquaculture for developing countries, coastal zone management must balance economic exploitation and environmental impacts in coastal lagoons. A reduction of untreated discharges of shrimp-farm effluents and wastewater treatment systems could be a first step to ensure conservation and rehabilitation of these valuable ecosystems.

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