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Trophic spectrum and feeding pattern of cannonball jellyfish *Stomolophus meleagris* (Agassiz, 1862) from central Gulf of California

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The diet and feeding pattern of scyphomedusa Stomolophus meleagris *(Rhizostomeae) was studied, by comparing stomach samples from different developmental stages and environmental zooplankton with the aim to determine diet composition, trophic niche breadth, selectivity and feeding overlap of this edible jellyfish species. Samplings were performed during April and December 2010 and in January 2011, in the coastal lagoon Las Guásimas (27°49′–27°54′N 110°40′–110°35′W), central Gulf of California, which consisted of zooplankton tows and jellyfish collections for stomach content. More than 39 prey items were identified in the gut contents (N = 69), from which eight taxa formed over 90% of the total. Fish eggs were considered main prey (58.6%), copepods (10.8%), veliger larvae of gastropod (13.0%) and bivalve (12.7%) were secondary prey while cirriped and decapod larvae were incidental prey (<3%). However, these proportions varied significantly between small, medium and large size classes of medusa as well as number and type of prey increasing as a function of medusa size. Values of Levin's index confirmed* S. meleagris *is a specialist predator and Pearre's index showed positive selection of fish eggs, gastropods, bivalves and cirripeds while selectivity was negative for copepods and appendicularians. The relative timing of these changes suggests that ontogenetic processes are closely related with shift in the diet, which indicates increasing predation pressure during development of the medusoid stage of this species, thus emphasizing their ecological importance in coastal ecosystems.*

Keywords: *Stomolophus meleagris*, stomach contents, diet composition, zooplankton, feeding pattern, ontogenetic shift, copepods, fish eggs, Gulf of California

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INTRODUCTION

Scyphozoan jellyfishes are a conspicuous component of the pelagic marine community. One of the most studied functions of this organisms is its feeding habits because they are considered voracious zooplankton predators that feed during day and night (Fancett & Jenkins, 1988) on a wide variety of taxa (Larson, 1991; Riascos *et al.*, 2014).

Most jellyfish are tactile predators that capture prey using nematocysts (Arai, 1997) by ambush or cruising strategies (Gerritsen & Strickler, 1977). Variation in feeding habits and prey selectivity in jellyfish is consistent with differences in functional morphology (Fancett & Jenkins, 1988; Larson, 1991; Costello & Colin, 1994; D'Ambra *et al.*, 2001) and type of nematocyst (Purcell & Sturdevant, 2001; Peach & Pitt, 2005). In addition, jellyfish diet may shift ontogenetically (Graham & Kroutil, 2001; Nogueira-Júnior & Haddad, 2008; Higgins *et al.*, 2008).

Despite the emphasis on the role of scyphomedusae as key species of coastal plankton, most inferences regarding their trophic interactions are derived from indirect evidence with limited laboratory experiments (Gibbons *et al.*, 1992; Toonen & Chia, 1993; Olesen *et al.*, 1994) on few cosmopolitan species (Arai, 1997; Purcell, 1997). Therefore, the comparison reliability of scyphomedusa feeding impacts is limited because relatively few species have been studied in sufficient detail (D'Ambra *et al.*, 2001). Nevertheless class Scyphozoa contains ~200 extant species (Mianzan & Cornelius, 1999); not all of them are relevant at community level. Much of the importance of jellyfish is due to the occurrence of seasonal outbreaks, which can cause negative impacts on human activities such as fishing (Graham *et al.*, 2003; Hong *et al.*, 2008; Nagata *et al.*, 2009; Quiñones *et al.*, 2013), aquaculture (Doyle *et al.*, 2008), tourism and nuclear power plants (Galil, 2007), and far less attention is given to the potential of such species to provide benefits, such as climate regulation, nutrient cycling, food provision amongst others (Doyle *et al.*, 2014).

Cannonball jellyfish *Stomolophus meleagris* (Agassiz, 1862) is a relatively big and conspicuous species that looks like a hemispherical mushroom-shaped organism swimming just

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under the sea surface, which inhabits the Atlantic and Pacific Ocean coastlines from Florida to Argentina and from California to Ecuador (Kramp, 1961; Balech & Ehrlich, 2008). Numerous outbreaks of this organism have been reported in several states of Mexico, such as Tabasco, Veracruz, Oaxaca, Nayarit, Sinaloa and Sonora (Gómez-Aguirre, 1991; Ocaña-Luna & Gómez-Aguirre, 1999; Álvarez-Tello, 2007). *Stomolophus meleagris* has been successfully exploited in Mexico since 2000 (López-Martínez & Álvarez-Tello, 2013) but there is still not enough information about its biology and ecology, as is the case with the vast majority of edible jellyfishes (Omori & Nakano, 2001; Kitamura & Omori, 2010).

As in most scyphozoans, cannonball jellyfish has a metagenic life cycle with a microscopic polypoid stage that can reproduce asexually (Calder, 1982) and a planktonic medusoid stage with short lifespan (Álvarez-Tello, 2007; López-Martínez & Álvarez-Tello, 2013), sexual reproduction and high fecundity (Carvalho-Saucedo *et al*., 2012). This medusa possesses developed oral arms that extend well below the margin of the swimming bell and are fused into complex oral arm cylinders containing hundreds to thousands of small mouthlets used to consume prey (Costello *et al*., 2008).

Regarding its function as a zooplankton predator, *S. meleagris* exhibits a cruising predator behaviour (Gerritsen & Strickler, 1977). Further studies on this species by Costello & Colin (1995) found that feeding and swimming are concurrent activities, and prey selection appears to depend first on prey vulnerability to entrainment in the flow created by swimming medusae. Larson (1991) and Puente-Tapia (2009) found that *S. meleagris* feeds mainly on zooplankton with emphasis on copepods followed by tintinnids, veliger larvae, and fish eggs from specimens captured in the Gulf of Mexico.

Recently, a study carried out by Padilla-Serrato *et al.* (2013) showed that fish eggs were the main item in stomachs of *S. meleagris* from the central Gulf of California, followed by bivalve and cirriped larvae, which contradict those of previous research. The main goal of this study was to determine diet composition and feeding patterns, particularly trophic niche breadth, dietary overlap and prey selectivity of *S. meleagris*, an important species for both coastal ecosystem and jellyfish fisheries from the central Gulf of California.

MATERIALS AND METHODS

Samplings

Five samplings were carried out in the coastal lagoon Las Guásimas (27°51.258′N 110°37.951′W) to cover all sizes of *S. meleagris* present in the environment (one in April 2010, two in December 2010 and two in January 2011). Note that no specimens were found from June to November. Samplings consisted of two fixed stations for zooplankton sampling and collections of jellyfish between these stations for stomach content analysis (Figure 1). Zooplankton were collected with a conical net (50 cm diameter, 300 μm mesh size) by horizontal tows while jellyfish were selected individually by random with a scoop net (40 cm diameter, 1 cm mesh size). A GPS was used to locate stations and estimate distance of plankton tows for 5 min. Filtered volume was calculated from the towed distance and the mouth area of the net (0.1963 m^2). Once on board, zooplankton samples were preserved with 5% formalin buffered with sodium borate. Jellyfish specimens were fixed immediately after catch with 10% formalin buffered with sodium borate and stored individually in plastic bags for subsequent analysis (Larson, 1991).

Sample processing

For zooplankton counting, each sample was adjusted to 100 mL, homogenized, and analysed by sequential aliquots (10 mL) until at least 1000 organisms were counted (Harris *et al*., 2000). The counts were performed using a stereomicroscope, and identification was carried out to the lowest taxonomic level using guides of Smith & Johnson (1996), Palomares-García *et al.* (1998), Harris *et al.* (2000) and Conway (2012). The zooplankters were recorded quantitatively in individuals by each 100 cubic metres filtered (ind 100 m^{-3}) and in terms of relative abundance (%N) (Smith & Richardson, 1979).

Each medusa was weighed to the nearest 1 g (W), and its length (L) determined to the nearest 1 mm (from top of umbrella to distal end of manubrium) before dissection was done to extract stomach contents. Prey were removed from jellyfish by extraction of gastric tissues and rinsing oral arms and gastric cavity on a 60 μm mesh-size sieve. Food items from pleated gastric membranes were extracted following Larson (1991). The items found in each stomach were identified with literature used for zooplankton.

Data analyses

The zooplankters were recorded quantitatively in individuals by each 100 cubic metres filtered (ind 100 m^{-3}) and in terms of relative abundance (%A) (Smith & Richardson, 1979). Zooplankton composition between months was compared using the Kruskal–Wallis test with $\alpha < 0.05$ significance level (McDonald, 2014).

Diet composition was evaluated by group of prey using three measures described by Hyslop (1980): numeric (%N); gravimetric (%W) and frequency of occurrence (%O). The Index of Relative Importance (IRI) was calculated using the equation proposed by Pinkas *et al.* (1971) and modified by Hacunda (1981).

$$\mathrm{IRI_i} = (\%N_i + \%G_i) \times \%O_i$$

where %N is the numeric percentage, %G is weight percentage and %O is the relative frequency of occurrence for each i prey group. To readily allow comparisons among prey items, the IRI was then standardized to %IRI for each prey group (Cortés, 1997).

Using the content of each stomach as sampling unit, a cumulative curve was performed plotting the number of stomachs analysed against corresponding number of prey taxa, applying 1000 randomizations with the software EstimateS (Colwell, 2013), which allowed assessment of sample size sufficiency by comparing the richness observed (S_{obs}) with the Chao1 non-parametric estimator (S_{Chao1}).

$$S_{\mathrm{Chao1}} = S_{\mathrm{obs}} + \frac{n_1^2}{2n_2}$$

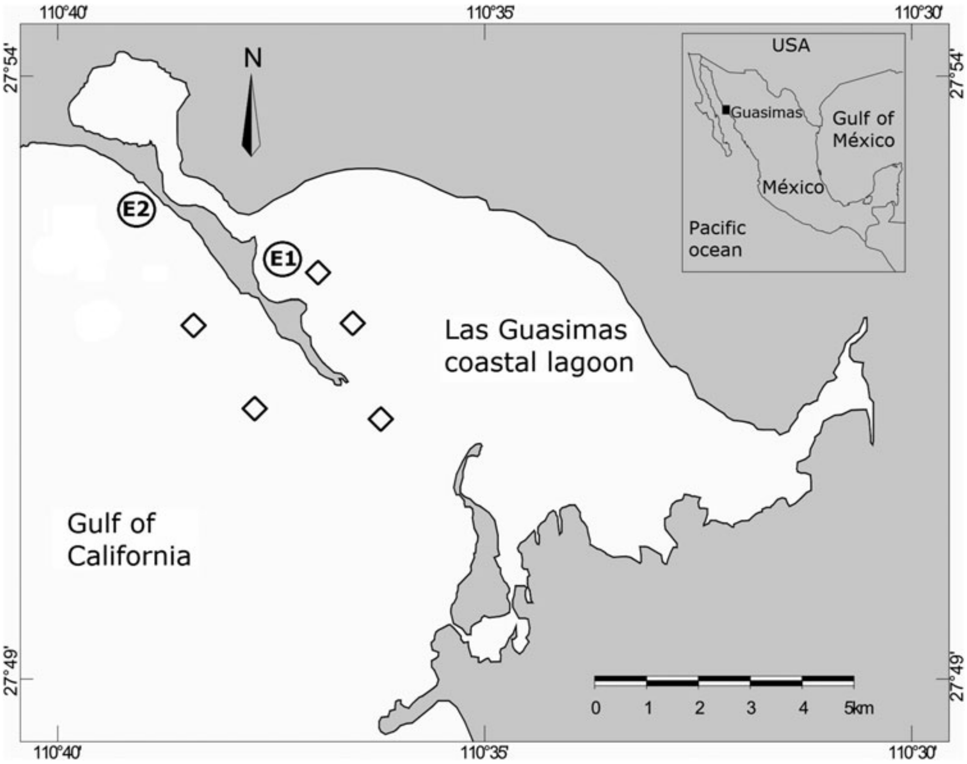

Fig. 1. Location of the coastal lagoon Las Guásimas in the central Gulf of California and stations for zooplankton (in circle) tows and jellyfish collections (rhombus) (modified from Arreola-Lizárraga, 2003).

where n_1 is the number of singletons (species found once) and n_2 is the number of doubletons (species found twice) (Chao *et al.*, 2009). We considered that the sampling effort was sufficient when the observed richness was at least 80% of S_{Chao1}, according to Jiménez-Valverde & Hortal (2003).

Stomolophus meleagris were separated into three arbitrary size classes to assess possible ontogenetic shifts, named 'small' ($L \leq 29$ mm), 'medium' (L from 30 to 69 mm) and 'large' ($L \geq 70$ mm). Kruskal-Wallis test with $\alpha < 0.05$ significance level was used to test differences in diet composition between size classes (McDonald, 2014). Association between size of specimens and stomach contents was evaluated with Spearman's correlation test, which does not require normally distributed data.

Feeding patterns of *S. meleagris* were assessed in general and by ontogenetic classes by means of trophic niche breadth, diet overlap between stages and selectivity toward main prey groups. Niche breadth was calculated using Levin's standardized index (Krebs, 1999):

$$B_i = \frac{1}{n-1\left(\frac{1}{\sum p_{ij}^2}-1\right)}$$

where B_i = Levin's standardized index for predator i, p_i = proportion in diet of predator i that is made up of prey j, and n = number of prey categories. This index ranges from 0 to 1, with low values indicating diets dominated by a few prey items (specialist predators) and higher values indicating generalist diets (Krebs, 1999).

Diet overlap among jellyfish ontogenetic classes was estimated with simplified Morisita's index of similarity C_H (Horn, 1966), which is not biased by sample size or number of resources (Wolda, 1981).

$$C_H = 2\cdot\frac{\sum(P_{ij}\cdot P_{ik})}{\sum P_{ij}{}^2+\sum P_{ik}{}^2}$$

where C_H = Simplified Morisita index of overlap between species j and k, P_{ij} = proportion resource i of the total resources used by species j, P_{ik} = proportion resource i of the total resources used by species k and n = total number of food items. Dietary overlap increases as the Morisita's index increases from 0 to 1. Overlap is generally considered to be biologically significant when the value exceeds 0.6 (Langton, 1982).

The selectivity 'C' index was calculated from the relative abundance (%N) of each prey item ingested in relation to prey availability in the zooplankton community (Pearre, 1982), which has been used previously in studies of jellyfish selectivity (Larson, 1991; Sullivan *et al.*, 1994; Graham & Kroutil, 2001) with the following equation:

$$C = \pm\sqrt{\left[\frac{(|a_d b_e - b_d a_e|)^2}{abde}\right]}$$

where, a and b represent the relative abundance of a particular species and all others, respectively, and subscripts d and e indicate the diet and the environment. The index ranges from +1 to −1. Positive values indicate selection, negative values indicate avoidance, and a value of zero indicates no selection (Pearre, 1982). Fisher's exact test was used for the analysis of contingency tables by food item to test for significance of selection indices (McDonald, 2014).

RESULTS

Zooplankton composition

Zooplankton densities were contrasting between months, with high values in April 2010 (30.5×10^3 ind. 100 m^3), lower values in December 2010 (12.5×10^3 ind. 100 m^3), and high values again in January 2011 (34.7×10^3 ind. 100 m^3). At a coarse taxonomic group level, the zooplankton community was dominated numerically by copepods, particularly during April when their relative abundance reached 98.5%. The most numerous copepods were *Acartia tonsa, Paracalanus* spp. and *Oithona* spp. Other abundant groups ($\%A > 1\%$) were appendicularians, ctenophores, polychaete larvae and chaetognaths (Table 1). Significant differences were found in composition of zooplankton groups between months ($H = 10.53$, $P < 0.01$).

Stomolophus meleagris catches

Fifteen specimens of *S. meleagris* were collected during April, both inside and outside of Las Guásimas lagoon. Jellyfish fishing season ended in mid-May and after that no jellyfish were observed until December. During this month 24 organisms were collected mainly inside the lagoon and during January 30 additional jellyfish were sampled. The longitudinal length of the specimens ranged from 12 to 110 mm, with a mean value of 48 mm ($SD = 28.2$, $n = 69$). Three of 69 stomachs analysed were empty. Only large organisms were captured in April while in December there were mainly small medusae. During January 2011 a wide range of sizes was collected, but medium jellyfishes clearly predominated. Size structure of samples was composed of 27 small, 23 medium and 19 large organisms (Figure 2A). Power regressions between jellyfish size and weight were significant and explained 97% of the data (Figure 2B).

General diet composition

A total of 9766 prey items were found in 66 stomachs, from which 39 food types were identified (Table 2). The most abundant were oval fish eggs (42.2%), bivalve larvae (20.2%), gastropod larvae (9.7%), spherical fish eggs (7.4%) and cirriped larvae (5.5%), which adds up to more than 85% of the total. Average content was 142 items per stomach although it ranged widely from one prey in small specimens (16 mm) to 2017 prey in one large organism (110 mm).

The cumulative curves from randomized counting of richness observed (S_{obs}) were convergent with the values of Chao1 estimator (S_{Chao1}) and reached sufficiency criteria (S_{obs}>80% of S_{Chao1}) after specimen number 39 (Figure 3). The likelihood of finding new food items at this sample size was very low (<0.05).

For subsequent analyses, prey were grouped in 13 major taxonomic categories shown in Table 3. Fish eggs were the most abundant by number ($\%N = 50.1\%$) and weight ($\%G = 84.9\%$) while copepods were the most common between stomachs ($\%O = 87.0\%$). Integrating the previous values into the index of relative importance (IRI) resulted that the main prey group of *S. meleagris* were fish eggs ($IRI = 58.6\%$). Secondary prey were gastropod larvae ($IRI = 13.0\%$), bivalve larvae ($IRI = 12.7\%$) and copepods ($IRI = 10.8\%$). Cirriped larvae ($IRI = 2.8\%$) and decapods ($IRI = 1.0\%$) were considered occasional prey (Figure 4). In

Table 1. Monthly mean of zooplankton densities and relative abundance (%*A*) in the coastal lagoon Las Guásimas.

		Apr 2010		Dec 2010		Jan 2011	
Key	**Group**	**ind. 100 m^{-3}**	**%A**	**ind. 100 m^{-3}**	**%A**	**ind. 100 m^{-3}**	**%A**
CO	Copepoda	30,067	98.5	7843	62.9	30,730	88.5
AP	Appendicularia	0	0.0	1609	12.9	645	1.9
CT	Ctenophore	0	0.0	891	7.1	909	2.6
PO	Polychaete larvae	12	0.0	74	0.6	1318	3.8
CH	Chaetognatha	25	0.1	575	4.6	242	0.7
CL	Cladoceran	0	0.0	563	4.5	0	0.0
BR	Brachyura larvae	91	0.3	124	1.0	303	0.9
GA	Gastropod larvae	103	0.3	114	0.9	196	0.6
HI	Hydromedusae	0	0.0	226	1.8	22	0.1
EG	Fish eggs	131	0.4	72	0.6	44	0.1
SI	Siphonophora	0	0.0	169	1.4	0	0.0
FL	Fish larvae	25	0.1	14	0.1	80	0.2
AM	Amphipoda	0	0.0	77	0.6	36	0.1
DE	Decapod larvae	57	0.2	9	0.1	33	0.1
BI	Bivalve larvae	25	0.1	17	0.1	35	0.1
CI	Cirriped larvae	0	0.0	30	0.2	43	0.1
PH	Phoronida larvae	0	0.0	0	0.0	43	0.1
SC	Scyphomedusae	0	0.0	3	0.0	35	0.1
AN	Anomuran larvae	0	0.0	26	0.2	0	0.0
BZ	Bryozoan larvae	0	0.0	10	0.1	4	0.0
TH	Thaliacea	0	0.0	12	0.1	0	0.0
CU	Cumacea	0	0.0	7	0.1	0	0.0
FO	Foraminifera	0	0.0	3	0.0	0	0.0
	Total	30,533		12,466		34,718	

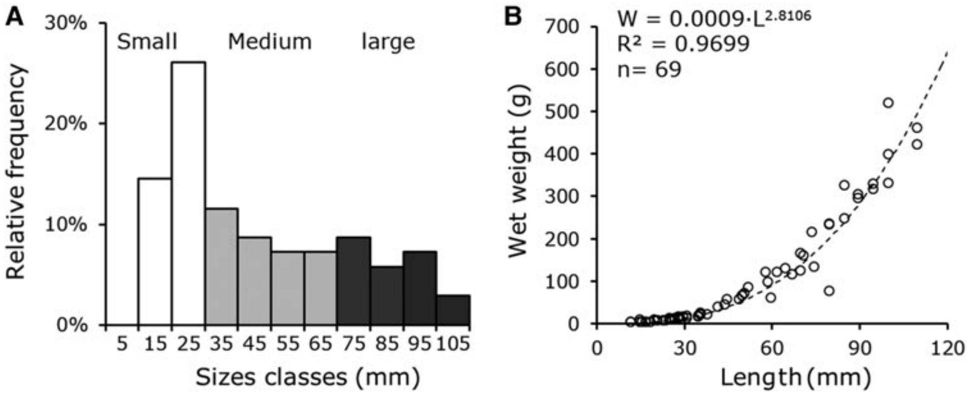

Fig. 2. Size structure (A) and Length-wet weight relationship (B) of *S. meleagris* dissected for stomach contents analyses from the coastal lagoon Las Guásimas, Sonora Mexico.

addition, another seven groups were present at less than 1%, which were treated as 'rare prey'.

Table 2. General diet composition of *Stomolophus meleagris* by food item. %*N*, %*G*, %*O* and %IRI represent percentages in number, wet weight, occurrence and index of relative importance.

Item	%*N*	%*G*	%*O*	%IRI
Fish eggs (type 2)	42.2	62.7	21.7	37.9
Bivalve larvae	20.2	6.9	39.1	17.6
Gastropod larvae	9.7	4.4	76.8	18.1
Fish eggs (type 1)	7.4	22.1	27.5	13.5
Cirriped larvae	5.5	1.3	26.1	2.9
Appendicularians	2.3	<0.1	23.2	0.9
Copepod larvae	2.2	0.5	50.7	2.2
Paracalanus sp.	1.5	0.3	39.1	1.2
Copepod undetermined	1.5	0.3	47.8	1.4
Brachyuran zoea	1.5	0.5	36.2	1.2
Oithona sp.	1.1	0.3	39.1	0.9
Polychaete larvae	1.1	<0.1	17.4	0.3
Copepodites	1.0	0.2	40.6	0.8
Acartia spp.	0.5	0.1	37.7	0.4
Amphipods	0.3	0.1	17.4	0.1
Fish eggs unknown	0.3	0.1	7.2	<0.1
Corycaeus spp.	0.2	0.1	17.4	0.1
Cirriped nauplii	0.2	<0.1	18.8	0.1
Oncaea sp.	0.2	0.1	18.8	0.1
Fish eggs (type 3)	0.2	<0.1	8.7	<0.1
Microsetella sp.	0.1	<0.1	15.9	<0.1
Bryozoan larvae	0.1	<0.1	7.2	<0.1
Hydroida	0.1	<0.1	14.5	<0.1
Decapod larvae	0.1	<0.1	11.6	<0.1
Chaetognatha	0.1	<0.1	10.1	<0.1
Insecta	0.1	<0.1	5.8	<0.1
Tintinida	0.1	<0.1	4.3	<0.1
Foraminifera	0.1	<0.1	4.3	<0.1
Nemertean larvae	<0.1	<0.1	4.3	<0.1
Pteropods	<0.1	<0.1	4.3	<0.1
Fish larvae	<0.1	<0.1	2.9	<0.1
Ostracod	<0.1	<0.1	2.9	<0.1
Labidocera spp.	<0.1	<0.1	2.9	<0.1
Clausocalanus sp.	<0.1	<0.1	2.9	<0.1
Coscinodiscus spp.	<0.1	<0.1	1.4	<0.1
Penilia avirostris	<0.1	<0.1	1.4	<0.1
S. meleagris ephyra	<0.1	<0.1	1.4	<0.1
Euterpina acutifrons	<0.1	<0.1	1.4	<0.1
Sapphirina sp.	<0.1	<0.1	1.4	<0.1

Feeding pattern

The trophic niche breadth value showed a specialist pattern of feeding ($B_i = 0.131$) based essentially on five (>80%) of 39 available prey. It was evident that prey composition in jellyfish stomach contents varied greatly from the zooplankton composition observed (Figure 5A). This medusa showed a clear positive selection for bivalves ($C = 0.28$, $P < 0.01$) and gastropods ($C = 0.30$, $P < 0.01$) in every month. Fish eggs and cirriped larvae only showed positive and significant selection during April. These prey were relatively scarce in zooplankton (<1%) while copepods, which were abundant in the environment, showed a significant and negative selectivity index every month ($C = -0.55$, $P < 0.01$) while appendicularians only during December. No significant values of selectivity were obtained for the rest of prey in stomachs (Figure 5B).

Ontogenetic changes

Prey number and richness in stomachs of *S. meleagris* were significantly correlated with specimen size ($rs = 0.8862$, $n = 66$, $P < 0.001$ and $rs = 0.7854$, $n = 66$, $P < 0.001$, respectively) and showed an exponential pattern in prey contents (Figure 6A) and a linear tendency for prey richness (Figure 6B). Small jellyfish averaged 11 prey (SD = 10, $n = 26$) in their stomachs, medium jellyfish ingested 58 (SD = 81, $n = 22$) while large organisms consumed 428 prey (SD = 619, $n = 18$).

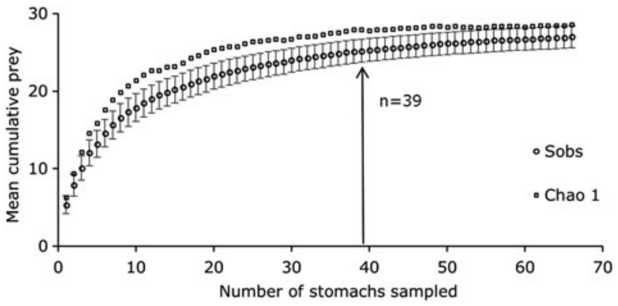

Fig. 3. Cumulative prey curves (±SD) for *S. meleagris* from Las Guásimas. Circle plots represent the average of 1000 permuted curves constructed using randomized ordering of samples (S_{obs}) and squares are data of prey species richness estimates (S_{Chao1}). The arrow indicates the point at which S_{obs} reaches sufficiency criteria (80% S_{Chao1}).

Table 3. Mean prey content of individual *S. meleagris* by size classes and index of relative importance (IRI) for each prey group.

		Prey medusa^{-1}				**%IRI**			
Key	**Prey group**	**Small (n = 27)**	**Medium (n = 23)**	**Large (n = 19)**	**Average**	**Small**	**Medium**	**Large**	**Total**
CO	Copepods	7.0	19.3	10.0	11.9	70.4	40.9	1.2	10.8
GA	Gastropods larvae	2.5	10.8	33.3	13.7	26.5	23.4	5.9	13.0
BI	Bivalve larvae	0.0	11.7	89.5	28.5	<0.1	14.4	13.9	12.7
EG	Fish eggs	0.7	7.6	247.1	70.8	2.0	15.8	74.1	58.6
CI	Cirriped larva	0.2	2.7	25.7	8.1	0.2	1.3	3.4	2.8
DE	Decapod larvae	0.1	1.7	5.9	2.2	0.1	1.9	0.8	1.0
AP	Appendicularia	0.0	1.8	9.4	3.2	<0.1	1.2	0.3	0.6
PO	Polychaete larvae	0.0	0.3	5.2	1.5	<0.1	0.1	0.3	0.2
AM	Amphipod	0.1	0.9	0.4	0.4	0.1	0.6	<0.1	0.1
QE	Chaetognatha	0.1	0.3	0.1	0.2	0.1	<0.1	<0.1	<0.1
HI	Hydroida	0.2	0.3	0.0	0.2	0.2	0.1	<0.1	<0.1
BR	Bryozoan larvae	0.0	0.0	0.7	0.2	<0.1	<0.1	<0.1	<0.1
RG	Rare groups	0.3	0.7	0.7	1.5	0.3	0.3	<0.1	0.1
	TOTAL	11.2	58.0	427.9	142.5				

The composition of main prey groups exhibited an evident change between size classes of *S. meleagris* (Figure 7). Copepod and gastropod IRI showed a strong tendency to decrease with jellyfish growth while fish eggs tended to increase. Small and medium jellyfish showed a diet based on copepods and gastropods while adults ingested primarily fish eggs and bivalves (Table 3). Composition of diets between size classes were statistically different ($H = 11.25$, $P = 0.0036$).

Trophic niche breadth values showed a specialist pattern of feeding for every medusa stage with the highest value for medium specimens ($B_i = 0.25$) and the narrowest for the smallest and largest classes ($B_i < 0.1$) (Figure 8A). Morisita's index of similarity indicated that small and medium jellyfishes were the most similar ($C_H = 0.534$) while small and large organisms were the least ($C_H = 0.014$). Large and medium sizes also had a slight niche overlap value with a Morisita's index of similarity of 0.122 (Figure 8B).

Selectivity was associated with change in size of medusa for the main groups of prey. Meroplanktonic larvae of gastropods, bivalves, fish eggs and cirripeds showed a tendency to be positively selected while copepods were negatively selected by medusae of medium and large size classes (Figure 9). Change in selection of copepods ($rs = -0.580$, $P < 0.01$) and gastropods ($rs = -0.515$, $P < 0.01$) was negatively correlated with change in size of *S. meleagris*, and the converse was observed for bivalves ($rs = 0.416$, $P = 0.03$), fish eggs ($rs = 0.657$, $P < 0.01$), cirripeds ($rs = 0.601$, $P < 0.01$) and decapods ($rs = 0.549$, $P < 0.01$).

DISCUSSION

Stomolophus meleagris exhibited a clearly carnivorous specialist diet with a tendency to select some of the food resources available in the environment, such as fish eggs, bivalve, gastropod, copepod, decapod and cirriped larvae, which is partially concurrent with findings of previous research in the Gulf of Mexico by Larson (1991) and Puente-Tapia (2009) and in the Gulf of California by Padilla-Serrato *et al.* (2013). In addition, the diet of medium cannonball jellyfish is comparable to other scyphozoans like *Chrysaora plocamia*, which consumes mainly fish eggs, copepod, bivalve, polychaete and cirriped larvae (Riascos *et al.*, 2014).

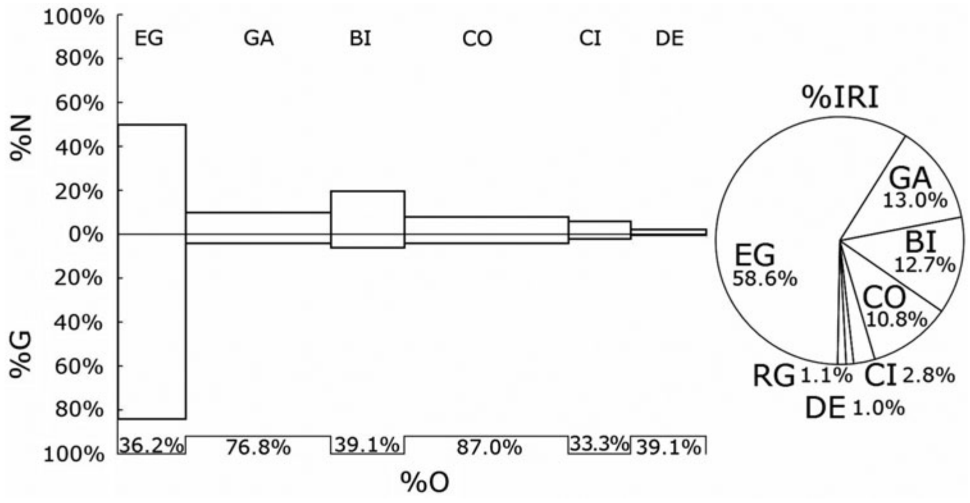

Fig. 4. Trophic spectrum of *S. meleagris* from Las Guásimas, Sonora Mexico. Where: CO, copepods; EG, fish eggs; GA, gastropod larvae; BI, bivalve larvae; DE, decapod larvae and RG, rare groups.

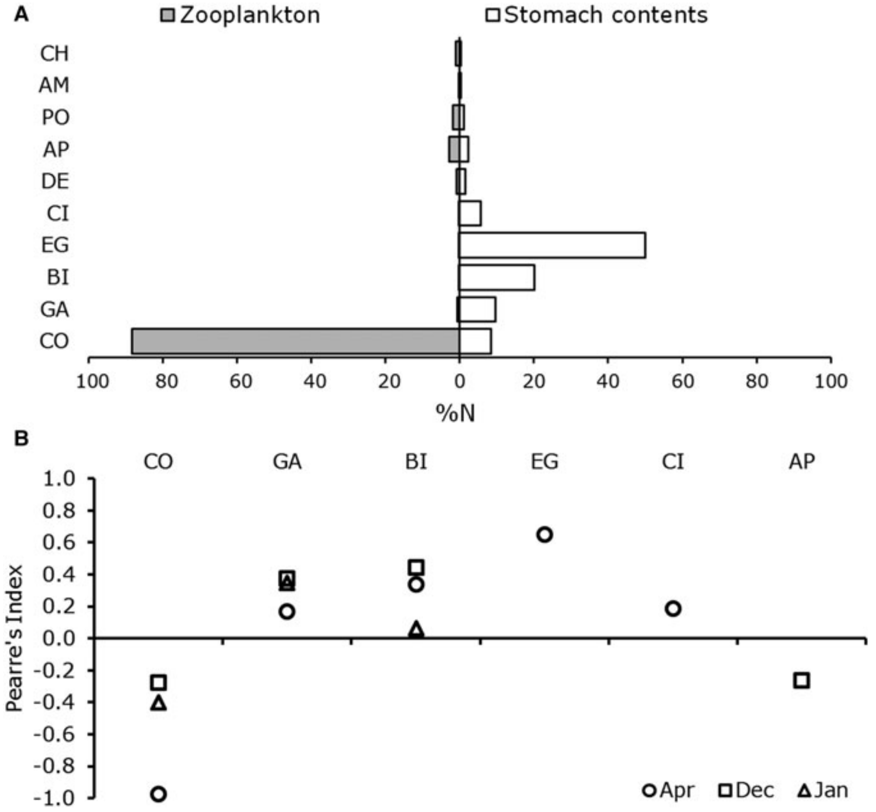

Fig. 5. General selectivity of *S. meleagris* from Las Guásimas. (A) Gross comparison between numeric percentage (%*N*) of main zooplankton groups in environment vs percentage of prey in stomach contents and (B) monthly selectivity of main prey groups. Where CO, copepods; EG, fish eggs; GA, gastropod larvae; BI, bivalve larvae; CI, cirriped larvae; DE, decapod larvae; AP, appendicularians; PO, polychaete larvae; AM, amphipods and CH, Chaetognaths.

We hypothesize that some differences in the general composition of diet between our work and previous research on feeding habits of *S. meleagris* were probably due to geographic and temporal differences of samples, but mainly due to the structure of size of samples for stomach content analyses. Interestingly, at size class levels we found some similarities with previous literature. Larson (1991) determined 24 taxa in the diet of *S. meleagris* composed of 20% small and 65% medium medusae where the main prey were bivalve, gastropods and copepods, which is similar to the diet found in our work if we only consider the proportion of small and medium sizes of jellyfish from our sample. More recently, Padilla-Serrato *et al.* (2013) identified 13 food items in the gut contents of *S. meleagris* composed of 90% large and 10% medium jellyfishes where fish eggs and bivalves comprised 90% of the diet, which is similar to our findings in the subsample of large medusae (88%). Puente-Tapia (2009) also analysed the diet for this species and reported a composition based mainly on copepods and fish eggs but the size structure of his sample is unknown.

In our study the dominant taxa from zooplankton samples, excluding copepods, did not dominate the jellyfish gut contents. Padilla-Serrato *et al.* (2013) found that *S. meleagris* is a specialist predator with $B_i = 0.12$, which is very similar to our estimate of Levin's index (0.13) for the entire sample. Values of selectivity were negative for copepods and positive for bivalve larvae, which is analogous to Larson's (1991) results. However, it is not possible to compare ontogenetic differences in the diet of *S. meleagris* or on any other rhizostome due to the lack of information in this field. The most

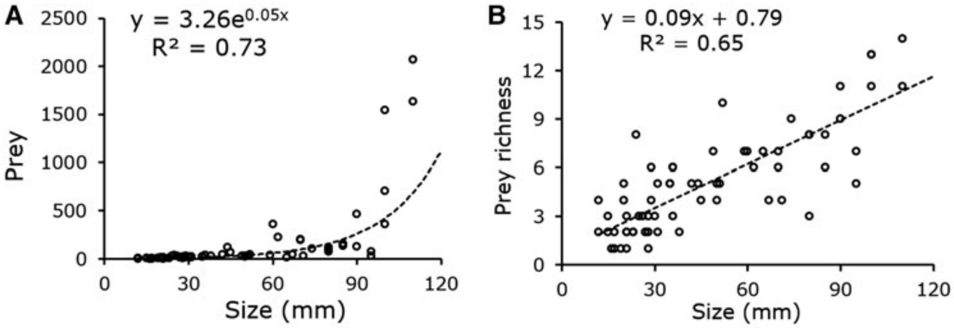

Fig. 6. Relationship between the size of *S. meleagris* with (A) number of prey and (B) prey richness of food items from the coastal lagoon Las Guásimas, Sonora, México.

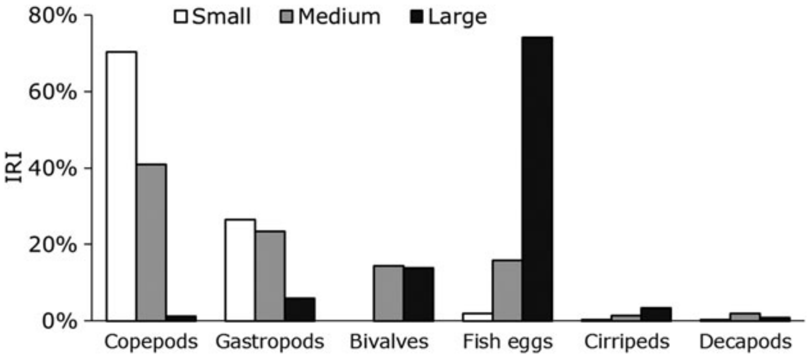

Fig. 7. Change of %IRI values in main prey groups related with ontogenetic classes of *S. meleagris* from Las Guásimas, Sonora Mexico.

similar studies on this matter are the estimation of predatory potential by *Phyllorhiza punctata* (García & Durbin, 1993), the analysis of gut contents on field-caught *Aurelia aurita* by Graham & Kroutil (2001), quantification of change of feeding in *Cyanea capillata* (Higgins *et al*., 2008) and study of dietary shift in cubomedusae *Chiropsalmus quadrumanus* (Nogueira-Júnior & Haddad, 2008), whose findings have confirmed that size change of predator can influence the clearance rates, quantity of prey ingested and diet composition.

In our work, we found an increase in prey numbers and taxa richness related with jellyfish size, which agrees with the findings of Graham & Kroutil (2001) in *Aurelia aurita*, Kanagaraj *et al*. (2011) in *Chrysaora* cf. *caliparea* and Riascos *et al*. (2014) in *C. plocamia*. However, Graham & Kroutil (2001) mentioned that it is not surprising that the number of prey increases with the size of the jellyfish, which is attributable to the fact that larger organisms have higher clearance rates because of the increased contact area with the environment, larger inertial forces and thus higher probabilities to contact a potential prey. Costello & Colin (1994) theorized that larger jellyfish could trap larger and faster organisms due to stronger inertial forces in jellyfish swimming. However, our results seem to contradict this prediction: while mollusc larvae showed little variability through ontogenetic stages, IRI values of copepods decreased whereas IRI of fish eggs increased, suggesting a gradual loss in the ability to capture more moving prey types and a growing dependence for slow or motionless food resources.

Change in feeding pattern of *S. meleagris* could be explained by the presence of more vulnerable prey to certain nematocysts, as in the case of larvaceans, fish larvae and gelatinous prey ('soft-bodied') that appear vulnerable to nematocysts of the isorhizas type from *Aequorea victoria* and *C. capillata* while 'hard-bodied prey' such as crustaceans and bivalve larvae were more vulnerable to euryteles from *Aurelia labiata* (Purcell, 2003). In another study, Peach & Pitt (2005) determined the composition of nematocysts and prey in *Catostylus mosaicus* and *Phyllorhiza punctata* captured at the same place and time, finding differences in the composition of nematocysts and in the proportion of prey between species. Calder (1983) investigated the composition of nematocysts of polyps, ephyrae and adult of *S. meleagris* and found a changing composition based on two basic types: isorhizas and euryteles, each one with different morphology and distribution in the body. This relates to the research by Arai (1997), who determined that discharged nematocysts were not reusable and therefore constituted a considerable cost of energy for the animal. More recent investigations in this field in *Chironex fleckeri* (Carrette *et al*., 2002), *C. quadrumanus* (Nogueira-Júnior & Haddad, 2008) and *C. capillata* (Higgins *et al*., 2008) confirmed the link between changes in morphology and composition of cnidome and dietary shifts, during jellyfish growth.

The information above suggests that observed changes in the diet of *S. meleagris* could be due to the gradual loss of certain types of nematocysts during ontogenetic development, along with changing inertial forces around the jellyfish body. However, for a better understanding of this feeding behaviour, future studies should focus on these patterns beyond the limits examined in this study, for example, considering the influence of cnidome development during the medusoid stage of *S. meleagris* and prey size.

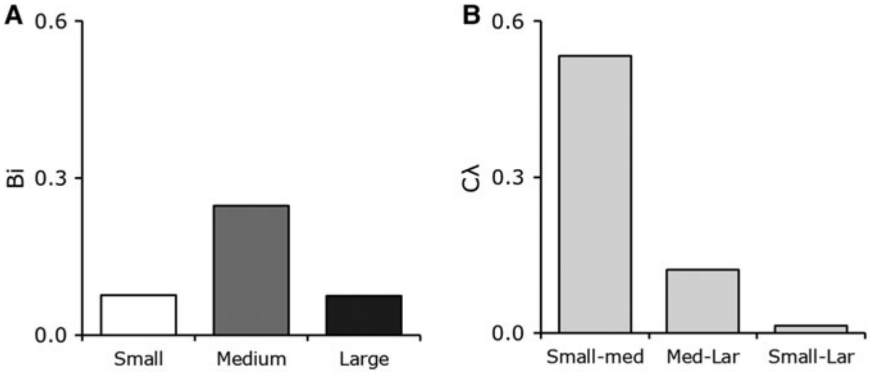

Fig. 8. (A) Trophic niche breadth and (B) diet overlap between ontogenetic classes of *S. meleagris* from Las Guásimas, Sonora Mexico.

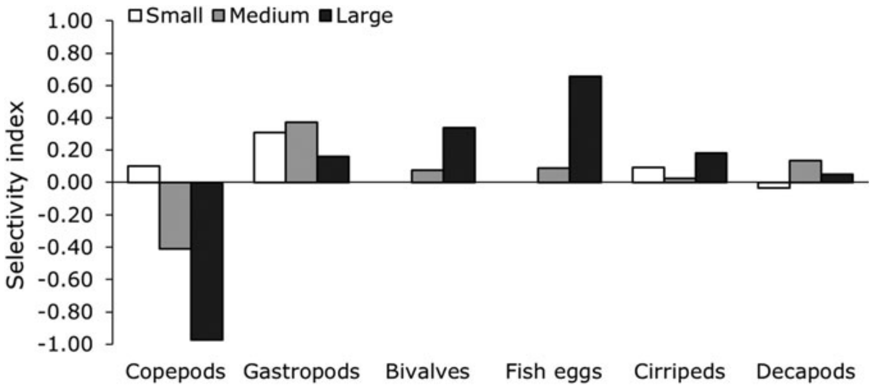

Fig. 9. Selectivity index of mean prey groups by ontogenetic classes of *S. meleagris* from Las Guásimas.

Remarkably, *S. meleagris* displayed a clear pattern of change in selection for copepods from slightly positive in early stages to strongly negative in adults. The existence of avoidance strategies, immunity to certain nematocysts and escape capacity as a possible explanation for the negative selection of copepods was suggested by Purcell (2003). Positive selection of fish eggs and larvae of molluscs (bivalves and gastropods) could be partially related to their limited ability to escape, which could imply a significant source of mortality for these species (Fancett & Jenkins, 1988; Purcell *et al.*, 1994; Purcell, 1997). Additionally, we are aware that sampling zooplankton with a 300 µm mesh-size net can cause an underestimation of the smallest planktonic larvae (nauplii, copepodites and early bivalve and gastropod veliger), which indirectly can influence selectivity values. Indeed, estimation of more reliable selection indices require good information on the prey abundance in the water column. Therefore, more exhaustive zooplankton studies, perhaps using a 200 µm mesh-size net for sampling, are needed to better understand the selective feeding behaviour of *S. meleagris*.

In the wild, most marine fish larvae feed on copepods and other small crustaceans during the first few weeks of life (Das *et al.*, 2014), and it is generally believed that copepods can meet the nutritional requirements of fish larvae (Evjemo *et al.*, 2003). Nogueira-Júnior & Haddad (2008) also reported a diet based on crustaceans for the larval and juvenile phases of cubomedusae *C. quadrumanus* before a shift in preference for fish and suggest that this behaviour may be a strategy to avoid competition between large and small individuals. Therefore, a similar phenomenon may be occurring for *S. meleagris*, which fed on copepods, mostly on copepodites and nauplii during larval and juvenile stages. On the other hand, Carvalho-Saucedo *et al.* (2010) discussed whether lipid increase in *S. meleagris* tissues registered during March and April 2005 and 2006 could be related with feeding and the need to store energy reserves for gonadal development. From an evolutionary point of view, this change in diet could be advantageous for the species, which initially can feed on prey rich in proteins, such as copepods, to grow rapidly and change when mature to a food rich in lipids, such as fish eggs, to improve gonadal development (Carvalho-Saucedo *et al.*, 2010; Padilla-Serrato *et al.*, 2013). This variable feeding pattern supports the hypothesis that *S. meleagris* is a species highly coupled with zooplankton abundance cycles (Larson, 1986) because it can select food sources to satisfy physiological needs through its ontogenetic development during the pelagic stage.

The results of this study allow us to suggest that *S. meleagris* is a relatively more passive predator than others that have been documented with zooplanktivorous habits since most of their prey were zooplankters with reduced or no swimming capabilities, and thus unable to escape the turbulent flow used by this jellyfish to swim and catch prey (Costello & Colin, 1995). However, despite its apparently low individual consumption (0.05% of wet weight), the presence of swarms of millions of organisms could involve a significant daily removal rate on plankton by massive effect. This extreme abundance of jellyfish is very plausible in this region where jellyfish fishery has been regular since 2000 with annual catches of more than 10,000 tonnes wet weight during recent years (López-Martínez & Álvarez-Tello, 2013).

Our results show that *S. meleagris* is a highly specialized and selective zooplanktivorous species, with a clear change in diet in terms of quantity and types of prey as it grows. The increase in number and types of prey in stomachs was proportional to the size of medusa, while the ontogenetic shift in the proportion of prey was possibly due to changes in the composition of nematocysts throughout the development of the medusa, changing inertial forces around jellyfish and prey availability in the environment. Copepods were the main prey of newly recruited small and medium size medusae while large animals mainly selected fish eggs, probably favouring initial growth of the jellyfish and later its gonadal maturation. Despite the feeding habits of *S. meleagris* seeming to be partially analogous to other jellyfish species, similar studies of shift in diets between ontogenetic stages of other jellyfishes will be necessary to determine whether it is a regular pattern of the feeding habits of other members of the class Scyphozoa, in order to gain a better understanding of the ecological importance of this conspicuous group of marine animals.

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