Floating nurseries? Scyphozoan jellyfish, their food and their rich symbiotic fauna in a tropical estuary

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The anthropogenic modification of basal trophic pathways is seemingly prompting the increase of jellyfish populations at the expense of planktivorous fishes. However, gross generalizations are often made because the most basic aspects of trophic ecology and the diverse interactions of jellyfish with fishes remain poorly described. Here we inquire on the dynamics of food consumption of the medusoid stage of the scyphozoan jellyfish *Stomolophus meleagris* and characterize the traits and diversity of its symbiotic community. *S. meleagris* and their associated fauna were sampled in surface waters between November 2015 and April 2017 in Málaga Bay, an estuarine system at the Colombian Pacific. Stomach contents of medusae were examined and changes in prey composition and abundance over time analysed using a multivariate approach. The associated fauna was identified and the relationship between the size of medusae and the size their symbionts tested using least-square fitting procedures. The presence of *S. meleagris* medusa in surface waters was seasonal. The gut contents analysis revealed that algae, copepods and fish early life stages were the more abundant items, and PERMANOVA analysis showed that the diet differed within the seasons ($P_{(perm)}$=0.001) but not between seasons ($P_{(perm)}$=0.134). The majority of the collected medusae (50.4 %) were associated to individuals of 11 symbiotic species, 95.3% of them fishes, 3.1% crustaceans and 1.6% molluscs. Thereby, this study reports 10 previously unknown associations. The bell diameter of *S. meleagris* was positively related to the body sizes of their symbionts. However, a stronger fit was observed when the size relationship between *S. meleagris* and the fish *Hemicaranx zelotes* was modelled. The ocurrence of S. meleagris was highly seasonal, and the observed patterns of mean body size through the seasons suggested the arrival of adult medusae to the estuary from adjacent waters. The diet of *S. meleagris* in the study area showed differences with previous reports, chiefly because of the consistent abundance of algae that are seemingly ingested but not digested. The low number of

zooplanktonic items in gut contents suggest the contribution of alternative food sources not easily identifiable. The observed changes in the composition of food in the guts probably reflect seasonal changes in the availability of prey items. The regular pattern in the distribution of symbionts among medusae (a single symbiont per host) and the positive host-symbiont size relationship reflects antagonistic intraspecific and interspecific behaviour of the symbiont. This strongly suggest that medusa represent an "economically defendable resource" that potentially increases the survival and recruitment of the symbionts to the adult population. We argue that, if this outcome of the symbiotic association can be proven, scyphozoan jellyfish can be regarded as floating nurseries.

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2   **symbiotic fauna in a tropical estuary**

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12 **Abstract**

13 **Background.** The anthropogenic modification of basal trophic pathways is seemingly prompting
14 the increase of jellyfish populations at the expense of planktivorous fishes. However, gross
15 generalizations are often made because the most basic aspects of trophic ecology and the diverse
16 interactions of jellyfish with fishes remain poorly described. Here we inquire on the dynamics of
17 food consumption of the medusoid stage of the scyphozoan jellyfish *Stomolophus meleagris* and
18 characterize the traits and diversity of its symbiotic community.

19 **Methods.** *S. meleagris* and their associated fauna were sampled in surface waters between
20 November 2015 and April 2017 in Málaga Bay, an estuarine system at the Colombian Pacific.
21 Stomach contents of medusae were examined and changes in prey composition and abundance
22 over time analysed using a multivariate approach. The associated fauna was identified and the
23 relationship between the size of medusae and the size their symbionts tested using least-square
24 fitting procedures.

25 **Results.** The presence of *S. meleagris* medusa in surface waters was seasonal. The gut contents
26 analysis revealed that algae, copepods and fish early life stages were the more abundant items,
27 and PERMANOVA analysis showed that the diet differed within the seasons ($P_{(perm)}$=0.001) but
28 not between seasons ($P_{(perm)}$=0.134). The majority of the collected medusae (50.4 %) were
29 associated to individuals of 11 symbiotic species, 95.3% of them fishes, 3.1% crustaceans and
30 1.6% molluscs. Thereby, this study reports 10 previously unknown associations. The bell
31 diameter of *S. meleagris* was positively related to the body sizes of their symbionts. However, a
32 stronger fit was observed when the size relationship between *S. meleagris* and the fish
33 *Hemicaranx zelotes* was modelled.

34 **Discussion.** The ocurrence of S. meleagris was highly seasonal, and the observed patterns of
35 mean body size through the seasons suggested the arrival of adult medusae to the estuary from
36 adjacent waters. The diet of *S. meleagris* in the study area showed differences with previous
37 reports, chiefly because of the consistent abundance of algae that are seemingly ingested but not
38 digested. The low number of zooplanktonic items in gut contents suggest the contribution of
39 alternative food sources not easily identifiable. The observed changes in the composition of food
40 in the guts probably reflect seasonal changes in the availability of prey items. The regular pattern
41 in the distribution of symbionts among medusae (a single symbiont per host) and the positive
42 host-symbiont size relationship reflects antagonistic intraspecific and interspecific behaviour of
43 the symbiont. This strongly suggest that medusa represent an "economically defendable
44 resource" that potentially increases the survival and recruitment of the symbionts to the adult
45 population. We argue that, if this outcome of the symbiotic association can be proven,
46 scyphozoan jellyfish can be regarded as floating nurseries.

Introduction

48 The magnitude and frequency of population blooms of jellyfish (pelagic cnidarian and
49 ctenophores) are seemingly increasing, along with strong impacts on marine ecosystems. The
50 collapse of formerly rich fisheries has been linked to increasing jellyfish populations in several
51 regions (Lynam *et al.*, 2006; Brodeur, Ruzicka & Steele 2011). However, much of the societal
52 and even scientific perception about jellyfish and their role in ecosystems is based on speculation,
53 limited evidence and flawed scientific practices (e.g. Haddock 2008; Richardson *et al.*, 2009;
54 Sanz-Martín *et al.*, 2016). Trophic interactions between jellyfish and planktivorous fishes have
55 been characterized as a combination of mutual predation and competition for planktonic food
56 (Purcell & Arai, 2001; Lynam, 2006; Brodeur *et al.*, 2008; Richardson *et al.*, 2009). Changes in

57 the balance of these trophic pathways in stressed and overfished ecosystems have been
58 hypothesized to explain massive local proliferations of jellyfish that displace planktivorous fishes
59 and form alternate jellyfish-dominated ecosystems (Richardson *et al.*, 2009). However, trophic
60 relationships are only known for a small portion of this polyphyletic assemblage spanning more
61 than 2000 species (Fleming *et al.*, 2015). As a result, trophic models assessing food web structure
62 and energy flow often ignore jellyfish or include them as a single functional group with the
63 characteristics of an 'average' jellyfish whose parameterization frequently varies greatly among
64 models (Pauly *et al.*, 2009). In fact, the hypotheses proposed to explain changes in jellyfish
65 dominated ecosystems remain untested, partially because there is a recognition that more basic
66 research on feeding ecology is still required (Pauly *et al.*, 2009; Richardson *et al.*, 2009; Naman
67 *et al.*, 2016).

68 Regarding scyphozoan jellyfish, two emerging issues are challenging the predominant view of
69 competitive trophic interactions between planktivorous fishes and jellyfish. First, recent
70 methodological approaches have shown that scyphozoans use unsuspected food sources,
71 including benthic organisms (Pitt *et al.*, 2008; Ceh *et al.*, 2015), microplankton and resuspended
72 organic matter (Javidpour *et al.*, 2015). These food sources have been traditionally overlooked,
73 because most studies on feeding ecology use gut content analysis that focuses on
74 mesozooplankton and ichthyoplankton, presumably because they are more visible and retained in
75 the gut for longer than other type of food (Pitt, Connoly & Meziane, 2009). Thus, the widely held
76 view that fishes and scyphozoan jellyfish compete for the same food source seems a gross
77 generalization. Second, mounting evidence suggests that mutual predation (i.e, medusae
78 predating on fish egg or larvae and fishes predating on medusae early life stages) is only one side
79 of the story. Scyphozoans can host a diverse range of symbionts, from fish to invertebrates, in a
80 variety of relationships including parasitism, mutualism and commensalism (Riascos, 2013;
81 Ohtsuka *et al.*, 2009; Ingram, Pitt & Barnes 2017). However, trophic modelling efforts
82 traditionally focus on predation and competition, despite mounting evidence showing that
83 alternative trophic pathways and relationships may positively affect fish populations (e.g. Lynam
84 & Brierley, 2007; Riascos *et al.*, 2012; Greer *et al.*, 2017).

85 Much of the prevalent view about fish-jellyfish trophic dynamics is derived from scyphozoans of
86 subtropical and temperate areas that support large pelagic fisheries. In estuarine systems, the
87 scarce evidence suggests a low trophic overlap between fish and jellyfish (Nagata *et al.*, 2015;
88 Naman *et al.*, 2016) and a high occurrence of symbiotic associations with juveniles of fish and
89 invertebrates (e.g., Rountree 1983; Costa, Albieri & Araújo, 2005; Martinelli *et al.*, 2008),
90 perhaps reflecting the abundance of early stages of coastal fauna in nursery areas. Hence there is
91 a need to study the trophic ecology of scyphozoan jellyfish and their multiple biological
92 interactions to truly understand population dynamics, their position in food webs and their
93 functional role in estuarine ecosystems.

94 Here we studied the canon ball jellyfish *Stomolophus meleagris* (Agassiz, 1862), in the estuarine
95 ecosystem of Malaga Bay, an area of high biodiversity in the Colombian pacific coast. This
96 species is widely distributed in the western Atlantic (United States to Brazil) and the Pacific
97 oceans (southern California to Ecuador; Sea of Japan to South China Sea) (Calder, 1982; Griffin
98 & Murphy, 2011) and has been described as a specialized predator of fish eggs, copepods and
99 mollusc larvae, with the capacity to regulate local populations of its prey (Larson, 1991).
100 Therefore, the aims of this study were (i) to assess changes in the structure of the diet in the study
101 area and (ii) analyse the traits, diversity and significance of the symbiotic associations in the
102 estuarine ecosystem.

103 **Materials & Methods**

104 Sampling

105 The study was performed in Málaga Bay, a south-facing bay located in the central region of the
106 Colombian Pacific coast (4°05´ N and 77°16´ W). The bay is located within the Chocó-Darien
107 region, one of the rainiest places in the western hemisphere (7,000–11,000 mm; Poveda,
108 Jaramillo & Vallejo, 2014), which has two wet seasons during the year: April-June and
109 September-November. The water depth in this bay averages 13 m but reaches a maximum of 40
110 m. Tides are semi-diurnal, with a tidal range of 4.1 m. Sea surface temperature varies between 25
111 and 30 °C and salinity between 19 and 28 in the mouth of the bay and 1.3 and 10 close to small
112 rivers (Lazarus and Cantera 2007). Sampling of *S. meleagris* was conducted around La Plata
113 Archipielago, at the innermost part of Málaga Bay. Samplings were allowed by the National
114 Autority (permission number 1070_28-08-2015). The medusoid phase showed a seasonal
115 occurrence in surface waters: December 2015 to May 2016 (hereafter season 1) and December
116 2016 to April 2017 (hereafter season 2). Sampling effort was relatively constant throughout the
117 seasons: when medusae were detected, three or four 3-hour sighting trips were performed per
118 month. Medusae were sampled from a small boat using dip nets, and the relative abundance was
119 estimated as the number of caught medusae per hour. As medusas where generally associated to
120 juvenile fish or invertebrates the sampling was limited to 15 to 20 medusae per month, to avoid
121 disturbing populations of fish potentially under conservation. Upon collection, medusae
122 discharged a sticky mucus that rapidly killed fish or associated invertebrates as reported by
123 Shanks & Graham (1988). Thereafter, medusae and their associated fauna were tagged and stored
124 in individual jars with 5% borate buffered formaldehyde solution in seawater.

125 In the laboratory, the bell diameter of each medusa and the standard length of associated fish and
126 invertebrates (crustaceans and molluscs) were measured using callipers. The medusa´s fused oral
127 arms and the mouth folds were excised and rinsed through a 100-µm mesh sieve to concentrate
128 food particles. The resulting material was transferred to ethanol and sorted for the presence of
129 prey items using a dissecting microscope. Prey items were determined to a taxonomic level
130 suitable for making meaningful comparisons with similar studies.

131 Associated fish were identified to species according to current keys and by comparison of their
132 morphological features against available descriptions (Jordan & Evermann 1898; Allen &
133 Robertson 1994; Fischer *et al.*, 1995, Chirichigno & Cornejo, 2001, Robertson & Allen, 2005).
134 Molluscs and crustaceans were sent to taxonomic experts for identification. Finally, all the
135 associated fauna was stored as reference material in the scientific collection at the Marine
136 Biology section at Universidad del Valle.

137 Data analyses

138 In order to understand spatial and temporal patterns in the occurrence of medusae, we compiled
139 published studies reporting temporal changes in the abundance of *S. meleagris* along the Atlantic
140 and the Pacific coast of North, Central and South America. Studies were classified as "inshore"
141 (inlets, estuaries, coastal lagoons) or "offshore" according to the type of environment where
142 samples were taken.

143 A multivariate approach was used to test changes in the structure (composition and abundance) of
144 the diet over time. For this, data were arranged in a matrix of abundance of each taxon (rows)
145 eaten by individual medusae in each month (columns). Prey taxa with few occurrences (< 0.1%

146   of total abundance; Table 1), were excluded from further analyses. Prior to the analyses data were
147   standardized to account for the difference in food quantity associated to distinct medusae body
148   sizes, by dividing the abundance of each prey item by the total abundance of prey for each
149   medusa. Moreover, data were square root transformed to slightly downweigh the contribution of
150   abundant food items.

151   Non-metric multidimensional scaling (nMDS; Clarke & Gorley 2006) was used to build an
152   ordination plot of medusae per month and season calculated from a Bray–Curtis matrix of
153   similarity in diet composition. The distance-based permutational multivariate analysis of variance
154   (PERMANOVA, Anderson 2001) was used to test for temporal differences in the structure of diet
155   between months and seasons. The model used "month" as a random factor nested within the fixed
156   factor "season". As the PERMANOVA approach is sensitive to differences in multivariate
157   dispersion within groups, the PERMDISP routine was used to test for homogeneity of
158   dispersions. Thereby, a preliminary analysis showed that multivariate dispersion was strongly
159   dependent of sample size, with less dispersion observed at the beginning of the season, when
160   medusae were scarce in the field and thus sample size was smaller. Therefore, samples from
161   December 2015 (N=2) January 2015 (N=2) and January 2016 (N=5) were excluded from the
162   analysis. Finally, when temporal differences were confirmed by the PERMANOVA, a Canonical
163   Ordination of Principal Coordinates (CAP, Anderson & Wills 2003) was used as a constrained
164   ordination that best defines groups (months) according to the diet structure.

165   To assess if the body sizes of medusae and their symbionts are related, length data were fitted to
166   linear, polynomial, logarithmic, exponential and power models. The best fit was chosen
167   according to the proportion of variance explained. Models were fitted by least squares procedures
168   using the algorithm Levenberg-Marquardt to estimate standard errors (SE) of the parameters.
169   Finally, we performed a literature review of the reported symbiotic fauna for *S. meleagris* to
170   compare the diversity of associations found in the study area. The terms "*Stomolophus*" and
171   "*Stomolophus meleagris*", excluding the terms "venom", "protein" and proteomics" from the title
172   or in combination with "association", "symbiosis" or "relationship", were used to search the ISI
173   Web of Science database and Google Scholar. The resulting literature was then manually scanned
174   for descriptions of symbiotic relationships

175   **Results**

176   1. Jellyfish seasonality

177   Two scyphozoan jellyfish were found during this study: *S. meleagris* and *Pelagia noctiluca*. The
178   latter was found only occasionally; one individual during season 1 and six during the season 2.
179   Such a small sample size circumvents any quantitative analysis and therefore only descriptive
180   details will be given. The relative abundance of *S. meleagris* consistently showed a unimodal
181   pattern with peaks during March or April (Fig. 1). Moreover the body did not show a consistent
182   pattern of growing or decreasing size over time.

183   2. The dynamics of food consumption by *S. meleagris*

184   The composition and abundance of food items consumed by *S. meleagris* is shown in Table 1.
185   The diet was prevalently comprised of bacillariophyte algae, copepods and fish early stages.
186   Small amounts of benthic items (e.g., juvenile polychaetes, amphipods and adult *Emerita* sp)
187   were found frequently and suggest that *S. meleagris* feeds near the bottom. A few nematods,
188   typically jellyfish parasites, were also found but included as food items because they were not

189 buried in the host's tissue, as observed by Phillips & Levin (1973), and showed obvious signs of
190 digestion.

191 Between-month differences in diet composition were apparent form the nMDS ordination (Fig.
192 2), particularly when the same month from different seasons were compared (e.g. March in each
193 season). However, as the PERMDISP test was significant for the factor "month" ($F_{9,111}$ = 4.242;
194 $P_{(perm)}$ = 0.006), a PERMANOVA might yield misleading results. To circumvent this problem,
195 months with small sample sizes (N$\leq$ 5) were excluded (PERMDISP test not significant: month:
196 $F_{6,105}$ = 2.183; $P_{(perm)}$ = 0.066; season: $F_{1,110}$ = 1-734; $P_{(perm)}$ = 0.211).

197 The PERMANOVA analysis (Table 2A) showed significant differences in the structure of the diet
198 of *S. meleagris* among months ($P_{(perm)}$=0.001) but not between seasons ($P_{(perm)}$=0.134). Pair-wise
199 comparisons (Table 2B) revealed between-months differences, which were best illustrated by the
200 CAP constrained ordination (Fig. 3A). Moreover, the CAP analysis showed that the temporal
201 changes in consumption of a few food items, among the more abundant in gut contents (Table 1),
202 were highly correlated with the axes illustrating the multivariate pattern (Fig. 3B).

203 3. Traits and diversity of the biological associations

204 The body size of the 121 collected *S. meleagris* ranged between 12.1 and 109.2 mm in bell
205 diameter. The prevalence of symbiotic associations (i.e., the percentage of medusa harbouring
206 symbionts) was high, with 50.4% of the collected specimens. With only three exceptions, a single
207 symbiont per medusa was found, clearly indicating that the distribution of symbionts among host
208 was not random but uniform. The symbiotic community of *S. meleagris* was composed of fishes
209 (95.3%), crustaceans (3.1%) and molluscs (1.6%) (Table 4). Generally, associated fish reacted to
210 disturbance by hiding within oral arms or below the bell´s host; it could be said that fish "resist
211 efforts to separate them", as stated by Hargit (1905). However, the prevalence of symbiotic
212 association might have been underestimated, because some may have escaped during the
213 sampling. Regularly only one symbiont per host was found, with only three exceptions, where
214 two fish per medusa where observed. *P. noctiluca* also had symbiotic associations: two out of six
215 medusae harboured individual fish (*Hemicaranx zelotes*).

216 The body size of the scyphozoan *S. meleagris* showed a significant positive correlation with the
217 body size of its symbiotic community as a whole, the fish assemblage and *H. zelotes* in particular
218 (Fig. 4; Table 3). Power models best fitted the positive body size relationships, and the model
219 including only *H. zelotes* had the highest proportion of variability explained (0.634). This
220 partially reflects the fact that *H. zelotes* was the most common symbiont of *S. meleagris*. Figure 4
221 shows that the symbionts were generally smaller than the host. However, less frequent symbionts
222 did not follow that pattern; for instance, *Centropomus medius*, *Lutjanus guttatus*, *Oligoplites*
223 *altus*, *Selene brevoortii* and *Gerres similimus* were larger, and *Hyporhamphus snyderi* almost
224 twice as large as its host.

225 The richness of the symbiotic fauna reported for *S. meleagris* in the study area was unexpectedly
226 high: 11 species, 10 of them being new reports of symbionts for this species. This richness
227 represents 39.2 % of the total diversity of associations found so far (28 symbiotic species
228 reported; Table 4) for this widely-distributed scyphozoan jellyfish.

229 **Discussion**

230 The occurrence of *S. meleagris* in the study area showed a consistent seasonal pattern that
231 coincides with the seasonal increase in the sea surface temperature from January to May in the
232 study area (IDEAM, 2004). The body size did not show an increasing trend through the seasons.

233 This suggest that the observed medusae did not recruit from local benthic polyps, but arrive to the
234 estuarine system as adults from adjacent areas, as discussed by Kraeuter & Seltzer (1975) for S.
235 meleagris in Georgian and North Carolina waters.

236 There are only three published studies on feeding ecology of *S. meleagris*. Taken together, these
237 studies highlight that a few taxa form a high percentage of the total gut content. Larson (1991)
238 found that in the north-eastern Gulf of Mexico 98% of *S. meleagris* diet was composed of bivalve
239 veligers, tintinnids, copepods, gastropod veligers and Oikopleura (Appendicularia). In the Gulf of
240 California, off the coast of Sonora, gut contents were dominated by fish eggs (ca. 83% in a study
241 by Padilla-Serrato *et al.*, 2013; and ca. 59% in a study by Álvarez-Tello, López-Martínez, &
242 Lluch-Cota, 2016), followed by mollusc larvae (~26%) and copepods (~11%) (Álvarez-Tello,
243 López-Martínez, & Lluch-Cota, 2016). Although our results (Table 1) also show that a few items
244 comprise high percentages of the diet, the composition and relative importance of those items
245 varied strongly among studies, suggesting strong spatial-temporal differences in food
246 composition. The main difference with previous studies is the consistency of Bacillariophyta
247 among ingested items, surprising for a scyphozoan considered carnivore. However, finding an
248 ingested item does not mean that it is digested, which is one general limitation of studying
249 feeding patterns of jellyfish by gut contents (Pitt, Connolly & Meziane, 2009). As
250 Bacillariophyceae (*Nitzschia*) and Coscinodiscophyceae (*Coscinodiscus, Rhizosolenia*) are
251 among the most abundant phytoplankton components in Málaga Bay (Prahl, Cantera &
252 Contreras, 1990), it seems reasonable to apply Ockham´s principle and assume that the presence
253 of algae in gut contents only reflect their abundance in the water column. Interestingly, Larson
254 (1991) also states that "*Coscinodiscus* sp. was abundant in gut contents" but it was not listed as
255 prey taxa. It is worth noting that the assumption that jellyfish feed on mesozooplankton and
256 ichthyoplankton is probably related with the essentially arbitrary use of 60-100 μm sieves to
257 concentrate the samples for gut content analysis. In fact, when complementary methods like
258 grazing experiments, microvideographic techniques, stable isotopes and fatty acid tracers are
259 used it becomes apparent that jellyfish can also feed on microzooplankton (Sullivan & Gifford,
260 2004; Colin *et al.*, 2005), demersal zooplankton (Pitt *et al.*, 2008) and resuspended organic matter
261 (Javidpour *et al.*, 2015). Therefore, our results should be regarded as a partial depiction of the
262 diet composition of *S. meleagris*.

263 As body size of *S. meleagris* did not show a consistent pattern of growth over time (Figure 1), the
264 intra-season variability observed in the structure of the diet could not be attributed to ontogenetic
265 changes in food habits. In fact, the diet composition of the on average smaller and larger medusae
266 observed in December 2015 and January 2016, respectively, (Fig. 1), was very similar (Fig. 2).
267 Therefore, the observed intra-season variability might be related with changes in the availability
268 of prey in the water column, but information to evaluate this hypothesis is lacking.

269 The lack of significant differences in the diet structure of *S. meleagris* between seasons was
270 surprising because the first medusoid season coincided with the major El Niño-La Niña cycle
271 2015-2016. It is known that the strong modification of freshwater nutrient subsidies through
272 precipitation in Málaga Bay drives changes in the population dynamics and reproductive cycle of
273 benthic estuarine bivalves (Riascos 2006; Riascos, Heilmayer & Laudien, 2008). Hence, it would
274 be reasonable to expect shifts in the abundance and composition of the zooplankton community
275 associated to El Niño-La Niña during the first season, which would be then reflected in
276 significant changes in the diet structure of *S. meleagris* between seasons. It is difficult to
277 speculate on reasons for this result, but perhaps El Niño-La Niña modified the composition of the
278 zooplankton community at lower taxonomic levels (e.g., species, families), which we were not
279 able to detect owed to our categorization of prey items at higher taxonomic levels (Table 1).

280 Marshes, mangrove forests and seagrass meadows have long been recognized as nursery grounds,
281 mainly because they have extremely high primary and secondary productivity and support a great
282 abundance and diversity of early life stages of fish and invertebrates (Beck *et al.*, 2001).
283 Recently, Doyle *et al.*, (2014) analysed the role of jellyfish as "service providers" in pelagic
284 habitats and described jellyfish as habitat and nurseries, because they are: (i) larger than most
285 planktonic organisms, (ii) slower swimmers than most nektonic animals and (iii) their diverse
286 morphology provide three-dimensional space for refuge or shelter. Clearly those facts alone do
287 not meet the premise that "a habitat is a nursery for juveniles of a particular species if its
288 contribution per unit area to the production of individuals that recruit to adult populations is
289 greater, on average, than production from other habitats in which juveniles occur" (Beck *et al.*,
290 2001). Strictly speaking, this is a hypothesis remaining to be tested, though some of our results
291 suggest that *S. meleagris* occurring in estuarine systems provide a valuable resource that may
292 significantly increase the survivorship and recruitment of juvenile fishes or invertebrates. First,
293 the great dominance of *H. zelotes* among a diversity of other symbionts suggest a higher
294 suitability to its host. This is in line with the fact that fish of the family Carangidae are the most
295 commonly reported symbiont of *S. meleagris* (Table 4). Secondly, the high prevalence of an
296 association and a uniform distribution of the symbiont within the host population as those
297 observed for *H. zelotes* and *S. meleagris* strongly suggest intraspecific and interspecific
298 interactions and territorial behaviour (Conell, 1963; Britayev *et al.*, 2007; Riascos *et al.*, 2011).
299 And thirdly, positive symbiont-host size relationships, as those observed when *H. zelotes*, the fish
300 assemblage and the whole symbiotic assemblage are analysed, suggest either parallel growth of
301 the host and the symbiont (Britayev & Fahrutdinov, 1994) or size-segregation behaviour by the
302 symbiont (Adams, Edwards & Emberton, 1985; Hobbs & Munday 2004).

303 Ecological theory predicts that competition and the "economic defendability" of a resource
304 (*sensu* Brown, 1964) facilitate or hinder the evolution of territoriality; resources are monopolized
305 whenever the benefits exceed the costs of defence. Individuals of a territorial species that fail to
306 obtain a limited resource often make no contribution to future generations (Begon, Harper &
307 Townsend, 2006). For jellyfish-fish associations, there is correlational data suggesting that the
308 shelter and/or food provided by jellyfish increase the survival of juvenile fish to adulthood
309 (Lynam & Brierley, 2007). In this context, if the seasonal occurrence of *S. meleagris* does
310 represent a defendable resource, and the influence on the survival of its symbiotic fauna could be
311 experimentally demonstrated, this species may be considered a floating nursery.

312 According to Castro, Santiago & Santana-Ortega (2001) 333 species of fish belonging to 96
313 families show aggregative or associative behaviour with floating algae, gelatinous zooplankton,
314 whales, flotsam or man-made fish aggregating devices and 14 of these families associate with
315 jellyfish. Therefore, one may reasonably argue that if the jellyfish-fish association have a
316 measurable effect on fish populations, it can be considered marginal. But, how complete is our
317 knowledge of these associations? Regarding *S. meleagris*, Table 4 hints on this question. First of
318 all, it shows that only a few areas of the species distribution range have been studied, particularly
319 the western coast of United States and the Gulf of Mexico. Second, and more importantly, the
320 fact that the findings of our short-term study performed in a small tropical estuarine system
321 represent ca. 40% of the known diversity of the symbiotic fauna of *S. meleagris* strongly suggest
322 that diversity of symbionts increase toward tropical areas and that it is heavily underestimated.
323 Indeed, the seven-year monitory of the bycatch in the trawl fishery of *S. meleagris* off Georgia by
324 Page (2015), rendered 38 species of finfish and 3 species of invertebrates. Of course, these cannot
325 per se be assumed to be symbionts of *S. meleagris*. But the fact that three species known to be
326 common associates (*Peprilus paru*, *P. triacanthus* and *Chloroscombrus chrysurus*; Phillips,

327 Burke & Keener, 1969; Rountree, 1983) comprised 63% of the bycatch strongly suggest that
328 some of the other species may actually be unrecognised symbionts.

Conclusion

330 The patterns of food consumption described here represent the trophic spectrum within a size
331 range of food particles, during a stage of the ontogenetic development of *S. meleagris*. A
332 complete depiction of prey should consider sampling at larger spatial and temporal scales and
333 complementary methods to identify the contribution of different food sources. The study of
334 symbiotic fish-jellyfish associations need to move beyond listing accounts of associations and use
335 experimental approaches to evaluation of their ecological significance; this may provide a more
336 balanced view of the relationship between fish and jellyfish in marine ecosystems.

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340 identifying crustaceans and molluscs, respectively.

Figures

342 Figure 1. Monthly variability of bell diameter (grey bars) and relative abundance (black lines) of
343 *Stomolophus meleagris* in La Plata Archipielago (Málaga Bay, Colombia) during two medusoid
344 seasons A) December 2015-May 2016; B) December 2016-May 2017

345 Figure 2. nMDS ordination plot on the diet composition of *Stomolophus meleagris* calculated
346 from Bray-Curtis dissimilarity measures with square-root transformed data of abundance per food
347 item during two medusoid seasons (December 2015-May 2016 and Jan 2017-Apr 2017)

348 Figure 3. Constrained Canonical Analysis of Principal Coordinates of the diet composition of
349 *Stomolophus meleagris* calculated from Bray-Curtis dissimilarity measures with square-root
350 transformed data of abundance per food item during two medusoid seasons (December 2015-May
351 2016 and Jan 2017-Apr 2017)

352 Figure 4. Body size relationships between *Stomolophus meleagris* and its symbiotic fauna. Lines
353 represent the model fits for *Hemicaranx zelotes*, fishes and the whole symbiotic community.
354 Parameter estimations and associated statistics for each model are given in Table 3. The dotted
355 lined circle represents a *H. zelotes,* excluded from the analysis, as its association to the respective
356 medusa could not be confirmed with certainty.

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Composition and mean abundance (number of food item per medusa and standard error in brackets) of food items in gut contents of *Stomolophus meleagris* during two seasons in Bahía Málaga, Pacific coast of Colombia.

Table 1. Composition and mean abundance (number of food item per medusa and standard error in brackets) of food items in gut contents of *Stomolophus meleagris* during two seasons in Bahía Málaga, Pacific coast of Colombia.

Food ítem	Season 1 (2015-2016)						Season 2 (2017)				Tot.	Rel. Ab (%)
	Dec	Jan	Feb	Mar	Apr	May	Jan	Feb	Mar	Apr		
Bacillariophyta: Coscinodiscophyceae	0 (0)	1.5 (2.1)	6.2 (9.4)	12.1 (30)	9.6 (13.2)	1.9 (4.9)	1.6 (1.9)	0.6 (0.7)	0.2 (0.5)	1.7 (3.9)	561	18.1
Arthropoda: Copepoda	37.5 (14.8)	4 (5.7)	5.5 (4.8)	3.2 (3.1)	6.1 (13.8)	1.8 (1.9)	2.4 (3.8)	0.9 (1.5)	0.7 (1)	3.4 (5.2)	444	14.3
Bacillariophyta: Bacillariophyceae	0.5 (0.7)	14.5 (7.8)	7.8 (15.6)	1.7 (5.2)	3.7 (6)	2.9 (5.9)	1.6 (1.7)	1.6 (2.5)	1.3 (2)	5.4 (8.1)	395	12.8
Chordata: Fish (eggs & larvae)	1 (0)	6 (1.4)	3.1 (3.8)	3.6 (4.1)	3.2 (6.2)	3.9 (10.6)	0.6 (1.3)	1.9 (2.5)	0.7 (1.3)	2.1 (2.7)	308	9.9
Arthropoda: Crustacea	0 (0)	0 (0)	0.9 (3.3)	0.7 (2.3)	2.7 (4.1)	1.8 (2.2)	1.6 (1.5)	1.8 (3.2)	4.3 (3.2)	5.4 (3.7)	286	9.2
Mollusca: Bivalve larvae	0 (0)	2 (2.8)	2.2 (2.8)	3.7 (5)	1.9 (4.3)	0.8 (1.4)	1 (1)	2.5 (2.5)	0.6 (0.8)	2.8 (3.3)	229	7.4
Mollusca: Gastropod larvae	0 (0)	6.5 (9.2)	3.4 (4.7)	1.9 (3.7)	1.4 (2.3)	0.7 (1.5)	0 (0)	3.2 (3.4)	0.5 (1.4)	0.2 (0.4)	193	6.2
Arthropoda: Cirripedia larvae	1 (0)	0 (0)	0.8 (1.3)	0.5 (1.1)	1.5 (2.4)	0 (0)	0.6 (0.5)	1.3 (1.9)	0.3 (0.8)	0.3 (0.7)	88	2.8
Chaetognatha: Sagittoidea	1 (1.4)	0 (0)	0.2 (0.8)	0.7 (1.3)	1.3 (2.1)	0.5 (1.2)	2.6 (2.4)	0.4 (0.9)	0 (0.2)	0.3 (0.7)	75	2.4
Ciliophora	0 (0)	0 (0)	0 (0)	0 (0)	0.6 (1.6)	0 (0)	6.4 (14.3)	0 (0)	0 (0)	0 (0)	46	1.5
Annelida: Polychaeta larvae/juvenile	0 (0)	0 (0)	0.1 (0.3)	0.3 (1)	0.1 (0.3)	0.2 (0.8)	0.4 (0.5)	0.3 (0.7)	0.4 (0.8)	0.3 (0.7)	31	1.0
Arthropoda: Brachiuran larvae	0 (0)	1 (1.4)	0.5 (0.9)	0.1 (0.3)	0.2 (0.7)	0.2 (0.6)	0 (0)	0.3 (0.4)	0.1 (0.3)	0.1 (0.3)	25	0.8
Nematoda	0 (0)	0 (0)	0 (0)	0.1 (0.5)	0 (0.2)	0.3 (0.6)	0.2 (0.4)	0.4 (0.7)	0.2 (0.5)	0 (0)	19	0.6
Arthropoda: Amphipoda	1 (1.4)	0 (0)	0 (0)	0 (0)	0 (0.2)	0 (0)	0.2 (0.4)	0 (0)	0 (0.2)	0.3 (1)	8	0.3
Arthropoda: Decapoda (*Emerita* sp)	0 (0)	0 (0)	0 (0)	0 (0)	0.2 (0.5)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	4	0.1
Unidentified	5.5 (2.1)	11.5 (6.4)	4.5 (4.6)	4.3 (4)	2.2 (3.4)	3.2 (4.8)	4.8 (3.8)	3 (2.9)	2.5 (3.1)	0.6 (0.9)	386	12.5
Average number of prey items	47.5 (9.3)	47 (4.5)	35.2 (2.6)	32.8 (3.1)	34.7 (2.6)	18.3 (1.3)	24 (1.8)	18.2 (1.1)	12 (1.1)	23.1 (1.9)	29.3	

Analysis of the differences in the structure of the diet of *Stomolophus meleagris*.

(A) the PERMANOVA analysis on the differences in the structure of the diet among months and seasons. (B) pair-wise tests for differences between pairs of months in each season. Significant factors (α = 0.05) are highlighted in bold.

Table 2. Results of A) the PERMANOVA analysis on the differences in the structure of the diet of *Stomolophus meleagris* among months and seasons and B) pair-wise tests for differences between pairs of months in each season. Significant factors ($\alpha = 0.05$) are highlighted in bold.

A	Source	df	SS	MS	Pseudo-F	P(perm)	Unique perms
	Season	1	10841	10841	2.2673	0.134	917
	Month(season)	5	24981	4996	2.4719	**0.001**	998
	Res	105	212230	2021			
	Total	111	249810				
B	Months		Season		T	P(perm)	perms
	February, March		1		1.440	0.077	999
	February, April		1		1.427	0.087	999
	February, May		1		1.395	0.083	998
	March, April		1		1.717	**0.017**	999
	March, May		1		1.510	**0.041**	999
	April, May		1		0.982	0.486	997
	February, March		2		2.101	**0.004**	999
	February, April		2		1.830	**0.016**	998
	March, April		2		1.270	0.151	999

Results of the model fitting procedure on the relationship of the body size of *Stomolophus meleagris* and its symbionts.

Pr.Var.: proportion of variability explained by the model.

Table 3. Results of the model fitting procedure on the relationship of the body size of *Stomolophus meleagris* and its symbionts. Pr.Var.: proportion of variability explained by the model.

Associates	Model	a (SE)	b (SE)	Pr. Var.	F-value	p
Fish	$Y=aX^b$	1.551 (1.202)	0.809 (0.189)	0.291	134.763	<0.001
All	$Y=aX^b$	1.775 (1.371)	0.775 (0.189)	0.269	138.378	<0.001
H. zelotes	$Y=aX^b$	1.204 (0.486)	0.830 (0.098)	0.634	412.441	<0.001

List of published reports on symbionts associated to the cannonball jellyfish *Stomolophus meleagris*.

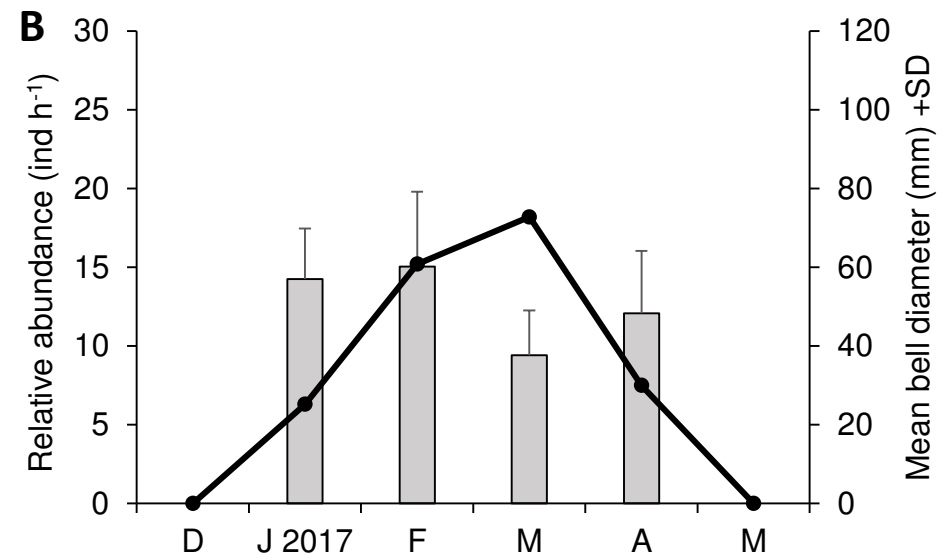
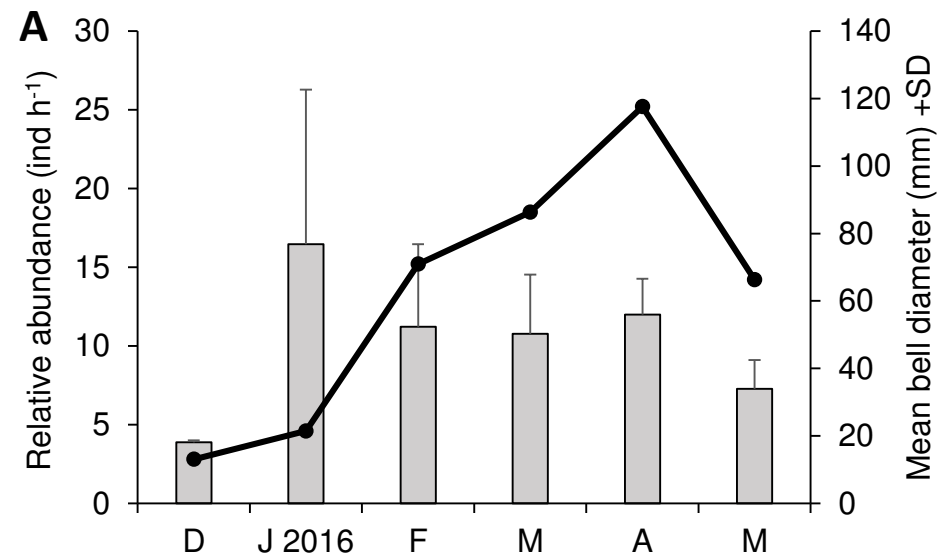
An unidentified cestode larva was reported by Phillips & Levin (1973), though it is not included in the list.

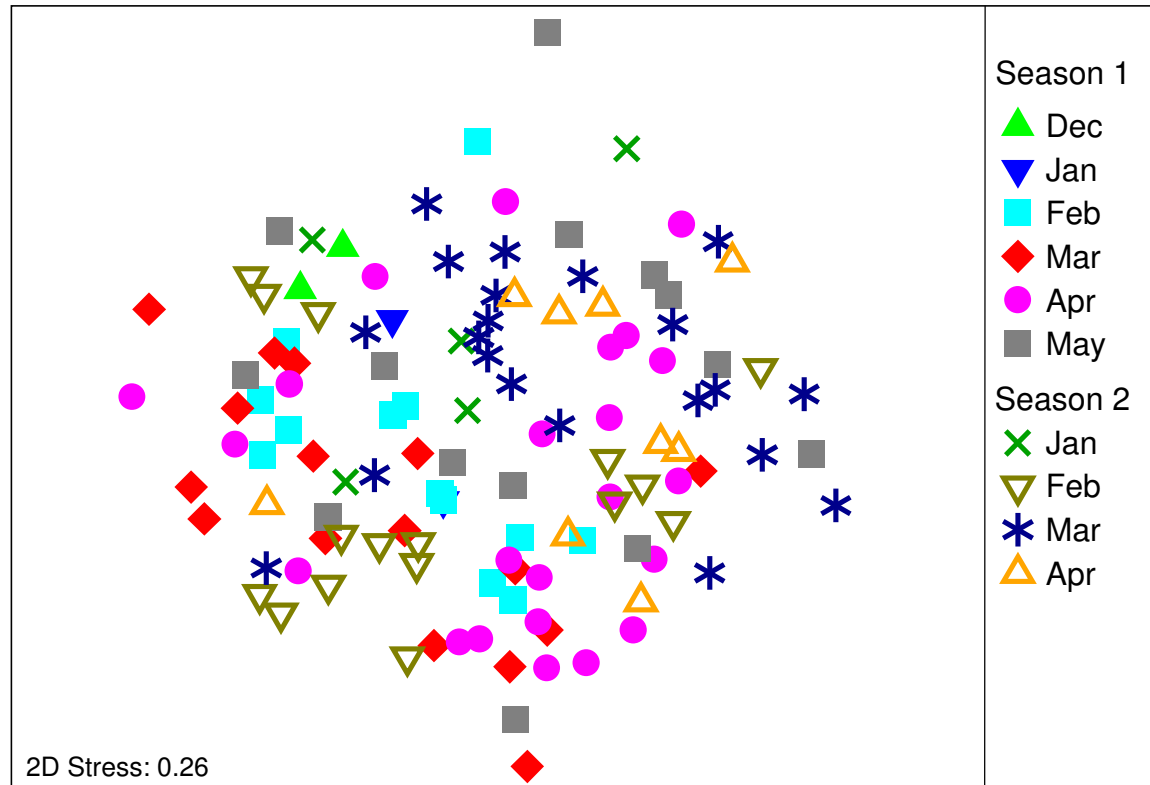
Table 3. List of published reports on symbionts associated to the cannonball jellyfish *Stomolophus meleagris*. An unidentified cestode larva was reported by Phillips & Levin (1973), though it is not included in the list.

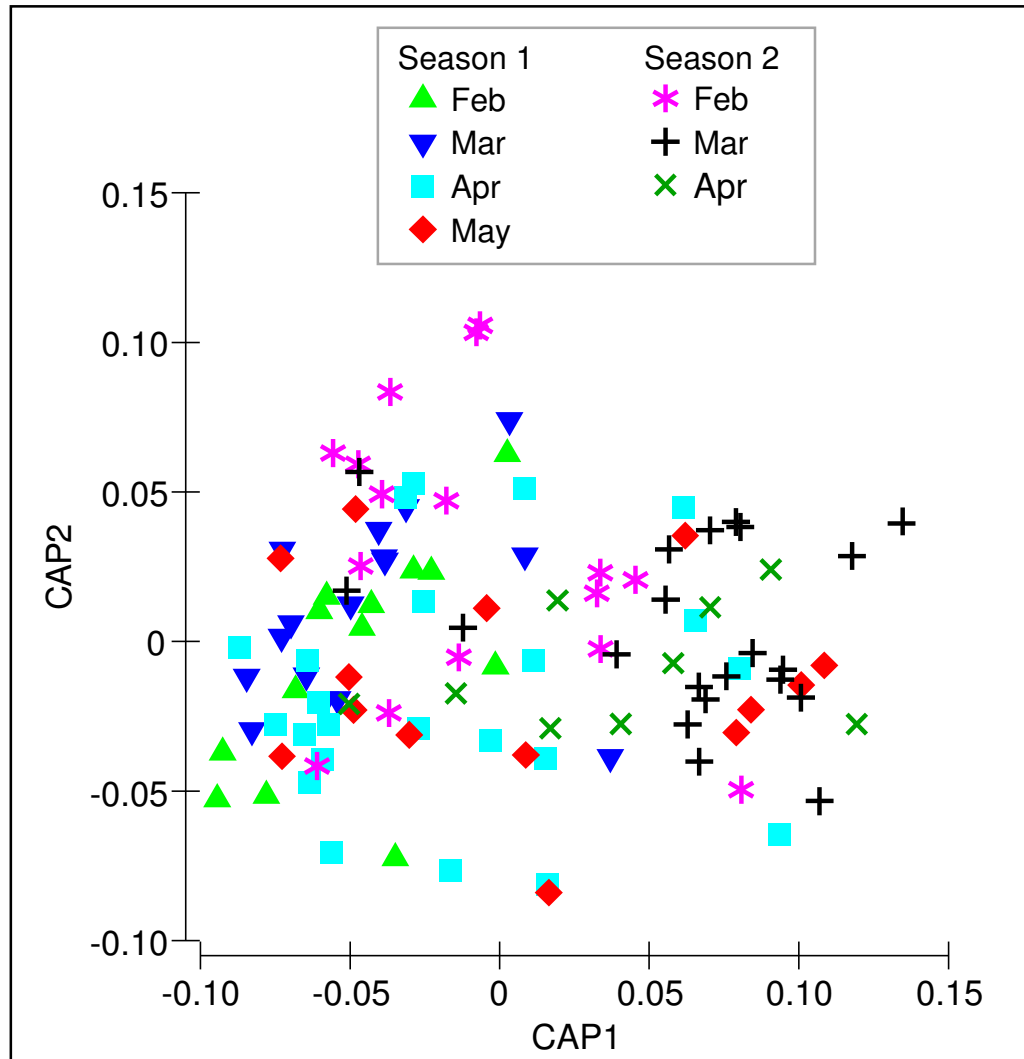
Class: family	Species	Locality and literatura source
Actinopterygii: Carangidae	*Chloroscombrus chrysurus* (Linnaeus, 1766)	Mississippi Sound, Mississippi, USA (Phillips et al. 1969)
		Wrightsville Beach, North Carolina, USA (Rountree, 1983)
		Onslow Bay, North Carolina, USA (Shanks & Graham, 1988)
		Texas USA (Baughman, 1950)
	Chloroscombrus orqueta Jordan & Gilbert, 1883	Málaga Bay, Pacific coast, Colombia (new report)
	Hemicaranx amblyrhynchus (Cuvier, 1833)	Western Golf of Mexico, USA & Mexico (Hildebrand, 1954)
	Hemicaranx zelotes Gilbert, 1898	Kino Bay, Sonora, Mexico (López & Rodríguez, 2008)
		Málaga Bay, Pacific coast, Colombia (This study)
	Caranx crysos (Mitchill, 1815)	Barataria Bay, Louisiana, USA (Gunter, 1935)
	Caranx hippos (Linnaeus, 1766)	Wrightsville Beach, North Carolina, USA (Rountree, 1983)
	Oligoplites altus (Günther, 1868)	Málaga Bay, Pacific coast, Colombia (new report)
	Selene brevoortii (Gill, 1863)	Málaga Bay, Pacific coast, Colombia (new report)
	Carangoides bartholomaei (Cuvier, 1833)	Wrightsville Beach, North Carolina, USA (Rountree, 1983)
Actinopterygii: Stromateidae	*Peprilus triacanthus* (Peck, 1804)	Wrightsville Beach, North Carolina, USA (Rountree, 1983)
		Beaufort, North Carolina, USA (Smith, 1907)
		Port Aransas, Texas, USA (Hoese et al. 1964)
		Western Golf of Mexico, USA & Mexico (Hildebrand, 1954)
		Gulf of Mexico, USA (Horn, 1970)
	Peprilus burti Fowler, 1944	Gulf of Mexico, USA (Horn, 1970)
	Peprilus paru (Linnaeus, 1758)	Mississippi Sound, Mississippi, USA (Phillips et al. 1969)
		Port Aransas, Texas, USA (Hoese et al. 1964)
Actinopterygii: Monacanthidae	*Stephanolepis hispida* (Linnaeus, 1766)	Mississippi Sound, Mississippi, USA (Phillips et al. 1969)
		Wrightsville Beach, North Carolina, USA (Rountree, 1983)
		Onslow Bay, North Carolina, USA (Shanks & Graham, 1988)
	Aluterus schoepfii (Walbaum, 1792)	Wrightsville Beach, North Carolina, USA (Rountree, 1983)

Actinopterygii: Nomeidae	*Nomeus gronovii* (Gmelin, 1789)	Woods Hole, Massachusetts, USA (Hargitt, 1905)
		Beaufort, North Carolina, USA (Smith, 1907)
		Japan & Hong Kong (Morton, 1989)
Actinopterygii: Atherinopsidae	*Atherinella argentea* Chernoff, 1986	Málaga Bay, Pacific coast, Colombia (new report)
Actinopterygii: Gerreidae	*Gerres simillimus* Regan 1907	Málaga Bay, Pacific coast, Colombia (new report)
Actinopterygii: Centropomidae	*Centropomus medius* Günther, 1864	Málaga Bay, Pacific coast, Colombia (new report)
Actinopterygii: Hemiramphidae	*Hyporhamphus snyderi*, Meek & Hildebrand, 1923	Málaga Bay, Pacific coast, Colombia (new report)
Actinopterygii: Lutjanidae	*Lutjanus guttatus* (Steindachner, 1869)	Málaga Bay, Pacific coast, Colombia (new report)
Malacostraca: Epialtidae	*Libinia dubia* H. Milne Edwards, 1834	Beaufort, North Carolina, USA (Gutsell, 1928)
		Mississippi Sound, Mississippi, USA (Phillips et al. 1969)
		South Carolina, USA (Corrington, 1927)
		Wrightsville Beach, North Carolina, USA (Rountree, 1983)
		Onslow Bay, North Carolina, USA (Shanks & Graham, 1988)
		Fort Pierce, Florida, USA (Tunberg & Reed, 2004)
	Libinia sp	Texas coast, USA (Whitten, Rosene & Hedgpeth, 1950)
	Libinia emarginata, Leach, 1815	Western Golf of Mexico, USA & Mexico (Hildebrand, 1954)
Malacostraca: Portunidae	*Charybdis (Charybdis) feriata* (Linnaeus, 1758)	Japan & Hong Kong (Morton, 1989)
Malacostraca: Penaeidae	*Penaeus stylirostris* Stimpson, 1871	Málaga Bay, Pacific coast, Colombia (new report)
Hexanauplia: Lepadidae	*Conchoderma virgatum* Spengler, 1789	Guaymas, Mexico (Álvarez-Tello et al. 2013)
Cephalopoda: Loliginidae	*Lolliguncula (Lolliguncula) panamensis* Berry, 1911	Málaga Bay, Pacific coast, Colombia (new report)
Cestoda: Otobothriidae	*Otobothrium dinoi* (Mendez, 1944) Palm, 2004	Cananéia, Sao Paulo, Brazil (Vanucci 1954)

Variability of body size and relative abundance of *S. meleagris*

Monthly variability of bell diameter (grey bars) and relative abundance (black lines) in La Plata Archipielago (Málaga Bay, Colombia) during two medusoid seasons A) December 2015-May 2016; B) December 2016-May 2017

nMDS ordination of the diet composition of *Stomolophus meleagris.*

nMDS calculated from Bray-Curtis dissimilarity measures with square-root transformed data of abundance per food item during two medusoid seasons (December 2015-May 2016 and Jan 2017-Apr 2017)

Constrained Canonical Analysis of Principal Coordinates (CAP) of the diet composition of *Stomolophus meleagris*

CAP calculated from Bray-Curtis dissimilarity measures with square-root transformed data of abundance per food item during two medusoid seasons (December 2015-May 2016 and Jan 2017-Apr 2017)

Body size relationships between *Stomolophus meleagris* and its symbiotic fauna.

Lines represent the model fits for *Hemicaranx zelotes*, fishes and the whole symbiotic community. Parameter estimations and associated statistics for each model are given in Table 3. The dotted lined circle represents a *H. zelotes,* excluded from the analysis, as its association to the respective medusa could not be confirmed with certainty.