Jellyfish as an alternative source of food for opportunistic fishes

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Abstract :

Although scientific interest on jellyfish ecology has substantially increased in the last decades, little is known on the role of potential predators shaping their population dynamics. Jellyfish were long considered as 'dead ends' within food webs, and therefore overlooked as potential food source for higher trophic levels, e.g. fishes. Here this question is tackled by using comprehensive laboratory experiments assessing fish predation on jellyfish. The approach included all the life stages (polyps, ephyrae and medusa) of *Aurelia* sp. versus more traditional aquaculture feeds in an easily farmed opportunistic fish, the gilthead seabream *Sparus aurata* (L.). Results revealed that all life stages of *Aurelia* sp. were accepted as a source of food by *S. aurata*, whose grazing pressure varies depending on the jellyfish life stage. Higher ingestion rates were observed on young stages (i.e. small medusa) indicating their higher vulnerability to fish predation and the potential negative impact this may have on *Aurelia* sp. population dynamics. These results provide new insights on the so far underestimated role fish predation can have on jellyfish population dynamics. In particular, opportunistic fish species, such as *S. aurata* may contribute to control jellyfish blooms, through top-down regulations of jellyfish biomass.

Highlights

► During bloom events, jellyfish might be a source of food for opportunistic fishes. ► All life stages of *Aurelia* sp. are used as a source of food by *Sparus aurata*. ► Higher ingestion rates of fish predation were observed on *Aurelia* sp. young stages. ► Opportunistic fish species might contribute to control jellyfish blooms.

50 **1. Introduction**

51 Jellyfish are ubiquitous components of marine food webs and acknowledged

52 indicators of ecosystem change (Richardson et al., 2009). In recent decades, however,

53 recurrent massive proliferations in temperate coastal waters (Brotz et al., 2012) warned

54 on dramatic consequences for the management of ecosystem assets, including fisheries

55 and tourism industries. Underlying mechanisms of jellyfish proliferations have been

56 ascribed to climate changes and anthropogenic disturbances in the marine environment,

57 i.e. mainly habitat modification and overfishing (Purcell, 2012; Richardson et al., 2009).

58 In addition, while high human population densities persist expanding in coastal areas,

59 the resulting anthropogenic stress continue fostering favorable conditions for jellyfish,

60 thereby challenging the sustainable management of coastal resources (Pauly et al., 2009;

61 Purcell et al., 2007; Purcell, 2012; Richardson et al., 2009).

62 Research on jellyfish ecology has long focused on bloom drivers (e.g. Purcell,

63 2005). However, little is known in regards to causes impairing blooms, i.e. jellyfish

64 mortality (Purcell and Arai, 2001), which is fundamental to understand their population

65 dynamics. In particular, jellyfish mortality during early life stages may have a major

66 effect on population recruitment, and subsequently on adults density (Lucas, 2001). For

67 instance, recent findings provided new insights on the role predation on polyps and

68 ephyrae may have on jellyfish outbreaks through enhancing jellyfish mortality (e.g. Ishii

69 et al., 2004; Takao et al., 2014).

70 Over decades, jellyfish were described as 'dead ends' in marine food webs,

71 because of their high water content and low nutritional value (e.g. 2.3-3.6 KJ.g.dry

72 mass^{-1} for *A. aurita*, Doyle et al., 2007), although gelatinous organisms are often

73 reported in lists of fish stomachs contents. For instance, some species, such as moon

74 fish (*Mola mola*) and butterfish (*Peprilus triacanthus*), are known to prey exclusively

on gelatinous zooplankton (Arai, 2005, 1988; Ates, 1988; Mianzan et al., 1996; Purcell and Arai, 2001). Also, in periods of massive proliferation, jellyfish are further suggested as a non-negligible source of energy for fishes (Arai, 2005; Arai et al., 2003; Cardona et al., 2012), however quantitative estimations on the impact of fish predation on jellyfish are rare (Cardona et al., 2012; Milisenda et al., 2014). Hence, to date the strength of the trophic linkage between fish and jellyfish is barely known.

This study sought to examine the trophic relationship between fish and jellyfish. To tackle this question laboratory experiments were performed to explore the intensity of predation of coastal harvested fish species on jellyfish. The jellyfish *Aurelia* sp. was used as prey model and *Sparus aurata* as predator. The main aim was to assess predation on different life stages of *Aurelia* sp., and their respective attractiveness as food sources, when compared to prey types used in aquaculture. Therefore, it was intended to answer three main questions: i) What is the ingestion rate of jellyfish prey?; ii) Is the ingestion of jellyfish prey items fostered by their high availability/concentration?; iii) Are jellyfish positively selected? The approach provides evidence that jellyfish are more important as food source for fish than previously thought.

2. Materials and Methods

The potential fish predation on jellyfish was investigated in laboratory conditions, bearing in mind the natural conditions occurring in the Thau lagoon, NW Mediterranean, 43°23'59.10'' N; 3°36'37.15'' E. This is a semi-enclosed brackish lagoon, which harbors a resident population of *Aurelia* sp. (Bonnet et al., 2012; Marques et al., 2015b), providing an ideal framework to understand the links between jellyfish and fish.

100   The gilthead seabream (*Sparus aurata*) is a common species in the northwestern

101   Mediterranean and the main target of commercial fishery in Thau lagoon, representing

102   at times up to 56.6% of total annual 'capéchade' catches (the most common fishing gear

103   in Thau lagoon) (Crespi, 2002). Irrespective of age, most of gilthead seabream spend

104   winter months at sea, where spawning occurs, and return to coastal lagoons around

105   April (Audouin, 1962; Mercier et al., 2012). Although some adults spend significant

106   amount of time in coastal lagoons (Mercier et al., 2012), in Thau Lagoon the population

107   of *S. aurata* is composed mainly by juveniles under maturity age (2-3 years, 27-33 cm

108   length; Lasserre, 1974 *in* Crespi, 2002). Moreover, gilthead seabream has been raised

109   for decades in aquaculture farms worldwide and its life history is therefore well known

110   (e.g. Moretti et al., 1999). All these criteria made it a particularly good candidate to

111   obtain homogeneous groups of individuals with similar size.

112   The experiments were performed at the IFREMER institute (Institut Français de

113   Recherche pour l'Exploitation de la Mer) in the research station of Palavas-les-Flots

114   (France), from April to June 2014. A total of 433 *S. aurata* were obtained from the 'Les

115   Poissons du Soleil' aquaculture farm. Two size classes were used in the experiments:

116   370 small individuals (Small Fish - SF: W of ca. 70 g; TL= 14-19 cm), and 63 large

117   individuals (Large Fish - LF: W of ca. 200 g; TL= 20-25 cm). Fishes were acclimated in

118   three 1500 L tanks filled with filtered sea water at 20-22°C. Every two days, fishes were

119   fed with commercial dry pellet food for sea bream (B-Nature, Le Gouessant) at 1% of

120   the fish biomass to meet their food requirements.

121   The predation on various prey items was compared. All preys were kept at

122   20±0.5°C. Live *Artemia* with about 1 cm length were collected in soft flats in Le Grau-

123   du-Roi and maintained in 60 L tank with air supply. Live *Aurelia* sp. ephyrae and small

124   medusae (Ø 1 cm) were obtained from 'Jellyfish Concept' company (Cherbourg,

125 France) and maintained in 15 L containers with air supply, fed with newly hatched

126 *Artemia*. Medium and large *Aurelia* sp. medusae (Ø 4 and 7-8 cm, respectively) and

127 colonies of *Aurelia* sp. polyps were collected in Thau Lagoon. Medium and large

128 medusae were collected with hand nets, while polyps, fixed on oyster or mussel shells,

129 were collected by SCUBA divers. They were all maintained in 60 L tanks with air

130 supply.

131 The experiment set up was composed by 24 separate tanks of 60 L (40 L of sea

132 water) with shared water and air supply, which ensure identical temperature and salinity

133 in all tanks. Experiments were performed at 20±0.5°C, since it is within the optimum

134 temperature range for *S. aurata* (Feidantsis et al., 2009) and it also corresponds to

135 temperatures at which blooms of *Aurelia* sp. occur in Thau lagoon (Bonnet et al., 2012;

136 Marques et al., 2015a). Photoperiod was determined according to field conditions at the

137 time of experiment (13 h of light and 11 h of dark period). As the maximum fish

138 biomass recommended in *S. aurata* aquaculture farms is of 7 $kg.m^{-3}$ (C. Pryzbyla pers.

139 comm.), all experiments were performed with three SF or two LF per tank. Before each

140 experiment, fishes were acclimated for four days in experimental tanks and maintained

141 in starvation to ensure that all individuals empty their stomachs.

142 This study consisted in three different experiments, using three replicates for

143 each treatment, the monospecific diets, the gradient of concentration and the selectivity

144 experiments (**Table 1**).

145

146 2.1. Monospecific diets

147 The main goal of the monospecific diets experiment was to compare *S. aurata*

148 ingestion rates for the various life stages of *Aurelia* sp. (polyps, ephyrae and different

149 sizes of medusae) with those for other types of food, live or not. As *S. aurata* were

150 acquired from aquaculture farms, dry pellets were used as control, since fishes were

151 previously reared with this diet. As the carbon content or dry weight of the prey items

152 was not determined, the comparison of the different prey items was performed

153 according to the concentration of prey per tank (item.tank^{-1}). Additionally, small,

154 medium and large medusae were also compared according to their weight, determined

155 according to theoretical calculations (Uye and Shimauchi, 2005).

156   The concentration of prey items in each treatment was calculated in order to

157 meet 1% of fish biomass of dry pellets in each tank. Therefore, in SF and LF treatments,

158 44 and 80 pellets.tank^{-1} were used, respectively. The same concentrations were then

159 used for *Artemia* and ephyrae, since they have equivalent dimensions (0.7-1 cm).

160   As small, medium and large medusae have considerably higher dimensions as

161 pellets, *Artemia* and ephyrae, these prey items were provided at lower concentrations:

162 50 and 1 prey item.tank^{-1} of small and medium medusae, respectively. Large medusa

163 was provided at the minimum possible concentration (1 prey item.tank^{-1}).

164   In order to mimic field conditions, one colony of polyps settled on oyster shell

165 was provided. Consequently, the initial concentration of this prey item was not

166 artificially fixed.

167

168   2.2. Gradient of concentration

169   The goal of the gradient of concentration experiment was to assess whether

170 *Aurelia* sp. ingestion could be proportional to its availability in the field. Based on the

171 results of the first feeding experiment, small medusae (Ø = 1 cm) were used for this test,

172 using six different treatments (with initial concentrations of 5, 10, 15, 30, 40 and 50

173 item.tank^{-1}) for both size classes of *S. aurata*.

174

175

176   2.3. Selectivity experiment

177   Selectivity experiments allowed the assessment of the influence of simultaneous

178 availability of high nutritional quality prey (crustacean) on the potential ingestion of

179 early life stages of *Aurelia* sp.. Therefore, two composite diets were supplied for both

180 SF and LF. Diet 1 was composed by ephyrae and *Artemia* with equal initial

181 concentrations, while diet 2 was composed by polyps and *Artemia* (**Table 1**). Total prey

182 concentrations were determined as previously described in monospecific diets

183 experiment section and equally distributed by the prey items (i.e. 0.5% for ephyrae and

184 *Artemia*)

185   The experiments were run for 2 h for all treatments, which is in accordance with

186 previous laboratory experiments on fish predation on jellyfish (Arai et al., 2003) and

187 allow an accurate estimation of ingestion rates, as further confirmed by a preliminary

188 test. Since the experiment time was short, control experiment to determine prey

189 mortality by predation from polyps/ephyrae was not required.

190   Prey items in each case were counted before and after the experiments, either by

191 direct visual observation (for larger medusae) or under a dissecting microscope after

192 filtering the water of the entire tank on a 200 μm mesh sieve. Polyps attached to oyster

193 or mussel shells were photographed with a Cannon PowerShot G16 camera at the

194 beginning and end of the experiment. Photographs were pre-treated with Adobe

195 Photoshop CS2 Version 9.0, in order to improve contrast and polyps were counted by

196 eye observation. In the end of the experiments, fishes were measured and weighted.

197

198   2.4. Calculations

199   Ingestion rate per gram of fish (I; prey item.g^{-1} fish.h^{-1}) was calculated according

200 to the equation:

$$I = ((Ci - Cf)/t.n)/m$$

Where Ci and Cf are the initial and final concentration (prey item.tank^{-1}) of prey in the water, respectively, t is the experiment duration (h), n is the number of fish in each experimental tank and m is the weight of each fish (g). The results are presented as the mean I of each treatment (i.e. three replicates).

Ingestion rates of small, medium and large medusae were also compared according to their wet weight. Medusa biomass (wet weight; WW) was calculated based on medusa bell diameter (BD; cm), according to the equation of Uye and Shimauchi (2005):

$$WW = 0.0748 \, BD^{2.86}$$

Corresponding ingestion rates in biomass (Im; g.g^{-1}fish.h^{-1}) were calculated, according to the equation:

$$Im=I*WW$$

The results are presented as the mean Im for each treatment (i.e. three replicates).

2.5. Statistical analysis

In monospecific diets experiments, differences in *S. aurata* ingestion rates among prey types were tested by Kruskal-Wallis test, followed by *post hoc* multiple comparison test by Dunn test, with Bonferroni correction ($\alpha < 0.0018$). The test of hypotheses explaining the *S. aurata* ingestion rates during the gradient of concentration experiment was done using a General Linear Model (GLM), including the initial prey concentration as predictor. Differences between SF and LF linear regressions of ingestion rates were tested with ANOVA test. Mann-Whitney-Wilcoxon test was performed to identify significant differences of ingestion rate between treatments in

226 selectivity experiments. All statistical analysis was performed using the software R

227 3.1.1 (The R Project for Statistical Computing 2014) and taking $\alpha < 0.05$ as the limit for

228 statistical significance.

229

230 **3. Results**

231 Predation activity was systematically observed during the feeding experiments

232 and occurred irrespective of *S. aurata* size class, the type of prey provided, and the tank.

233 Furthermore, in several treatments, all the provided prey was consumed within the two

234 hours of experiment, indicating the suitability of the experiment time.

235

236 3.1. Monospecific diets experiments

237 Predation activity on dry pellets (i.e. control) was consistently observed in all

238 experiments and occurred for both size classes of *S. aurata,* showing the suitability of

239 this type of food as control.

240 Both size classes displayed predatory activity over both benthic and pelagic

241 stages of *Aurelia* sp. life cycle (**Fig. 1**). Large medusae were not totally consumed by

242 any size class of fish, but bites on the edge of umbrellas were consistently observed. In

243 these cases though, the biomass of *Aurelia* sp. consumed by the fish was not

244 quantifiable with our protocol.

245 Ingestion rates for monospecific diets varied significantly according to the type

246 of prey offered, both for the SF (Kruskal-Wallis test, $p<0.01$) and for the LF (Kruskal-

247 Wallis test,$p<0.01$). Significant differences (Kruskal-Wallis test, $p < 0.05$) were

248 observed between the two size classes of *S. aurata*. The highest mean ingestion rates for

249 SF was obtained for small medusa (0.15 ± 0.03 prey item.g^{-1}fish.h^{-1}), polyps (0.14 ± 0.07

250 prey item.g^{-1}fish.h^{-1}) and *Artemia* (0.11 ± 0.00 prey item.g^{-1}fish.h^{-1}), while ephyrae

251 (0.05±0.02 prey item.g^{-1}fish.h^{-1}), medium (0.003±0.001 prey item.g^{-1}fish.h^{-1}) and large

252 medusa (no consumption) presented lower values (**Fig. 1**). The multiple comparison,

253 though revealed that only medium medusa and large medusa presented significant lower

254 values as control (Dunn *post hoc* test with Bonferroni correction, $p < 0.0018$), while the

255 remaining were not significantly different. For LF, *Artemia* (0.11±0.00 prey item.g^{-}

256 ^{1}fish.h^{-1}) and small medusa (0.07±0.00 prey item.g^{-1}fish.h^{-1}) were the most consumed

257 preys, followed by polyps (0.04±0.02 prey item.g^{-1}fish.h^{-1}), ephyrae (0.03±0.02 prey

258 item.g^{-1}fish.h^{-1}), medium (0.001±0.001 prey item.g^{-1}fish.h^{-1}) and large medusa (no

259 consumption). Significant lower values than dry pellets were only revealed by large

260 medusae (Dunn *post hoc* test with Bonferroni correction, $p < 0.0018$) (**Fig. 1**). Fish

261 predation on medium medusae of *Aurelia* sp. was limited, when considering the

262 quantity of individuals consumed, irrespective of fish life stage (**Fig. 1**). However, when

263 considering ingestion rates in terms of biomass, *Aurelia* sp. medusae of medium size (Ø

264 = 4 cm) proved to be at least as important as small ones as a source of food for *S.*

265 *aurata*. Indeed, because one medusae of 4 cm bell diameter provides approximately the

266 same wet weight of food (3.94 g) than 50 individuals with bell diameters of 1 cm (3.74

267 g), ingestion rates in terms of biomass were in fine similar between the two size classes

268 of *Aurelia* sp. medusae, irrespective of the fish size class (Dunn *post hoc* test, $p = 0.46$;

269 $p = 0.36$, for SF and LF respectively). It is worth noticing that the ingestion of *Aurelia*

270 sp. small and medium medusae was consistently higher (Kruskal-Wallis test $p < 0.05$) in

271 the SF fishes (0.0112 ± 0.002 and 0.0116 ± 0.003 g.g^{-1}fish.h^{-1}, respectively) than LF

272 (0.005 ± 0.000 and 0.004 ± 0.003 g.g^{-1}fish.h^{-1}, respectively), suggesting different food

273 preferences for this species according to the size class.

274

275

276   3.2. Gradient of concentration experiments

277   The results of ingestion rate obtained from the gradient of concentrations

278   experiment suggested that the predation of *S. aurata* on *Aurelia* sp. individuals in the

279   wild could be proportional to their availability, at least for the small medusae (**Fig. 2**).

280   The ingestion rates increased with increasing concentration supply, for both size classes,

281   showing a significant correlation ($p < 0.01$) and significant differences between the two

282   size classes of fish ($p < 0.01$). They reach the maximum value of 0.15 ± 0.03 prey item.g^{-}

283   ^{1}fish.h^{-1} for SF and 0.07 ± 0.00 prey item.g^{-1}fish.h^{-1} for LF, which represents the

284   ingestion of all available prey in the tank.

285

286   3.3. Selectivity experiments

287   Selectivity experiments showed that the attractiveness of *Aurelia* sp. as a prey

288   depended on both its life stage (benthic or pelagic) and that of the fish (SF or LF) (**Fig.**

289   **3**). Although the results indicate higher ingestion rates for *Artemia* in both diets for SF,

290   significant differences were obtained only when provided together with polyps

291   (Wilcoxon test, $p < 0.05$). For LF, *Artemia* was significantly selected when compared

292   with ephyrae (Wilcoxon test, $p < 0.05$). In diet 2, however, the reverse situation was

293   observed with the polyps presenting higher ingestion values (Wilcoxon test, $p < 0.05$),

294   despite the high variability in polyp ingestion rates among replicate tanks.

295

296   **4. Discussion**

297   The trophic interaction between fish and *Aurelia* sp. was assessed and found

298   novel insights on the so far underestimated role fish predation can have on jellyfish

299   population size. It is here hypothesised that oportunistic fish species, such as *S. aurata*

300   (Escalas et al., 2015; Pita et al., 2002), might take advantage of local peaks in *Aurelia*

301 sp. densities to partially sustain their growth. This study provide evidences that jellyfish

302 are not 'dead ends' of the food web, as they are actively predated when an alaternative

303 prey is not available, thereby favouring alternative energy pathways in food webs.

304   Both size classes of *S. aurata* feed on all life stages of *Aurelia* sp. offered as

305 prey. This predator is an opportunistic feeder which commonly adapts its diet to the

306 food resources available in its environment (Pita et al., 2002; Wassef and Eisawy, 1985)

307 and can therefore prey on *Aurelia* sp. during blooms events. In contrast with former

308 descriptions of the feeding preferences of this species (Escalas et al., 2015; Pita et al.,

309 2002), the results provide evidence of the active predation of *S. aurata* on jellyfish. In

310 line with this, several species of Sparidae family have been reported as jellyfish

311 consumers (Ates, 1988; Mianzan et al., 1996), stressing the aptness of *S. aurata* as

312 jellyfish predator.

313   The ingestion rates of both size classes of *S. aurata* varied significantly

314 according to the type of prey offered. Firstly, it is worth noticing the high consumption

315 of polyps by the SF. In the wild, younger individuals of *S. aurata* prey mainly on

316 epibenthic polychaetes, small fishes, crustaceans and gastropods (Escalas et al., 2015;

317 Tancioni et al., 2003), but with a clear dominance on bivalves in some habitats (Pita et

318 al., 2002). As the polyps of *Aurelia* sp. in the experiments were provided fixed on the

319 shells of living bivalves (oyster and mussel), it is possible that the actual target of fish

320 predation was the settling substrate, rather than on the polyps themselves. Anyhow,

321 bivalves are commonly colonized by polyps in the wild and particularly in Thau lagoon

322 (Marques et al., 2015b), where bivalves play a crucial role in the development of

323 *Aurelia* sp. benthic population. For instance, on submersed metal structures, oysters

324 represent 90.4% of the biofouling that is colonized by the polys of *Aurelia* sp. in Thau

325 lagoon (Marques et al., 2015b). Therefore *S. aurata* probably has a non negligible

326   impact on the benthic population of *Aurelia* sp. in this ecosystem, either by direct

327   predation on its polyps or by indirect mortality when feeding on the bivalves.

328   With regard to the vulnerability of *Aurelia* sp. pelagic life stages the results

329   revealed that the intensity of *S. aurata* predation depends on prey size range. That is,

330   small medusa appeared to be preferred by both size classes, but more evident for SF of

331   *S. aurata*, which showed ingestion rates as high as those observed with the control

332   pelleted food or with live adult *Artemia*. In contrast, large medusae with 7-8 cm bell

333   diameter were bitten but never fully consumed, while predation on medium sized

334   medusae (Ø 4cm) was intermediate. Large medusae are highly vulnerable to capture by

335   fish because their size increases their visibility in the water column and they have low

336   escape capacities (Houde, 2001), which favour their consumption by fish. The

337   preference of *S. aurata* for the smallest pelagic stages of *Aurelia* sp. may be therefore

338   linked to prey size, which is largely controlled by mouth size in this species (Goldan et

339   al., 1997; Russo et al., 2007; Wassef and Eisawy, 1985). Still, fish bites were observed

340   in the edge of large medusae umbrella, suggesting that the quality of prey is not the

341   hamper factor of its ingestion. Although just partially consumed, large jellyfish may

342   provide a potential source of food for *S. aurata* and in turn, its bites damage the

343   umbrellas of this jellyfish, reducing their capability to swim and capture prey.

344   Results showed that the small medusa (Ø 1cm) is the most consumed *Aurelia* sp.

345   stage by *S. aurata*, however when considering the contributions according to prey

346   biomass, both small and medium medusae appear suitable as food source, highlighting

347   the vulnerability of *Aurelia* sp. early pelagic stages to fish predation. Indeed, *Aurelia* sp.

348   within this size range are found from March to May in Thau lagoon (Bonnet et al.,

349   2012), which matches the annual period for *S. aurata* individuals settlement in the

350 lagoon, either as post larvae or as sub-adults (corresponding to SF and LF size range)

351 after a few months of overwintering at sea (Crespi, 2002; Mercier et al., 2012).

352   The observed trophic interactions between *S. aurata* and *Aurelia* sp. has wide

353 implications for the population dynamics of the two species as the results showed that

354 increasing availability of *Aurelia* sp. medusae boosts ingestion rates of *S. aurata*. In the

355 experiments the fishes were exposed to higher concentrations of medusae than the

356 maximum abundance recorded in Thau lagoon (3.30 x 10^{-3} ind.L^{-1}, Marques et al.,

357 2015a), but in most tanks all the prey available was totally consumed. This suggests that

358 even higher ingestion rates can be achieved if higher abundance of jellyfish are

359 encountered in the wild as previously reported for other ecosystems (e.g. 2.48 x 10^{-1}

360 ind.L^{-1} in Kertinge Nor, Denmark; Olesen et al., 1994). Such observations are in line

361 with former empirical evidence of *S. aurata* behavior, which increase food intake when

362 proteins and lipids levels in the diet provided are low (Santinha et al., 1999). Because

363 *Aurelia* sp. medusae are mainly composed of water (ca. 96%) and have very low

364 nutritional value (Lucas, 1994), higher volumes of these organisms must be ingested to

365 meet predators energetic requirements (Cardona et al., 2012). In addition, as revealed

366 here by significant differences of ingestion rates between the two size classes of fishes,

367 larger predators may have a bigger impact on jellyfish population, as their food

368 requirements are superior and greater numbers of jellyfish must be consumed.

369 Nevertheless, the digestion rates of jellyfish (Arai et al., 2003) suggest higher ingestion

370 as predator guts are cleared faster when feeding on these prey. Therefore the hypothesis

371 is raised that important amounts of *Aurelia* sp. medusae are consumed punctually by

372 both size classes of *S. aurata* each spring, contributing to the population size of the

373 species in the Thau lagoon.

374   The intensity of trophic link however, is probably dependent on the relative

375 densities of the various preys available in the lagoon at that time of the year. Indeed, the

376 results of the prey selectivity trial pointed out that jellyfish are not preferred by *S.*

377 *aurata* individuals when a type of prey with higher nutritional quality is equally

378 available in the tank. Although carbon concentration was not estimated and considering

379 that prey abundance was equally determined according to their size, it is realistic to

380 assume that crustaceans represent a much important input of carbon as prey than

381 jellyfish. Similar results were reported for the threadsail filefish (*Stephanolepis*

382 *cirrhifer*), which was shown to preferentially ingest gelatinous prey when the high

383 quality prey was less visible in the tanks (Miyajima et al., 2011). Likewise, prey

384 accessibility was also pointed as a key factor in prey selectivity by *S. aurata* in the field

385 (Pita et al., 2002). During bloom events, though, jellyfish dominance occurs as an

386 outcome of their predation on zooplankton (Bonnet et al., 2012; Hansson et al., 2005;

387 McNamara et al., 2013; Pereira et al., 2014; Purcell and Sturdevant, 2001), and can

388 reduce the mesozooplankton stock by ca. 81%, as reported in Thau lagoon (Bonnet et

389 al., 2012). Such shifting from high energetically zooplankton community to low quality

390 jellyfish dominating system, might promote an adjustment of prey selectivity of *S.*

391 *aurata* favouring the most abundate prey item, i.e. jellyfish. Jellyfish energy content

392 also increases during the period of gonad maturation (Milisenda et al., 2014), which, in

393 Thau lagoon, occurs from April to June (Bonnet et al., 2012). Hence, given the high

394 ingestion rates that were observed for this life stage in the present study, massive

395 concentrations of jellyfish during blooms have been suggested to satisfy fish energy

396 requirements within a very small area, thereby minimizing energy waste in foraging and

397 prey capture (Cardona et al., 2012; Mianzan et al., 1996).

398   The results suggest that jellyfish like *Aurelia* sp. can be a non-negligible source

399   of food for opportunistic fish species, which has important implications on energy

400   fluxes within food webs and on the population dynamics of both the jellyfish prey and

401   their predators. Furthermore, these laboratory experiments revealed that *Sparus aurata*

402   could prey on benthic (by direct or/and indirect predation) and pelagic stages of *Aurelia*

403   sp., which might have an important impact on *Aurelia* sp. by increasing its predation

404   rates, when the availability of prey with higher nutritional quality is reduced in the wild.

405   These results offer insights on two important issues on jellyfish ecology; that is,

406   fish, especially the opportunistic species, at least partially contribute to control jellyfish

407   blooms, through top-down regulations by preying on different stages of their life cycle.

408   The exploitation and consequent reduction of fish stocks is not only depleting jellyfish

409   food competitors but also releasing jellyfish from the predation pressure. Purcell and

410   Arai (2001) and Arai (2005) stated that predation by a large number of fish species with

411   broad diets is more ecologically important than the predation by the relatively few

412   specialized fishes with primarily gelatinous diets. Hence, this provides support on the

413   role overfishing has in promoting jellyfish outbreaks (Roux et al., 2013). Second, during

414   bloom events jellyfish may provide an alternative source of food which might favour

415   the more opportunistic fish species. The energy from the lower trophic levels might

416   therefore be diverted to fish species with less commercial value. Such modification of

417   the energy pathways within the food webs should be further explored, included in

418   ecosystem based models and considered in management strategies.

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423   5. **References**

424   Arai, M.N., 2005. Predation on pelagic coelenterates: a review. J. Mar. Biol. Assoc. UK

425   85, 523–536. doi:10.1017/S0025315405011458

426   Arai, M.N., 1988. Interactions of fish and pelagic coelenterates. Can. J. Zool. 66, 1913–

427   1927.

428   Arai, M.N., Welch, D.W., Dunsmuir, A.L., Jacobs, M.C., Ladouceur, A.R., 2003.

429   Digestion of pelagic Ctenophora and Cnidaria by fish. Can. J. Fish. Aquat. Sci. 60,

430   825–829. doi:10.1139/F03-071

431   Ates, R.M.L., 1988. Medusivorous fishes, a review. Zool. Meded. Leiden 62, 29–42.

432   Audouin, J., 1962. La daurade de l'étang de Thau *Chrysophrys aurata* (LINNÉ). Rev.

433   Trav. Inst. Péches marit. 26, 105–126.

434   Bonnet, D., Molinero, J.C., Schohn, T., Yahia, M.N.D., 2012. Seasonal changes in the

435   population dynamics of *Aurelia aurita* in Thau lagoon. Cah. Biol. Mar. 53, 343–

436   347.

437   Brotz, L., Cheung, W.W.L., Kleisner, K., Pakhomov, E., Pauly, D., 2012. Increasing

438   jellyfish populations: trends in Large Marine Ecosystems. Hydrobiologia 690, 3–

439   20. doi:10.1007/s10750-012-1039-7

440   Cardona, L., Álvarez de Quevedo, I., Borrell, A., Aguilar, A., 2012. Massive

441   consumption of gelatinous plankton by Mediterranean apex predators. PLoS One

442   7, e31329. doi:10.1371/journal.pone.0031329

443   Crespi, V., 2002. Recent evolution of the fishing exploitation in the Thau lagoon,

444   France. Fish. Manag. Ecol. 9, 19–29.

445   Doyle, T.K., Houghton, J.D.R., McDevitt, R., Davenport, J., Hays, G.C., 2007. The

446   energy density of jellyfish: Estimates from bomb-calorimetry and proximate-

447   composition. J. Exp. Mar. Bio. Ecol. 343, 239–252.

448   doi:10.1016/j.jembe.2006.12.010

449   Escalas, A., Ferraton, F., Paillon, C., Vidy, G., Carcaillet, F., Salen-Picard, C., Le

450   Loc'h, F., Richard, P., Darnaude, A.M., 2015. Spatial variations in dietary organic

451   matter sources modulate the size and condition of fish juveniles in temperate

452   lagoon nursery sites. Estuar. Coast. Shelf Sci. 152, 78–90.

453   doi:10.1016/j.ecss.2014.11.021

454   Feidantsis, K., Pörtner, H.O., Lazou, A., Kostoglou, B., Michaelidis, B., 2009.

455   Metabolic and molecular stress responses of the gilthead seabream *Sparus aurata*

456   during long-term exposure to increasing temperatures. Mar. Biol. 156, 797–809.

457   doi:10.1007/s00227-009-1135-z

458   Goldan, O., Popper, D., Karplus, I., 1997. Management of size variation in juvenile

459   gilthead . I : Particle size and frequency of feeding dry and live food. Aquaculture

460   152, 181–190.

461   Hansson, L., Moeslund, O., Kiørboe, T., Riisgård, H., 2005. Clearance rates of jellyfish

462   and their potential predation impact on zooplankton and fish larvae in a neritic

463   ecosystem (Limfjorden, Denmark). Mar. Ecol. Prog. Ser. 304, 117–131.

464   doi:10.3354/meps304117

465   Houde, E.D., 2001. Fish larvae. Encycl. Ocean Sci. Vol. 2.

466   Ishii, H., Kojima, S., Tanaka, Y., 2004. Survivorship and production of *Aurelia aurita*

467   ephyrae in the innermost part of Tokyo Bay , Japan. Plankt. Benthos Res. 51, 26–

468   35.

469   Lucas, C.H., 2001. Reproduction and life history strategies of the common jellyfish ,

470   *Aurelia aurita* , in relation to its ambient environment. Hydrobiologia 451, 229–
471   246.

472   Lucas, C.H., 1994. Biochemical composition of *Aurelia aurita* in relation to age and
473   sexual maturity. J. Exp. Mar. Bio. Ecol. 183, 179–192.

474   Lynam, C.P., Gibbons, M.J., Axelsen, B.E., Sparks, C. A. J., Coetzee, J., Heywood,
475   B.G., Brierley, A.S., 2006. Jellyfish overtake fish in a heavily fished ecosystem.
476   Curr. Biol. 16, R492–3. doi:10.1016/j.cub.2006.06.018

477   Marques, R., Albouy-Boyer, S., Delpy, F., Carré, C., Le Floc'H, É., Roques, C.,
478   Molinero, J.-C., Bonnet, D., 2015a. Pelagic population dynamics of *Aurelia* sp. in
479   French   Mediterranean   lagoons.   J.   Plankton   Res.   0,   1–17.
480   doi:10.1093/plankt/fbv059

481   Marques, R., Cantou, M., Soriano, S., Molinero, J.-C., Bonnet, D., 2015b. Mapping
482   distribution and habitats of *Aurelia* sp. polyps in Thau lagoon, north-western
483   Mediterranean Sea (France). Mar. Biol. 162, 1441–1449. doi:10.1007/s00227-015-
484   2680-2

485   McNamara, M.E., Lonsdale, D.J., Cerrato, R.M., 2013. Top-down control of
486   mesozooplankton by adult *Mnemiopsis leidyi* influences microplankton abundance
487   and composition enhancing prey conditions for larval ctenophores. Estuar. Coast.
488   Shelf Sci. 133, 2–10. doi:10.1016/j.ecss.2013.04.019

489   Mercier, L., Mouillot, D., Bruguier, O., Vigliola, L., Darnaude, A., 2012. Multi-element
490   otolith fingerprints unravel sea−lagoon lifetime migrations of gilthead sea bream
491   *Sparus aurata*. Mar. Ecol. Prog. Ser. 444, 175–194. doi:10.3354/meps09444

492   Mianzan, H.W., Mari, N., Prenski, B., Sanchez, F., 1996. Fish predation on neritic
493   ctenophores from the Argentine continental shelf: A neglected food resource? Fish.

494   Res. 27, 69–79. doi:10.1016/0165-7836(95)00459-9

495   Milisenda, G., Rosa, S., Fuentes, V.L., Boero, F., Guglielmo, L., Purcell, J.E., Piraino,

496   S., 2014. Jellyfish as prey: frequency of predation and selective foraging of *Boops*

497   *boops* (Vertebrata, Actinopterygii) on the mauve stinger *Pelagia noctiluca*

498   (Cnidaria, Scyphozoa). PLoS One 9, e94600. doi:10.1371/journal.pone.0094600

499   Miyajima, Y., Masuda, R., Yamashita, Y., 2011. Feeding preference of threadsail

500   filefish *Stephanolepis cirrhifer* on moon jellyfish and lobworm in the laboratory.

501   Plankt. Benthos Res. 6, 12–17.

502   Moretti, A., Fernandez-Criado, M.P., Cittolin, G., Guidastri, R., 1999. Manual on

503   Hatchery Production of Seabass and Gilthead Seabream, Volume 1, Organization.

504   Olesen, N.J., Frandsen, K., Riisgard, H.U., 1994. Population dynamics , growth and

505   energetics of jellyfish *Aurelia aurita* in a shallow fjord. Mar. Ecol. Prog. Ser. 105,

506   9–18.

507   Pauly, D., Graham, W., Libralato, S., Morissette, L., Deng Palomares, M.L., 2009.

508   Jellyfish in ecosystems, online databases, and ecosystem models. Hydrobiologia

509   616, 67–85. doi:10.1007/s10750-008-9583-x

510   Pereira, R., Teodósio, M.A., Garrido, S., 2014. An experimental study of *Aurelia aurita*

511   feeding behaviour: Inference of the potential predation impact on a temperate

512   estuarine nursery area. Estuar. Coast. Shelf Sci. 146, 102–110.

513   doi:10.1016/j.ecss.2014.05.026

514   Pita, C., Gamito, S., Erzini, K., 2002. Feeding habits of the gilthead seabream (*Sparus*

515   *aurata*) from the Ria Formosa (southern Portugal) as compared to the black

516   seabream (*Spondyliosoma cantharus*) and the annular seabream (*Diplodus*

517   *annularis*). J. Appl. Ichthyol. 18, 81–86. doi:10.1046/j.1439-0426.2002.00336.x

518 Purcell, J.E., Sturdevant, M., 2001. Prey selection and dietary overlap among
519   zooplanktivorous jellyfish and juvenile fishes in Prince William Sound, Alaska.
520   Mar. Ecol. Prog. Ser. 210, 67–83. doi:10.3354/meps210067

521 Purcell, J.E., Uye, S., Lo, W., 2007. Anthropogenic causes of jellyfish blooms and their
522   direct consequences for humans: a review. Mar. Ecol. Prog. Ser. 350, 153–174.
523   doi:10.3354/meps07093

524 Purcell, J.E., 2012. Jellyfish and Ctenophore Blooms Coincide with Human
525   Proliferations and Environmental Perturbations. Ann. Rev. Mar. Sci. 4, 209–235.
526   doi:10.1146/annurev-marine-120709-142751

527 Purcell, J.E., 2005. Climate effects on formation of jellyfish and ctenophore blooms: a
528   review. J. Mar. Biol. Assoc. UK 85, 461–476. doi:10.1017/S0025315405011409

529 Purcell, J.E., Arai, M.N., 2001. Interactions of pelagic cnidarians and ctenophores with
530   fish : a review 27–44.

531 Richardson, A.J., Bakun, A., Hays, G.C., Gibbons, M.J., 2009. The jellyfish joyride:
532   causes, consequences and management responses to a more gelatinous future.
533   Trends Ecol. Evol. 24, 312–22. doi:10.1016/j.tree.2009.01.010

534 Roux, J.-P., van der Lingen, C.D., Gibbons, M.J., Moroff, N.E.,Shannon, L.J., Smith,
535   A.D.M., Cury, P.M., 2013. Jellyfication of marine ecosystems as a likely
536   consequence of overfishing small pelagic fishes: lessons from the Benguela. B.
537   Mar. Sci. 89(1): 249-284. doi: dx.doi.org/10.5343/bms.2011.1145

538 Russo, T., Costa, C., Cataudella, S., 2007. Correspondence between shape and feeding
539   habit changes throughout ontogeny of gilthead sea bream *Sparus aurata* L., 1758.
540   J. Fish Biol. 71, 629–656. doi:10.1111/j.1095-8649.2007.01528.x

541 Santinha, P.J.M., Medale, F., Corraze, G., Gomes, E.F.S., 1999. Effects of the dietary

542   protein : lipid ratio on growth and nutrient utilization in gilthead seabream (*Sparus*

543   *aurata L.*). Aquac. Nutr. 5, 147–156.

544 Takao, M., Okawachi, H., Uye, S., 2014. Natural predators of polyps of *Aurelia aurita*

545   s.l. (Cnidaria: Scyphozoa: Semaeostomeae) and their predation rates. Plankt.

546   Benthos Res. 9, 105–113.

547 Tancioni, L., Mariani, S., Maccaroni, A., Mariani, A., Massa, F., Scardi, M.,

548   Cataudella, S., 2003. Locality-specific variation in the feeding of *Sparus aurata* L.:

549   evidence from two Mediterranean lagoon systems. Estuar. Coast. Shelf Sci. 57,

550   469–474. doi:10.1016/S0272-7714(02)00376-1

551 Uye, S., Shimauchi, H., 2005. Population biomass, feeding, respiration and growth

552   rates, and carbon budget of the scyphomedusa *Aurelia aurita* in the Inland Sea of

553   Japan. J. Plankton Res. 27, 237–248. doi:10.1093/plankt/fbh172

554 Wassef, E., Eisawy, A., 1985. Food and feeding habits of wild and reared gilthead

555   bream *Sparus aurata* L. Cybium 9, 233–242.

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562   **6. Acknowledgments**

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580   **7. Figure captions**

581   **Fig. 1**: Mean ingestion rates (in number of prey item) observed in SF (top) and LF

582   (bottom) of *S. aurata* for all prey types during the monospecific diets experiments. Error

583   bars represent standard deviations in each case. Letters indicate significant differences

584   between groups after Bonferroni correction ($p < 0.0018$). Note that the initial number of

585   prey item offered (n) varied according to prey type (for more details, refer to **Table 1**).

586   **Fig. 2:** Mean ingestion rates (in number of prey items) observed for SF and LF of *S.*

587   *aurata* for increasing initial abundances (n) of small medusae (Ø = 1cm) of *Aurelia* sp.

588   in the tanks. Error bars represent standard deviations in each case.

589   **Fig. 3:** Mean ingestion rates (in number of prey items) observed in SF (top) and LF

590   (bottom) of *S. aurata* for the various types of live prey (*Artemia* and ephyrae or polyps

591   of *Aurelia* sp.) included in the two mixed diets used for the prey selectivity experiments.

592   Error bars represent standard deviations in each case. Symbols above horizontal bars

593   indicate when differences among groups were significant (*) or not (ns) at the risk level

594   α = 0.05.

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603 **Table 1**: Initial concentration of prey (tank^{-1} and L^{-1}) provided in the tanks during the different experiments, for SF and LF. Concentration of

604 polyps represents the mean concentration of three replicates except for some treatments where one replicate was eliminated, as a result of polyps

605 counting errors (*).

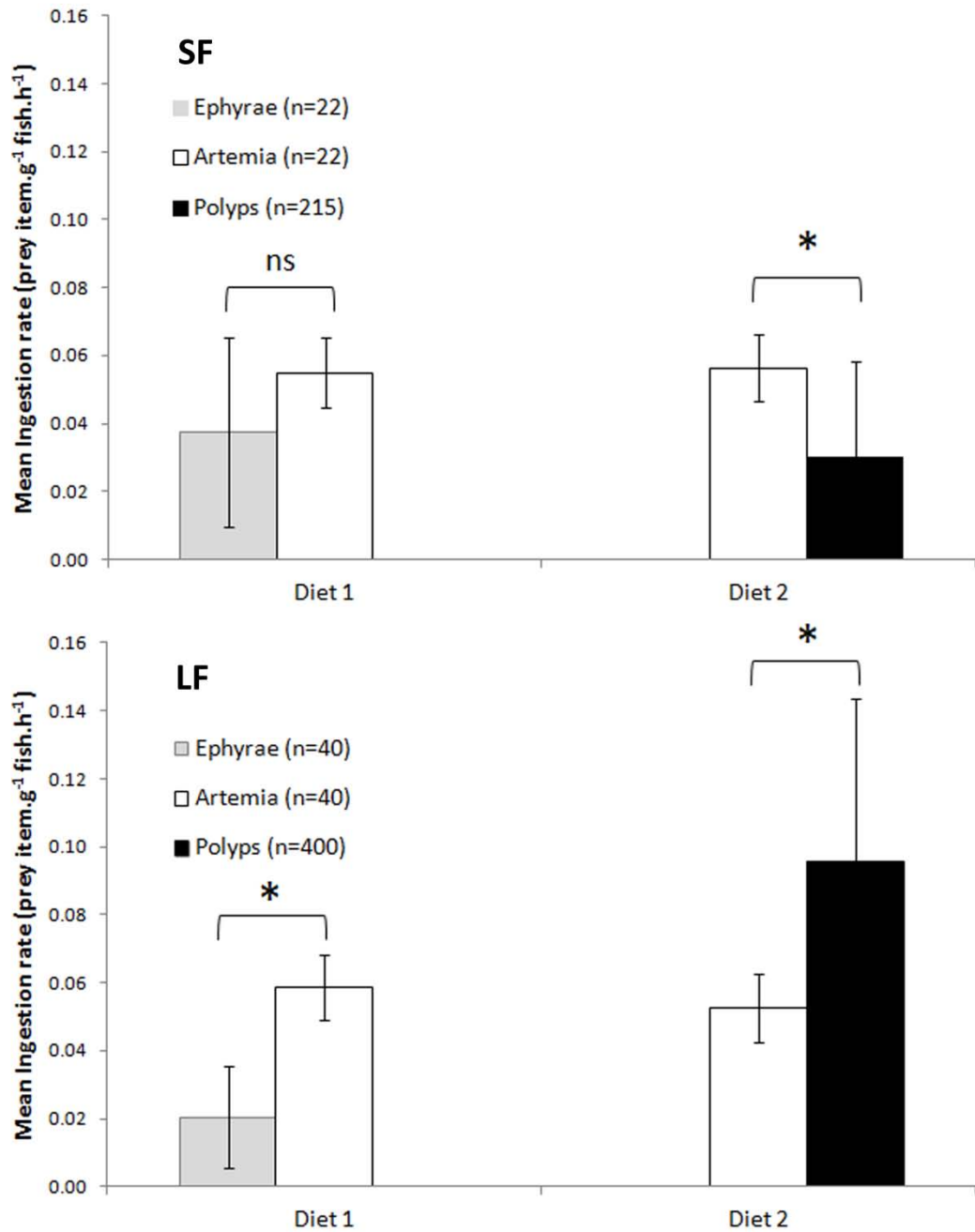| Experiment	Prey type	SF (n= 3 per tank)		LF (n= 2 per tank)	
		prey item.tank^{-1}	prey item.L^{-1}	prey item.tank^{-1}	prey item.L^{-1}
Monospecific diets	Dry pellets	44	1.10	80	2.00
	Artemia	44	1.10	80	2.00
	Polyps*	390	9.75	448	11.20
	Ephyrae	44	1.10	80	2.00
	Small Medusae (Ø1cm)	50	1.25	50	1.25
	Medium Medusae (Ø4cm)	1	0.03	1	0.03
	Large Medusae (Ø7-8cm)	1	0.03	1	0.03
Gradient of concentration	Medusae (Ø1cm)	5	0.13	5	0.13
	Medusae (Ø1cm)	10	0.25	10	0.25
	Medusae (Ø1cm)	15	0.38	15	0.38
	Medusae (Ø1cm)	30	0.75	30	0.75
	Medusae (Ø1cm)	40	1.00	40	1.00
	Medusae (Ø1cm)	50	1.25	50	1.25
Selectivity	Ephyrae + Artemia	22 + 22	0.55 + 0.55	40 + 40	1 + 1
	Polyps* + Artemia	215 + 22	5.38 + 0.55	400 + 40	10 + 1

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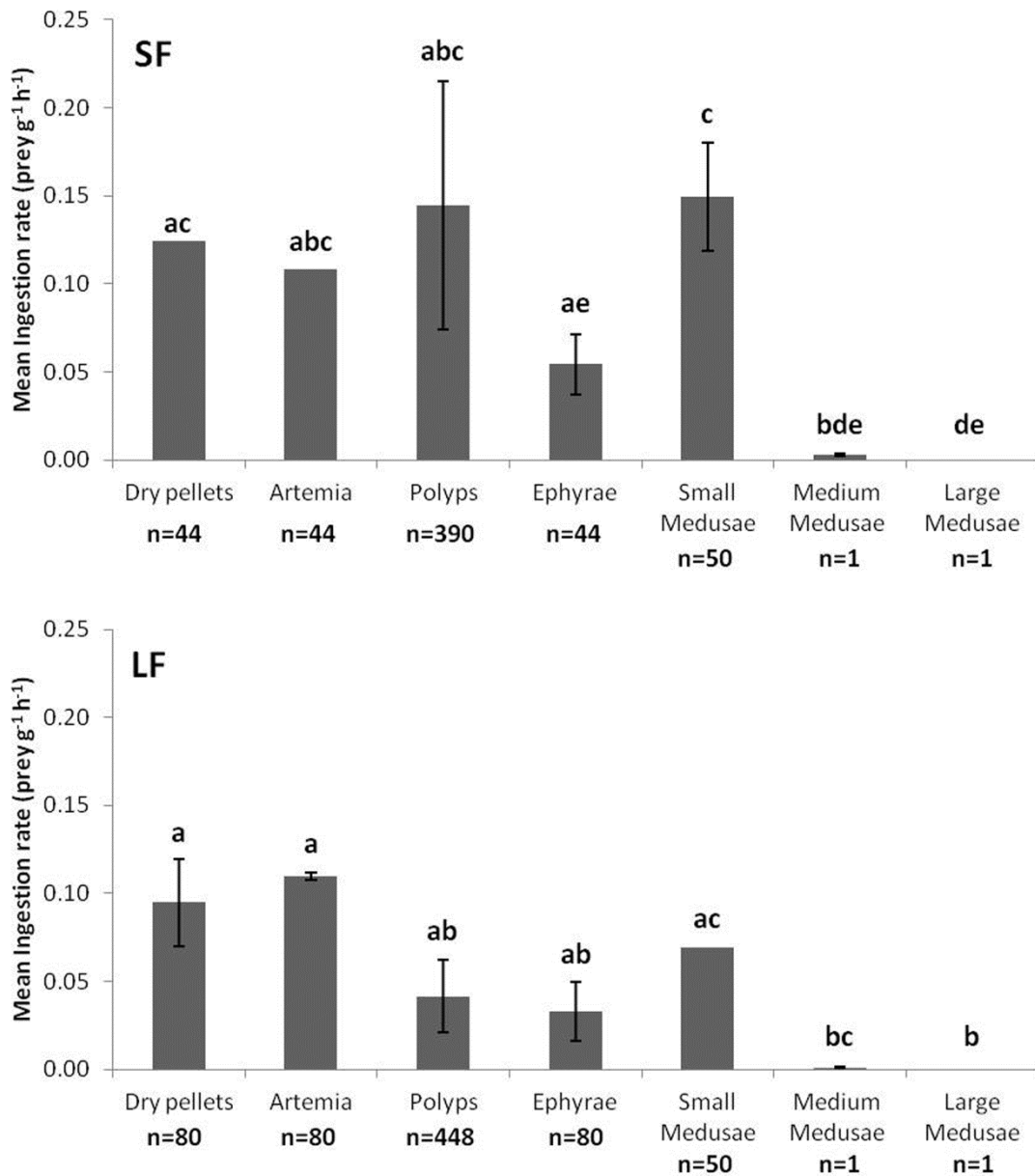
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Fig. 1: Mean ingestion rates (in number of prey item) observed in SF (top) and LF (bottom) *S. aurata* for all prey types during the monospecific diets experiments. Error bars represent standard deviations in each case. Letters indicate significant differences between groups after Bonferroni correction (p <0.0018). Note that the initial number of prey item offered (n) varied according to prey type (for more details, refer to **Table 1**).
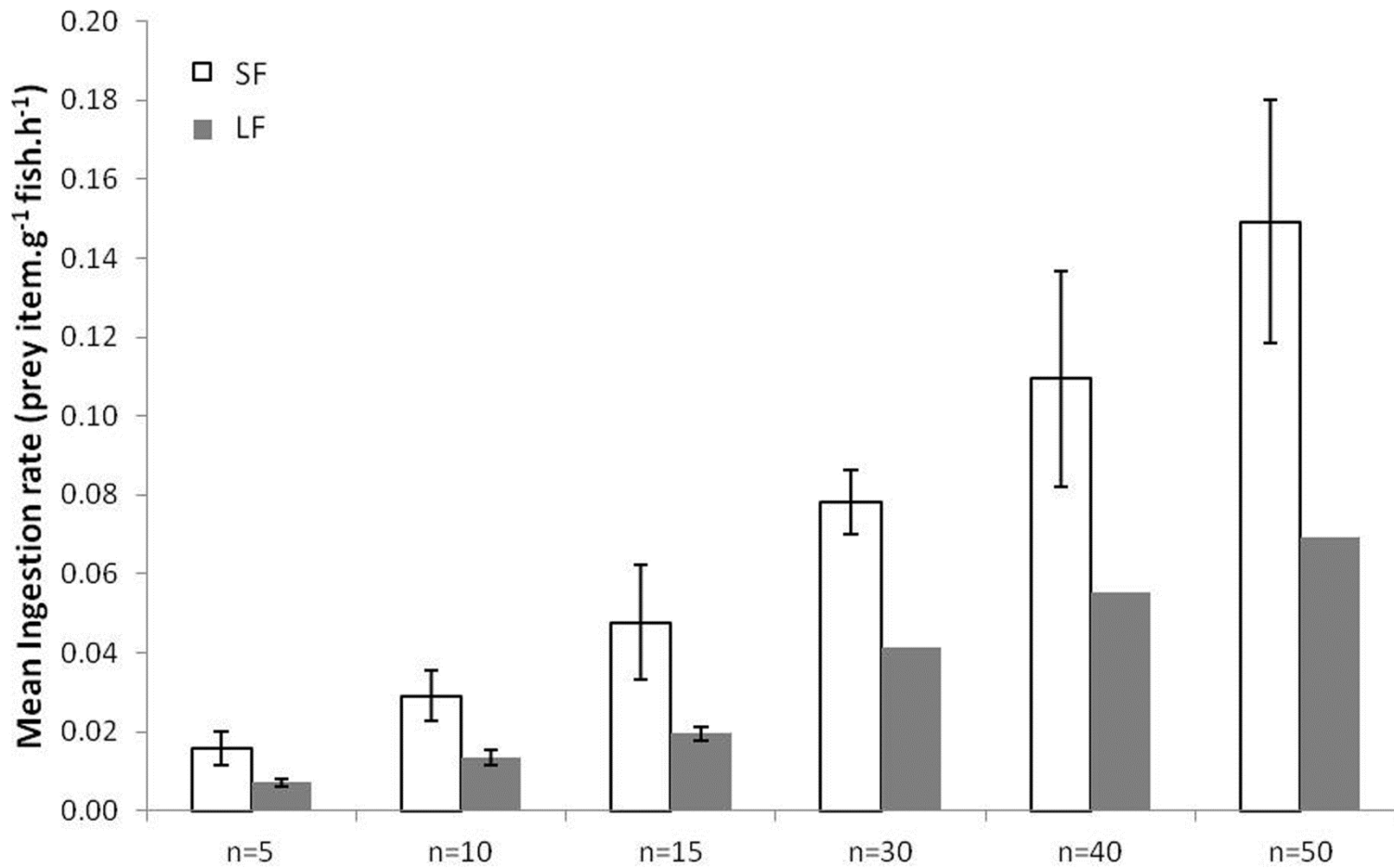
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8 **Fig. 2:** Mean ingestion rates (in number of prey items) observed for SF and LF of *S. aurata* for increasing initial abundances (*n*) of small

9 medusae (Ø = 1cm) of *Aurelia* sp. in the tanks. Error bars represent standard deviations in each case.

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Fig. 3: Mean ingestion rates (in number of prey items) observed in SF (top) and LF (bottom) of *S. aurata* for the various types of live prey (*Artemia* and ephyrae or polyps of *Aurelia* sp.) included in the two mixed diets used for the prey selectivity experiments. Error bars represent standard deviations in each case. Symbols above horizontal bars indicate when differences among groups were significant (*) or not (ns) at the risk level $\alpha = 0.05$.