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Differences in predator composition alters the direction of structure-mediated predation risk in macrophyte communities

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21   **Abstract**

22   Structural complexity strongly influences the outcome of predator-prey interactions in benthic

23   marine communities affecting both prey concealment and predator hunting efficacy. How habitat

24   structure interacts with species-specific differences in predatory style and antipredatory strategies

25   may therefore be critical in determining higher trophic functions. We examined the role of

26   structural complexity in mediating predator-prey interactions across macrophyte habitats

27   encompassing different levels of structural complexity in three different bioregions: Western

28   Mediterranean Sea (WMS), Eastern Indian Ocean (EIO) and Northern Gulf of Mexico (NGM).

29   Using sea urchins as model prey, we measured survival rates of small (juveniles) and medium

30   (young adults) size classes in different habitat zones: within the macrophyte habitat, along the

31   edge and in bare sandy spaces. At each site we also measured structural variables and predator

32   abundance. Generalised linear models identified biomass and predatory fish abundance as the

33   main determinants of predation intensity but the efficiency of predation was also influenced by

34   urchin size class. Interestingly though, the direction of structure-mediated effects on predation

35   risk was markedly different between habitats and bioregions. In WMS and NGM, where

36   predation by roving fish was relatively high, structure served as a critical prey refuge, particularly

37   for juvenile urchins. In contrast, in EIO, where roving fish predation was low, predation was

38   generally higher inside structurally complex environments where sea stars were responsible for

39   much of the predation. Larger prey were generally less affected by predation in all habitats,

40   probably due to the absence of large predators. Overall, our results indicate that, while the

41   structural complexity of habitats is critical in mediating predator-prey interactions, the direction

42   of this mediation is strongly influenced by differences in predator composition. Whether the

43   regional pool of predators is dominated by visual roving species or chemotactic benthic predators

44   may determine if structure dampens or enhances the influence of top-down control in marine

45   macrophyte communities.

46   *Key words: bottom predators, fish predators, seagrass, sea urchin, structure, top-down control.*

47   **Introduction**

48   As a key ecological driver, predation strongly influences community structure and

49   ecosystem processes (Menge 2000). Besides controlling direct trophic pathways, the presence of

50   predators in a system can also influence other species interactions and have cascading effects to

51   lower trophic groups, with far-ranging consequences for the overall functioning of the ecosystem

52   (Schmitz, Krivan and Ovadia 2004). However, the ability of predators to influence ecosystem

53   structuring is far from universal, and in many ecosystems, predation plays a relatively small role

54   (Matson and Hunter 1992). Several factors contribute to explaining the importance of predation

55   within a community, including predatory guild composition within a region, habitat structural

56   complexity or site-specific predatory strategies.

57   The ability of predators to control ecosystem processes is strongly mediated by the

58   architectural or structural complexity of habitats, which can, paradoxically, work both to enhance or

59   reduce predation, depending on the circumstance (Bartholomew, Diaz and Cicchetti 2000).

60   Specifically structure can significantly lower predation risk when it serves as a refuge for prey

61   (Masahiro, N, Y, M, Y, F and M 2013) but can also increase susceptibility to predators that use

62   structure for ambush or camouflage (Hoese, Law, Rao and Herberstein 2006, Rawlins 2011).

63   Therefore, the value of aquatic macrophyte ecosystem as a refuge is strongly dependent on the

64   relationship between vegetation density and the predator-prey community that inhabits it

65   (Manatunge, Asaeda and Priyadarshana 2000, Scheinin, Scyphers, Kauppi, Heck and Mattila 2012).

66   Whether structure facilitates or dampens the strength of predation pressure in ecosystems is heavily

67   dependent on the dominant predatory strategies employed by the carnivore guild. Predators that

68   depend on vision and speed in sighting and capturing their prey are often seriously disadvantaged

69   by habitat complexity (Crowder and Cooper 1982, McGinley, J.E. and Weis 2009). This is because

70 highly structured environments do not only significantly reduce a visual predator's hunting

71 efficiency (Duffy and Hay 2001), but also provide plenty of shelter for prey species (Gotceitas and

72 Colgan 1989). In contrast, predators that use cryptic sit-and-wait or sit-and-pursue strategies

73 perform much better in structurally complex environments (Preisser, Orrock and Schmitz 2007).

74 Because of these differential evolutionary strategies, the composition of the predator guild can make

75 all the difference to the strength and type of predation occurring within an ecosystem, depending on

76 whether the dominant predators benefit from, or are hampered by, increasing habitat complexity.

77 Terrestrial and aquatic systems differ considerably in the generation times of their principal

78 primary producers which potentially explain why aquatic systems are generally more strongly

79 influenced by top-down processes than terrestrial systems (Shurin, Gruner and Hillebrand 2006).

80 This has served to make them ideal model systems to test the influence of predatory processes on

81 community organization (Orth, Heck and van Montfrans 1984) . In these systems, as on land,

82 predator composition is determined by a suite of interacting forces operating at different scales,

83 from local habitat-specific resource availability and, inter-specific competitive interactions, to larger

84 scale variations in juvenile recruitment, population dynamics and migration (Connolly and

85 Roughgarden 1999). In addition, variations at biogeographic scales arising from historical

86 distribution patterns and evolutionary history can also strongly influence predator guilds and

87 predator-prey interactions (Jackson, Kirby, Berger, Bjorndal, Botsford, Bourque, Bradbury, Cooke,

88 Erlandson, Estes, Hughes, Kidwell, Lange, Lenihan, Pandolfi, Peterson, Steneck, Tegner and

89 Warner 2001). These affect the ability to predict the importance of predation at a particular location.

90 In this study, we examined the importance of habitat and biogeographic differences in

91 predatory guilds in modifying structure-mediated predation patterns across a range of macrophyte

92 habitats. Apart from being among the most productive nearshore communities in temperate and

93 subtropical seas, macrophyte habitats encompass widely different levels of structural complexity,

94 from thin filamentous algae to large vertical expansions. We quantified structure-mediated

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95   predation patterns in eleven macrophyte habitats distributed across three ocean basins (Indian

96   Ocean, Mediterranean Sea and Gulf of Mexico), representing a range of structural types with widely

97   varying predator communities. Predation risk was estimated inside the habitat, in the edge and

98   outside. Generally the edges are less structurally complex than the inner zones allowing greater

99   possibilities of movement for example for predatory fish (Gorman, Gregory and Schneider 2009),

100   but it can still provide a certain degree of habitat influence on predation with respect to the sandy

101   areas totally exposed.

102   We used a test on thetering sea urchin to evaluate the proportion of roving and habitat-

103   associated predation at every zone (Fig.1). To determine if predation patterns were mediated by

104   prey size, we quantified predation rates on small and medium size classes of sea urchins. At each

105   location we measured biomass and canopy heights to estimate habitat complexity (Orth, Heck and

106   van Montfrans 1984) and predator abundance to determine the relative importance of macrophyte

107   habitat structure and regional predatory guild composition in determining the strength of predation

108   across these three distinct biogeographic areas.

109

110   **Materials and methods**

111   We used the survival ratio of the most common species of sea urchin in each region (see below) as

112   model prey, using tethering techniques to quantify prey survival. We used both small (juveniles)

113   and medium (young adults) size classes of urchins as prey, since they are the most vulnerable to

114   predators, whereas larger adult urchins are rarely preyed on by extant predator communities

115   (Guidetti 2004, Sala 1997). In order to expose urchins to different conditions of structure and

116   predator complexes, we estimated survival ratios in three treatments: (i) prey placed within

117   vegetated habitat (structure present, habitat-associated predators and roving predatory fish present);

118   (ii) prey placed at the edge of vegetated habitat (no structure, habitat-associated predators and

119 roving predatory fish present); and (iii) prey placed in sandy open space away from vegetated

120 habitats (no structure and no habitat-associated predators, roving predatory fish present; Fig. 1).

121 Thus, predation assays were designed to estimatethe influence of habitat structure on predation

122 while still exposing model prey to specific habitat-associated predators, using habitat edges and

123 nearby sandy open spaces as proxies of predation processes that occur independent of structure

124 (Smith, Hindell, Jenkins and Connolly 2010).

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126 *1. Study area and study design*

127 This study took place in the Western Mediterranean Sea (Catalonia; Spain), Eastern Indian

128 Ocean (Perth; Western Australia) and Northern Gulf of Mexico (Florida; United States) (see

129 Appendix 1 for geographical references). In each region, we selected a range of dominant and

130 representative macrophyte habitats with varying levels of structural complexity (see below), and

131 performed urchin predation assays at two replicate locations for each habitat (site A and B) except

132 for the Northern Gulf of Mexico, where predation was measured in only one location (site A). For

133 this reason, we restrict our comparisons to the Western Mediterranean Sea and the Eastern Indian

134 Ocean, and use observations from the Northern Gulf of Mexico to supplement and reinforce our

135 principal results.

136 *1.1. Western Mediterranean Sea* (WMS). Predation assays and surveys were carried out in two

137 locations 4 km apart along the Costa Brava (Spain): "Site A" (Fenals) and "Site B" (Canyelles). We

138 tested the survival ratio of small (less than 3 cm test diameter, TD) and medium (3 to 5 cm TD)

139 sized *Paracentrotus lividus* (Lamarck) that approximately can reach up to 7 cm diameter

140 (Boudouresque and Verlaque 2001) in four of the most representative macrophyte habitats of the

141 region between 5-10m depth. In the WMS, these comprised two types of seagrass meadows,

142 *Posidonia oceanica* (L.) Delile and *Cymodocea nodosa* (Ucria) Asch., and two algae assemblages,

143 namely: 'turf-forming algae', consisting of brushy and sparsely-branched, small filamentous algae

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144 (e.g. Cladophoraceae, Rhodomelaceae), and 'erect algae', consisting of erect algal growth forms

145 such as Dictyotaceae and Stypocaulaceae (Ballesteros 1992, Sala, Ballesteros, Dendrinos, Di

146 Franco, Ferretti, Foley, Fraschetti, Friedlander, Garrabou, Güçlüsoy, Guidetti, Halpern, Hereu,

147 Karamanlidis, Kizilkaya, Macpherson, Mangialajo, Mariani, Micheli, Pais, Riser, Rosenberg, Sales,

148 Selkoe, Starr, Tomas and Zabala 2012).

149 *1.2. Eastern Indian Ocean* (EIO). The study was performed in two locations 45km apart in

150 Perth (Western Australia): "Site A" (Marmion reef) and "Site B" (Bird Rock). We measured

151 the survival ratio of small (around 3 cm TD) and medium size (5-6 cm TD) classes of the sea

152 urchin *Heliocidaris erythogramma* (Valenciennes), which can reach 9 cm diameter in Australia

153 (Keesing 2007), in four of the most representative macrophyte habitats in the region at 5m

154 depth. The habitats used in EIO were: meadows of the seagrasses *Posidonia sinuosa*

155 Cambridge and Kuo and *Amphibolis griffithii* J.M. (Black) den Hartog, and two algal-

156 dominated reef habitats comprising the kelp *Ecklonia radiata* (C.Agardh) J.Agardh and 'turf-

157 forming algae' assemblages (e.g. Sargassaceae, Dasyaceae).

158 *1.3. Northern Gulf of Mexico* (NGM). The study was conducted at the T.H. Stone Memorial

159 Park in St. Joseph Bay, in the North-east Gulf of Mexico (Florida; United States). The survival

160 ratio of small (< 3 cm TD) and medium sized (3 to 3.5 cm TD) sea urchin, *Lytechinus*

161 *variegatus* (Lamarck), which can grow to 9 cm diameter (Watts, McClintock and Lawrence

162 2001), were evaluated in three representative shallow seagrass habitats (1-1.5m depth):

163 *Thalassia testudinum* Banks & Sol. ex K.D.Koenig, *Halodule wrightii* Ascherson and

164 *Syringodium filiforme* Kützing.

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166 *2. Habitat structure*

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167   We classified structural complexity macrophyte habitat using canopy height and shoot

168   biomass (Heck and Crowder 1991, Orth, Heck and van Montfrans 1984) without, however,

169   considering the heterogeneity of rocky substrate on which algae grow. Since it would offset the

170   comparison with habitats placed on sandy bottom, abiotic shelters, such as crevices and holes,

171   were carefully avoided when sea urchins were placed on rocky bottoms

172   *2.1. Canopy height.* We measured canopy height *in situ* for each macrophyte community as the

173   maximum height of seagrass leaves or algae thalli of 35-50 haphazardly selected areas

174   distributed within the habitat.

175   *2.2. Biomass.* Ten replicates of seagrass shoots and three replicates of kelp fronds were

176   randomly collected by hand. Three replicates of algae assemblages of "turf-forming" and

177   "erect" algae were randomly collected with a flat-bladed paint scraper from a 0.10 m^2 quadrat.

178   All samples (except kelp, see below) were dried in an oven for 48 h at 80°C and then weighed.

179   Since individual kelp were too big to be dried and weighed whole, its biomass was estimated

180   using dry weights of equal circular-cut samples of stipe, lamina and lateral parts of the thallus,

181   which were used to estimate the dry weight of the entire kelp thallus based on known

182   proportions of these parts. The dry weights (DW) were calculated in grams per m^2 and

183   multiplied by density when necessary.

184

185   *3. Predator abundance*

186   We classified fish and invertebrate bottom predators dependent on their mode of predation

187   in relation to habitat structure: (i) habitat-associated fish predators, with limited movements, and

188   largely restricted to the habitat, (ii) roving predatory fish that move over large areas, often moving

189   between habitats, and (iii) habitat-associated bottom predators (cryptic invertebrate predators), such

190   as crustaceans, molluscs and sea stars. At each habitat, we measured the abundance of habitat-

191 associated bottom predators and predatory fish (e.g. species of Labridae, Sparidae or Muricidae).

192 Large size classes of roving predatory fish, such as *Sparus Aurata* in the Mediterranean Sea, are

193 characterized by a very high mobility and they usually are very difficult to count using standard

194 underwater visual census techniques especially outside Marine Protected Areas. Scuba divers

195 estimated the abundance of predators using five replicate underwater visual transects (25x2m) as a

196 modified version of the methodology used in García-Rubies (1997).

197   Transects were conducted for each habitat independently, with the exception of turf-forming

198 and erect algae in the Western Mediterranean Sea (or turf and kelp in the case of Eastern Indian

199 Ocean) since they were interspersed within a rocky matrix. Visual transects were conducted along

200 the inside and the edge zones of habitats.

201 We could not conduct visual censuses for habitat-associated fish predators in the Northern Gulf of

202 Mexico, and, as a result fish data from this region were treated as absent from the statistical

203 analysis.

204

205 *4. Survival ratio*

206   The experiments were carried out during the summer in each region, when predator

207 activity is generally highest (Heck and Valentine 1995, Sala and Zabala 1996, Vanderklift,

208 How, Wernberg, MacArthur, Heck and Valentine 2007). Sea urchins were collected from rocky

209 reefs near the study sites using SCUBA. Ten individual sea urchins per size class (small and

210 medium) were marked by tethering (Aronson and Heck 1995, Ebert 1965, McClanahan 1998)

211 and placed randomly inside the habitat (inside, n=10 per size class and habitat), at the edge of

212 the habitat (edge, n=10 per size class and habitat) and on bare sandy spaces (sand, n=10 per

213 size class). Urchins were tied with a fishing line to metal pegs firmly fixed to soft substrates or

214 attached to pieces of concrete brick on rocky substrates. In all cases, sea urchins were able to

215   move within a range approximately of 0.5m^2 to seek shelter, but they could not get out of the

216   effect of the zone conditions to which they were exposed. After the experiment was set up, we

217   checked urchin survival every day. We considered that predation had occurred if we found the

218   monofilament intact but without the urchin, if some urchin skeletal remains were found or

219   when the Aristotle's lantern membrane was removed (Guidetti 2004, Sala 1997). All samples

220   that had the nylon line broken or absent were excluded (this occurred in very few cases). The

221   experiment was stopped when a minimum of 50% of individuals were consumed in at least one

222   of the habitats being observed. As a result, the time of estimation of predation between

223   bioregions was not equal and was determined based on local predation activity. Although this

224   manipulative technique has associated artefacts such as reduced escape capacity or chemical

225   attraction to pierced prey (Curran and Able 1998) that might affect absolute estimates, it

226   allowed for a uniform comparison of relative predation risk between locations and structural

227   complexities (Farina, Tomas, Prado, Romero and Alcoverro 2009, Pagès, Farina, Gera, Arthur,

228   Romero and Alcoverro 2012).

229

230   *5. Data analysis*

231   For each bioregion, we ranked habitats based on their structural complexity from the lowest

232   to the highest biomass in grams of dry weight per square metre (g DWm^{-2}) and canopy height (cm).

233   We estimated survival as the ratio between the number of days an individual urchin survived and

234   the total days of the experiment, expressed on a scale from 0 to 1. A linear regression model was

235   carried out to determine the importance of the predictor variables biomass, canopy height, density

236   of habitat-associated predators (fish and bottom predators) and the size class of prey in influencing

237   survival ratio inside each habitat. In order to compare predation patterns at the bioregional scale, we

238   calculated average urchin survival ratio inside, at the edge and outsidehabitats. We selected the

239   zones with a gradually decreasing of structure influencing predator-prey interactions and one is

240 totally exposed. The inner zones reflect the highest influence of the habitat structure, while the edge

241 zones, taken outside but very close the vegetation, are only under the influence of the canopy

242 shadow (Gorman, Gregory and Schneider 2009). Finally the outside zones do not receive any

243 influence of the structure, but it allows to measure the potential pressure of roving predatory fish in

244 the area.

245 We compared differences among zones with a nonparametric Mann-Whitney U-Test and we

246 represented it in boxplots. We also generated cumulative survival curves to identify potential

247 patterns at the habitat scale. To do this we compared survival curves between "inside habitat" and

248 "habitat edge" on a daily basis (Kaplan-Meier estimation of censored survival data); differences

249 over the time of experiments were tested with the nonparametric Coxph-test and they were

250 summarized in boxplots. All analyses were performed using R software (R Development Core

251 Team 2010).

252

253 **Results**

254 *Habitat structure*

255 We used canopy height values measured at each location to classify habitats based on their

256 complexity. As expected, canopy height was highest in *Posidonia* spp. (average values of

257 36.21±2.32 cm in Western Mediterranean Sea and 40.60±1.71 cm in Eastern Indian Ocean) and

258 kelp forests (average value of 47.83±2.51cm) and lowest in turf algae (average value of 1.83±0.15

259 cm in WMS and 6.9±0.5 cm in EIO; see Fig. 2a).

260 However, biomass was highest in the macrophyte communities dominated by erect algae and

261 *Posidonia oceanica* in the WMS (1448.96±57.12 and 998.2±7.79 g DWm^2 respectively), and by

262 kelp forests and turf algae in EIO (977.775±13.84 and 870 ± 360.75 g DWm^2 respectively), while

263   some of the smaller seagrasses had very low biomass values (e.g. *Cymodocea nodosa* 56.73±1.655

264   g DWm^2; see Fig.2b).

265   *Predator abundance*

266   Visual census estimation of predator composition and abundance showed large

267   differences between regions and habitats (Fig.3). In the WMS, *P. oceanica*, turf and erect algae

268   assemblages had a high density of habitat-associated predatory fish such as *Coris julis*

269   (Linnaeus) (e.g. 11 ±2.2 ind/50m^2), *Diplodus vulgaris* (Forster) (4.7 ±0.3 ind/50m^2) and

270   *Diplodus sargus* (Linnaeus) (1.9 ±1.1 ind/50m^2). In contrast, bottom predator abundance was

271   lower and we found 0.9 ±0.5 ind/50m^2 of bottom predatory snails *Hexaplex trunculus*

272   (Linnaeus) in *P. oceanica* and 0.5 ±0.1 ind/50m^2 in turf and erect algae, while none of these

273   known predator species were found in *C. nodosa* (Fig.3a).

274   In the EIO, we estimated very high densities of habitat-associated bottom predators. The

275   common carnivorous sea star *Patiriella brevispina* (Clark) was found in *Posidonia sinuosa* and

276   *Amphibolis griffithii* at average densities of 26.6 ±6.1 and 36.6 ±6.14 ind/50m^2, respectively.

277   We also detected the large sea star *Coscinasterias calamaria* (0.1± 0.1 ind/50m^2 in seagrasses

278   and 0.2 ±0.1 ind/50m^2 in algae habitats), as well as a few unidentified species of habitat-

279   associated predatory fish in kelp and turf-forming algae on rocky bottoms (Fig.3b).

280   Finally, in the NGM we found the lowest densities of predators. The crab *Libinia*

281   *emarginata* (Hinsch) and the predatory snail *Fasciolaria tulipa* (Linnaeus) were detected in

282   *Thalassia testudium* (0.8 ±0.4 and 0.4 ±0.2 ind/50m^2 respectively), and the crab *Callinectes*

283   *sapidus* was found in *Syringodium filiforme* (0.2 ±0.2 ind/50m^2; Fig.3c). Roving predatory fish

284   and habitat-associated predatory fish were not estimated at this location (see methods).

285   *Survival ratio*

286   The linear model identified macrophyte biomass and predatory fish abundance as the most

287   important factors explaining overall urchin survival ratio (p=0.018; R^2=0.33), but size class of prey

288   influenced predator efficiency almost significantly (p=0.051;see Appendix 2 for the full linear

289   model Table). In the model, that included only explanatory variables relevant to the habitats

290   (biomass, canopy height), size class of prey and predator composition (habitat-associated predatory

291   fish and habitat-associated bottom predators), an important part of the variance associated with the

292   survival ratio was still unexplained. In fact, when introducing bioregions and habitats as factors

293   additional important differences emerged. On the whole, sea urchin predation generally differed

294   significantly among the three habitat zones (inside, on the edge and outside macrophyte habitats),

295   but with contrasting patterns observed in the three bioregions (Fig.4 supported by Appendix 3). In

296   the WMS and the NGM, survival ratio of the juveniles was significantly lower outside and at the

297   edge of habitats than inside habitats. For example, in WMS an average of 30% of urchins survived

298   inside habitats, while at the edge and outside only 10% did. The opposite trend was observed in EIO

299   where, for both juveniles and young adults sea urchins, survival was higher outside the habitat (70

300   and 100%, respectively) than at the edge (10% and 40%, respectively) or inside the habitat (10%

301   and 60%, respectively). In the WMS, there was no difference in survival ratio among habitat zones

302   (inside-edge-outside) in medium sizes that generally survived better than small sizes in all habitats

303   (Fig.4). In the NGM, survival of the medium size class mirrored the effects on smaller urchins, i.e.

304   survival was highest inside (100%) compared with the edge or outside habitats (~75%).

305   At the habitat scale (Fig.5 supported by Appendix 4), we found that the survival of juveniles

306   sea urchins in WMS was significantly higher inside than at the edge of all habitats with the

307   exception of turf assemblages, where there was no difference. In contrast, for the young adults,

308   urchin survival was not significantly different in any of the habitats. In EIO, differences in survival

309   trends between inside and the edge of habitats were not significant for either small or medium sizes

310   of sea urchins, with the exception of *A. griffithii*, where values were higher at the edge of habitats.

311   The trends in urchin survival ratio in NGM for the two size classes of prey were significantly higher

312   inside the habitat than at the edge.

313

314   **Discussion**

315   While habitat structure (biogenic or otherwise) is clearly an important agent

316   determining predation risk, our results suggest that it is strongly dependent on regional

317   predator pools, which can drive predation risk in habitats with very similar structure in

318   completely opposite directions, either reducing or enhancing top-down control within the

319   ecosystem. Thus, while complex macrophyte habitats serve as an effective shelter from

320   predation in the Western Mediterranean Sea, where roving or habitat-associated fish are the

321   dominant predators, highly structured macrophytes constitute dangerous habitats for prey in

322   the Eastern Indian Ocean due to the abundance of bottom predators. Although not replicated

323   fully, the Northern Gulf of Mexico showed similar trends as the Mediterranean, with

324   macrophyte habitats providing efficient shelters from roving predatory fish, and urchins being

325   safer inside rather than on the edge or outside macrophyte habitats.

326   The large variations in growth form and spatial configurations of dominant plant

327   species are often a significant contributor to habitat structure in vegetated habitats (Crowder

328   and Cooper 1982, Madsen, Chambers, James, Koch and Westlake 2001). Within the same

329   bioregion, the macrophyte communities in our study encompassed a range of biogenic

330   structures and complexity with varying biomass and canopy heights that differ considerably in

331   their refuge value for prey. The model indicates that structural complexity was an adequate

332   predictor of prey survival across all bioregions (Fig.5). In areas like the Mediterranean Sea

333   and the Gulf of Mexico, complex habitats offered far better refuge for prey, particularly for

334   smaller size classes. In fact, when roving and habitat-associated fish are the dominant

335   predators (as in the WMS), increasing structural complexity can strongly reduce predation

336   risk. Highly structured habitats like *P. oceanica* and erect algae constitute a much safer

337   refuge for juvenile urchins than turf algae. In the WMS, *C.nodosa* is an exception to this

338   general trend and may be driven more by the configuration of the landscape, which has been

339   observed to strongly influence predation depending on the spatial attributes of the habitats and

340   the surrounding matrix within which it is housed (Farina et al. unpublished). Meadows of *C.*

341   *nodosa* in the WMS typically grow close to the coast, are very isolated from other macrophyte

342   communities, and house very low densities of habitat-associated fish (Guidetti and Bussotti

343   2000), which combined, potentially explain the relatively high urchin survival here despite its

344   structure.

345   In contrast with the WMS, structurally complex habitats offered very little refuge for

346   small sea urchins in the Eastern Indian Ocean. Survival rates were lower in EIO where bottom

347   predators were more abundant than fish. Strikingly different from that observed in holder

348   experiments (Keough and Butler 1979), bottom predators like *Patiriella brevispina* feed

349   inside structurally complex environments and were found inside *Amphibolis griffithii*,

350   *Posidonia sinuosa* as well as turf habitats. It is likely that these bottom species are the

351   dominant predators of juvenile urchins in the EIO, and their presence inside structurally

352   complex habitats makes dense macrophyte stands very dangerous for small size classes of

353   urchins.

354   Interestingly, our results indicate that predation on large adult urchins was generally

355   low across all habitats and bioregions. Habitat structure did not constitute a refuge for larger

356   urchin size classes, as they were visible to predators in even the most structured habitats.

357   However, as observed elsewhere, adult urchins probably do not need to rely on structural

358   complexity, their size itself being refuge enough, with few sufficiently large extant visual

359   predators able to prey on them, even within Marine Protected Areas (Guidetti 2004). This was

360   particularly important because predation on small sizes was very high across all three

361 bioregions, indicating that survival of juveniles may be a critical bottleneck shaping urchin

362 population structure.

363   Our results show that habitat structure can work both ways in mediating predator-

364 prey interactions, either by reducing or enhancing top-down control. The effect is largely a

365 function of predator identity, which determines whether habitat complexity serves as a major

366 restriction that prevents effective hunting (through refuge) or enhances predation by providing

367 a camouflage or hiding space for predators (Bartholomew, Diaz and Cicchetti 2000). This

368 dual mediatory role results in a dynamic arms race among predators capable of exploiting

369 habitats of different structural characteristics within the ecosystem mosaic. Predators in our

370 large-scale study spanned a spectrum of predatory strategies (visual hunt, camouflage,

371 ambush and chemotaxis). Evolutionary and behavioral predispositions enable species that rely

372 on acute visual senses and speed to perform much better over large, relatively open expanses

373 (Canion and Heck 2009). In contrast, species that rely more on camouflage, ambush or

374 chemotaxis (James and Heck 1994) may be much more effective in the dense undergrowth

375 provided by structurally complex macrophyte communities (Martin, Fodrie, Heck and Mattila

376 2010). A clear example of these two strategies is evident by comparing the seagrasses

377 *Posidonia oceanica* in the WMS with *Amphibolis griffithii* in EIO; both have very similar

378 canopy height and biomass (Fig.2), but have very different types of predators. Although *A.*

379 *griffithii* has a structure characterized by tree-like fronds and an open space below its canopy

380 that may facilitate access for medium-sized fish (Hyndes, Kendrick, MacArthur and Stewart

381 2003), predation signs found on urchin prey tests in our study were typically made by sea

382 stars. In contrast, most predation signs in *P. oceanica* could be clearly assigned to fish that

383 most likely hunted visually. This reflects, the dominant predator groups observed in the two

384 regions (Fig. 3). These compositional differences appear to be critical in determining survival

385 ratios in the community with *P. oceanica* being one of the safest habitats for urchins in the

386   WMS, while *A. griffithii*, despite having a similar canopy height and biomass, is one of the

387   most predation-prone habitats we observed in the EIO.Our observed trends are most likely

388   driven by compositional differences in predators among habitats. In our study, predation

389   inside the habitat structure in the WMS and NGM was almost always lower than predation at

390   the edges and in the sand indicating that fish predators clearly dominated the predatory pool.

391   At least in the Mediterranean, this trend was also confirmed by our in-water surveys that

392   showed fish predators were by far the most dominant in this system compared with bottom

393   predators. This supports the observation that fish predators may be the main consumers of sea

394   urchins in macroalgal and seagrass communities in the Mediterranean (Sala 1997). In striking

395   contrast, predation inside and at the edge of the habitats tended to be higher when compared

396   to sand predation in EIO (Fig.4), a pattern that holds in almost every habitat from simple turf

397   forming algae to the more complex kelp *E. radiata* (Appendix 4). This was also related to the

398   predator guild composition that, in this region, was characterized by a high density of bottom

399   predators which can move up inside the structure to the edge (Fig.3). In fact, seagrass

400   meadows had very high densities of sea stars while fish predators were practically absent.

401   These observations conform with similar results by Vanderklift, How, Wernberg, MacArthur,

402   Heck and Valentine (2007) and Tuya, Vanderklift, Hyndes, Wernberg, Thomsen and Hanson

403   (2010), which indicate that fish were restricted to habitats close to rocky reefs and roving fish

404   predators were very rare in the area.

405   While natural differences in predator composition between habitats may play a large

406   role in determining predation rates, we cannot discount directed human harvest as an agent

407   influencing differences in predator composition. All of our studied habitats have been subject

408   to sustained fishing pressure (Halpern, Walbridge, Selkoe, Kappel, Micheli, D'Agrosa, Bruno,

409   Casey, Ebert, Fox, Fujita, Heinemann, Lenihan, Madin, Perry, Selig, Spalding, Steneck and

410   Watson 2008). As top predatory fish are selectively removed from coastal waters, there is an

411 increasing simplification of trophic webs that can have major modifications on the predator

412 pool in any given region (Jackson, Kirby, Berger, Bjorndal, Botsford, Bourque, Bradbury,

413 Cooke, Erlandson, Estes, Hughes, Kidwell, Lange, Lenihan, Pandolfi, Peterson, Steneck,

414 Tegner and Warner 2001). In extreme cases, the removal of top predators can lead to meso-

415 predator release (for instance, invertebrate predators), which could dramatically modify the

416 structure-predation relationship and change the landscape of risk that prey species experience

417 in these regions (Oksanen, Fretwell, Arruda and Niemela 1981).

418   When the prey concerned are themselves key functional elements in the ecosystem,

419 as sea urchins often are in macrophyte communities (Alcoverro and Mariani 2002, Woodley

420 1999), these distributional differences in the predatory pool can have vital consequences for

421 the functioning of the system. Modifications of predator guilds of sea urchins can affect the

422 abundance and distribution of these species, and their effects may cascade and affect other

423 ecosystem processes (top-down control). For instance, the sea urchin *P. lividus* we used in this

424 study is among one of the most important herbivores in the Mediterranean (Hereu, Zabala,

425 Linares and Sala 2005, Prado, Tomas, Pinna, Farina, Roca, Ceccherelli, Romero and

426 Alcoverro 2012) and has often been observed to overgraze macrophyte communities when

427 released from predation (Boudouresque and Verlaque 2001). In contrast, sea urchins are

428 relatively rare in the Australian macrophyte communities we studied (Vanderklift and

429 Kendrick 2004) and may be functionally less important to ecosystem structure. Of course,

430 their low numbers may, at least in part, be influenced by the high levels of predation observed

431 inside Australian macrophyte communities. Consequently, in areas that are controlled by

432 roving and habitat-associated predatory fish (i.e. Mediterranean and Gulf of México), a much

433 higher impact of overfishing is expected in macrophyte communities. In contrast, in areas

434 where the main predators are bottom invertebrate predators (i.e. Australia), the impact of

435 overfishing may not manifest so directly, although it may still appear through indirect

436 pathways. These differences make it difficult to generalize about the nature of habitat

437 structure-predation relationship across regions and local contexts. To fully understand and

438 manage ecosystem function, it is therefore crucial to determine the main types of predators

439 (fish versus invertebrate) dominant in each habitat, as structure can strongly modify

440 ecosystem function. Whether it enhances or limits predation is contingent completely on the

441 predatory pool, and may imply potentially very different habitat-specific management

442 directions.

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585   **Figure legends**

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587   **Fig.1** Diagram representing an example of a seagrass and algae assemblage mosaic and its

588 associated predator guild, including roving predatory fish , habitat-associated fish predators and

589 bottom predators. In nature sea urchins are present inside the habitats but also in the edge. The

590 innner zone may be infested by bottom predators, but in all likelihood it constitutes a barrier to fish

591 predators, which are forced to hunt visually outside the canopy. On the contrary the edge is highly

592 subjected to predatory fish, especially those that are very mobile, and the bottom predators at the

593 same time, coming from the inner of the habitat structure.

594

595   **Fig.2** a) Canopy height mean (±SE) and b) biomass mean (±SE) are used to determine

596 structural complexities of turf-forming and erect algae, *Cymodocea nodosa, Posidonia oceanica* in

597 the Western Mediterranean Sea (WMS); turf-forming algae, *Amphibolis griffithii, Posidonia*

598 *sinuosa, Ecklonia radiata* in Eastern Indian Ocean (EIO); *Halodule wrightii, Thalassia testudinum,*

599 *Syringodium filiforme* in the Northern Gulf of Mexico (NGM). Each region's habitats are listed in

600 increasing order of canopy height, from left to right.

601

602   **Fig.3** Abundance mean (±SE) of fish predators and bottom predators in 50m^2. a) Western

603 Mediterranean Sea (*Cymodocea nodosa*, turf-forming and erect algae assemblages, *Posidonia*

604 *oceanica*); b) Eastern Indian Ocean (*Amphibolis griffithii, Posidonia sinuosa, Ecklonia radiata* and

605 turf-forming algae), and c) the Northern Gulf of Mexico (Syringodium filiforme, Halodule wrightii,

606 Thalassia testudinum and). Visual census was not effective in detecting roving predatory fish

607 abundance which were underestimated, especially in the Mediterranean Sea and in the North Gulf

608 of Mexico where urchin survival was lowest outside the habitats (see Methods for details).

609

610   **Fig.4** Boxplots (median and interquartile range) showing bioregional patterns in urchin

611 survival ratio in the three habitat zones (inside, in the edge and outside). Results were analysed with

612 the non-parametrical Mann-Whitney U-test (p-level<0.05) and significant differences were

613 represented with lower-case letters above each bar.

614

615   **Fig.5** Boxplots (median and interquartile range) representing survival ratio of urchin size

616 classes inside and at the edge of each habitat: a) Western Mediterranean Sea (*Cymodocea nodosa*,

617 turf-forming algae, *Posidonia oceanica*, erect algae assemblages); b) Eastern Indian Ocean

618 (*Amphibolis griffithii, Posidonia sinuosa*, turf-forming algae, and *Ecklonia radiata*) and c) the

619 Northern Gulf of Mexico (*Syringodium filiforme, Halodule wrightii, Thalassia testudinum*).

620 Significant differences were estimated comparing the cumulative curves of survivorship with the

621 nonparametric Coxph-test (Appendix 4) and represented with asterisks.

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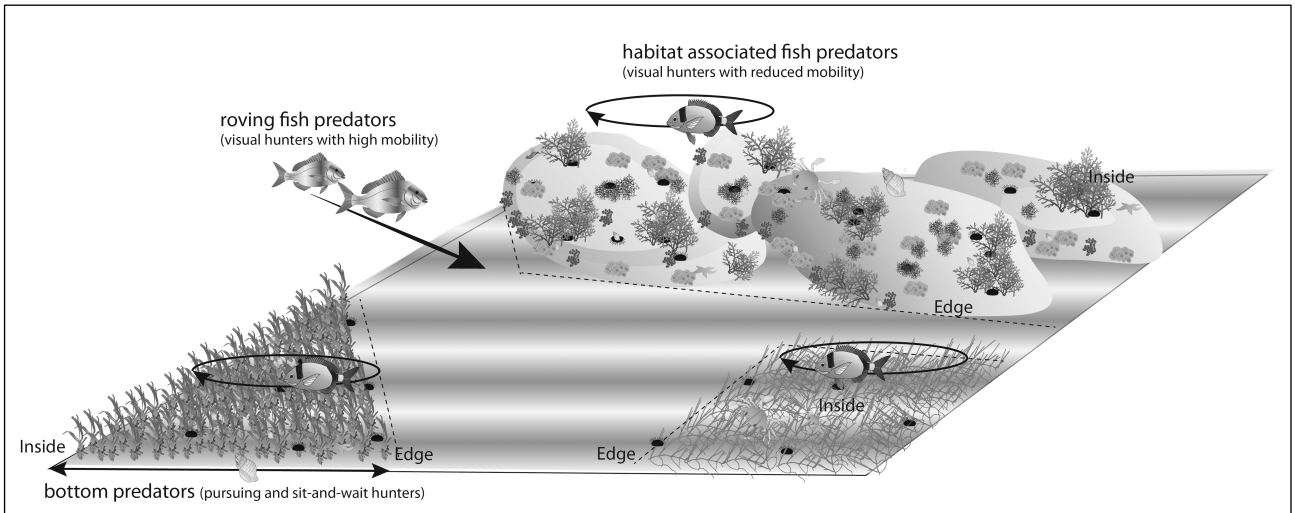626

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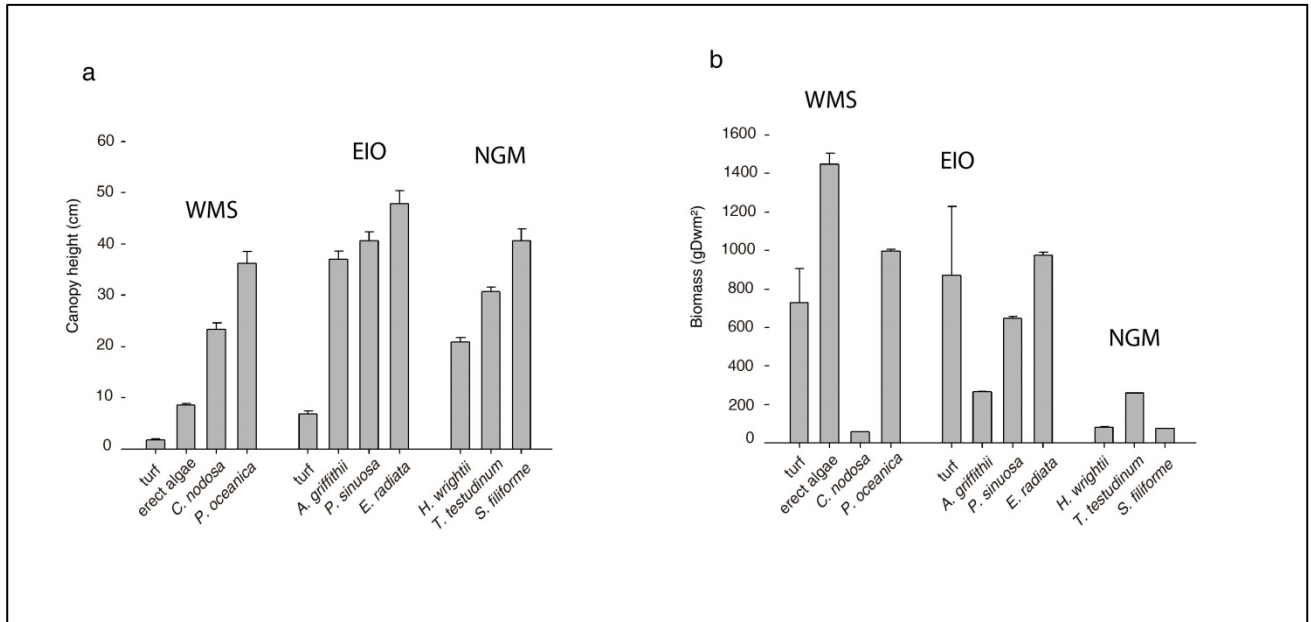632

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Fig.1

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Fig.2

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Fig.3

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Fig.4
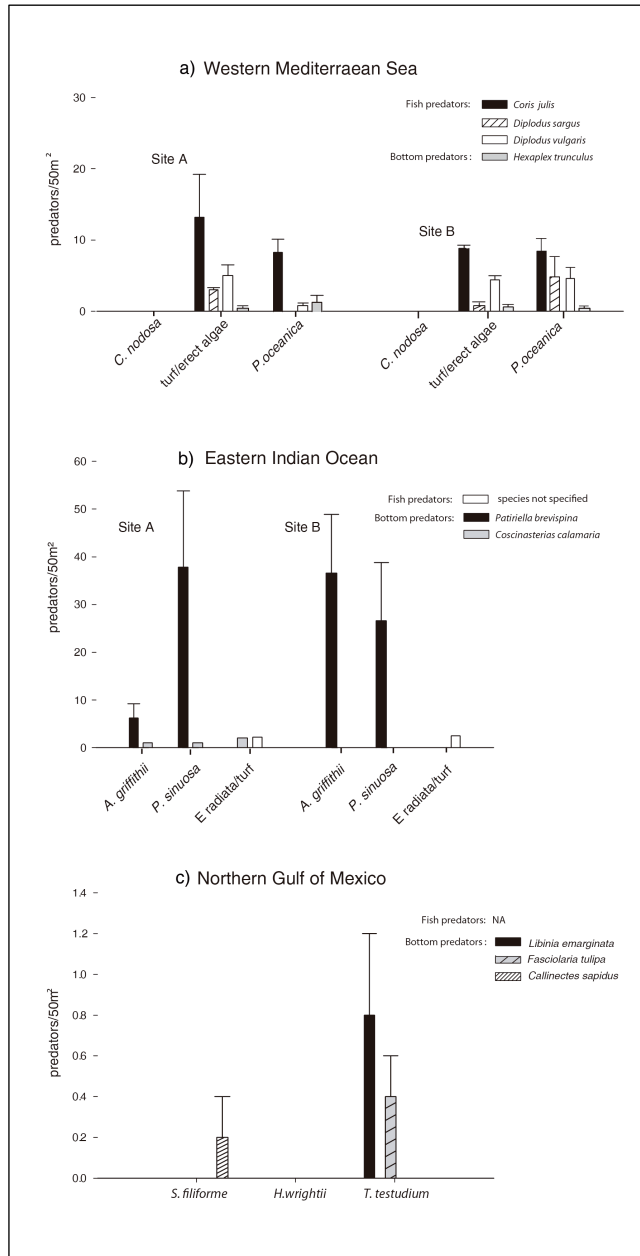
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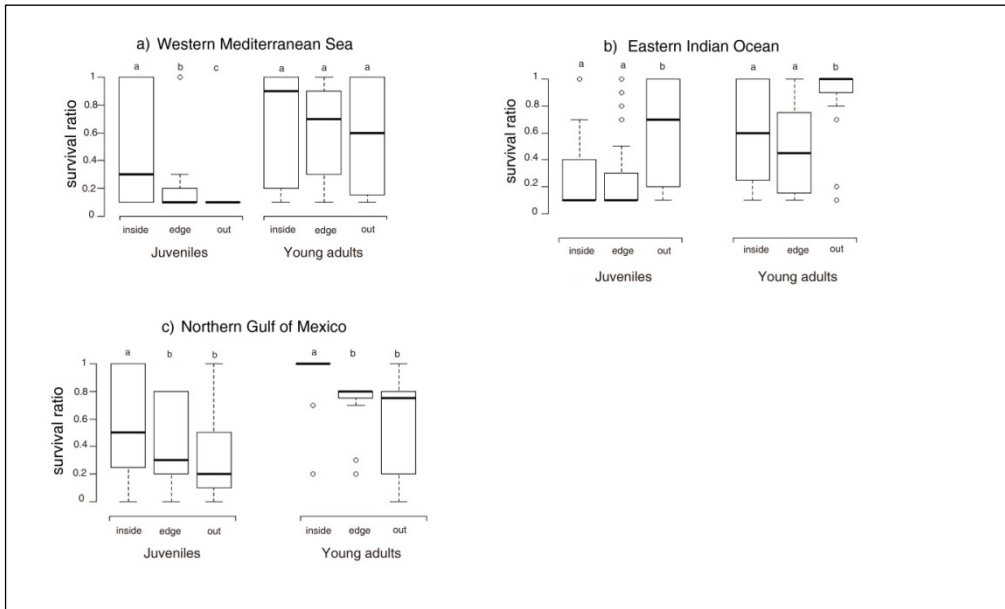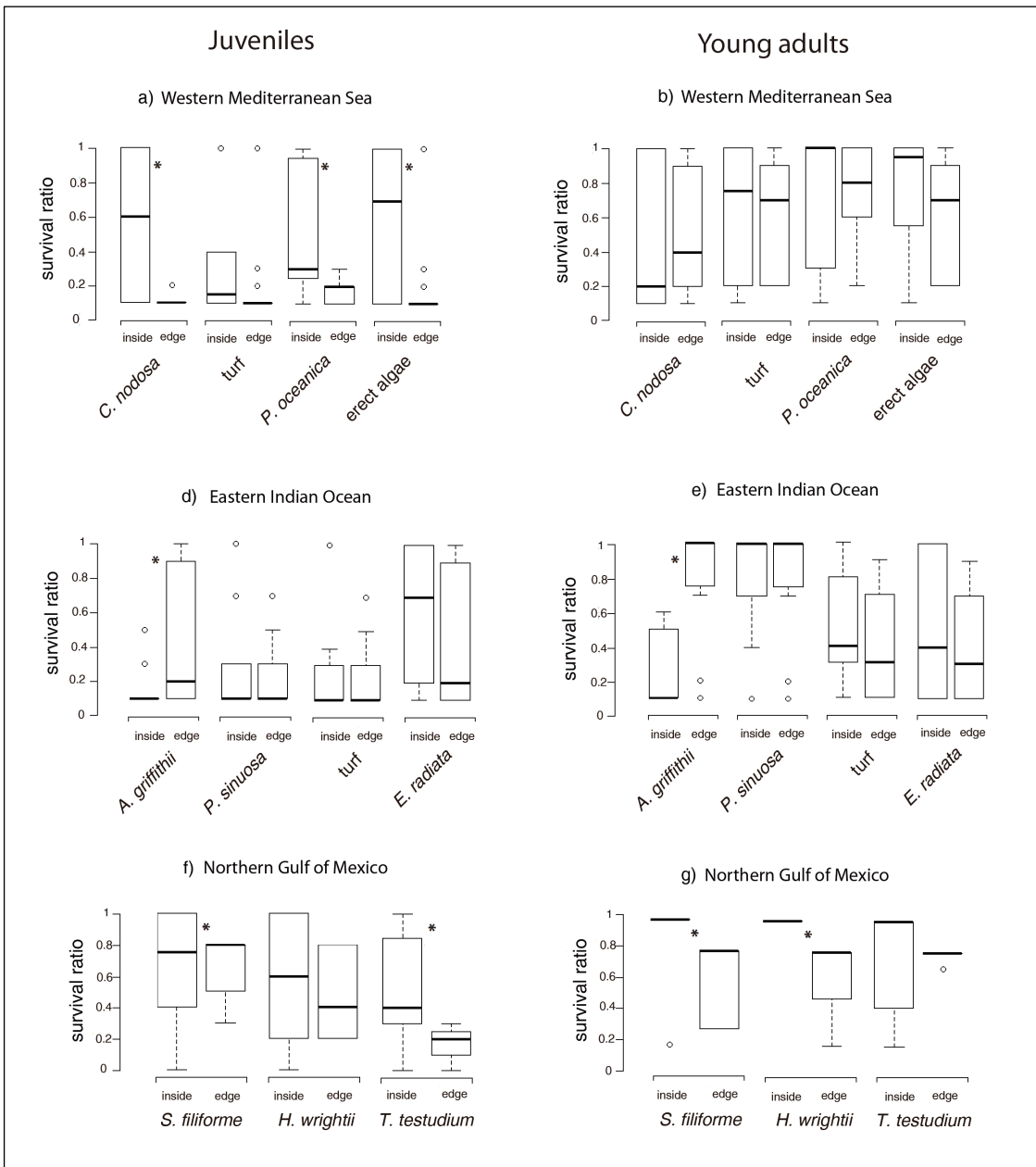
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675   **Fig.5**

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