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Unravelling the macro-evolutionary ecology of fish-jellyfish associations: life in the 'gingerbread house'

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1 **Unravelling the macro-evolutionary ecology of fish-jellyfish associations: life in the**
2 **'gingerbread house'**

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26 **Abstract**

27 Fish-jellyfish interactions are important factors contributing to fish stock success. Jellyfish can
28 compete with fish for food resources, or feed on fish eggs and larvae, which works to reduce
29 survivorship and recruitment of fish species. However, jellyfish also provide habitat and space for
30 developing larval and juvenile fish which use their hosts as means of protection from predators and
31 feeding opportunities, helping to reduce fish mortality and increase recruitment. Yet, relatively little
32 is known about the evolutionary dynamics and drivers of such associations which would allow for
33 their more effective incorporation into ecosystem models. Here, we found that jellyfish association
34 is a probable adaptive anti-predator strategy for juvenile fish, more likely to evolve in benthic (fish
35 living on the sea floor), benthopelagic (fish living just above the bottom of the seafloor) and reef-
36 associating species than those adapted to other marine habitats. We also found that jellyfish
37 association likely preceded the evolution of a benthic, benthopelagic and reef-associating lifestyle
38 rather than its evolutionary consequence, as we originally hypothesised. Considering over two thirds
39 of the associating fish identified here are of economic importance, and the wide-scale occurrence
40 and diversity of species involved, it is clear the formation of fish-jellyfish associations is an important
41 but complex process in relation to the success of fish stocks globally.

42 **Keywords:** anti-predator strategies; demersal fishes; early life stages; evolution; fisheries

43 Introduction

44 Over past decades, many studies have documented how jellyfish blooms (Phylum Cnidaria, Class
45 Scyphozoa) have pronounced consequences for human endeavour (1,2). Be it impacts on coastal
46 tourism, the clogging of fishing nets or the blocking of power station cooling-water intakes (1), the
47 result has been an overall negative perception of gelatinous species (3). While the scientific
48 community has concentrated efforts on investigating the deleterious effects of large aggregations of
49 jellyfish in our seas (2,4), the counterbalancing positive roles of jellyfish have typically received less
50 attention (3,5). However, recent efforts to address this gap are gaining momentum and a more
51 nuanced picture of jellyfish ecology is emerging (5).

52 Broadly, jellyfish contribute to the four main categories of ecosystem services defined by the
53 Millennium Ecosystem Assessment: regulating, provisioning, supporting and cultural services (3).
54 Furthermore, the traditional view of jellyfish as trophic dead ends, i.e. energy and nutrients directed
55 towards jellyfish are lost to taxa higher up the food chain, is now overturned thanks to numerous
56 studies demonstrating how jellyfish are key prey for apex marine predators and species of
57 commercial value (6). For example, predation on jellyfish by commercially important species in the
58 Irish Sea is far from rare, with >20% of sampled Atlantic herring (*Clupea harengus*) having jellyfish
59 detected in their stomachs (7). Opportunistic jellyfish predators also include species such as mallard
60 ducks (*Anas platyrhynchos*) (8), albatross (9), Adélie penguins (*Pygoscelis adeliae*) (10) and deep sea
61 octopods (11).

62 However, jellyfish also provide habitat for juvenile fishes in what is generally considered a facultative
63 symbiotic relationship (Fig. 1), and greater food acquisition opportunities for the fish is often cited
64 as an important causal factor in the formation of such interactions (12,13). Juvenile fish can feed on
65 the zooplankton entrained by jellyfish swimming pulses or captured on their tentacles, or even on
66 crustacean parasites on their jellyfish host (6,14,15). Moreover, stable isotope analysis has revealed

67 that associating juvenile Atlantic bumper (*Chloroscombrus chrysurus*) feed directly on their jellyfish
68 hosts (*Aurelia sp.* and *Drymonema larsoni*), constituting up to 100% of their diet during this life stage
69 (16). This study does not stand alone but reinforces previous evidence of how juvenile fish often feed
70 on their jellyfish hosts (17–20). Beyond food acquisition, protection from predators is also believed
71 to be a key driver behind fish-jellyfish associations (12). For example, 0-group (<12 months old)
72 gadoid fish avoid predation by retreating among jellyfish tentacles which may improve survival
73 during this critical time in their development (21). Similarly, Sassa et al. (22) reported correlational
74 evidence that the abundance of jack mackerel (*Trachurus japonicus*) juveniles in the North Pacific
75 was higher when concurrent increases in jellyfish *Pelagic noctiluca* were recorded. The ability of
76 juvenile associative fishes to feed directly on the host under which they are sheltering, arguably sets
77 fish-jellyfish associations apart from the straightforward predator-prey relationship described
78 previously, where marine predators consume the entire jellyfish. However, the benefits gained by
79 associating with jellyfish may be broader and differ to some extent among fish species with diverse
80 life histories, ecology and/or behaviour.

81 Mansueti (17) proposed that fish-jellyfish associations persist when the host provides protection
82 from predators on a sustaining basis. Larger juveniles or adults of benthic, benthopelagic and reef-
83 associating fish can achieve protection from predators by living on or close to the sea bed and
84 structurally complex habitats such as coral reefs. However, these species often have an earlier
85 pelagic developmental phase until they are of sufficient size to recruit into benthic or reef habitats
86 (23). For fully pelagic species, schooling behaviour is a common anti-predator adaptation which
87 typically begins after fin formation is complete, early in their development (24). There is currently
88 little evidence that early life stages of demersal fish employ schooling behaviour in a similar way (24).
89 Conversely, they are often found in association with jellyfish (12,17) or floating or static objects in
90 the ocean. This tendency suggests that benthic and benthopelagic fish have evolved an alternative
91 adaptive strategy against predation in the form of jellyfish association, where the jellyfish acts as a
92 structured refuge in the pelagic habitat, before recruitment to other, e.g. benthic habitats. If anti-

93 predator schooling behaviour in benthic, benthopelagic and reef associating fish is less common than
94 in fully pelagic species, then the former species should gain a greater evolutionary advantage from
95 displaying jellyfish association than pelagic species.

96 Here, we test the hypothesis that jellyfish association was more likely to evolve in benthic,
97 benthopelagic and reef-associating species (broadly defined here as demersal type fishes), than in
98 species adapted to other marine habitats. To do this we compiled a global scale dataset of jellyfish-
99 fish associations to date and used phylogenetic comparative approaches, better suited to unravel
100 generality of patterns and processes than studies based on one or few species (25,26). The
101 hypothesis predicts that association with jellyfish and demersal type – are more likely to be found
102 together than not (i.e. positively correlated). However, it is silent with regard to how pelagic non-
103 associating fish species have evolved into demersal type associating ones, and so whether they first
104 evolved demersal type and next association with jellyfish, or the opposite. Our phylogenetic
105 comparative approach specifically investigated which evolutionary pathway appeared more likely.

106 **Methods**

107 **Data collection**

108 Following Castro et al. (12), we defined fish-jellyfish association as a close spatial relationship
109 between a larval or juvenile fish with gelatinous zooplankton species ('jellyfish') that span the Phyla
110 Cnidaria (Class Scyphozoa, Cubozoa and Hydrozoa), Chordata (Class Thaliacea), and Ctenophora. We
111 conducted a literature search in Web of Science using English keywords such as 'jellyfish fish
112 association' and 'gelatinous zooplankton AND juvenile fish' to collate a list of fish species observed
113 as associating with jellyfish during early developmental stages. Information on associating species
114 was then extracted from peer-reviewed primary and review publications, and supplemented with
115 data from unpublished datasets, personal observations and museum collections. To test whether
116 fish that associate with jellyfish were more likely to be demersal type, we also needed to include

117 species in the dataset that are not known to associate with jellyfish and for which information on
118 lifestyle was available. To this end we collected data on lifestyle (see below) for a randomly selected
119 sample of fish species, which were not known to associate with jellyfish but that belong to the same
120 families of those that do, leading to a total sample size of 145 fish species with and without
121 associations with jellyfish. We extracted lifestyle data from online databases (27) on whether each
122 species in our dataset was benthic, benthopelagic or reef associating ('demersal') or fully pelagic
123 ('pelagic').

124 The absence of an observed association between a given fish species and jellyfish in the literature
125 may reflect either the true absence of such an association in nature, or the fact that it has not been
126 observed yet, leading to a misclassification of some fish species. To account for this issue, we
127 employed the commonly used procedure of using number of citations in WoS for a given species as
128 a measure of the research intensity on that species (28–30), under the expectation that highly
129 studied species should be more likely to be correctly classified as not associating with jellyfish. From
130 our full dataset (n=145 fish species) we then excluded 'non-associating' fish species with fewer than
131 10 citations (remaining species: n=130 fish species) or fewer than 25 citations (remaining species:
132 n=119) as potentially misclassified. Results of all analyses were highly consistent between the two
133 reduced data sets, suggesting that they are robust to sampling. Here we present results from the
134 larger dataset of 130 taxa (jellyfish associating and demersal n=43, associating and pelagic n=18, non-
135 associating and demersal n=51, non-associating and pelagic n=18). The dataset is available as
136 Supplementary File 1. Finally, we coded each fish species for two behavioural traits: association with
137 jellyfish (Yes=1/No=0) and lifestyle (Pelagic=0/Demersal=1).

138 Evolutionary history of fish-jellyfish association

139 We first investigated the evolutionary history of the association with jellyfish and lifestyle separately
140 to assess how frequently each trait evolved and was lost over time across the phylogeny. We thus
141 ran ancestral state reconstructions for discrete data in maximum likelihood, using the R package

142 'ape' (31) and a comprehensive fish phylogeny (32) (see Supplementary File 2). This analysis
143 estimates the likely character states of ancestors in the phylogeny and the rates of transitions
144 between states across the whole tree (i.e. the rate of gain and losses) (25,33). We fitted two
145 alternative evolutionary models to the data; one in which the rate of gain and rate of loss were the
146 same (Equal Rate model - ER), thus estimating one parameter (i.e. the rate of change), and the other
147 in which the rates of gain and losses could differ, estimating two rate parameters (All Rates Different
148 model - ARD). We then assessed the fit to the data of these two alternative models using a likelihood
149 ratio test with degrees of freedom (DF) equalling the difference in the number of estimated
150 parameters of the two competing models (here $df = 1$) (33).

151 Independent and dependent models of evolution

152 We tested whether associating with jellyfish was evolutionary correlated with lifestyle using
153 maximum likelihood estimation and the programme *BayesTraits* V.3 (34). Specifically, we compared
154 the fit to the data of two alternative evolutionary models: the Independent Model of evolution
155 where jellyfish association and lifestyle evolve independently of each other, and the Dependent
156 Model of evolution in which they evolve in a correlated fashion (33). The independent model
157 estimates four parameters (the rates of gain and losses for each of the two traits independently),
158 while the dependent model estimates eight parameters which are the transition rates among the
159 four combination of character states that the two traits can jointly take (i.e. non-associating pelagic
160 0/0, non-associating demersal 0/1, associating pelagic 1/0, and demersal associating 1,1; see Figure
161 4). We used a likelihood ratio test with four degrees of freedom to assess which model fitted the
162 data significantly better. If the LR test is significant, this indicates that the dependent model had a
163 significantly better fit to the data, and so the two traits are evolutionary correlated. The dependent
164 model of evolution can also reveal the evolutionary pathway through which two traits have evolved
165 together, and so whether the evolution of one trait precedes and facilitates the evolution of the
166 other (33). Specifically, should the dependent model provide a better fit to the data, the examination

167 and comparison of the magnitude of the transition rates between the four combination of character
168 states of the two traits can reveal whether associating with jellyfish in demersal fish species
169 (condition 1,1, see Figure 4) evolved from non-associating pelagic fish (condition 0,0) by gaining first
170 a demersal lifestyle (transition rates q_{12} to condition 0,1, see Figure 4) and subsequently the
171 association with jellyfish (transition rates q_{24}), or the other way round (transition rates q_{13} to
172 condition 1,0, see Figure 4). Thus, if one evolutionary pathway is more likely, this indicates that the
173 trait evolving first is more likely to promote the evolution of the other, which is evidence consistent
174 with causation (33). Conversely, if the dependent model provides a better fit than the independent
175 model but both evolutionary pathways exhibit transition rates of equal magnitude, we can infer that
176 the two traits are evolutionary correlated but there is no specific evolutionary (causal) pathway.

177 The analysis with dependent and independent models was run in triplicates and all runs produced
178 identical results to the third decimal place for the model fit and all parameter estimates, suggesting
179 that the analysis consistently converged on the same maximum likelihood estimates and are robust.

180 **Results**

181 **Fish-jellyfish associations in the literature**

182 In the literature we found 173 instances of specific fish-jellyfish associations from across the globe,
183 involving 86 species of fish spanning 24 families and 84 jellyfish taxa. Fish species from the
184 Carangidae family were most numerous (n=28) followed by the Centrolophidae, Nomeidae and
185 Monacanthidae families (n=11, n=8 and n=7 respectively) (Figure 2a).

186 Of all the jellyfish-fish associations, the Atlantic bumper (*Chloroscrombrus chrysurus*) and shrimp
187 scad (*Alepes djedaba*), both from the family Carangidae, associated with the most diverse range of
188 jellyfish species (both n=9), while *Cyanea capillata* and *Aurelia aurita* were the most common jellyfish
189 species for which fish-jellyfish associations were recorded (Figure 2b). Indeed, fish associating with

190 *Cyanea sp.* accounted for 12.5% of the total associations documented. Demersal type fish species
191 were recorded in 57% (n=49) of associations, with the remainder classified as fully pelagic (43%,
192 n=37).

193 Evolutionary history of fish-jellyfish association and lifestyle

194 An ARD model for the association with jellyfish did not improve the fit to the data relative to an ER
195 model (LR=2.12, df = 1, p=0.15), thus gains and losses of the association with jellyfish occurred at
196 equal rates (0.034 ± 0.001) across the fish phylogeny. The ER model estimated at least two gains and
197 seven losses of associations with jellyfish throughout the tree (Figure 3a). Conversely, the ARD model
198 for lifestyle better fitted the data relative to the ER model (LR=7.34, df = 1, p=0.007), and indicated
199 that the transition rate from demersal to pelagic was significantly lower than the reverse (demersal
200 to pelagic: 0.004 ± 0.001 ; pelagic to demersal: 0.013 ± 0.004). This model identified at least five
201 evolutionary origins and nine losses of the demersal lifestyle among the recent ancestors of extant
202 fish species (Figure 3b).

203 Correlated evolution between fish-jellyfish association and lifestyle

204 The analysis of correlated evolution between lifestyle and association with jellyfish revealed that
205 these two traits evolved in a correlated fashion for the sample of fish species of our dataset, as the
206 dependent model of evolution fitted the data better than the independent model (LR = 9.72, df = 4,
207 p=0.045). The dependent model also estimated that from a condition of no association and pelagic
208 lifestyle (0,0), the association with jellyfish was gained first while the gain of a demersal type lifestyle
209 in the absence of association with jellyfish was estimated to be 0 (association first: $q_{13}=4.52$;
210 demersal first: $q_{12}=0$; Figure 4). Once pelagic fish evolved an association with jellyfish (1,0), a
211 demersal lifestyle was gained quickly ($q_{34} = 8.13$; Figure 4). This finding suggests that associating with
212 jellyfish may be an important driver that facilitated the evolution of a demersal lifestyle. Finally, the
213 dependent model showed that a demersal lifestyle without association with jellyfish (0,1) was likely

214 to evolve from associating demersal fish (1,1) by losing the association with jellies while retaining a
215 demersal lifestyle ($q_{42}=9.78$); however, this condition was highly likely to be reverted by regaining
216 the association with jellyfish ($q_{24}=5.15$) (Figure 4). Thus, the combined ‘associating’ and ‘demersal’
217 character state (1,1) was relatively evolutionary stable.

218 Discussion

219 We tested the hypothesis that jellyfish association was more likely to evolve in benthic,
220 benthopelagic and reef-associating species than species adapted to other marine habitats. We find
221 support for this idea and show that both demersal type lifestyle and association with jellyfish traits
222 have been gained and lost multiple times across the fish phylogeny. However, our analysis revealed
223 that associating with jellyfish is more likely to be one evolutionary driver of adapting to a demersal
224 lifestyle, rather than its evolutionary consequence as we find that fish-jellyfish association is very
225 likely to precede, not follow, the evolution of a demersal lifestyle. This pattern is perhaps not
226 surprising given that predation pressure is extremely high when larvae and juveniles are in the water
227 column (35,36). If the demersal fish lifestyle trait evolved first, but without the predatory defence
228 mechanisms of jellyfish association or schooling, they would presumably face a very high risk of
229 mortality. Larval mortality in fish is strongly size-related: modelling studies suggest that a significant
230 proportion (56%-99%) of total larval mortality occurs before a critical size is achieved (fish total
231 length), after which mortality due to predation decreases sharply (35). Thus, pre-settlement benthic
232 or reef fish that lack schooling behaviour as anti-predator strategy (24) should be under intense
233 selection to evolve or retain alternative adaptations that allow them to survive the high predation
234 levels in the upper water column. Our analysis shows that associating with jellyfish might play an
235 important evolutionary role in this context. Jellyfish offer a complex three-dimensional structure that
236 provides juvenile fish with a refuge in an environment that is otherwise remarkably devoid of physical
237 habitat (37). The presence of such physical structure has been linked strongly to increased larval
238 recruitment in fishes (38). Our findings suggest that it is more likely that the association with jellyfish

239 evolves in pelagic species prior to the evolution of a demersal lifestyle. Therefore, other evolutionary
240 drivers, rather than antipredator strategies in non-schooling juvenile fish, have promoted the
241 evolutionary origin of jellyfish association in pelagic fishes. To investigate jellyfish association
242 evolutionary drivers further, future studies should explore how fully benthic, reef-associating and
243 benthopelagic fish as individual groups evolved with regard to the association with jellyfish given the
244 potential for different evolutionary pathways leading to jellyfish association, once more data become
245 available for a larger number of species.

246 While Mansueti (17) noted how only a very small proportion of pelagic fish globally are reported as
247 displaying associative behaviour, the implication of dismissing the potential impact of such
248 behaviours for the fishing industry may be great, considering over 72% of the jellyfish associating fish
249 species in this study are of commercial value. Unlike benthic fishes, pelagic fish can rely on schooling
250 to reduce predation risk when juveniles. We suggest that one potential driver of jellyfish associations
251 is the enormous potential as a food source that jellyfish represent for juvenile fish, especially
252 considering that jellyfish can often form large aggregations (39). Although jellyfish have a low
253 calorific value compared to other prey items, their gonads can be very large, representing over 20%
254 of their total body in some species and have higher energetic content than bell or oral arm tissues
255 (40). Indeed, a recent study has revealed that jellyfish represent a highly rewarding food source to
256 commercial fish (*Boops boops*) (41). In our dataset, many jellyfish associating species are carangids,
257 a large and diverse family considered among the most economically important fishes in the world
258 (42). The ability to exploit jellyfish as trophic resource may therefore offer a huge advantage to the
259 growth and survival of both demersal type and pelagic juvenile fishes.

260 Our ancestral state reconstruction showed that associating with jellyfish in extant fishes is likely to
261 have independently evolved multiple times across the fish phylogeny. We propose that the
262 evolutionary cost of evolving the suite of adaptations required to associate with jellyfish is small (i.e.
263 ability to locate and move close to jellyfish host for protection and realising opportunistic food

264 acquisition opportunities). Furthermore, the immediate costs of associating with jellyfish (e.g. risk of
265 injury/death from jellyfish nematocyst stings) are likely less than the consequences of not doing so;
266 namely an increased predation risk and decreased food opportunities. Indeed, even momentary
267 disturbances in fish-jellyfish associations that caused juvenile scads (*Trachurus lathami*) to desert
268 their jellyfish hosts, resulted in immediate predation by grouper (*Mycteroperca acutirostris*) (43).

269 Our study highlights how large-scale comparative approaches can be used to answer important
270 questions on the evolutionary ecology of fish-jellyfish associations, at least from the perspective of
271 the fish. To fully understand the evolution of these associations however, we need to also study how
272 such associations evolved from the perspective of the jellyfish and their characteristics. Our study
273 has revealed that some jellyfish taxa are in fact far more frequently involved in fish-jellyfish
274 associations than others. Thus, future studies could investigate whether the frequency of
275 associations of juvenile fish with different jellyfish species reflect the relative abundance of different
276 jellyfish species and distribution worldwide, or are determined by the jellyfish morphological
277 characteristics, such as size, volume, tissue complexity or strength of nematocyst sting, that make it
278 more likely for fish to associate with them. Jellyfish morphology varies hugely, from micro-through
279 to macro-zooplankton species weighing >200kg (e.g. *Nemopilmea nomurai*), so their potential for
280 providing shelter against predators and food resources should be very different (44). Furthermore,
281 jellyfish also differ in swimming mode, foraging and feeding strategies; traits that could elucidate the
282 role and importance of food acquisition in fish-jellyfish associations. Specifically the two main
283 foraging modes that jellyfish exhibit, ambush or cruise predators, result in interspecific dietary
284 differences (45) and may influence the success of associating juvenile fish that take advantage of
285 prey entrained in the pulse of the jellyfish or prey captured in the tentacles. To address these
286 questions over large comparative scale and exploit powerful phylogenetic comparative methods to
287 reveal generality of principles, we urgently need to build comprehensive jellyfish phylogenies and
288 collect data on a variety of jellyfish characteristics, including whether juvenile associating fish also
289 associate with non-gelatinous Floating Aggregating Devices (FADs) or floating objects. A number of

290 jellyfishes associating fish species identified by Castro et al. (12) were also documented as associating
291 with FADs or drift objects and it is possible that they may gain similar benefits from these types of
292 association to some degree such as the redistribution of food and a change in the behaviour of
293 predators (46). However, jellyfish precede human flotsam and FADs by millions of years and could
294 provide better or additional protection from predators by way of deterrence, as predators seek to
295 avoid their nematocyst stinging cells (17). Furthermore, jellyfish may provide a greater range of
296 indirect feeding opportunities by actively hunting for food which is subsequently stolen by
297 associating fish before ingestion as well as direct feeding opportunities via their energy rich gonads
298 (40). Thus, when appropriate data for a large number of fish species become available, we can
299 explore intricate ecological and evolutionary questions such as whether jellyfish are a uniquely
300 important habitat for juvenile fish, or whether they are just one of the many floating structures in
301 the sea which act as potential shelter and source of food for juvenile fishes, using phylogenetic
302 comparative approaches as shown in this study.

303 Together with recent studies (47–49), our findings suggest that jellyfish have important evolutionary
304 and ecological roles such as providing shelter from predators and trophic resources to juvenile fish,
305 an ecological service with huge implications for the population dynamics and long term persistence
306 of marine fish biodiversity. Here we propose the term ‘gingerbread house’ interaction from classic
307 folklore (i.e. a house you can eat) to describe the specific coaction whereby juvenile fish benefit from
308 the positive impacts offered to them via their association with jellyfish; shelter and food. Considering
309 that pressure on fin-fish stocks is increasing globally and that 72% of the fish species identified in our
310 study as displaying this association are economically important, understanding how and why fish-
311 jellyfish associations evolved we advocate further research to quantify the exact benefits of jellyfish
312 to juvenile fish recruitment.

313 **Competing interests**

314 The authors have no competing interests.

315 **Authors' contributions**

316 Funding DG, CH, IC and JDRH conceived the idea of the study. DG and IC undertook analyses. DG
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467 **Figures**

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469 Figure 1. Examples of juvenile fish swimming associating with jellyfish; (a) juvenile Atlantic horse mackerel (*Trachurus*
470 *trachurus*) around the oral arms of a large *Rhizostoma octopus* jellyfish off the South England coast, (b) juvenile gadoids
471 shelter among the oral arms and tentacles of a compass jellyfish (*Chrysaora hysoscella*) in Irish coastal waters, (c) a single
472 juvenile gadoid swimming above the bell of a blue jellyfish (*Cyanea lamarcki*) off the Isle of Man and, (d) three juvenile
473 gadoids camouflaged (shown above by red asterisk) against the frilly oral arms of a compass jellyfish (*Chrysaora hysoscella*)
474 off the North East coast of Ireland (photos courtesy of (a) Steve Trewhalla, (b) Sarah Tallon, (c) Sarah Bowen, and (d) Karen
475 Patterson).

476 Figure 2. (a) The carangids, a family of fish which includes the jacks, pompanos, jack mackerels, runners and scads, are the
477 most numerous with 28 individual species reported in the literature as displaying associative behaviour with jellyfish, (b) a
478 broad range of jellyfish, including medusa and non-true jellyfishes such as ctenophores and salps, are involved in fish-
479 jellyfish associations (n=64). While *Cyanea capillata*, *Aurelia aurita*, *Stomolophus meleagris* and *Nemopilema nomurai* are
480 the most widely reported species involved in these associations around the world, together accounting for 33.1% of the
481 individual instances of fish-jellyfish associations in the literature, most associations are from single observations of specific
482 interactions.

483 Figure 3. Evolutionary history of fish-jellyfish association (a) and demersal type versus pelagic lifestyle (b) in a sample of
484 130 fish species as estimated using Maximum Likelihood. In (a) the ancestral state reconstruction of fish associative

485 behaviour based on the Equal Rate model identifies at least 7 evolutionary losses and 2 evolutionary gains of association
486 with jellyfish (associative behaviour with jellyfish is coded as black, non-associative as grey). In (b) the ancestral state
487 reconstruction of lifestyle based on the All Rates Different model identifies at least 9 evolutionary events whereby the
488 demersal lifestyle is likely lost and 5 gains (demersal is coded in black, pelagic in grey). In both (a) and (b) the area of the
489 pie for the internal nodes is coloured in proportion of the probability that a node takes either of the two alternative states
490 for the tested trait.

491 Figure 4. Dependent model of correlated evolution for the combined traits of association with jellyfish lifestyle. The
492 arrows indicate the direction of change between the 4 possible combination of character states, with the arrow thickness
493 proportional to the magnitude of transition rates estimated by the model (also reported as number). Transition rates
494 estimated to be equal to 0 are indicated with dotted lines. Sample size of species by combination of character states as
495 used in the analysis (jellyfish association and demersal type or pelagic): (0,0) n=18, (0,1) n=51, (1,0) n=18 and (1,1) n=43.
496 Sample size of species by combination of character states based on lifestyle; associating and pelagic n=18, non-
497 associating and pelagic n=18, associating and benthic n=8, non-associating and benthic n=26, associating and reef
498 associating n=21, non-associating and reef associating n=16, associating and benthopelagic n=14, non-associating and
499 benthopelagic n=9.

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