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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'**

3   Donal C. Griffin[a], Chris Harrod[b,c], Jonathan D.R. Houghton[a], Isabella Capellini[d, e]

4   [a] School of Biological Sciences, Queen's University of Belfast, Belfast, Northern Ireland, United

5   Kingdom

6   [b] Universidad de Antofagasta, Fish and Stable Isotope Ecology Laboratory, Instituto de Ciencias

7   Naturales Alexander von Humbolt, Avenida Angamos, 601 Antofagasta, Chile.

8   [c] Núcleo Milenio INVASAL, Concepción, Chile

9   [d] Institute of Energy and Environment, University of Hull, Hull, HU6 7RX United Kingdom

10   [e] Department of Biological and Marine Sciences, University of Hull, Hull, HU6 7RX United Kingdom

11   Corresponding author: Jonathan D.R. Houghton (j.houghton@qub.ac.uk)

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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

Introduction

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

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

However, jellyfish also provide habitat for juvenile fishes in what is generally considered a facultative symbiotic relationship (Fig. 1), and greater food acquisition opportunities for the fish is often cited as an important causal factor in the formation of such interactions (12,13). Juvenile fish can feed on the zooplankton entrained by jellyfish swimming pulses or captured on their tentacles, or even on 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-

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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).

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.

Results

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 presumable 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

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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.

Authors' contributions

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

317   led the writing of the manuscript supported by IC, JDRH and CH.

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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

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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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(a)   (b)