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

Donal C. Griffin\(^a\), Chris Harrod\(^{b,c}\), Jonathan D.R. Houghton\(^a\), Isabella Capellini\(^d\).

\(^a\) School of Biological Sciences, Queen’s University of Belfast, Belfast, Northern Ireland, United Kingdom

\(^b\) Instituto de Ciencias Naturales Alexander von Humbolt & Instituto Antofagasta, Universidad de Antofagasta, Avenida Angamos, 601 Antofagasta, Chile.

\(^c\) Núcleo Milenio INVASAL, Concepción, Chile

\(^d\) Institute of Energy and Environment, University of Hull, Hull, HU6 7RX United Kingdom

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

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

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

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

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

**Methods**

**Data collection**

Following Castro et al. (12), we defined fish-jellyfish association as a close spatial relationship between a larval or juvenile fish with gelatinous zooplankton species (‘jellyfish’) that span the Phyla Cnidaria (Class Scyphozoa, Cubozoa and Hydrozoa), Chordata (Class Thaliacea), and Ctenophora. We conducted a literature search in Web of Science using English keywords such as ‘jellyfish fish association’ and ‘gelatinous zooplankton AND juvenile fish’ to collate a list of fish species observed as associating with jellyfish during early developmental stages. Information on associating species was then extracted from peer-reviewed primary and review publications, and supplemented with data from unpublished datasets, personal observations and museum collections. To test whether fish that associate with jellyfish were more likely to be demersal type, we also needed to include species in the dataset that are not known to associate with jellyfish and for which information on lifestyle was available. To this end we collected data on lifestyle (see below) for a randomly selected
sample of fish species, which were not known to associate with jellyfish but that belong to the same families of those that do, leading to a total sample size of 145 fish species with and without associations with jellyfish. We extracted lifestyle data from online databases (27) on whether each species in our dataset was benthic, benthopelagic or reef associating ('demersal') or fully pelagic ('pelagic').

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

Evolutionary history of fish-jellyfish association

We first investigated the evolutionary history of the association with jellyfish and lifestyle separately to assess how frequently each trait evolved and was lost over time across the phylogeny. We thus ran ancestral state reconstructions for discrete data in maximum likelihood, using the R package ‘ape’ (31) and a comprehensive fish phylogeny (32) (see Supplementary File 2). This analysis estimates the likely character states of ancestors in the phylogeny and the rates of transitions
between states across the whole tree (i.e. the rate of gain and losses) (25,33). We fitted two alternative evolutionary models to the data; one in which the rate of gain and rate of loss were the same (Equal Rate model - ER), thus estimating one parameter (i.e. the rate of change), and the other in which the rates of gain and losses could differ, estimating two rate parameters (All Rates Different model - ARD). We then assessed the fit to the data of these two alternative models using a likelihood ratio test with degrees of freedom (DF) equalling the difference in the number of estimated parameters of the two competing models (here df = 1) (33).

Independent and dependent models of evolution

We tested whether associating with jellyfish was evolutionary correlated with lifestyle using maximum likelihood estimation and the programme *BayesTraits* V.3 (34). Specifically, we compared the fit to the data of two alternative evolutionary models: the Independent Model of evolution where jellyfish association and lifestyle evolve independently of each other, and the Dependent Model of evolution in which they evolve in a correlated fashion (33). The independent model estimates four parameters (the rates of gain and losses for each of the two traits independently), while the dependent model estimates eight parameters which are the transition rates among the four combination of character states that the two traits can jointly take (i.e. non-associating pelagic 0/0, non-associating demersal 0/1, associating pelagic 1/0, and demersal associating 1,1; see Figure 4). We used a likelihood ratio test with four degrees of freedom to assess which model fitted the data significantly better. If the LR test is significant, this indicates that the dependent model had a significantly better fit to the data, and so the two traits are evolutionary correlated. The dependent model of evolution can also reveal the evolutionary pathway through which two traits have evolved together, and so whether the evolution of one trait precedes and facilitates the evolution of the other (33). Specifically, should the dependent model provide a better fit to the data, the examination and comparison of the magnitude of the transition rates between the four combination of character states of the two traits can reveal whether associating with jellyfish in demersal fish species (condition 1,1, see Figure 4) evolved from non-associating pelagic fish (condition 0,0) by gaining first
a demersal lifestyle (transition rates $q_{12}$ to condition 0,1, see Figure 4) and subsequently the
association with jellyfish (transition rates $q_{24}$), or the other way round (transition rates $q_{13}$ to
condition 1,0, see Figure 4). Thus, if one evolutionary pathway is more likely, this indicates that the
trait evolving first is more likely to promote the evolution of the other, which is evidence consistent
with causation (33). Conversely, if the dependent model provides a better fit than the independent
model but both evolutionary pathways exhibit transition rates of equal magnitude, we can infer that
the two traits are evolutionary correlated but there is no specific evolutionary (causal) pathway.

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

Results

Fish-jellyfish associations in the literature

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

Of all the jellyfish-fish associations, the Atlantic bumper (Chloroscombrus chrysurus) and shrimp
scad (Alepse djedaba), both from the family Carangidae, associated with the most diverse range of
jellyfish species (both n=9), while Cyanea capillata and Aurelia aurita were the most common jellyfish
species for which fish-jellyfish associations were recorded (Figure 2b). Indeed, fish associating with
Cyanea sp. accounted for 12.5% of the total associations documented. Demersal type fish species
were recorded in 57% (n=49) of associations, with the remainder classified as fully pelagic (43%,
n=37).
Evolutionary history of fish-jellyfish association and lifestyle

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

Correlated evolution between fish-jellyfish association and lifestyle

The analysis of correlated evolution between lifestyle and association with jellyfish revealed that these two traits evolved in a correlated fashion for the sample of fish species of our dataset, as the dependent model of evolution fitted the data better than the independent model (LR = 9.72, df = 4, p=0.045). The dependent model also estimated that from a condition of no association and pelagic lifestyle (0,0), the association with jellyfish was gained first while the gain of a demersal type lifestyle in the absence of association with jellyfish was estimated to be 0 (association first: q₁₃=4.52; demersal first: q₁₃=0; Figure 4). Once pelagic fish evolved an association with jellyfish (1,0), a demersal lifestyle was gained quickly (q₃₁₄ = 8.13; Figure 4). This finding suggests that associating with jellyfish may be an important driver that facilitated the evolution of a demersal lifestyle for some fishes. Finally, the dependent model showed that a demersal lifestyle without association with jellyfish (0,1) was likely to evolve from associating demersal fish (1,1) by losing the association with jellies while retaining a demersal lifestyle (q₂₄=9.78); however, this condition was highly likely to be reverted by regaining the association with jellyfish (q₂₄=5.15) (Figure 4). Thus, the combined ‘associating’ and ‘demersal’ character state (1,1) was relatively evolutionary stable.
Discussion

We tested the hypothesis that jellyfish association was more likely to evolve in benthic, benthopelagic and reef-associating species than species adapted to other marine habitats. We find support for this idea and show that both demersal type lifestyle and association with jellyfish traits have been gained and lost multiple times across the fish phylony. However, our analysis revealed that associating with jellyfish is more likely to be one evolutionary driver of adapting to a demersal lifestyle, rather than its evolutionary consequence as we find that fish-jellyfish association is very likely to precede, not follow, the evolution of a demersal lifestyle. This pattern is perhaps not surprising given that predation pressure is extremely high when larvae and juveniles are in the water column (35,36). If the demersal fish lifestyle trait evolved first, but without the predatory defence mechanisms of jellyfish association or others such as schooling for example, they would presumable face a very high risk of mortality. Larval mortality in fish is strongly size-related: modelling studies suggest that a significant proportion (56%-99%) of total larval mortality occurs before a critical size is achieved (fish total length), after which mortality due to predation decreases sharply (35). Thus, pre-settlement benthic or reef fish that lack schooling behaviour as anti-predator strategy (24) should be under intense selection to evolve or retain alternative adaptations that allow them to survive the high predation levels in the upper water column. Our analysis showed that associating with jellyfish might play an important evolutionary role in this context. Jellyfish offer a complex three-dimensional structure that provides juvenile fish with a refuge in an environment that is otherwise remarkably devoid of physical habitat (37). The presence of such physical structure has been linked strongly to increased larval recruitment in fishes (38). Our findings suggest that it is more likely that the association with jellyfish evolves in pelagic species prior to the evolution of a demersal lifestyle. Therefore, other evolutionary drivers, rather than antipredator strategies in non-schooling juvenile fish, have promoted the evolutionary origin of jellyfish association in pelagic fishes. To investigate jellyfish association evolutionary drivers further, future studies should explore how fully benthic, reef-associating and benthopelagic fish as individual groups evolved with regard to the
association with jellyfish given the potential for different evolutionary pathways leading to jellyfish association, once more data become available for a larger number of species.

While Mansueti (17) noted how only a very small proportion of pelagic fish globally are reported as displaying associative behaviour, the implication of dismissing the potential impact of such behaviours for the fishing industry may be great, considering over 70% of the jellyfish associating fish species in this study are of commercial value. Unlike benthic fishes, pelagic fish can rely on schooling to reduce predation risk when they are juveniles. We suggest that one potential driver of jellyfish associations is the enormous potential as a food source that jellyfish represent for juvenile fish, especially considering that jellyfish can often form large aggregations (39). Although jellyfish have a low calorific value compared to other prey items, their gonads can be very large, representing over 20% of their total body in some species and have higher energetic content than bell or oral arm tissues (40). Indeed, a recent study has revealed that jellyfish represent a highly rewarding food source to commercial fish (Boops boops) (41). In our dataset, many jellyfish associating species are carangids, a large and diverse family considered among the most economically important fishes in the world (42). The ability to exploit jellyfish as trophic resource may therefore offer a huge advantage to the growth and survival of both demersal type and pelagic juvenile fishes.

Our ancestral state reconstruction showed that associating with jellyfish in extant fishes is likely to have independently evolved multiple times across the fish phylogeny. We propose that the evolutionary cost of evolving the suite of adaptations required to associate with jellyfish is small (i.e. ability to locate and move close to jellyfish host for protection and realising opportunistic food acquisition opportunities). The immediate costs of associating with jellyfish (e.g. risk of injury/death from jellyfish nematocyst stings) are likely less than the consequences of not doing so; namely an increased predation risk and decreased food opportunities. Furthermore, possible mechanisms for juvenile fish to evade the potential negative effects of jellyfish stinging cells include avoiding contact, resistance to nematocyst toxin and reduced nematocyst discharge due to mucus on the fish skin (43).
Whereas, even momentary disturbances in fish-jellyfish associations that caused juvenile scads (*Trachurus lathami*) to desert their jellyfish hosts, resulted in immediate predation by grouper (*Mycteroperca acutirostris*) (44).

Our study highlights how large-scale comparative approaches can be used to answer important questions on the evolutionary ecology of fish-jellyfish associations, at least from the perspective of the fish. To fully understand the evolution of these associations however, we need to also study how such associations evolved from the perspective of the jellyfish and their characteristics. Our study has revealed that some jellyfish taxa are in fact far more frequently involved in fish-jellyfish associations than others. Thus, future studies could investigate whether the frequency of associations of juvenile fish with different jellyfish species reflect the relative abundance of different jellyfish species and distribution worldwide, or are determined by the jellyfish morphological characteristics, such as size, volume, tissue complexity or strength of nematocyst sting, that make it more likely for fish to associate with them. Jellyfish morphology varies hugely, from micro through to macro-zooplankton species weighing >200kg (e.g. *Nemopilema nomurai*), so their potential for providing shelter against predators and food resources should be very different (45). Furthermore, jellyfish also differ in swimming mode, foraging and feeding strategies; traits that could elucidate the role and importance of food acquisition in fish-jellyfish associations. Specifically the two main foraging modes that jellyfish exhibit, ambush or cruise predators, result in interspecific dietary differences (46) and may influence the success of associating juvenile fish that take advantage of prey entrained in the pulse of the jellyfish or prey captured in the tentacles. To address these questions over large comparative scale and exploit powerful phylogenetic comparative methods to reveal generality of principles, we urgently need to build comprehensive jellyfish phylogenies and collect data on a variety of jellyfish characteristics, including whether juvenile associating fish also associate with non-gelatinous Floating Aggregating Devices (FADs) or floating objects. A number of jellyfish species identified by Castro et al. (12) were also documented as associating with FADs or drift objects and it is possible that they may gain similar benefits from these types of
association to some degree such as the redistribution of food and a change in the behaviour of predators (47). However, jellyfish precede human flotsam and FADs by millions of years and could provide better or additional protection from predators by way of deterrence, as predators seek to avoid their nematocyst stinging cells (17). Furthermore, jellyfish may provide a greater range of indirect feeding opportunities by actively hunting for food which is subsequently stolen by associating fish before ingestion as well as direct feeding opportunities via their energy rich gonads (40). Thus, when appropriate data for a large number of fish species become available, we can explore intricate ecological and evolutionary questions such as whether jellyfish are a uniquely important habitat for juvenile fish, or whether they are just one of the many floating structures in the sea which act as potential shelter and source of food for juvenile fishes, using phylogenetic comparative approaches as shown in this study.

Together with recent studies (48–50), our findings suggest that jellyfish have important evolutionary and ecological roles such as providing shelter from predators and trophic resources to juvenile fish, an ecological service with huge implications for the population dynamics and long term persistence of marine fish biodiversity. Here, we propose the ‘gingerbread house hypothesis’ from classic folklore (i.e. a house you can eat) to describe the specific coaction whereby juvenile fish gain both shelter and food shelter from jellyfish. Considering that pressure on fin-fish stocks is increasing globally, and that 72% of the associating fish species in our study are economically important, we advocate further research to quantify the overall benefit of jellyfish to fish recruitment over a range of scales.
Figures

Figure 1. Examples of juvenile fish swimming associating with jellyfish; (a) juvenile Atlantic horse mackerel (*Trachurus trachurus*) around the oral arms of a large *Rhizostoma octopus* jellyfish off the coast of Southern England, (b) juvenile gadoids shelter among the oral arms and tentacles of a compass jellyfish (*Chrysaora hysoscella*) in Irish coastal waters, (c) a single juvenile gadoid swimming above the bell of a blue jellyfish (*Cyanea lamarcki*) off the Isle of Man and, (d) three juvenile gadoids camouflaged (shown above by red asterisk) against the frilly oral arms of a compass jellyfish (*Chrysaora hysoscella*) off the northeast coast of Ireland (photos courtesy of (a) Steve Trewhalla, (b) Sarah Tallon, (c) Sarah Bowen, and (d) Karen Patterson).
Figure 2. (a) The carangids, a family of fish which includes the jacks, pompanos, jack mackerels, runners and scads, are the most numerous with 28 individual species reported in the literature as displaying associative behaviour with jellyfish, (b) a broad range of jellyfish, including medusa and non-true jellyfishes such as ctenophores and salps, are involved in fish-jellyfish associations (n=64). While *Cyanea capillata*, *Aurelia aurita*, *Stomolophus meleagris* and *Nemopilema nomurai* are the most widely reported species involved in these associations around the world, together accounting for 33.1% of the individual instances of fish-jellyfish associations in the literature, most associations are from single observations of specific interactions.
Figure 3. Evolutionary history of fish-jellyfish association (a) and demersal type versus pelagic lifestyle (b) in a sample of 130 fish species as estimated using Maximum Likelihood. In (a) the ancestral state reconstruction of fish associative behaviour based on the Equal Rate model identifies at least 7 evolutionary losses and 2 evolutionary gains of association with jellyfish (associative behaviour with jellyfish is coded as black, non-associative as grey). In (b) the ancestral state reconstruction of lifestyle based on the All Rates Different model identifies at least 9 evolutionary events whereby the 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 pie for the internal nodes is coloured in proportion of the probability that a node takes either of the two alternative states for the tested trait.

Figure 4. Dependent model of correlated evolution for the combined traits of association with jellyfish lifestyle. The arrows indicate the direction of change between the 4-possible combination of character states, with the arrow thickness proportional to the magnitude of transition rates estimated by the model (also reported as number). Transition rates estimated to be equal to 0 are indicated with dotted lines. Sample size of species by combination of character states as 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. Sample size of species by combination of character states based on lifestyle; associating and pelagic n=18, non-associating and pelagic n=18, associating and benthic n=8, non-associating and benthic n=26, associating and reef associating n=21, non-associating and reef associating n=16, associating and benthopelagic n=14, non-associating and benthopelagic n=9.

Competing interests

The authors have no competing interests.
Authors’ contributions

Funding DG, CH, IC and JDRH conceived the idea of the study. DG and IC undertook analyses. DG led the writing of the manuscript supported by IC, JDRH and CH.

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Data accessibility

Data presented here can be found in the supplementary material File 1. The Rabosky et al. (2013) phylogeny can be found as an excel worksheet in supplementary material file 2.

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