

Seafarers or castaways: ecological traits associated with rafting dispersal in tropical reef fishes

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ABSTRACT

Aim Rafting with natural flotsam is an important mechanism of long-distance oceanic dispersal for many near-shore marine organisms. Identifying the species-level traits associated with this behaviour would aid in understanding and predicting a species' capacity for dispersal between isolated areas of benthic habitat.

Location The tropical and subtropical Atlantic.

Methods We assessed the relationships between species-level traits (habitat use, position in water column, diet, body size, schooling activity) and rafting behaviour among 985 species of reef fish using generalized linear mixed-effect modelling. To assess whether the relationships between rafting behaviour and species traits were mediated by raft type, our analysis included interactions between raft type and our predictor variables.

Results The following species-level traits are positively associated with rafting for reef fishes: (1) position in water column above reef substratum, which indicates a species' dependency on the substratum; (2) schooling behaviour, a trait linked to predation avoidance; (3) large adult size, which may be associated with enhanced survivorship and growth of rafting juveniles; and (4) broad habitat use, which may facilitate use of atypical habitats, including flotsam. Some correlations varied depending on the type of flotsam – broad habitat use is only positively correlated with the use of seaweed rafts, which may resemble patches of benthic macroalgal and seagrass beds that the reef fishes often use as ancillary habitat. In contrast, schooling behaviour is only positively correlated with rafting among logs and similar objects, perhaps because they represent poor refuges from predation.

Main conclusions A species' propensity to use rafts is associated with specific ecological traits, some of which are contingent on characteristics of the raft. Thus, our findings suggest that increasing amounts of man-made flotsam entering the ocean may differentially influence future rafting opportunities among tropical reef fishes, depending on their traits, which may have important implications for their biogeographical distributions.

Keywords

Atlantic Ocean, debris, floating seaweed, flotsam, logs, long-distance dispersal, pelagic environment, *Sargassum*, tropical reef fish

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INTRODUCTION

Rafting – the passive transport of organisms in association with flotsam – has been observed in diverse taxa, including

fishes, sessile aquatic organisms (e.g. barnacles and corals) and terrestrial vertebrates such as lizards and small mammals (Thiel & Gutow, 2005a; de Queiroz, 2014). Among terrestrial taxa, rafting dispersal is well known to influence the

composition of island communities (Thornton, 2007), and is increasingly recognized as a driver of geographical distributions for species of animals and plants (de Queiroz, 2005, 2014; Rowe *et al.*, 2010; Gillespie *et al.*, 2012). By contrast, among marine taxa, including reef fishes, few studies have investigated the effect of rafting on species' geographical distributions.

For fishes, rafting involves aggregating around flotsam, a behaviour observed among the pelagic species by fishermen many centuries ago (Dempster & Taquet, 2004). However, many species of reef fishes as well as the pelagic fishes have been recorded in association with flotsam rafts (Castro *et al.*, 2002). Flotsam may function as a habitat substitute for fish in transition from a pelagic to a demersal life stage (Hunter & Mitchell, 1967), acting as a nursery refuge for juvenile reef fishes that have not yet located the reef habitat at the end of the pelagic-larval stage (Kingsford, 1993; Wells & Rooker, 2004).

Large expanses of open ocean represent essentially impassable barriers to terrestrial and near-shore marine organisms that are unable to survive in the pelagic realm, or that have either no pelagic dispersal stage or one of short duration (Lessios & Robertson, 2006; Kleiber *et al.*, 2011). For reef fishes, rafts can provide a suitable substratum at the stage when they would normally settle into benthic habitats, and thus can potentially enhance the probability of long-distance dispersal (Mora *et al.*, 2001; Robertson *et al.*, 2004). Successful colonization depends, in part, on a sufficiently large number of individuals arriving simultaneously at one location (Thornton, 2007), the chance of which decreases with the increasing distance for pelagic-larval dispersal (Cowen *et al.*, 2006). Consequently, given that rafting provides a mechanism by which several conspecifics can arrive simultaneously at a new location (Teske *et al.*, 2005), rafting of juveniles may provide a more effective means of colonizing remote areas than larval dispersal alone. Thus, rafting may facilitate the gene flow between otherwise isolated marine populations, and thereby connect the populations separated by large stretches of open ocean (Thiel & Haye, 2006; Nikula *et al.*, 2013).

Despite the potential importance of rafting dispersal to the biogeography of reef fishes, we have a poor understanding of the factors that influence its prevalence. In particular, the probability of successful colonization via rafting may be influenced by species-specific traits that facilitate the use of flotsam. Alternatively, if all organisms are similarly adapted to being rafters, then the species that make use of flotsam for dispersal should be a random subset of the regional species pool.

Several hypotheses have been proposed to explain the association of fishes with rafts. Flotsam may function as a substitute substratum for reef-associated species that are poorly adapted to a pelagic life or that undergo a change from a pelagic to a benthic mode of existence (Hunter & Mitchell, 1967). It may also offer refuge from predators by providing shelter or by serving as a form of predation

interference (e.g. camouflage; Gooding & Magnuson, 1967; Hunter & Mitchell, 1967; Castro *et al.*, 2002). The flotsam may also directly serve as a food source (e.g. seaweed) or as habitat for potential prey (e.g. invertebrates, small fishes; Gooding & Magnuson, 1967; Castro *et al.*, 2002). Finally, the presence of flotsam may aid the fish in finding food sources even if the flotsam itself provides no resources. The 'indicator-log' hypothesis, for example, proposes that fishes are attracted to rafts because they originate in and remain within resource-rich areas (i.e. river mouth, mangrove swamps) or aggregate in frontal zones and convergences where planktonic food accumulates (Franks, 1992; Castro *et al.*, 2002).

Characteristics of different types of flotsam may determine the assemblages of organisms that they transport (Thiel & Gutow, 2005a; Bravo *et al.*, 2011). The most common materials found in the flotsam today are seaweeds, wood, seeds, terrestrial plants, volcanic pumice, and plastic litter (Thiel & Gutow, 2005a). Seaweeds typically harbour a diverse fauna of grazing invertebrates that feed on seaweed substrata (Thiel & Gutow, 2005a). Floating seaweeds, especially *Sargassum* in the North Atlantic (cf. the Sargasso Sea), can form thick, highly structured mat aggregations that provide food to a diverse assemblage of organisms. By contrast, individual flotsam items, such as logs, driftwood and plastic litter, are not food sources for their fish passengers, but may harbour a fouling community that fish can feed upon. These items are smaller and less structured than seaweed mats, and generally accommodate a less diverse assemblage of associated invertebrates and fishes (Coston-Clements *et al.*, 1991; Moser *et al.*, 1998; Casazza & Ross, 2008). While the role of material type in determining suitability for rafting is fairly well known for marine invertebrates (Thiel & Gutow, 2005a), this is not the case for demersal fishes, particularly with respect to man-made flotsam (Bravo *et al.*, 2011; Goldstein *et al.*, 2014).

In the past few decades, various types of man-made flotsam, comprising mainly plastic waste and derelict fishing gear, have become increasingly abundant in the sea (Barnes, 2002; Barnes *et al.*, 2009). Today, in many regions, plastic waste is by far the most common man-made item in the flotsam (Riera *et al.*, 1999; Barnes, 2002). Floating plastic debris accumulates along large-scale convergences in surface currents, forming immense garbage patches in the major oceanic subtropical gyres in the north-west Atlantic and in the north-east Pacific (Cózar *et al.*, 2014). Many plastic objects enclose large volumes of air, are extremely resistant to decay (Bravo *et al.*, 2011), and remain buoyant for much longer than natural flotsam. Consequently, plastic objects may travel far longer distances, and thus may provide much greater dispersal opportunities for rafters (Barnes, 2002). As a result, marine organisms capable of using man-made flotsam may now be experiencing unprecedented rates of dispersal.

There is solid evidence that marine invertebrate species that are capable of rafting share some common traits (Thiel & Gutow, 2005b). Among amphipods and copepods, species that are generalists in terms of diet and habitat preferences often dominate rafting communities (Vandendriessche *et al.*,

2006). Moreover, the diets of dominant species tend to vary among raft types. Suspension feeders dominate abiotic rafts, whereas grazers and borers proliferate on seaweed and wood, respectively (Thiel, 2003). However, among fish, hypotheses put forward to explain associations with flotsam are generally based on circumstantial evidence such as occasional observations (Gooding & Magnuson, 1967; Rountree, 1989; Castro *et al.*, 2002). A rigorous test of alternative hypotheses and mechanisms for rafting among fish would involve applying a trait-based approach to a comprehensive data set on the use of flotsam by different taxa.

Here, we aim to achieve a better understanding of the factors influencing rafting dispersal by reef fish, and the long-term probability for their range expansion between isolated areas of benthic habitat, by analysing data compiled on the use of flotsam by 985 species. In this analysis, we address the following question: are fish rafters more like seafarers, which possess special traits that facilitate long oceanic journeys, or more like castaways, that represent a random subset of species marooned by chance in the flotsam? To do so, we examined rafting propensity in relation to five previously proposed species-level traits: (1) habitat breadth (Vandendriessche *et al.*, 2006); (2) species position in water column, which indicates a species dependency on the substratum (Hunter & Mitchell, 1967); (3) schooling behaviour (Castro *et al.*, 2002); (4) maximum adult body size (Gooding & Magnuson, 1967); and (5) diet (Gooding & Magnuson, 1967; Castro *et al.*, 2002; Thiel & Gutow, 2005a). In addition, we assessed what role the raft type might play in mediating correlations between rafting propensity and species traits by examining relationships with seaweed flotsam versus single-object flotsam items (e.g. logs, buoys).

MATERIALS AND METHODS

Data collection

Our analysis was conducted using data compiled for 985 reef-associated species of tropical fish in the Atlantic Ocean (see Appendix S1 in Supporting Information). The database includes demersal and semi-pelagic taxa that typically associate with coral, rocky and/or coralline algal reefs. Although pelagic fish species also associate with floating material passing over a reef, they are normally temporary visitors in such situations. The present analysis was restricted to the tropical and subtropical Atlantic because a large corpus of data is available on many species of Atlantic rafters, and the Atlantic is noted for the occurrence of large *Sargassum* rafts, such as those that accumulate in the Sargasso Sea.

We classified each of the 985 species as using or not using each of two types of flotsam – seaweed rafts, single-object rafts – based on the data compiled by Castro *et al.* (2002), augmented by records gathered from a literature search and by our own visual observations (O.J.L., D.R.R. and S.R.F.) while doing field surveys in the Caribbean, Brazil and the tropical eastern Atlantic. Seaweed rafts are floating mats of

detached seaweeds. Single-object rafts included logs, pumice, driftwood, and man-made objects such as buoys, oil barrels, fishing gear and fish aggregation devices (FADs). FADs are man-made structures, floating at or just below the surface, which are deployed to enhance fisheries by attracting pelagic fish (Castro *et al.*, 2002; Dempster & Taquet, 2004) and are structurally similar to aggregations of flotsam such as logs. We did not consider species that were only recorded in association with oilrigs as rafters because these large structures essentially represent small permanent reefs, with fully developed communities of benthic marine organisms. Consequently, oilrigs can support substantial numbers of reef fish species, many of which are not known to associate with smaller, more ephemeral natural flotsam (Galloway & Lewbel, 1982). For our analysis, we assumed that species that were not recorded in association with either flotsam type either do not raft or do so less frequently than species that were recorded in association with flotsam. Data on species abundance, ontogenetic stage and individual fish size were not available for all species, and therefore could not be considered as potential predictors of rafting in our analyses.

When selecting potential predictors of rafting for our analysis, we focused on benthic-phase ecological traits that potentially influence the ability of species to live associated with marine flotsam during some stage of their lives. Among the variables considered were: habitat generalization (two categories: broad, reef exclusively); water column position (three categories: bottom-dwellers, low-level swimmers, high-level swimmers); diet type (six categories adapted from Ferreira *et al.*, 2004, definitions for each category are given below); maximum body size (length); and schooling behaviour (two categories: present, absent).

Habitat generalist species might be more capable of exploiting unusual environments and therefore be more likely to colonize rafts. Here, we define generalists to include species that use other habitats in addition to structural reefs such as soft bottoms, seagrass and macroalgae beds, mangroves and estuaries (see Luiz *et al.*, 2012). The position in the water column in which species usually forage is a good indicator of their swimming ability. We assigned species to one of three categories based on the position in the water column where they usually forage as adults and/or juveniles: (1) bottom-dwellers are species that remain on or within benthic habitats and usually are sedentary or territorial; (2) low-level swimmers are demersal fishes that roam around just above the reef (usually within 1–2 m from the substrate); and (3) high-level swimmers are semi-pelagic species that normally swim well above (> 2 m) the substratum, usually roaming from one reef to another within the same day or over a short period of time (Mouillot *et al.*, 2014).

Variation in the capacity to take advantage of specific feeding opportunities provided by different rafting materials could be expected to affect rafting capacity. Omnivores, which might have broader feeding opportunities from both plant and animal origin, could be better represented among rafters in general than species whose diet is restricted to

either plant (herbivores) or animal (macrocarivores, mobile- and sessile-invertebrate feeders and planktivores) material. In addition, herbivorous fish might be more likely to associate with floating seaweeds than other types of flotsam. Finally, the ‘indicator-log’ hypothesis predicts that planktivores will be better represented among raft-associated species. We assigned a major diet type for each species to one of six categories: (1) benthic feeding herbivore–detritivores; (2) macrocarivores that consume larger benthic mobile invertebrates (e.g. crabs, lobsters, cephalopods, echinoderms) and fishes of any size; (3) mobile-invertebrate feeders, which feed on small benthic mobile invertebrates (e.g. small crustaceans, mobile worms, small molluscs); (4) omnivores, which feed on both benthic animal and plant material; (5) planktivores; and (6) sessile-invertebrate feeders that feed on sessile animals (e.g. sponges, corals, ascidians). Body size is known to determine species survivorship by influencing susceptibility to predators and resource acquisition (Munday & Jones, 1998). Therefore, juveniles of species that grow faster can quickly reach a size refuge or take advantage of opportunistic food items. Because there is a correlation between species maximum body size and growth rate (Buesa, 1987; Legendre & Albaret, 1991) and few empirical estimates of growth rates are available for reef fishes, we used species maximum adult body size as a proxy for juvenile growth rate. Finally, schooling behaviour may be a mechanism that influences predation risk and persistence not only on reefs (Pitcher & Parrish, 1993; Sandin & Pacala, 2005; Luiz *et al.*, 2013) but also in the rafting environment. Hence we assigned species as schooling or non-schooling based on their gregariousness. We considered as schooling species those that regularly form polarized, cohesive groups of 20 or more conspecific individuals (Luiz *et al.*, 2013).

Data on the use of non-reef habitats, schooling behaviour, position in water column, maximum total length (our metric for body size) and diet type, were mostly obtained from the literature (see references in Appendix S1) and FishBase (<http://www.fishbase.org/>) and complemented by our own observations.

Data analysis

The effect of different species-level traits on the probability of rafting behaviour were analysed using generalized linear mixed-effect modelling (GLMM), assuming a binomial distribution for the response (non-rafter = 0 and rafter = 1) and a logit link function for the predictor variables (Zuur *et al.*, 2009). Two observations were made for each species, one for each raft type. Taxon (genus nested within family) was included as a random variable to account for the non-independence of species owing to shared ancestry. This nested random variation is represented as taxon-level differences of families and genera around the overall ‘fixed’ effects, attributable to other variables, that can then be generalized to the entire fauna (Pinheiro & Bates, 2000). For model selection, we followed the backward stepwise procedure

recommended by Zuur *et al.* (2009), which entailed sequential removal of non-significant fixed-effect terms ($P > 0.05$) from the full model based on log-likelihood ratio tests. The GLMMs were fitted using the function ‘lmer’ in the package `LME4` (Bates *et al.*, 2012) of R (R Core Team, 2014). Partitioning of variance to determine the relative importance of each explanatory variable in the model was calculated using the R package `HIER.PART` (Walsh & Mac Nally, 2013). All variables were tested for collinearity prior to analyses using rank order correlation (collinearity = $|r| > 0.7$; Dormann *et al.*, 2013), except for diet categories that were non-ordered; however, diet was not included in the final model.

To assess whether relationships between rafting behaviour and species traits were, in part, mediated by raft type (seaweed rafts versus single-object rafts), we included additional terms in our model representing interactions between raft type and each of our predictive variables. Diets of reef fishes often change ontogenetically (Crossman *et al.*, 2005), and younger stages are those most frequently acting as rafters (Castro *et al.*, 2002). Therefore, we conducted two analyses, one including adult traits (maximum body size and adult diet), and another with maximum body size removed and juvenile diet substituted for adult diet where such data were available (31 species).

The significance of predictor variables in the final models were evaluated based on 95% confidence intervals (CIs) for the fitted parameters, which represent odds ratios on the log scale. Following exponential transformation of estimates and CIs, odds ratios correspond to the probability of a trait being associated with flotsam divided by the probability of not being associated with flotsam. This likelihood is expressed in comparison with the reference category for dichotomous variables, or as the change in likelihood with one unit difference for a continuous variable. An odds-ratio-coefficient value of one indicates that a trait state is unrelated to association with flotsam, while coefficient values less and greater than one indicate that the trait’s state is, respectively, negatively and positively correlated with association with flotsam association.

RESULTS

Among the 985 species included in our analyses, 88 species from 57 genera and 26 families were recorded as rafters (see Appendix S1). Among those, 72 used seaweed rafts (45 of them exclusively) and 43 used single-object rafts (16 of them exclusively). Twenty-seven species used both types of rafts, and these represented a higher proportion of the species found in single-object rafts than in seaweed rafts (Fig. 1a). Single-object rafts contained a higher proportion of high-level swimmers and schooling species than seaweed rafts (Fig. 1b,c). On the other hand, seaweed rafts contained a higher proportion of habitat generalist species than did single-object rafts (Fig. 1d).

Species from 23 families used seaweed rafts (10 of them exclusively). In contrast, only 16 families used single-object

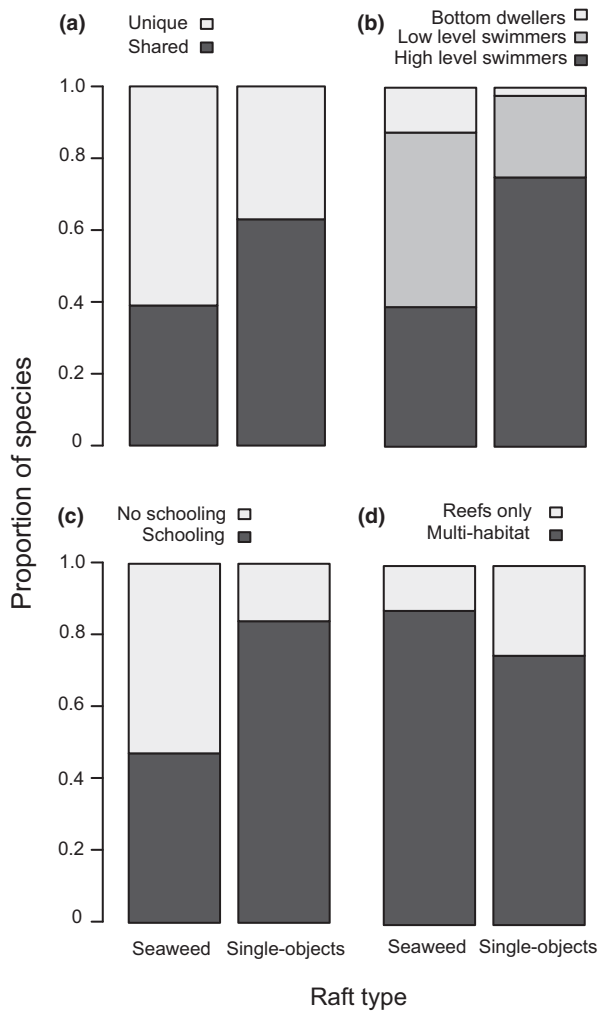


Figure 1 The proportion of tropical reef fish species recorded in the literature associating with seaweed rafts ($n = 72$) and single-object rafts ($n = 43$) in the Atlantic Ocean grouped by (a) species unique to a single raft type ($n = 61$) and shared between both raft types ($n = 27$), (b) position in water column, (c) schooling behaviour, and (d) habitat use.

rafts, including three of them exclusively (Fig. 2). Thus, a greater diversity of taxa, at both the species and family level are associated with seaweed rafts than to single-object rafts. However, this result should be interpreted with caution, as the opportunistic nature of most of the rafting observations precludes control for variability in observation effort among raft types. According to binomial tests, the families Carangidae, Monacanthidae, Balistidae and Diodontidae (all $P < 0.05$), and perhaps Syngnathidae ($P < 0.06$), each had significantly more species associated with seaweed rafts (Fig. 2a) than expected by chance after controlling for the number of species per family, and Carangidae and Balistidae each had significantly more species associated with single-object rafts than expected by chance (both $P < 0.05$, Fig. 2b).

Results of the first GLMM analysis, conducted using adult traits, indicate that species associated with flotsam tend to

swim high in the water column, to be habitat generalists, to exhibit schooling behaviour and to be larger in adult size, so water column position, habitat generalization, schooling behaviour, and body size were all retained as predictors in the final model (Table 1). Habitat generalization and schooling behaviour also exhibited significant interactions with raft type (Table 1). Water column position was the most important predictor of rafting, accounting for more than 58% of the variance, followed by schooling behaviour (26.9%), habitat generalization (11.2%) and raft type (3%) as indicated by estimated independent effects (see IEs in Table 2). While water column position and body size were general predictors, multi-habitat use was positively correlated only for association with seaweed rafts and schooling behaviour only for association with single-object rafts (Fig. 3). Results of the second GLMM analysis, conducted using juvenile traits, indicate that neither removal of adult body size, nor substitution of (available) juvenile diets for adult diet fundamentally changes the overall results (see Appendix S2).

DISCUSSION

Our analysis demonstrates for the first time that rafting behaviour among the members of a major regional fauna of tropical reef fishes is significantly correlated with specific ecological traits. Hence, the improved potential for oceanic dispersal that rafting provides (Luiz *et al.*, 2012) favours dispersal among a select group of species with a particular suite of traits. Semi-pelagic reef fishes are more likely to associate with flotsam items, and to persist in the rafting environment, due to their greater capacity for active swimming. Colonization of experimental rafts by numerous species of juvenile fish can occur within a few hours (Dempster & Kingsford, 2004). This suggests that fishes detect and actively seek out rafts rather than encountering them by chance. When seeking a raft, fishes probably use olfactory clues, as indicated by observations that fishes aggregate more rapidly around drifting FADs that are encrusting with invertebrates than FADs without associated organisms (Nelson, 2003; Dempster & Kingsford, 2004). Among fish that encounter rafts by chance, semi-pelagic species likely have the capacity to leave rafts that provide inadequate food or protection, increasing their chances of encountering better quality rafts. Gooding & Magnuson (1967) observed rafting reef fishes from an underwater chamber, and reported that semi-pelagic species ranged far from the raft, sometimes being out of view for several hours before returning.

The degree of species reliance on the hard-reef substrata is inversely correlated with probability of rafting. This result indicates that flotsam in general likely represents a poor substitute for reefs. In fact, most flotsam items lack the complex physical structure of reefs that is important for many reef fishes, particularly single-object rafts such as logs and plastic objects, which have relatively smooth surfaces. While a substantial fouling community may build-up to cover all the submerged parts of these items (Thiel & Gutow, 2005b), this

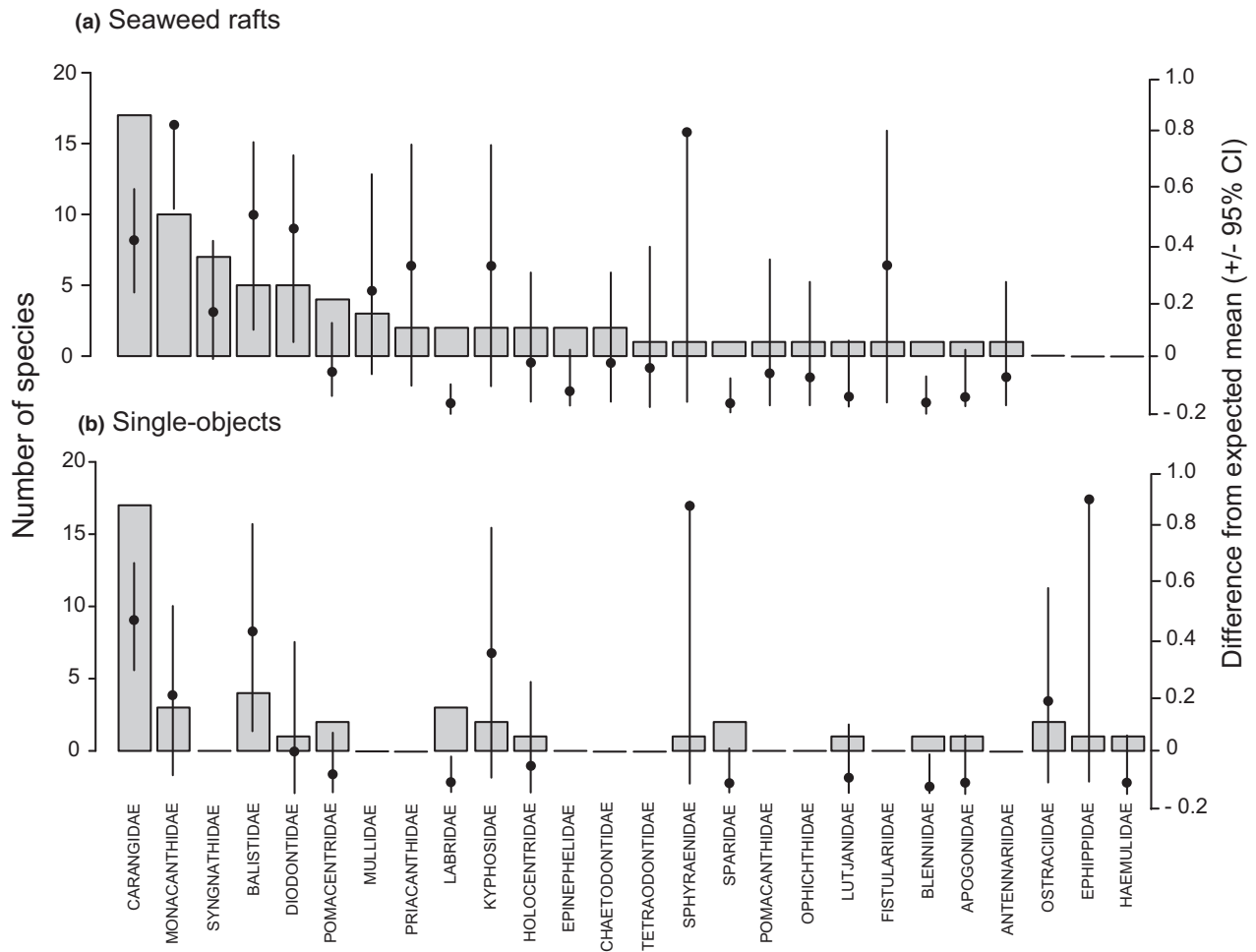


Figure 2 The number of tropical reef fish species recorded in the literature associating with (a) seaweed rafts ($n = 72$) and (b) single-object rafts ($n = 43$), in the Atlantic Ocean, grouped by family. The black dots are differences in family proportions of number of rafter species relative to the expected proportion for all families (i.e. dots above zero indicate that a family has more rafter species on average and vice versa). 95% binomial confidence intervals (vertical lines) show if proportions can be distinguished from expectation at a significance level of $P < 0.05$ for lines that do not overlap with zero.

biotic cover is unlikely to provide the same variety of food and shelter opportunities provided by crevices and holes of reefs. On the other hand, aggregations of floating seaweed rafts, particularly of *Sargassum* in the North Atlantic, can extend for many kilometres and individual patches can be up to 3 m thick (Moser *et al.*, 1998; Casazza & Ross, 2008), providing greater opportunities for shelter and food compared to single-object rafts. In addition, several species take advantage of coloration that matches the coloration of the floating seaweed (Casazza & Ross, 2008). These structural differences may explain why seaweed rafts are used by many more species of reef fishes than single-object rafts.

The importance of habitat generalism and schooling behaviour as correlates of flotsam association depends on flotsam type. The fact that multi-habitat use is positively correlated with flotsam association only for seaweed is perhaps not surprising because generalist species use equivalent vegetated-bottom habitats near reefs. This is reflected in different taxonomic compositions of the reef fish assemblages found

associated with each raft type: representatives of many families of habitat generalist reef fishes were found exclusively in seaweed rafts (Fig. 2). Generalist reef fishes living in close association with macroalgal-covered habitats are likely to find suitable resources on rafts formed when such substrata become detached from the bottom (Gutow *et al.*, 2015). For example, seahorses and pipefishes (Syngnathidae) are well represented in the seaweed raft community (Kleiber *et al.*, 2011; Gutow *et al.*, 2015) despite being very poor swimmers and lacking a pelagic dispersal phase due to brooding fully developed young (Teske *et al.*, 2005).

Schooling behaviour, a trait that is largely linked to predation reduction (Pitcher & Parrish, 1993; Sandin & Pacala, 2005), is positively correlated with association with single-object rafts. Single-object rafts have a much simpler physical structure than seaweed rafts and are relatively small. Hence pelagic predators can easily survey the entire single-object rafts. Fishes schooling with flotsam might be using it as a barrier between themselves and a predator (Gooding &

Table 1 The best generalized linear mixed-effect model for the association between species-level traits of tropical reef fishes ($n = 985$) and occurrences in rafts on the Atlantic Ocean was selected by recording the effect of (a) dropping interactions of each variable and with raft type, and (b) dropping each variable independently in a backward stepwise manner. We have shown the Akaike information criterion (AIC) values and the significance (P -value). The P -value shown in each line refers to the significance for the retention of the factor excluded, and the final model is indicated in bold. Coefficient in bold indicates that P -value is significant ($P < 0.05$).

Variables	d.f.	AIC	P -value for retention
(a) Interactions			
Full model	24	480.50	–
Raft type*Diet	19	476.97	0.263
Raft type*Position in water column	17	475.40	0.259
Raft type*Body Size	16	477.91	0.098
Raft type*Habitat	15	483.99	0.010
Raft type*School	15	491.08	< 0.001
(b) Single factors			
Raft*Schooling + Raft*Habitat + Position in water + Body Size + Diet	16	474.12	0.286
Raft*Schooling + Raft*Habitat + Position in water + Body Size	11	488.58	0.006
Raft*Schooling + Raft*Habitat + Position in water	9	479.60	< 0.001
Raft*Schooling + Raft*Habitat + Body Size	8	497.10	< 0.001

Magnuson, 1967; Hunter & Mitchell, 1967; Rountree, 1989). Protection offered by single-object rafts may be effective if combined with anti-predation traits like schooling behaviour. The high proportion of plastic debris bearing bite-marks from fish predators (Carson, 2013) could be due to predators trying to capture smaller fish hiding behind such flotsam, although it could also be due to fish treating or testing the plastic as a food item. Although almost the same numbers of schooling species associate with both raft types, schooling species are largely dominant among single-object rafts, whereas they represent less than half of the species found among seaweed rafts. This suggests that non-schooling species either avoid single-object rafts or are more easily weeded out by predators, and that seaweed rafts offer better conditions to survival and persistence on the rafting environment for solitary species.

Species maximum body size was the third most important general predictor for association with flotsam, although considerably less important than position in water column and schooling. As most rafting species associate with flotsam only at their juvenile stage, the adult body-size effect might arise due to its relationship to juvenile size: juveniles of large species tend to be growing faster and be larger than juveniles of smaller species (Buesa, 1987; Legendre & Albaret, 1991). Because there are strong relationships between maximum body size and many other species characteristics (Munday &

Table 2 Parameter estimates for the final generalized linear mixed-effect model for the association between species-level traits of tropical reef fishes ($n = 985$) and occurrences in rafts on the Atlantic Ocean, including the significant interactions among raft type and fixed variables and with genus nested within family as a random variable. Coefficient estimates of fixed variables, standard error (SE), test statistic (z -value), probability (P -value) and the independent effect (IE) of each explanatory variable on the response variable are shown; the latter calculated by separately using hierarchical partitioning. Coefficients in bold indicate significance ($P < 0.05$). Reference levels for this regression were set as 'seaweed' for raft type, 'low swimmer' for level in water and as 'no' for both schooling behaviour and multi-habitat use.

Variable	Estimate	SE	z -value	P -value	IE (%)
Intercept	–6.986	1.185	–5.891	< 0.0001	
Raft type					
Floating objects	–0.898	0.712	–1.262	0.207	3.04
Schooling behaviour	0.073	0.681	0.108	0.913	23.03
Position in water column					
Bottom dweller	–2.380	0.891	–2.669	0.007	50.24
High swimmer	3.006	0.746	4.026	< 0.001	
Multi-habitat use	1.979	0.539	3.666	< 0.001	8.48
Body size	0.754	0.302	2.497	0.012	15.20
Raft type:					
Schooling behaviour	2.432	0.677	3.588	< 0.001	
Raft type:					
Multi-habitat use	–1.959	0.695	–2.817	0.004	

Jones, 1998), it is difficult at present to delineate a specific mechanism that may be driving this relationship. Whatever the mechanism by which body size favour rafting, it is significant, and so its removal reduces the explanatory power of model (see Appendix S2).

Variation in diet type, which could plausibly have some effect on rafting behaviour, did not act as a significant predictor for species associated with either floating seaweed or single-object rafts. These results indicate that no particular diet type is favoured in the rafting environment. However, because the diets of juveniles of many species that associate with flotsam as juveniles are presently unknown, this result should be interpreted with caution until more information on age-related data on feeding preference becomes available.

Flotsam-associated species are more likely to cross long-distance oceanic barriers (Luiz *et al.*, 2012) and thus they may influence the functional composition of neighbouring biogeographical provinces. The prevailing view is that the Tropical Western Atlantic (TWA), the most diverse part of the tropical Atlantic, exports species to the Tropical Eastern Atlantic (TEA) (Briggs, 2003; Floeter *et al.*, 2008; Briggs & Bowen, 2013). Recent phylogeographical analyses support this viewpoint (Floeter *et al.*, 2008; Briggs & Bowen, 2013). If this is correct then the TEA regional fauna should have a higher proportion of species with the different rafting-associated traits than the TWA. We compared the proportions of each of the traits in our final model between the TEA and the TWA using a binomial test of proportions (Crawley,

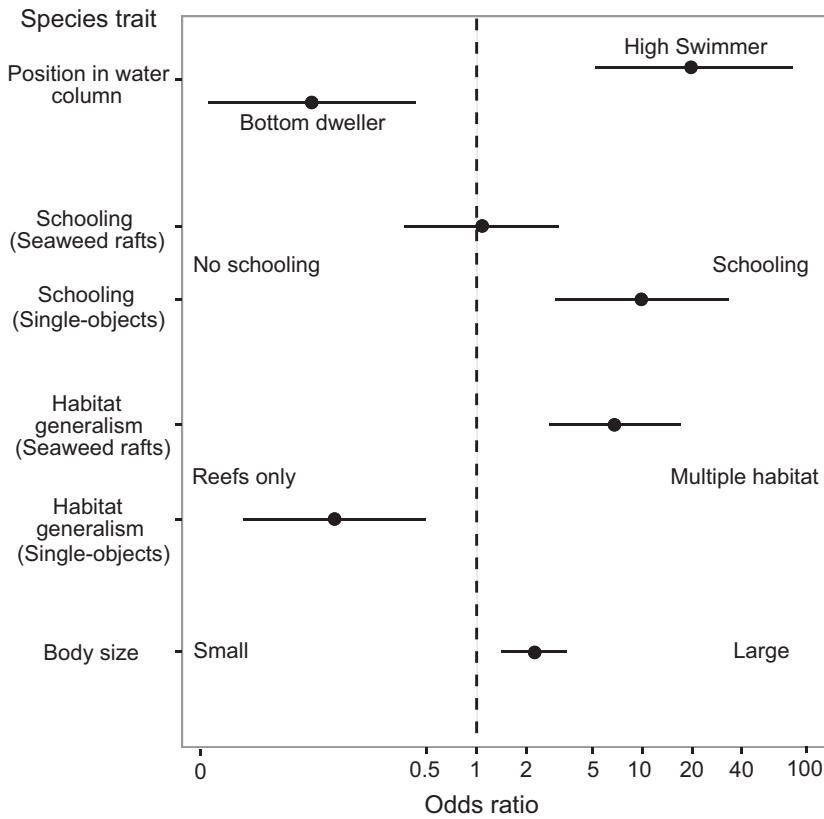


Figure 3 Relationships of tropical reef fish species traits with the likelihood that a species associates with flotsam in the Atlantic Ocean. Values plotted are model odds ratios (OR; points) with 95% confidence intervals (CIs; solid horizontal lines). Where CIs do not encompass 1 (vertical dashed line), the trait was significantly more likely (OR > 1) or less likely (OR < 1) among flotsam-associated species. Multi-habitat use and schooling behaviour interacted significantly with raft type, so seaweed rafts and single-object rafts are shown separately for these traits. Position in water column levels ‘bottom-dwellers’ and ‘high-level swimmers’ are compared against the baseline level ‘low-level swimmers’.

Table 3 Summary of binomial test of proportions of resident tropical reef fish species, from two biogeographical provinces in the Atlantic Ocean, bearing traits that are associated with rafting dispersal (showing χ^2 -test statistics, degrees of freedom and *P*-values). Coefficient in bold indicates that *P*-value is significant (*P* < 0.05).

	Province		χ^2	d.f.	<i>P</i> -value
	TEA	TWA			
% High-level swimmers	12.9	0.5	18.930	1	0.001
% Schooling	21.2	11.3	17.204	1	0.003
% Multi-habitat	59.1	53.4	2.539	1	0.111

TEA, Tropical Eastern Atlantic; TWA, Tropical Western Atlantic.

2015). That comparison showed that species with the various traits that correlate positively with flotsam association are proportionately more common in the TEA regional fish assemblages than in the TWA assemblage (Table 3). This finding, in combination with phylogeographical evidence and the observation that the majority of the species observed associated with the flotsam environment have a trans-Atlantic distribution (Luiz *et al.*, 2012), provides strong evidence that long-distance oceanic dispersal by rafting is a biologically significant factor driving large-scale biogeographical patterns among marine shore fishes.

Rafting may enhance dispersal of reef fishes over oceanic barriers not only by extending drift time in the pelagic environment, but also by facilitating the simultaneous arrival of

multiple conspecifics at a new location (Teske *et al.*, 2005; Luiz *et al.*, 2013). Arrival of rafting recruits at larger sizes than is the case with non-rafters and displaying defensive behaviours such as schooling should increase their chances of survival and successful establishment at the new site (Luiz *et al.*, 2013).

Are future prospects for oceanic dispersal via flotsam likely to be different from those in the recent past, before the advent of significant amounts of artificial and other human-generated flotsam (Gregory, 2009)? Increasing amounts of man-made flotsam, particularly large aggregations of durable flotsam such as derelict fishing nets (netballs), will probably enhance future oceanic dispersal. The likely picture for species that associate with seaweed rafts is less clear. Scenarios based on effects of ongoing climate-change predict that seaweed rafts will perish faster and decline in abundance in the tropics (Macreadie *et al.*, 2011; Rothäusler *et al.*, 2012), lowering dispersal potentials for some species. However, increasing ocean temperatures should allow seaweed rafts to spread farther polewards (Rothäusler *et al.*, 2011, 2012; Afonso *et al.*, 2013) assisting the potential for latitudinal range shifts by fish species that tend to associate with seaweed rafts. In addition, netballs, which do represent suitable flotsam habitat for some species that associate with seaweed rafts (Goldstein *et al.*, 2014), are much more persistent than floating seaweeds, and are distributed differently to seaweeds through the different oceans. Detailed studies of reef fishes, among other organisms, that raft with derelict nets and other

manmade flotsam are needed to assess what positive and negative effects it will have on the dispersal potential.

Here, we have identified some of the ecological traits for raft-associated reef fishes. Our analyses suggest that, in the tropical Atlantic: (1) the persistence of these fishes with flotsam at sea does enhance successful dispersal capability and is not a haphazard process, (2) the characteristics of the floating substrata have an important role in determining the composition of the associating reef fish assemblage, and (3) flotsam dispersal does have a measurable influence on large-scale biogeographical patterns among those fishes. Reef-fish faunas of the three tropical oceans exhibit both general taxonomic similarities at the family and genus levels, and general similarities in their ecology. Hence, our results are likely to be general for other tropical regions, although this remains to be tested. In summary, rafting fishes tend to be seafarers that depend on specific traits to successfully survive in the raft environment and disperse over the oceans, rather than accidental castaways drifting by chance.

ACKNOWLEDGEMENTS

Financial support was provided by an International Macquarie University Research Excellence Scholarship (O.J.L.), the Australian Research Council (J.S.M), the Smithsonian Tropical Research Institute (D.R.R.; STV grant to S.R.F.), the National Geographic Society (grant 7937-05 to S.R.F.), and CNPq (S.R.F.). We are grateful to Michelle Gaither, Martin Thiel, Nicholas Ory, Michel Kulbicki, and an anonymous referee for the comments on the manuscript.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Data set used in the study and references used for compile the data.

Appendix S2 Additional tables showing the model selection and the coefficients for the alternative model for the association between species-level traits of tropical reef fishes and occurrences in rafts on the Atlantic Ocean, with maximum body size removed and juvenile diet substituted for adult diet.

BIOSKETCH

Osmar Luiz has investigated the role of species-level traits in the dispersal of coral reef fishes for his PhD thesis. His research interests include macroecology, biogeography and conservation of the reef-associated biota.

Author contributions: O.J.L. and S.R.F. conceived the ideas; O.J.L., D.R.R. and S.R.F. compiled the data set; O.J.L., A.P.A. and J.S.M. analysed the data. All authors wrote the manuscript.

Editor: Michelle R. Gaither