



10 Patterns and processes in geographic range size in coral reef fishes

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Coral reef fishes vary dramatically in the extent of their geographic distributions, and the patterns, causes, and consequences of this extensive variation have long interested coral reef fish ecologists. Although there is still a great deal of uncertainty regarding the drivers of range size variation in coral reef fishes, research over the last several decades has greatly improved our understanding. Ecologists once suspected that larval traits, primarily pelagic larval dispersal potential, had a strong influence on species' ranges, but recent synthetic work has shown that larval dispersal only impacts range sizes when ranges cross the greatest dispersal barriers in the Pacific. Emerging work suggests that adult traits, such as body size, habitat preferences, and even nocturnal activity are correlated with range size, likely by increasing persistence of newly established populations. Processes that operate over evolutionary scales are also likely important, but it has been challenging to empirically examine these factors. However, the quantity and availability of biological information are increasing rapidly, providing reef fish ecologists with richer datasets with which to evaluate a broader range of hypotheses.

One of the most fundamental traits of a species is the size of its geographic range. Coral reef fishes show dramatic variation in range size, and even closely related species can have vastly different geographic extents. For example, the surge wrasse *Thalassoma purpuraceum* extends from South Africa to Central and South America, a span of nearly 28 000 km, while the Clipperton wrasse *Thalassoma robertsoni* is endemic to Clipperton Atoll in the tropical eastern Pacific, an island approximately 6 km long (Figure 10.1). Therefore, it is not surprising that this variation has interested coral reef biologists and biogeographers for decades.

The size of a species' range is likely the product of a wide variety of biotic and abiotic forces and as such can provide great insight into biogeographic and evolutionary patterns. Geographic range size can also have a large impact on a species' extinction risk, since widespread species are thought to be much less vulnerable to extinction than geographically restricted species [357,915]. However, despite its importance, there is still considerable uncertainty about the factors that influence the range sizes of coral reef fishes.

A variety of evolutionary and ecological mechanisms for range size variation have been suggested, including niche breadth or environmental tolerance, body size, population abundance, latitude, environmental variability, colonization and extinction dynamics, and dispersal ability [357,912,915,2421]. In marine systems, larval dispersal ability is one of the most commonly investigated factors to explain range size variation [757,1031,1220,1476,1477,1543,2345], particularly for mollusks and reef fishes. This is because many marine species, particularly those that are reef-associated, are generally site-attached as adults and have a pelagic larval phase and thus the most significant dispersal likely occurs during the larval phase. Furthermore, many of these reef species have geographic ranges spanning deep water, suggesting that larval dispersal could have a strong influence on range size.

However, despite extensive research into the relationship between range size and dispersal ability, results are equivocal and suggest that larval dispersal is only a driving factor for range size variation in limited instances [1477]. There is clearly a need to focus on a broader set of potential biological mechanisms that influence range size variation in marine organisms.

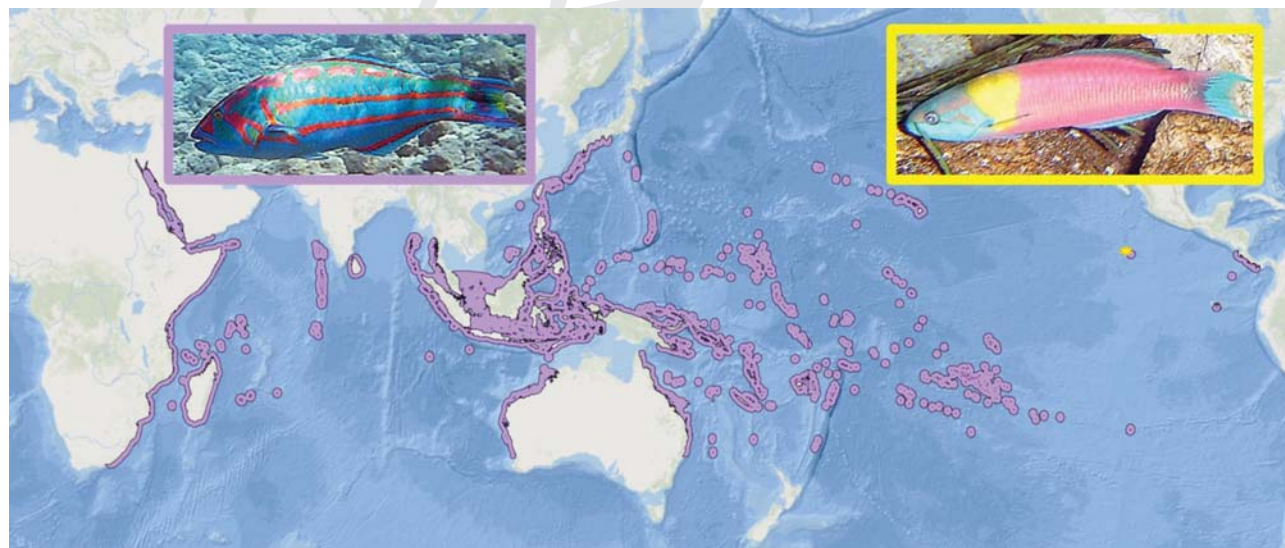
Coral reef fishes are an ideal group for studying patterns and processes in range size in the marine realm. They are conspicuous members of shallow coral reef ecosystems, facilitating the surveys that provide presence/absence data needed to quantify range sizes. There is also a great deal of information about adult and larval traits, such as body size, habitat use, and length of the larval duration [877], enabling investigation into the factors that may influence range size. Furthermore, they are a species-rich group, with many closely related species that vary greatly in both their range size and in many of the potential biological traits that may influence range size. In this chapter, we review the current state of our knowledge on patterns of range size variation for coral reef fishes, the processes that may drive this variation, and key research questions looking forward.

PATTERNS IN RANGE SIZE VARIATION

Defining range size

Unfortunately, quantifying the size of a species' range is rarely straightforward. Commonly used metrics include number of

Figure 10.1 Geographic range maps for congeners *Thalassoma purpuraceum*, found throughout the Indian and Pacific Oceans (in purple; photo: National Park Service) and *Thalassoma robertsoni*, endemic to Clipperton Atoll (single yellow star; photo: Wikimedia commons). Geographic range data from IUCN [1217].



arbitrarily defined areas occupied, distance from a proposed center of diversity or center of speciation, maximum distance in latitude and/or longitude, maximum gap distance between areas of suitable habitat, maximum linear distance between the furthest two range endpoints, and total area occupied [915]. Of course, different metrics will be more relevant for different mechanistic explanations for range size variation, requiring careful consideration when selecting or evaluating a potential metric. Given that different metrics have been used by different researchers, it is often hard to compare results across studies. Seemingly conflicting results are in some cases an artifact of the use of different range size metrics [e.g. 1476].

Patterns across ocean basins

Range size in reef fishes obviously varies considerably among ocean basins since the size of the basin will constrain maximum range size. The maximum range size of reef fishes in the Indo-Pacific is over twice as large as in the Atlantic (27 200 km vs. 12 400 km) and maximum range size is smaller still (7500 km) for species restricted to the tropical eastern Pacific [1476]. Barriers to range expansion within and across basins will also strongly influence patterns of range size. Specifically, there are several large biogeographic barriers in the Pacific. Both the Hawai'ian and Pitcairn Islands are separated from the nearest reef habitat by ~2000 km of open ocean, and the Eastern Pacific barrier is the largest marine biogeographic barrier, spanning ~5000 km of open water from the Central Pacific to the tropical eastern Pacific. Despite its formidable size, many species ranges do cross this barrier. For example, Lessios and Robertson [1474] found no significant genetic differentiation between Eastern Pacific and Central Pacific populations in 16 of 18 species of trans-Pacific reef fish species, suggesting that dispersal events across the barrier are not uncommon over evolutionary time scales, at least for species that have successfully crossed it. While not as large, the Atlantic also has several range barriers. The most notable are the Mid-Atlantic Barrier, an open ocean barrier of 2800–3500 km with a few islands along the Mid-Atlantic Ridge, and the Orinoco–Amazon discharge plume, a span of 2300 km along the northeastern coast of South America that is dominated by freshwater outflow from the Orinoco and Amazon Rivers, with little hardbottom habitat [828,1542]. However, similar to the case in the Pacific, there is significant overlap in species composition and extensive genetic exchange within species across barriers [828], suggesting that Atlantic barriers are also permeable, at least for some species [1542].

Despite the large differences in maximum range size and the presence of range barriers in the Atlantic and Indo- and Eastern Pacific, there is still extensive variation in geographic range size within each ocean basin. The range size frequency distribution in the Atlantic has multiple peaks, with prominent modes at small range sizes – for species that span the Caribbean only – and at larger range sizes – for species that extend from the Caribbean to

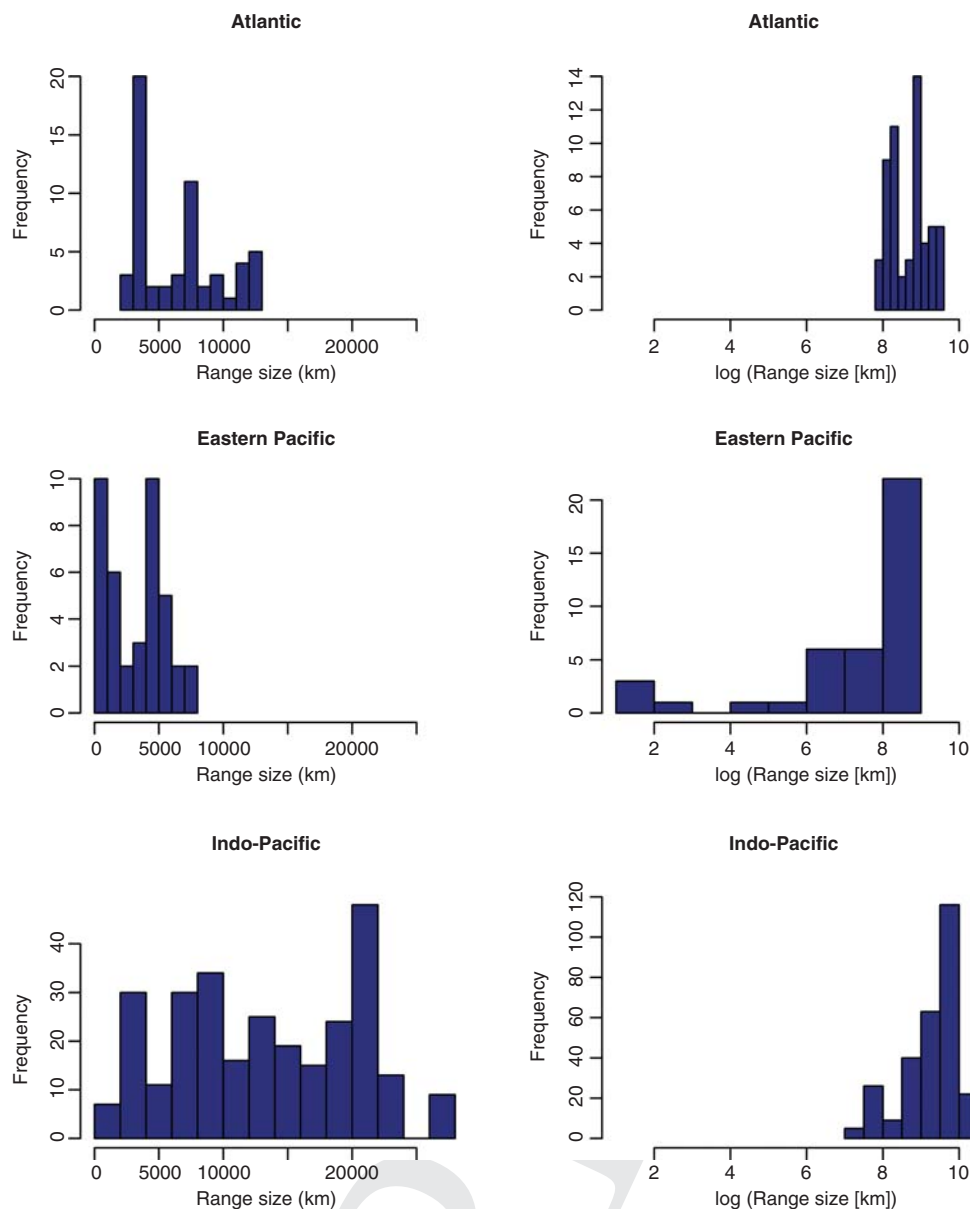
Brazil (Figure 10.2, [828,1477,1542]). The size frequency distribution in the tropical Eastern Pacific is also bimodal, with a small peak at small range sizes representing island endemics, and a peak at larger range sizes representing more widespread species (Figure 10.2, [1734]). The mode at larger range sizes illustrates that the tropical eastern Pacific is a small basin with few barriers, allowing many species to be distributed throughout the region. The range size distribution in the Indo-Pacific is much more varied, but there are two peaks in the distribution at larger range sizes, one for those species that span the full Indo-Pacific basin excluding the tropical Eastern Pacific, and a smaller peak for trans-Pacific species (Figure 10.2, [1191]). However, related research found that distributions of a subset of common reef fish families in the Indo-Pacific was right skewed toward smaller ranges [1290]. Clearly, the distribution and availability of habitats and the existence of range barriers play important roles in generating or constraining range size distributions.

POTENTIAL MECHANISMS DRIVING RANGE SIZE VARIATION

There are numerous mechanisms that may create variation in range size in reef fishes. These are likely operating over both ecological and evolutionary time scales, and may not be mutually exclusive, further complicating the search for causation. Below, we start by examining mechanistic explanations that focus on species' characteristics, including both larval and adult traits, which have the potential to impact species' distributions by influencing colonization ability and/or post-colonization survival or persistence. Second, we examine non-equilibrium processes that operate over evolutionary rather than ecological time scales, such as speciation and extinction rates. Lastly, we explore the special case of island endemics, since their extremely limited distributions provide an interesting test of hypotheses for drivers of range size variation.

Dispersal potential

For a species to expand its range, it first must be able to reach and colonize a new area. The likelihood of colonization is related to several factors. For one, investigators have long expected that the length of the larval stage should be a strong determinant of the ability of a species to reach new coral reef habitats separated by open water. For many benthic-associated marine organisms, dispersal occurs primarily or exclusively in the larval phase, during which larvae have the ability to move great distances on ocean currents. This is particularly true for most shallow-water coral reef fishes, since shallow reef areas can be separated by hundreds or thousands of kilometers of open water uninhabitable by adults. While estimating the length of the larval phase is challenging for many marine organisms, research in the 1980s demonstrated that daily growth increments in the otoliths (earstones) of fish larvae can be used to



estimate the PLD [2568,2570], and researchers have generated PLD data for hundreds of species of reef fishes [e.g. 352,1543,2572].

Using these quantitative estimates of PLD, numerous researchers have tested the hypothesis that larval dispersal is the main factor influencing range size variation in coral reef fishes, yielding surprisingly conflicting results. Some found no relationship [1290,2486,2572], while others found evidence of a link between PLD and range size. But even in these cases, the nature of that relationship varied, such as species only have larger range sizes above a threshold PLD value [352] or there is a significant correlation only at the generic level [2488]. Other

Figure 10.2 Range size frequency distributions for coral reef fishes, by ocean basin. Range size is quantified as the maximum linear distance between the furthest two range endpoints. Data from Luiz *et al.* [1543].

analyses found significant relationships between PLD and range size, but only when examining a taxonomic subset of reef fishes, such as within one or a few families [287,1733,2757]. For example, Zapata and Herron [2757] found a correlation between PLD and longitudinal range (but not for overall range size) for five snappers in the tropical eastern Pacific, and Mora *et al.* [1733] reported a correlation between mean PLD at a location and

distance from a center of origin for Indo-Pacific labrids and pomacentrids.

In an attempt to resolve these conflicting results, Lester and Ruttenberg [1476] conducted a synthetic analysis using all published PLD data. They found a positive relationship between range size and PLD but only in the Indo-Pacific basin and only when including those species whose ranges extended to the isolated Central Pacific islands (e.g. Hawai'i) and the tropical eastern Pacific. Recognizing that evolutionary processes may be important, Mora *et al.* [1748] controlled for evolutionary age, and still found no relationship between PLD and range size within several reef fish families. They developed an ocean circulation model that suggests all but the most remote reef areas of the tropical oceans are reachable by most reef fish species during the pelagic period, which may explain the lack of relationship between range size and PLD. A similar dispersal study using oceanographic models found that PLD increases larval connectivity over smaller spatial scales, but that the probability of connectivity decreased sharply beyond a few hundred kilometers [2520]. In the most thorough synthesis to date, Luiz *et al.* [1543] included several factors in a model to explain range size, including ocean basin and PLD. At the ocean basin scale, PLD was only significant in the Indo-Pacific, and only when including trans-Pacific species. When these species were removed from the global model, PLD became the least important of the five statistically significant traits in the global model [1543]. These results reinforce the idea that PLD may influence species' ranges only at the largest scales and only when ranges span large dispersal barriers [352,1476,1733,2488].

In addition to using PLD as a proxy for dispersal potential, other researchers have attempted to use genetic data to infer dispersal ability. For example, in a genetic analysis of Hawai'ian surgeonfishes, Eble *et al.* [728] found that Indo-Pacific species whose ranges extend to Hawai'i are genetically homogenous throughout the Hawai'ian Islands, but species endemic to the Hawai'ian archipelago show genetic structure throughout the islands. They interpret these data to support the hypothesis that Hawai'i's endemic species evolved from ancestors with reduced dispersal ability, and were not only unable to maintain connectivity with ancestral populations after rare colonization events, but also show low genetic connectivity across the islands. In contrast, widespread Indo-Pacific species continue to exchange individuals throughout the Hawai'ian Islands. However, a recent meta-analysis found a only a weak relationship between PLD and genetic structure in marine species, and this relationship became non-significant when direct developers (i.e. no pelagic larval phase) were removed from the analysis [2638], suggesting that PLD is a poor proxy for genetic connectivity and dispersal over evolutionary time scales.

Other larval traits may also influence dispersal ability. Larval rafting, the ability of larvae and juveniles to associate with floating objects, may allow these species to remain in pelagic

environments much longer than implied by their PLD [1205], thus increasing their dispersal ability. For example, sergeant major damselfish (genus *Abudefduf*), can remain in pelagic environments much longer than their estimated PLD of 21–22 days when they are associated with floating objects [1205,2643]. Indeed, rafting is positively associated with species whose ranges cross the Mid-Atlantic Barrier [1542]. Larval swimming ability may also influence dispersal. Recent work has shown that coral reef fish larvae are capable of complex behaviors and have much greater swimming abilities than previously thought, although this varies greatly among species [1459-1461]. In addition, some species have the ability to delay metamorphosis and extend the larval phase [2643]. Together, these larval traits have the potential to influence dispersal distance, probability of colonization, and ultimately range size. However, taken together, studies examining the role of dispersal ability in driving range size strongly suggest that factors other than dispersal are at least partly responsible for determining range size in tropical reef fishes.

Reproductive output

Propagule pressure, or the number of offspring released from a source population that may colonize new areas [1512], is likely to have a strong influence on colonization ability and thus could impact geographic range size. Species with high reproductive output and large populations can generate many more propagules, thereby increasing the probability of colonizing new areas. However, estimating reproductive output requires detailed life-history and population abundance information from a large number of locations, and these data have not yet been synthesized. Still, modeling studies have found that increased reproductive output (which would be expected from large populations) can increase among populations [2520]. Increased connectivity may increase the probability that a species is able to colonize a new area and expand its geographic range. However, island endemics are often locally abundant [649,1132,1133,2137], and by definition have restricted ranges, suggesting that large population sizes are not always correlated with large geographic ranges. Clearly, additional research is warranted to further investigate the degree to which local population abundance influences range size.

Habitat use

Habitat specificity may influence colonization success and ultimately range size since species able to use multiple habitats may be able to use those habitats as "stepping stones". Habitat generalists may also be able to occupy areas that are suboptimal for habitat specialists. For example, while many reef fishes have close associations with the benthos, others swim higher in the water column, potentially allowing them to occupy broader areas; Mora and Robertson [1734] found that species not tightly associated with the benthos – a group termed "coastal pelagics" that

includes jacks, silversides, and herrings, among others – were more widespread than those strictly associated with reefs in the Eastern Pacific, presumably because of their improved colonization ability as adults. They also found that the most widespread species in the tropical eastern Pacific were able to use both continental and island habitats, allowing them to occupy a larger overall range than insular endemics, some of which are found on multiple islands separated by greater distances than from the islands to the mainland. They suggest that habitat specificity may prohibit these insular endemics from colonizing the mainland. Similarly, Luiz *et al.* [1542] found that species able to use non-reef habitats were much more likely to have ranges that crossed the Amazon–Orinoco plume. They hypothesize that such habitat generalists may be able to establish adult populations in the lower salinity soft-bottom habitats within the plume which subsequently provide propagules to reef areas in Brazil and the Caribbean.

Body size

Body size has been found to correlate with range size in many other taxa including temperate and tropical mammals, Australian and North American birds, and even some insect groups [915], and is a trait that can potentially influence both colonization and persistence in reef fishes. Several recent studies have found positive relationships between body size and geographic range size for a broad group of marine fishes [2441] and a subset of reef fishes [1543]. Luiz *et al.* [1543] hypothesize that body size may facilitate persistence in reef fishes; larger species tend to have fewer predators and reach larger sizes faster [2378], which should reduce overall predation pressure and subsequent mortality. Larger species also tend to use a wider range of food types and a wider range of habitats [1786], which may also increase survivorship of newly colonizing individuals and increase persistence of newly established populations. Lastly, larger body size results in increased reproductive output in fishes [279], which may increase the probability of colonization.

Behavioral adaptations

Behavioral adaptations may also influence persistence and range size. Recent research has found that nocturnal species are more active diurnally when predators are absent, suggesting that nocturnal activity is in part a mechanism to reduce predation [1600]. Emerging work has also shown that schooling can reduce per capita mortality in coral reef fishes [2256,2666]. Following these findings, Luiz *et al.* [1543] found that both nocturnal activity and schooling behaviors were significantly correlated with geographic range size across multiple ocean basins. They interpreted these results to suggest that these behaviors may reduce predation pressure and increase the likelihood of persistence of populations in newly expanded areas. However, the dynamics of predator–prey interactions have complex outcomes on

population and community dynamics; for example, Holt *et al.* [1169] examined range size and range expansion in the context of predator–prey dynamics in a theoretical model. They found that the degree of specialization of both predators and prey can influence range size and rates of range expansion in positive and negative directions, which will make it more difficult to predict how such interactions will ultimately influence range sizes of both predators and prey.

Evolutionary processes

Many of the larval and adult traits discussed above operate over ecological time scales. However, range size is fundamentally a species-level attribute, and therefore will be affected by processes operating at evolutionary time scales. By definition, allopatric speciation events result in two species with ranges smaller than that of the parent species. However, accounting for these processes in large analyses is challenging in part because evolutionary history will impact species traits but actual phylogenetic relationships are often unknown. Researchers have taken several approaches to account for phylogeny. Lester and Ruttenberg [1476] found a negative relationship between species richness at the family level and mean PLD of the family. They suggest that species within families with shorter PLDs are more likely to become isolated, speciate, and subsequently have smaller ranges. Similarly, data from the fossil record on mollusks found a negative relationship between range size and speciation rate [1221]. In contrast, Mora *et al.* [1748] found no relationship between PLD and range size even when controlling for species' evolutionary ages. The relatively small number of studies that have attempted to account for evolutionary processes when examining range size – and their conflicting results – suggests that a great deal of additional work is needed on this topic.

The special case of island endemics

To further complicate the search for generalities in the factors that influence range size in reef fishes, there is the special case of species endemic to small islands. Reef fish ecologists have sought to understand the unique biological attributes that lead to endemism in the hopes that these features may shed light on broader processes that influence reef fish biogeography [2137,2572]. However, researchers have found few if any traits that clearly distinguish endemic species from their widespread congeners. Endemic species are often representative of the regional species pool, and are similar in many biological characteristics to widespread species, including trophic group and body size [2137]. Larval and reproductive traits are also similar; endemics include pelagic and demersal spawners in similar proportions [2137] and PLDs are similar, if slightly longer, for endemics when compared to their widespread congeners [1133,2572]. Island endemics are often locally abundant [649,1132,2137], and may greatly exceed the density of widespread congeners [1133]. There is some

evidence that island endemics may be more specialized for island habitats, since some island endemics are found on multiple oceanic islands that are separated by greater distances than from the islands to the mainland [1734]. Unfortunately, research on these special cases has not revealed any generalities about what factors lead to endemism, but continued work in this area may eventually help in the search for a broader understanding of the factors that determine range size in reef fishes.

SUMMARY AND FUTURE RESEARCH DIRECTIONS

Despite several decades of research, the causes and consequences of range size variation in reef fishes remains unclear. However, recent synthetic and modeling studies have begun to shed light on some of the factors that are more, and less, important in driving the extensive variation that we observe. First, despite its intuitive appeal, the length of the PLD is not a primary determinant of range size [1476,1543,1748]. It appears to be important only when ranges span large barriers to dispersal, such as the East Pacific Barrier [1476,1543], and larval rafting may also allow species to cross these barriers [1542]. Juvenile and adult traits, on the other hand, may be much more important to determining range size than once thought, likely by increasing survivorship in newly established populations. Emerging work has found that body size, nocturnal activity, schooling behavior, and the ability to

use multiple habitats are positively associated with increased range size [1543].

Looking forward, there are some important opportunities for further research. Evolutionary processes including speciation and endemism may be important; this idea is supported by some recent research [1476] but not by others [1748]. Increasingly available molecular phylogenetic data should allow researchers to better account for evolutionary processes in future analyses. Population-level reproductive output may also greatly impact range size by providing a larger pool of potential propagules. Past work has not been able to account for population size or potential reproductive output, but survey data are becoming more readily available from more locations [e.g. 1744,1895], and such analysis may be possible. Lifespan may also influence persistence; populations of longer-lived species are more likely to persist in new locations [2616], thereby expanding range size. A few studies have mentioned longevity, making the implicit assumption that body size and longevity are related [1543]. In fact, this assumption may be erroneous; emerging data has found that many species of small-bodied reef fish can live to be 20–40 years old [387,1678,2198], as long or longer than some of the largest predatory reef fish [376]. Incorporating estimates of longevity into these analyses may explain additional variance. We anticipate that the rapidly increasing quantity and availability of relevant biological and ecological data will lead to further insights about the drivers of range size in tropical reef fish.

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