

The relationship between pelagic larval duration and range size in tropical reef fishes: a synthetic analysis

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We address the conflict in earlier results regarding the relationship between dispersal potential and range size. We examine all published pelagic larval duration data for tropical reef fishes. Larval duration is a convenient surrogate for dispersal potential in marine species that are sedentary as adults and that therefore only experience significant dispersal during their larval phase. Such extensive quantitative dispersal data are only available for fishes and thus we use a unique dataset to examine the relationship between dispersal potential and range size. We find that dispersal potential and range size are positively correlated only in the largest ocean basin, the Indo-Pacific, and that this pattern is driven primarily by the spatial distribution of habitat and dispersal barriers. Furthermore, the relationship strengthens at higher taxonomic levels, suggesting an evolutionary mechanism. We document a negative correlation between species richness and larval duration at the family level in the Indo-Pacific, implying that speciation rate may be negatively related to dispersal potential. If increased speciation rate within a taxonomic group results in smaller range sizes within that group, speciation rate could regulate the association between range size and dispersal potential.

Keywords: dispersal; range size; reef fish; biogeography; pelagic larval duration; Indo-Pacific

1. INTRODUCTION

Understanding the patterns and mechanisms regulating species' geographic distributions is a critical goal of ecology and biogeography (Brown *et al.* 1996). Species' range sizes vary by orders of magnitude (Brown *et al.* 1996) and a number of mechanisms have been proposed to account for range size variation (Brown *et al.* 1996; Gaston 1996). However, because tests of these hypotheses have been limited by the large scales involved and the diverse taxa in question, a general explanation has yet to emerge.

Dispersal potential is a frequently cited causal factor for range size variation, in both terrestrial (Juliano 1983; Edwards & Westoby 1996; Duncan *et al.* 1999; Thompson *et al.* 1999; Clarke *et al.* 2001) and marine systems (Shuto 1974; Hansen 1980; Scheltema & Williams 1983; Perron & Kohn 1985; Jablonski 1986; Emler 1995; Bonhomme & Planes 2000; Victor & Wellington 2000). Species with greater dispersal potential are expected to establish and maintain larger ranges than similar species with more limited dispersal capabilities. This explanation has received particular attention in the marine literature because closely related taxa can show remarkable variations in both dispersal potential (Kinlan & Gaines 2003) and range size (Brown *et al.* 1996). Many marine organisms are relatively sedentary as adults, dispersing primarily during a pelagic larval phase. Thus, the duration of this larval phase will strongly influence a species' dispersal potential (Shanks *et al.* 2003; Siegel *et al.* 2003). While dispersal potential may also be affected by complex oceanography, larval behaviour, and propagule supply

(itself influenced by population size, body size and fecundity, and reproductive frequency), tests of the impact of these factors are hampered by the absence of sufficient quantitative data. However, several recent studies demonstrate that despite these potential complexities, larval durations correlate well with alternative quantitative estimates of dispersal (Riginos & Victor 2001; Shanks *et al.* 2003; Siegel *et al.* 2003). Therefore, given our current understanding of larval biology and physical factors, the length of the larval phase is the best quantitative estimate of dispersal potential.

Difficulties in quantifying the duration of the larval phase have resulted in a paucity of tests of the relationship between dispersal potential and range size for most marine taxa. However, marine fishes are a model system for evaluating this relationship because the length of their pelagic larval durations (PLD) can be estimated from otolith increments (see §2) and they vary in both dispersal potential and range size (Jones *et al.* 2002; Kinlan & Gaines 2003).

There is an increasing wealth of PLD data available for tropical reef fishes (e.g. Wellington & Victor 1989; Victor 1991) and some of these data have been used to examine the relationship between dispersal ability and range size (e.g. Thresher 1991; and references in table 1) with strikingly contradictory results. Several studies document a positive relationship between PLD and range size either at the species level (Bonhomme & Planes 2000; Zapata & Herrón 2002; Mora *et al.* 2003), or at the generic level (Thresher *et al.* 1989; Wellington & Victor 1989). Others found no significant relationship at the species level (Jones *et al.* 2002; Thresher & Brothers 1985; Thresher *et al.* 1989; Victor & Wellington 2000). However, most

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Table 1. Studies examining PLD and geographic distribution in tropical reef fishes. (Abbreviations used: spp., species; n.s., non-significant relationship; no., number.)

reference	family (no. of sp.)	region	range metric	results
Thresher & Brothers (1985)	Pomacanthids (31)	Indo-Pacific	no. of 28 areas occupied	n.s.: PLD and no. of areas occupied
Brothers & Thresher (1985)	22 families (115)	Indo-Pacific	no. of 29 areas occupied	spp. with PLD greater than 45 d tend to have broad ranges spp. with PLD less than 45 d vary in their distributional extent
Thresher <i>et al.</i> (1989)	Pomacentrids (67)	Indo-Pacific	no. of 28 areas occupied	positive correlation only at generic level spp. found on and off west margin of Pacific plate have longer mean PLD than spp. found only on or off
Wellington & Victor (1989)	Pomacentrids (100)	all	widespread versus restricted genera and spp.	n.s.: mean PLD of widespread versus restricted spp. genera with shorter mean PLD tend to be those restricted to the Indo-Pacific
Victor & Wellington (2000)	Labrids (29); Pomacentrids (20)	East Pacific	max linear distance max gap distance between habitat	n.s.: PLD and max linear or gap distance for both families endemic species have longer PLD than widespread congeners for both families
Bonhomme & Planes (2000)	Pomacentrids (98)	Indo-Pacific	no. of 23 localities occupied	positive correlation between PLD and no. of localities occupied
Zapata & Herrón (2002)	Lutjanids (5)	East Pacific	max gap distance between locations longitudinal range	n.s.: PLD and max gap distance positive correlation between PLD and longitudinal range
Jones <i>et al.</i> (2002)	five families (150)	Indo-Pacific	range of occurrence (km ²)	n.s.: PLD and range size (families pooled: $R^2 = 0.08$) spp. with longest PLD have largest ranges
Mora <i>et al.</i> (2003)	Labrids (95); Pomacentrids (116)	Indo-Pacific	distance from proposed centre of origination	significant positive correlation between mean PLD of spp. at a location and the distance of the location from origination centre, for both families

of these studies focus on only one or a few families, usually in a single ocean region. Range size is also described differently across studies, complicating attempts to resolve the issue.

A more comprehensive survey comparing multiple families and ocean basins is needed to determine the conditions under which dispersal potential is associated with range size, and to investigate the mechanisms that may regulate this association. We synthesize all published tropical reef fish PLD data (362 species from 28 families) and determine each species' range size using a consistent, quantitative measure—maximum linear distance within a species' range.

The relationship between dispersal potential and range size may take one of three general forms. First, dispersal

potential may have little or no effect on species' geographic ranges. This idea predicts no relationship between PLD and range size in any ocean basin and within few, if any, taxonomic groups (i.e. families). Second, dispersal potential may strongly influence species' range sizes. If dispersal potential is a primary determinant of range size, we would expect to find a strong positive relationship between PLD and range size in all ocean basins and within most taxonomic groups. Finally, dispersal potential may affect species' ranges only under certain circumstances. For example, dispersal potential may only be important over distances beyond a threshold (e.g. Brothers & Thresher 1985). Additionally, dispersal might influence species' geographic distributions only for particular spatial arrangements of available habitat. If some habitat

is considerably isolated and peripheral, such as distant oceanic islands, species will require greater dispersal potential to colonize these areas. In doing so, these species will achieve the largest possible range size. In this case, the relationship between range size and larval duration might actually be a sideways U-shape; species with short to medium dispersal potential would tend to have small to medium ranges, while species with the greatest dispersal potential would have both the largest ranges (they can reach the most distant and isolated areas) and smallest ranges (if after colonizing a distant area, they remain genetically isolated and speciate, becoming endemics with restricted distributions). The presence of such endemics would obscure a stronger positive relationship among the more widespread species. Using our larval duration database, we test which of these forms best describes the relationship between dispersal potential and range size.

2. METHODS

We compiled PLD data from the studies in table 1, along with any published tropical reef fish PLD data collected for other purposes (see Electronic Appendix for references). We chose to limit our analysis to tropical reef fishes because (i) PLD and reliable distributional information exist for many species; (ii) their coral reef habitat is abundant worldwide throughout the tropics; (iii) areas of suitable habitat are often separated by expanses of uninhabitable open ocean across which they must disperse as larvae to extend their range; and (iv) adults have limited home ranges, such that dispersal occurs almost exclusively during the larval phase.

We only included PLD estimates determined by ageing otoliths, calcium carbonate accretions within the semicircular canals of bony fishes. Otoliths are used to estimate PLD by examining their daily growth increments and distinct 'settlement marks' (Victor 1991). We used the mean larval duration reported, and when multiple studies estimated PLD for a given species, we averaged the mean from each study. When available, we also recorded the overall minimum and maximum PLD (across all studies). The resulting dataset includes 362 species from 28 families.

We collected distributional information for each species (see Electronic Appendix). Species were designated as either Atlantic ($n=50$) or Pacific ($n=312$). Pacific species were further categorized as East Pacific endemics ($n=40$), Hawaiian Islands endemics ($n=15$) or Indo-Pacific species, which excluded all East Pacific endemics and Hawaiian Islands endemics ($n=257$). A final category, West Pacific species, was composed of the Indo-Pacific species excluding species with ranges extending to the East Pacific, Hawaii, and/or Easter Island ($n=206$). We collected data for a proportionate number of species from each ocean basin with respect to relative regional reef fish diversity (approximately 7% and 9% of the Atlantic and Indo-Pacific reef fish species, respectively; Lieske & Myers 2002).

We defined a species' range as the maximum extent of established, breeding populations, excluding locations from which only vagrants or recruits had been reported. For each species, we determined the locations of range endpoints (north, south, east, west, northeast, northwest, southeast, southwest). Endpoint geographic coordinates (latitude and longitude) were determined to the nearest half degree using the Times Atlas of the World (Anon. 1999) and entered into a

Table 2. Comparison of R^2 values for linear regressions of PLD (days) on the three range size metrics (maximum linear distance, in km and longitudinal and latitudinal range, in degrees) in each ocean region. (*indicates $p<0.0001$. All other regressions are non-significant.)

range metric	Indo-Pacific	West Pacific	Atlantic
max linear distance	0.26*	0.12*	0.005
longitudinal range	0.26*	0.12*	0.014
latitudinal range	0.16*	0.083*	0.001

geographical database. We then calculated three measures of range size: (i) latitudinal extent, (ii) longitudinal extent, both in degrees, and (iii) maximum linear surface distance, in km, from the furthest two range endpoints. Maximum linear distance was determined using the distance function in the mapping toolbox in MATLAB 6.1 (MathWorks, Inc.) to calculate the rhumb line distance between the furthest two range endpoints. The rhumb line is the path between two points on the earth, maintaining a constant heading, and is thus an accurate measure of the maximum linear distance within the species' range, calculated from the surface of the globe. We regressed each of our range size metrics (degrees or kilometres) against PLD (days). We log-transformed PLD for all analyses to achieve normality. Statistical tests were conducted using JMP 4.0 (SAS Institute).

3. RESULTS

All three of our range metrics (latitude, longitude and maximum linear distance within the range) are highly collinear ($r=0.818$ and 0.997 for maximum distance versus latitudinal and longitudinal extent respectively, and $r=0.802$ for latitudinal versus longitudinal extent), suggesting that fishes with broad ranges in one dimension tend to have broad ranges in all dimensions. These metrics all yield qualitatively similar results, and quantitatively similar results for maximum linear distance and longitude (table 2). Given that the latitudinal ranges of tropical reef fishes are likely to be constrained by factors other than available habitat (e.g. temperature tolerance), it is not surprising that we find a stronger relationship between PLD and longitudinal range and maximum linear distance than between PLD and latitudinal range. We subsequently report results only for maximum linear distance, as it is a more complete descriptor of a species' geographic extent.

The relationship between PLD and range size differs between oceans. There is no relationship between PLD and range size in the Atlantic (figure 1a; $p=0.628$), but there is a highly significant positive relationship in the entire Pacific (figure 1b; $p<0.0001$). However, the relationship is weak ($R^2=0.07$) and the significance is probably caused in part by the large sample size (greater than 300 species). There is some indication that the relationship follows a sideways U-shaped distribution in the Pacific, possibly the result of endemics in the dataset. The Hawaiian Island and East Pacific endemics groups (figure 1c,d) contain some species with relatively long larval durations, but small ranges constrained by available habitat. These species comprise the data in the lower right portion of the 'U' in figure 1b. When these two groups are removed, and only widespread

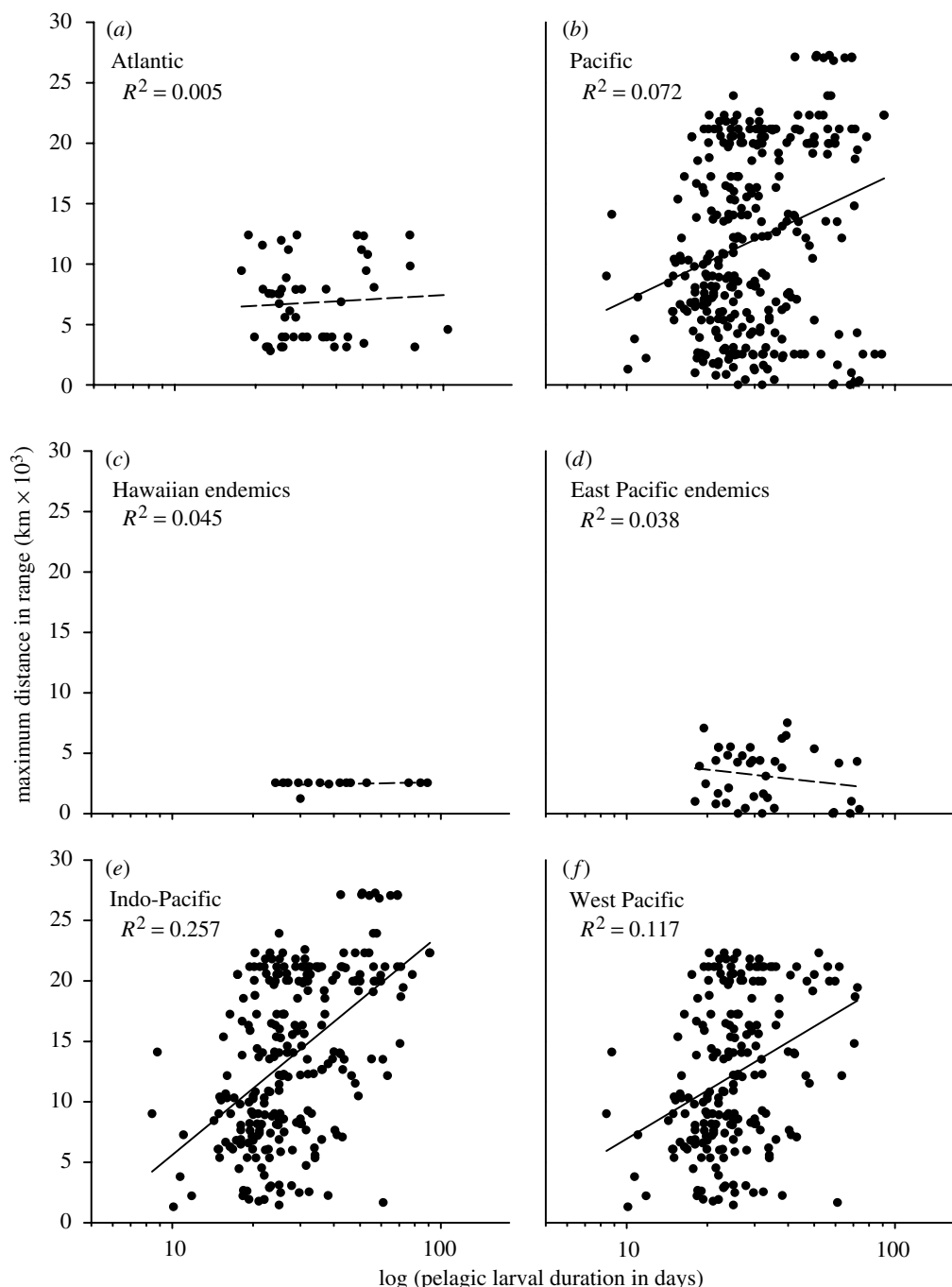


Figure 1. Relationship between maximum linear distance within a species' range and pelagic larval duration. Data are shown for Atlantic species ((a) $n=50$, $p=0.628$), all Pacific species ((b) $n=312$, $p<0.0001$), Hawaiian island endemics ((c) $n=15$, $p=0.449$), East Pacific endemics ((d) $n=40$, $p=0.231$), Indo-Pacific species ((e) $n=257$, $p<0.0001$), and West Pacific species ((f) $n=206$, $p<0.0001$). Solid lines indicate significant relationships, while dotted lines indicate non-significant relationships. Refer to §2 for an explanation of regional designations.

Indo-Pacific species are included, the positive relationship between PLD and range size is much stronger ($R^2=0.257$; figure 1e).

Much of the previous work (table 1) has examined patterns only within fish families. Positive relationships within individual families could be masked when combining data from multiple families. However, we find positive within-family patterns in the same regions as across-family patterns (table 3). Three of the five families for which we have sufficient data show significant relationships in the Indo-Pacific. All other relationships

are non-significant, although small sample sizes limit the power of some of these tests.

The PLDs of related species may be constrained phylogenetically and thus may not be truly independent. Furthermore, if PLDs are phylogenetically constrained, within-group (i.e. within-family) analyses may not capture the full range of variation in PLD. However, it is impossible to make true phylogenetic contrasts at the species level because the evolutionary distances among species are unknown. Thus, to correct for the effect of phylogeny, we examined patterns at higher taxonomic levels. We calculated the mean PLD and range size for

Table 3. Results of linear regressions of PLD (days) on maximum linear distance within a species' range (km), in the Indo-Pacific, for the five families best represented in the dataset.

(Results for the Atlantic, East Pacific, and Hawaii regressions are not shown because they are non-significant.)

family	<i>n</i>	<i>p</i>	<i>R</i> ²	slope
Pomacentridae	92	0.0002	0.143	+
Labridae	68	0.0002	0.193	+
Pomacanthidae	28	0.731	0.005	—
Acanthuridae	14	0.136	0.176	+
Chaetodontidae	14	0.020	0.376	+

each genus and family with data for three or more species. There is no relationship in the Atlantic (Genus: $p=0.262$; Family: $p=0.370$), but a highly significant positive relationship in the Indo-Pacific (Genus: $R^2=0.540$, $p<0.0001$, $n=28$; Family: $R^2=0.851$, $p<0.0001$, $n=11$; figure 2a).

Rare, long dispersal events may be disproportionately important in extending species' ranges. If true, maximum PLD may be a more relevant measure of dispersal potential. We are unable to critically examine the relationship between maximum PLD and range size because we only have reliable ($n \geq 20$ individuals per species) maximum PLD data for approximately 20% of the entire dataset, and less than 10% of the Indo-Pacific dataset. However, there is a tight relationship between mean and maximum PLD for those species for which we do have reliable data ($R^2=0.94$, $p<0.0001$, $n=66$), suggesting that mean PLD may be a reliable predictor of maximum PLD, and therefore of a species' relative dispersal potential.

4. DISCUSSION

Our data suggest that dispersal potential, described as mean PLD, is not a universal driver of range size in reef fishes, but does appear to be important under certain circumstances (e.g. in the Indo-Pacific). A few explanations may account for this result, most notably ocean basin size and the spatial distribution of habitat and dispersal barriers. The Pacific is considerably larger than the Atlantic; the maximum potential range is approximately 28 000 km in the Indo-Pacific, compared to 12 500 km in the Atlantic. Thus, the relationship between PLD and range size may only be apparent over large scales if dispersal potential does not limit range size in smaller oceans, where range size is more constrained. Since there is no comparably large tropical ocean, it is difficult to determine whether basin size *per se*, or other unique aspects of the Pacific, drive our results.

Variations in the spatial arrangement of habitat among ocean basins may also account for our results. The Pacific contains vast expanses of ocean between suitable reef fish habitat and has few islands that could function as dispersal 'stepping stones' to its most remote areas. The Hawaiian Islands and Easter Island are isolated from the nearest tropical reef area by approximately 2000 km, and trans-Pacific species must cross almost 5000 km in a single dispersal event to reach the tropical eastern Pacific.

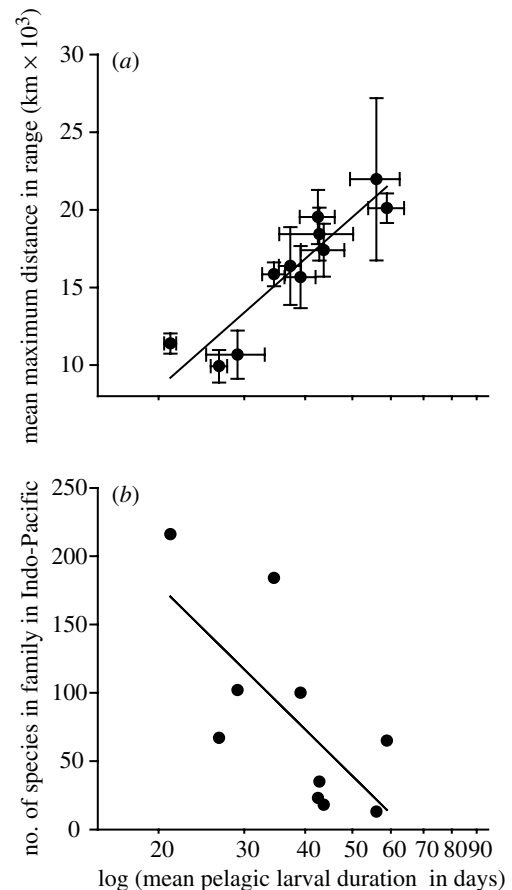


Figure 2. Indo-Pacific family means. (a) Average range size versus the average pelagic larval duration for each Indo-Pacific family comprised of data from three or more species. Error bars indicate plus or minus one standard error (Linear regression: $n=11$, $p<0.0001$, $R^2=0.851$). (b) Indo-Pacific species richness versus mean pelagic larval duration for each family, as above (Linear regression: $n=10$, $p=0.023$, $R^2=0.494$).

Furthermore, the few islands nearest to the eastern Pacific tend to be small, and hence may be unable to sustain large populations. Smaller populations will produce fewer offspring, thereby limiting the number of potential long-distance dispersers. In contrast, while transatlantic species must cross a large oceanic stretch (the minimum distance is 2800 km from Brazil to Senegal), the oceanic Atlantic as a dispersal barrier is bounded on either side by extensive continental habitat, increasing population sizes and the subsequent pool of dispersing larvae, as well as the size of potential targets (i.e. continental coasts) where larvae may settle after long-distance dispersal. However, due to the number of factors that may influence species' range sizes, such as environmental tolerance, historical factors (e.g. rise of the Panamá Isthmus) and biotic interactions, the absence of a relationship between PLD and range size in the Atlantic may not be surprising.

Given the spatial arrangement of habitat in the Pacific, species whose ranges extend to more isolated, peripheral areas like Hawaii and the East Pacific tend to have the largest ranges. These species may therefore be disproportionately important in strengthening the relationship between PLD and range size if they require a long PLD to reach such areas. We conducted two tests of this hypothesis. First, we compared the relationship

among Indo-Pacific species (figure 1e) to that among species restricted to the West Pacific (figure 1f), excluding the 51 species whose ranges extend to Hawaii, Easter Island and/or the East Pacific. The R^2 value drops by more than half (from 0.257 to 0.117) when widespread species are excluded. For comparison, a simulation randomly excluding 51 of the 257 Indo-Pacific species iterated 100 times produced a mean R^2 value of 0.253. This suggests the strength of the PLD and range size relationship in the Indo-Pacific is reinforced by the inclusion of these widespread species. Second, we compared the PLDs of the 51 widespread species to the PLDs of the West Pacific species; widespread species have significantly longer larval durations (mean=48 and 27 days, respectively; t -test: $p < 0.0001$, $n = 257$). This result is consistent with that of some previous work (Brothers & Thresher 1985; Thresher *et al.* 1989). In contrast, transatlantic species do not have longer PLDs than species restricted to the western Atlantic (t -test: $p = 0.128$, $n = 45$). These results support the idea that certain configurations of habitat strengthen the relationship between range size and PLD.

While a long PLD may be necessary for species to expand their ranges to the peripheries of ocean basins, rare colonization events of these distant areas may also result in endemics with long PLD and small range (i.e. the points in the bottom right of the 'U' in figure 1b). Hawaiian endemics have significantly longer PLD than their more widely distributed congeners (paired t -test: $p = 0.0009$, $n = 11$). Other studies confirm that island endemics, despite their small ranges, are not limited in their dispersal potential. In a recent review of the biological characteristics of tropical reef fishes endemic to small, isolated islands, Robertson (2001) concluded that endemics do not tend to have a shorter PLD than related species with more widespread ranges. Victor & Wellington (2000) found that island endemics from two fish families in the East Pacific have a longer PLD than their widespread congeners. That species colonizing these islands are subsequently able to speciate despite their great larval dispersal potential highlights the importance of local retention mechanisms (Swearer *et al.* 2002) and/or limited larval supply.

The positive relationships between dispersal potential and range size that we found are stronger at higher taxonomic levels. There is a considerable increase in explanatory power from the species to the genus to the family level in the Indo-Pacific (R^2 : 0.26, 0.54 and 0.85, respectively; figures 1e and 2a). An unmeasured factor that is phylogenetically constrained and is correlated with both PLD and range size may be causing the stronger relationships at higher taxonomic levels. Potential factors include body size, habitat specificity, reproductive output, generation time and speciation rate. Body size is relatively uncorrelated with larval duration and range size for the Indo-Pacific species in our dataset ($r = 0.29$ and 0.30 , respectively; body size estimates from distributional references listed in the Electronic Appendix). Habitat specialization could be correlated to dispersal potential, assuming habitat specialists experience greater selective pressure for limited dispersal than habitat generalists; but habitat specificity is unlikely to be constrained by family, at least for most fish families.

High reproductive output or short generation times could be related to effective dispersal by increasing the absolute number of individuals that comprise the tail of the dispersal kernel, thereby enhancing the number of long-distance dispersal events. However, reproductive output has not been quantified for most reef fishes and our data lends little support for generation time, as relatively long lived families are found on both extremes of the range of data plotted in figure 2.

Speciation rate is a more plausible mediating mechanism, assuming taxa with a shorter PLD are more likely to speciate (due to genetic isolation and local adaptation) and speciation results in smaller range sizes (younger species have less evolutionary time for range expansion). We predict that families with short mean PLD should be more speciose if they have a higher speciation rate. To test this prediction, we determined the approximate number of species within the Indo-Pacific for each family (Lieske & Myers 2002); there is a significant negative relationship between family-level species richness and the mean larval duration for that family ($n = 10$, $p = 0.023$, $R^2 = 0.494$; figure 2b). While these data support the idea that speciation rate could help drive the relationship between PLD and range size, additional evidence regarding species' evolutionary ages and the relative importance of extinction rates, both of which may be influenced by dispersal potential (see Jablonski 1986 and references therein), is necessary to further evaluate this hypothesis.

In summary, by incorporating data from multiple oceans and families, we have addressed the conflicting evidence regarding the relationship between dispersal potential and range size in tropical reef fishes. We demonstrate that PLD appears to influence range size only over large scales when significant barriers to dispersal are present. The tails of dispersal distributions may therefore potentially be critical in allowing species to colonize the most isolated areas. This highlights the need for more complete data describing dispersal kernels, particularly better estimates of maximum PLD. Our mechanistic investigation of this relationship has implications for other taxa and makes predictions which could be tested in other systems.

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