Research

High connectivity among habitats precludes the relationship between dispersal and range size in tropical reef fishes

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The hypothesis that pelagic larval duration (PLD) influences range size in marine species with a benthic adult stage and a pelagic larval period is intuitively attractive; yet, studies conducted to date have failed to support it. A possibility for the lack of a relationship between PLD and range size may stem from the failure of past studies to account for the effect of species evolutionary ages, which may add to the dispersal capabilities of species. However, if dispersal over ecological (i.e. PLD) and across evolutionary (i.e. species evolutionary age) time scales continues to show no effect on range size then an outstanding question is why? Here we collected data on PLD, evolutionary ages and range sizes of seven tropical fish families (five families were reef-associated and two have dwell demersal habitats) to explore the independent and interactive effects of PLD and evolutionary age on range size. Separate analyses on each family showed that even after controlling for evolutionary age, PLD has an insignificant or a very small effect on range size. To shed light on why dispersal has such a limited effect on range size, we developed a global ocean circulation model to quantify the connectivity among tropical reefs relative to the potential dispersal conferred by PLD. We found that although there are several areas of great isolation in the tropical oceans, most reef habitats are within the reach of most species given their PLDs. These results suggest that the lack of habitat isolation can potentially render the constraining effect of dispersal on range size insignificant and explain why dispersal does not relate to range size in reef fishes.

Identifying factors shaping the geographical distribution of species is a fundamental aim of macroecology (Gaston 2003). For tropical reef fishes, the role of dispersal ability, quantified as the duration of the pelagic period (i.e. pelagic larval duration; PLD), has received considerable attention as a driver of range size because as adults these species are mostly sedentary (Thresher and Brothers 1985, 1989, Thresher et al. 1989, Wellington and Victor 1989, Zapata and Herron 2002, Goodwin et al. 2005, Lester and Ruttenberg 2005, Lester et al. 2007). The rationale is that species with longer PLDs can disperse over longer distances, resulting in larger geographical ranges compared to species with shorter PLDs. Although dispersal distances can be affected by additional factors such as currents and larval behaviors (reviewed in Mora and Sale 2002), the use of PLD as a quantitative measure of dispersal potential in reef fishes has been previously supported (Riginos and Victor 2001, Shanks et al. 2003, Siegel et al. 2003, Lester and Ruttenberg 2005, Lester et al. 2007). Interestingly, however, numerous studies explicitly comparing PLD to range size have failed to demonstrate a significant or important relationship between the two (Thresher and Brothers 1985, 1989, Tresher et al. 1989, Wellington and Victor 1989, Victor and Wellington 2000, Jones et al. 2002, Zapata and Herron 2002, Goodwin et al. 2005, Lester and Ruttenberg 2005, Lester et al. 2007).

Although recent meta-analyses, including all available data on PLDs, have concluded that dispersal is not a general determinant of range size (Lester and Ruttenberg 2005, Lester et al. 2007), the nullification of the hypothesis that PLD influences range size may be premature due to the failure of previous studies to account for species evolutionary ages (i.e. older species ought to have had more time to disperse and if dispersal influences range size then older species would be expected to have larger ranges than younger species). Species evolutionary ages may also confound the effects of PLD because species with large PLDs may have small geographic ranges if they are relatively young; alternatively, species with short PLDs could potentially have larger ranges if they have been dispersing over longer evolutionary time scales. This situation calls for analyzing the combined effects of PLD and species ages on range size. Consequently, if even after accounting for evolutionary age, PLD does not affect range size, then a critical question is why?

In this study, we gathered data on PLD, evolutionary age and range sizes of tropical reef and demersal fishes to evaluate the relative effect and interaction strength of evolutionary (i.e. species age) and ecological (i.e. PLD) dispersal on range size. We found that even after controlling for species age, PLD has a very small or statistically insignificant effect on range size. To gain further insight as to why dispersal does

not affect range sizes, we developed a global ocean circulation model to quantify the isolation of tropical reefs relative to the potential dispersal conferred by species-specific PLD. We found that although there are areas of great isolation in tropical oceans, most reef habitats are within reach of most species' PLD. These results suggest that the lack of isolation of habitats likely renders insignificant the potential constraints of PLD on range size.

Methods

We assembled three independent databases on the PLD, evolutionary age and range size of tropical reef fishes. We started with an extensive literature search on published PLDs of reef fishes. We then searched for available phylogenies of fish families for which we collected data on PLD for ten or more species. All phylogenies were digitized and analyzed with the programs treesnatcher v1.0 (Laubach and von Haeseler 2007) and the 'ape' package in R (R Development Core Team 2010, <www.r-project.org>) to obtain the age of each species in the case of ultrametric trees (i.e. where branch lengths represent the actual evolutionary age in millions of years) or the genetic distance between pairs of species in the case of phylogenetic trees. Most phylogenies were already dated using fossils or time of known bifurcation events, but, in one family (i.e. Pomacentridae) trees were only available as genetic difference, in which case genetic dissimilarity to the most recent sister species was assumed to be a surrogate of age since divergence (Webb and Gaston 2000, Coyne and Orr 2004, Stelkens et al. 2010). When a species had more than one sister species, we calculated the average pairwise genetic distance between the one species and all sister species in the clade (see Webb and Gaston 2000 for details). In most cases, phylogenies were based on multiple markers (i.e. mitochondrial and nuclear) to accommodate differential modes of inheritance (i.e. maternal vs biparental), differences in effective population size (i.e. small vs large), variable recombination (no recombination in mtDNA) and mutation (i.e. nuclear-slower, mtDNA faster) rates.

For species with data on PLD and evolutionary age, we gathered biogeographical records from multiple sources, including the Ocean Biogeographic Information System (<www.iobis.org>), the Global Biodiversity Information Facility (<www.gbif.org>), and 70 check lists of reef fish species used in Mora et al. (2003). To remove records that were clearly outside the established range of each species and which likely reflected known errors in these data sources (Robertson 2008), all records were grouped into an ArcGIS shapefile and compared against the distribution of each species as reported in general reef fish books (Randall et al. 1990, Allen and Robertson 1994, Allen et al. 1997). Once all records were validated, species-specific ranges were measured as the distance between the two most separated locations where the species was recorded (none of the species analyzed have antitropical distributions). For the families for which we obtained data on all variables, we ran generalized linear models with range size as the dependent variable and PLD and evolutionary age as independent variables. Given our expectation that evolutionary age and PLD may interact, the model also included an interaction term between these

two variables. We also included ocean as a factor to allow for differences between ocean basins.

To quantify the isolation of reef habitats in tropical oceans and the barriers it imposes on the dispersal of reef fishes, we calculated the fraction of species whose PLDs are not long enough to bridge the different gaps between reef habitats. For this, we modeled the long-term average dispersal of reef fish larvae from every potential reef habitat in the world in the band between 45°N and 45°S. We started by creating a global database on available habitats for the establishment of reef fishes. Our data included the distribution of coral reefs [global data from Mora et al. (2006), which concatenates data from digitized maps and satellite images], rocky reefs from the tidal zone down to 100 m depth [global data from Halpern et al. (2008)] and seamounts whose peaks are <100 m below the surface of the water (global data from Wessel 2001, Yesson et al. 2011). We considered both coral and rocky reefs as previous studies have indicated that, with very few exceptions, most reef fish species can inhabit both reef types (Robertson 1998). We also included seamounts to consider their role as stepping stones in the expansion of species ranges. There are additional sources of potential habitats to reef fishes that we did not include given the lack of global data such as seaports, wrecks, oil rigs, etc. Yet the inclusion of these artificial structures should make patterns of isolation less pronounced as such habitats could also act as stepping stones, making our results about connectivity conservative. The habitat database was divided in cells of 25 km² (i.e. we created a global grid of 25 km² cells and selected all cells that overlapped any of the habitats considered). This coarsening of the habitat data was necessary to optimize the computational approach described below.

We modeled the potential larval dispersal among all habitat patches (connectivity) given contemporary patterns of ocean currents using the modeling framework of Treml et al. 2008, implemented by the Marine Geospatial Ecology Tools software (Roberts et al. 2010) ver. 0.8. This framework simulates the dispersal of larvae from each habitat patch by dynamic ocean currents using an advection transport algorithm (Smolarkiewicz and Margolin 1998) and by turbulent diffusion. In this scheme, larvae are treated as a dye concentrated initially at the source habitat patch and spread by advection and diffusion as the simulation progresses (see example in the animation provided in the Supplementary materials). When larvae encounter downstream habitat patches, they settle and are removed from the water. The simulator tracks the quantity of larvae settled at each time step and calculates an asymmetric dispersal matrix giving the minimum time required for larvae to disperse between all pairs of habitat patches. To drive the model's advection algorithm, we used ocean surface currents from the HYCOM + NCODA Global 1/12° Analysis (Chassignet et al. 2009, downloaded from <www.hycom.org/dataserver/glb-analysis> in July 2010). This database provides high-resolution daily estimates of the state of the global ocean by assimilating sea surface height, temperature, salinity, and ice concentration measurements obtained by satellites and in situ sources. The model describes well the deep open ocean, shallow coastal areas, and the mixed layer (Chassignet et al. 2009). To account for seasonal and inter-annual variabil-

ity in currents, we performed four dispersal simulations per year for the entire time span available in the HYCOM + NCODA dataset (i.e. 2004–2009, for a total of 24 simulations). The time period for which hydrodynamic data was available encompasses enough variability in episodic events known to affect water circulation (Supplementary material Appendix 1 Fig. A1), suggesting that our results reflect the generality of larval connectivity in the tropical ocean. It is clear, however, that a longer time frame would likely increase the chances of infrequent dispersal events making our results more conservative.

We released larvae at the midpoint of each season (i.e. 2 February, 5 May, 6 August, and 11 November) and simulated dispersal for 100 d, a duration encompassing the majority of PLDs in tropical reef fishes (Supplementary material). After completing the 24 simulations, we created a single asymmetric dispersal matrix giving the minimum dispersal time between all pairs of habitat patches obtained over the entire set of simulations. We then compared these times to the database of PLDs to calculate the fraction of species whose PLD was shorter than the time it took to cross the different gaps between patches, thereby highlighting where biogeographical barriers to the dispersal of reef fishes are likely to exist in the world's tropical reefs.

Results

We collected data on PLD for 547 species in 67 families from 137 sources (Supplementary material). Only 13 families had data on PLD for more than 10 species (i.e. Pomacentridae, Labridae, Pomacanthidae, Gobiidae, Acanthuridae, Chaetodontidae, Lutjanidae, Anguillidae, Serranidae, Sparidae, Blenniidae, Scombridae and Pleuronectidae). Of these, we found representative phylogenies for seven families [i.e. Pomacentridae (Cooper et al. 2009), Labridae (Cowman et al. 2009), Pomacanthidae (Bellwood et al. 2004), Chaetodontidae (Bellwood et al. 2010), Anguillidae (Minegishi et al. 2005), Serranidae (Craig and Hastings 2007) and Sparidae (Chiba et al. 2009)]. Most of these families comprise reef-associated species with the exception of Anguillidae and Sparidae, which are mostly dermersal (Supplementary material Appendix 1). We maintained data on all seven families as the hypothesis that dispersal influences ranges size is relevant to all families with benthic habitat associations. In combination, we obtained data on species PLDs and evolutionary ages for 183 species in the seven families. For the species in these seven families, we obtained 98, 385 biogeographical records, all of which were verified visually against their reported distribution in general reef fish books (Methods). All of the seven families analyzed have relatively large body sizes suggesting that these species have a high sighting probability. Additionally, fish assemblages on reefs are the best sampled in the world's oceans (Mora et al. 2008) and for both the Pacific and Indian Oceans we used published checklists of species, which are known to be relatively complete. These facts combined suggest that the records we obtained are very likely to provide a reliable indication on the distribution of the analyzed species.

We found that neither the main effects of PLD or evolutionary age nor their interaction were important

determinants of species geographical ranges in the seven independently analyzed families (Fig. 1). We kept the analyses for each family independent because the lack of phylogenetic data on the relatives among families and inconsistency of the genetic markers among studies prevents the concatenation of all families into a single phylogenetic 'supertree'. The analyses on each family show that geographical ranges were equally variable in size along the entire series of PLDs and species evolutionary ages (Fig. 1). Only Pomacentrids showed a significant but weak relationship with PLD, which explained <4% of the variance in range sizes (Fig. 1). In the other six families, the relationships between range size and PLD, evolutionary age and their interaction were statistically non-significant (Fig. 1).

The world's tropical oceans have several regions of great isolation for reefs, such as the region between the central and eastern Pacific, the central Atlantic, and the central Indian Ocean, where distances to the nearest potential reef habitat can be as large as 1700 km (Fig. 2a). When considering isolation under hydrodynamic conditions many of these distances can be traversed over relatively short time periods. Only for a few reefs were there travel times >100 d (Fig. 2b); this was due to a combination of long distances of separation and slow current speeds (i.e. the eastern and southern Pacific and the south Indian Ocean) (Fig. 2b). For the majority of tropical oceans, travel times between reef patches were on the order of 30–100 d (Fig. 2c). Among the 547 species for which we collected data on PLD, the average PLD was 42.6 d (SD = 41.5) with several species having PLDs of over 100 d (Supplementary material Appendix 1). As result, when comparing the duration of the pelagic larval stage to the times to cross between reef patches, we found that few species are filtered by isolation across the tropical oceans. Only two geographical locations could potentially filter reef fish species through dispersal limitations at PLDs >70–80 d (~88% of species filtered). One occurred along the fringes between the central and eastern Pacific (i.e. the Eastern Pacific Barrier) and the other between the western and eastern Atlantic (Fig. 2c, d). Other than these two gaps, which are known to define different biogeographical regions with distinctive fish faunas (MacPherson 2002, Mora and Robertson 2005a, b, Floeter et al. 2008), most of the habitats in the ocean are within the travel time conferred by the PLD of most reef fishes (Fig. 2d). Note that this pattern on the isolation by dispersal of reef fishes is highly conservative because we considered average PLD and average daily currents at a 25 km^2 resolution. If maximum PLDs and higher resolution currents were used, the levels of isolation may have been smaller given the greater current speeds and dispersal potential. Similarly, we did not consider the potential extreme events of dispersal that some species may experience through their association with floating objects (Mora et al. 2001, Castro et al. 2002). We did not use maximum PLD in our analyses because the availability of such data was variable among sources; furthermore, sampling size to estimate PLDs was often small and variable among studies making maximum PLD an unreliable metric for comparison among species; that is, extreme events of dispersal are expected to be rare and therefore extensive sampling is required to reliably quantify them.
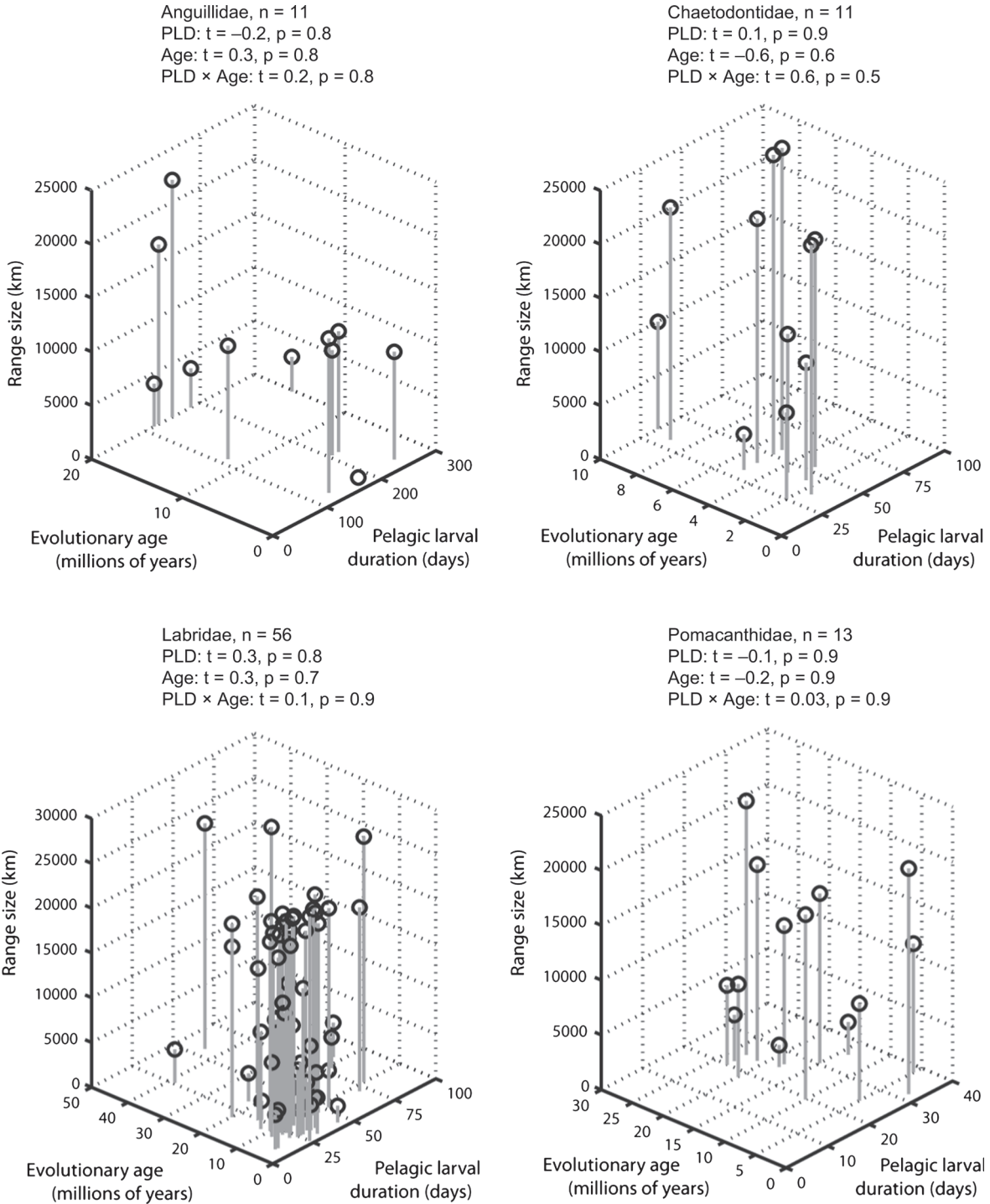
Figure 1. Interaction between range size, pelagic larval duration (PLD) and species evolutionary ages in seven fish families. Also plotted are the summary results of generalized linear models, including range size as the dependent variable and PLD, evolutionary age and their interaction as independent variables and ocean as a factor.

Discussion

Dispersal during the pelagic larval stage has been an appealing variable to marine macroecologists for explaining variations in range size among species with a pelagic larval period and a benthic adult life (Thresher and Brothers 1985, 1989, Thresher et al. 1989, Wellington and Victor 1989, Victor and Wellington 2000, Jones et al. 2002, Zapata and Herron

2002, Goodwin et al. 2005, Lester and Ruttenberg 2005, Lester et al. 2007). Although it is reasonable to think that longer larval periods should relate to larger geographical ranges, this hypothesis has received little empirical support (Lester and Ruttenberg 2005, Lester et al. 2007). However, the outright rejection of this hypothesis may be premature because previous work failed to incorporate aspects of the evolutionary time over which species have been dispersing.
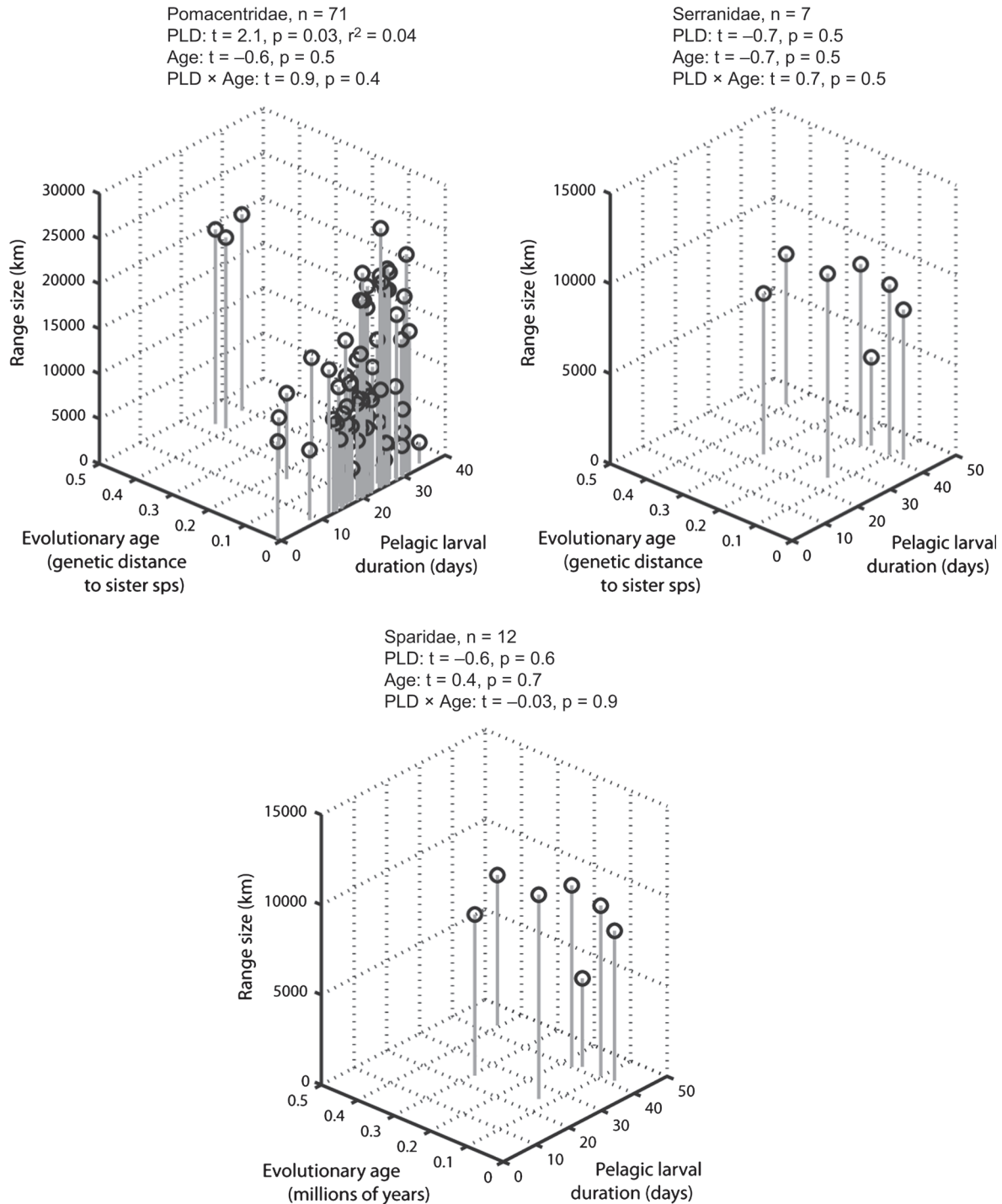
Figure 1. *Continued.*

In this study, we carried out independent tests in seven different families and showed that even after controlling for evolutionary age, the duration of the pelagic larval stage has little effect in determining range size. To explain why dispersal does not influence range size, we demonstrated that shallow reef habitats, although variably isolated, are commonly within reach of most species PLDs when taking ocean currents into account. In fact, empirical studies suggest that even some of the dispersal barriers identified in this study, such as that between the central and eastern Pacific (Lessios

and Robertson 2006) and that in the central Atlantic (Rocha et al. 2002, Carlin et al. 2003) are sporadically permeable to propagules on either side.

The hypothesis that dispersal affects range size assumes a gradient of suitable habitat isolation such that species with different dispersal capabilities are capable of moving differentially along the gradient, which should in turn yield a positive relationship between range size and dispersal capabilities. Our results indicate that with the exception of two major oceanic gaps between the central and eastern Pacific
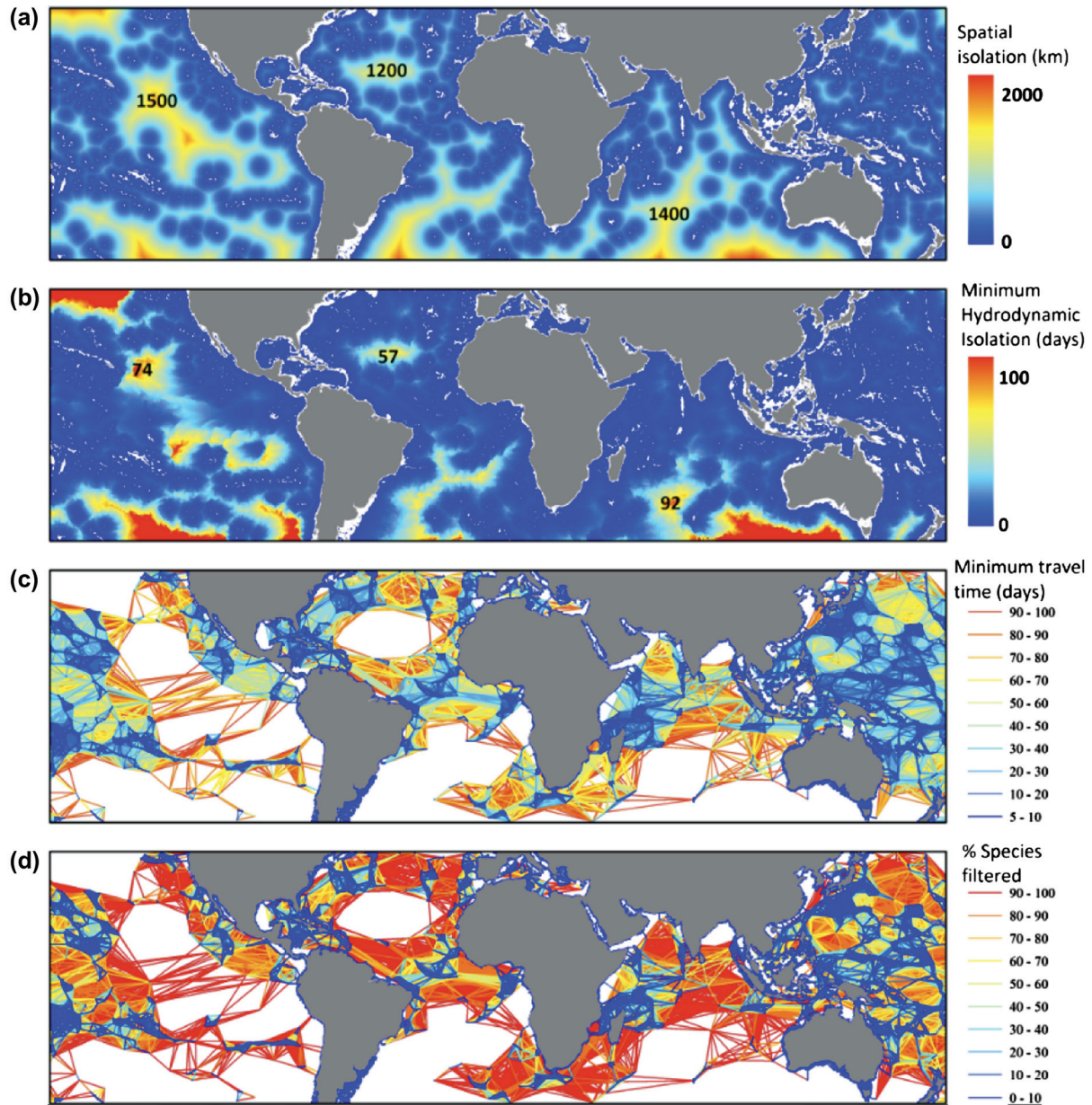
Figure 2. Connectivity of the world's tropical reef habitats. (a) Spatial isolation of tropical reef habitats quantified as the shortest distance to reef habitats. (b) Oceanographic isolation of tropical reef habitats quantified as the minimum time it takes to reach all reef habitats as determined by ocean currents (see animation in Supplementary materials). (c) Minimum time required to disperse from every reef patch to every other habitat patch. The lines between habitat patches represent dispersal connections color coded according to their travel time. These connections are represented as lines; however, they constitute voyages followed by particles given ocean circulation (see animation in Supplementary materials). (d) Network representing the proportion of species whose pelagic larval duration is insufficient to connect habitat patches.

and the western and eastern Atlantic (Fig. 2c), most tropical reef habitats in the world can be colonized during the pelagic larval duration of most reef fish species. This high degree of connectivity between tropical reefs is supported by recent genetic studies suggesting high population connectivity across the Indo-Pacific (Craig et al. 2007, Horne et al. 2008) and Atlantic (Rocha et al. 2002, Carlin et al. 2003, Purcell et al. 2006) Oceans [some of these studies include microsatellite markers (Purcell et al. 2006), which are known to evolve at relatively fast rates indicating that connectivity is established rather quickly, at least for the purpose of maintaining integrated geographical ranges]. These results suggest

that the assumption about a gradient of habitat isolation does not hold true for many reef fish species across the tropics, which likely explains the poor correlation between dispersal ability and range size in reef fishes.

Support for the limited isolation of marine habitats to the dispersal of reef fishes is also available from the fact that some species without a larval period can be broadly distributed (e.g. the genus *Acanthochromis*) and from recent studies on invasive reef fish species. For instance, less than a decade after it was first observed off Florida, the Indo-Pacific lionfish *Pterois volitans*, which likely has a typical larval duration ranging between 20 and 40 d (Whitfield et al. 2002),

is now widely distributed throughout the southeast coast of the United States, Bahamas, Dominican Republic and several other countries in the Caribbean (Whitfield et al. 2002, 2007, Guerrero and Franco 2008, Green and Cote 2009). The contemporary and rapid expansion of this species' geographical range highlights the relatively low impedance of habitat isolation to the expansion of species ranges and the short time required to colonize new habitats relative to the evolutionary time-scales on which species live. A similar example concerns the introduction of grouper and snapper species in Hawaii in the early 1960s. In an attempt to improve fisheries, the Bureau of Commercial Fisheries and the Division of Fish and Game of the state of Hawaii introduced eleven species of Serranidae and Lutjanidae to several Hawaiian reefs (Oda and Parrish 1981, Randall 1987). Of the eleven introduced species, three established resident populations and two became broadly distributed throughout the entire Hawaiian Archipelago (Oda and Parrish 1981, Randall 1987). The rapid spread of these species supports the limited effects of isolation in preventing the expansion of species. The fact that many species failed to establish is also interesting because it suggests that the potential for colonization or reachability of adequate habitats alone is unlikely to cause range expansion, as most species succeeded in reaching new habitats but most failed to establish within them. The reasons for why species fail to establish populations or the factors limiting their geographical expansion can be varied and could include physiological tolerances to environmental factors such as temperature and salinity (Marshall et al. 2010), ecological factors such as predation and competition, specific habitat requirements (e.g. terrestrial inputs, habitat size and quality, etc.) and potentially many others (reviewed by Gaston 2003, Lester and Ruttenberg 2005, Lester et al. 2007). Such a wide variety of factors may well explain why in some species PLD is proportional to traveled distance while in others it is not (Shanks et al. 2003). Discussion of these factors, however, is outside the scope of this paper which was to demonstrate the role, or lack thereof, of dispersal on range size.

In combination, our results indicate that habitat isolation plays a minor role in limiting the geographical expansion of reef fishes through dispersal, and perhaps much less so considering the long evolutionary time-scales over which most species have been dispersing. Identifying the factors limiting the geographical extent of reef fish species remains a challenge to reef fish biogeography; yet our study suggests that the focus should be shifted to attributes other than dispersal over ecological (i.e. PLD) or evolutionary (i.e. species age) time.

References

Allen, G. R. and Robertson, D. R. 1994. Fishes of the tropical eastern Pacific. – Univ. of Hawaii Press.

Allen, G. R. et al. 1997. Marine fishes of tropical Australia and south-east Asia, 3rd rev. ed. – Western Australian Museum, Perth.

Bellwood, D. R. et al. 2004. Evolution and biogeography of marine angelfishes (Pisces: Pomacanthidae). – Mol. Phylogenet. Evol. 33: 140–155.

Bellwood, D. R. et al. 2010. Evolutionary history of the butterfly-fishes (f: Chaetodontidae) and the rise of coral feeding fishes. – J. Evol. Biol. 23: 335–349.

Carlin, J. et al. 2003. Ancient divergences and recent connections in two tropical Atlantic reef fishes *Epinephelus adscensionis* and *Rypticus saponaceous* (Percoidei: Serranidae). – Mar. Biol. 143: 1057–1069.

Castro, J. J. et al. 2002. A general theory on fish aggregation to floating objects: an alternative to the meeting point hypothesis. – Rev. Fish Biol. Fish. 11: 255–277.

Chassignet, E. P. et al. 2009. US GODAE: Global Ocean Prediction with the HYbrid Coordinate Ocean Model (HYCOM). – Oceanography 22: 64–75.

Chiba, S. N. et al. 2009. Comprehensive phylogeny of the family Sparidae (Perciformes: Teleostei) inferred from mitochondrial gene analyses. – Genes Genet. Syst. 84: 153–170.

Cooper, W. J. et al. 2009. Exploring the radiation of a diverse reef fish family: phylogenetics of the damselfishes (Pomacentridae), with new classifications based on molecular analyses of all genera. – Mol. Phylogenet. Evol. 52: 1–16.

Cowman, P. F. et al. 2009. Dating the evolutionary origins of wrasse lineages (Labridae) and the rise of trophic novelty on coral reefs. – Mol. Phylogenet. Evol. 52: 621–631.

Coyne, J. A. and Orr, H. A. 2004. Speciation. – Sinauer.

Craig, M. and Hastings, P. A. 2007. A molecular phylogeny of the groupers of the subfamily Epinephelinae (Serranidae) with a revised classification of the Epinephelini. – Ichthyol. Res. 54: 1–17.

Craig, M. T. et al. 2007. High genetic connectivity across the Indian and Pacific oceans in the reef fish *Myripristis berndti* (Holocentridae). – Mar. Ecol. Prog. Ser. 334: 245–254.

Floeter, S. R. et al. 2008. Atlantic reef fish biogeography and evolution. – J. Biogeogr. 35: 22–47.

Gaston, K. J. 2003. The structure and dynamics of geographic ranges. – Oxford Univ. Press.

Goodwin, N. B. et al. 2005. Macroecology of live-bearing in fishes: latitudinal and depth range comparisons with egg-laying relatives. – Oikos 110: 209–218.

Green, S. J. and Cote, I. M. 2009. Record densities of Indo-Pacific lionfish on Bahamian coral reefs. – Coral Reefs 28: 107.

Guerrero, K. A. and Franco, A. L. 2008. First record of the Indo-Pacific red lionfish *Pterois volitans* (Linnaeus, 1758) for the Dominican Republic. – Aquat. Invasions 3: 267–268.

Halpern, B. S. et al. 2008. A global map of human impact on marine ecosystems. – Science 319: 948–952.

Horne, J. B. et al. 2008. High population connectivity across the Indo-Pacific: congruent lack of phylogeographic structure in three reef fish congeners. – Mol. Phylogenet. Evol. 49: 629–638.

Jones, G. P. et al. 2002. Rarity in coral reef fish communities. – In: Sale, P. F. (ed.), Coral reef fishes: dynamics and diversity in a complex ecosystem. Academic Press, pp. 81–101.

Laubach, T. and von Haeseler, A. 2007. TreeSnatcher: coding trees from images. – Bioinformatics 23: 3384–3385.

Lessios, H. A. and Robertson, D. R. 2006. Crossing the impassable: genetic connections in 20 reef fishes across the eastern Pacific barrier. – Proc. R. Soc. B 273: 2201–2208.

Lester, S. E. and Ruttenberg, B. I. 2005. The relationship between pelagic larval duration and range size in tropical reef fishes: a synthetic analysis. – Proc. R. Soc. B 272: 585–591.

Lester, S. E. et al. 2007. The relationship between dispersal ability and geographic range size. – Ecol. Lett. 10: 745–758.

Macpherson, E. 2002. Large-scale species richness gradients in the Atlantic Ocean. – Proc. R. Soc. B 269: 1715–1720.

Marshall, D. J. et al. 2010. Phenotype-environment mismatches reduce connectivity in the sea. – Ecol. Lett. 13: 128–140.

Minegishi, Y. et al. 2005. Molecular phylogeny and evolution of the freshwater eels genus *Anguilla* based on the whole mitochondrial genome sequences. – Mol. Phylogenet. Evol. 34: 134–146.

Mora, C. and Sale, P. F. 2002. Are populations of coral reef fishes open or closed? – Trends Ecol. Evol. 17: 422–428.

Mora, C. and Robertson, D. R. 2005a. Causes of latitudinal gradients in species richness: a test with fishes of the tropical eastern Pacific. – Ecology 86: 1771–1782.

Mora, C. and Robertson, D. R. 2005b. Factors shaping the ranges size frequency distribution of fishes in the Tropical Eastern Pacific. – J. Biogeogr. 32: 277–286.

Mora, C. et al. 2001. Dispersal of juvenile and adult reef fishes associated with floating objects and their recruitment into Gorgona Island Reefs, Colombia. – Bull. Mar. Sci. 68: 557–561.

Mora, C. et al. 2003. Patterns and processes in reef fish diversity. – Nature 421: 933–936.

Mora, C. et al. 2006. Coral reefs and the global network of marine protected areas. – Science 312: 1750–1751.

Mora, C. et al. 2008. The completeness of taxonomic inventories for describing the global diversity and distribution of marine fishes. – Proc. R. Soc. B 275: 149–155.

Oda, D. K. and Parrish, J. D. 1981. Ecology of commercial snappers and groupers introduced to Hawaian reefs. – Proc. 4th Int. Coral Reef Symp. 1: 59–67.

Purcell, J. et al. 2006. Weak genetic structure indicates strong dispersal limits: a tale of two coral reef fish. – Proc. Biol. Sci. 273: 1483–1490.

Randall, J. E. 1987. Introduction of marine fishes to the Hawaiian Islands. – Bull. Mar. Sci. 41: 490–502.

Randall, J. E. et al. 1990. Fishes of the Great Barrier Reef and Coral Sea. – Univ. of Hawaii Press.

Riginos, C. and Victor, B. C. 2001. Larval spatial distributions and other early life-history characteristics predict genetic differentiation in eastern Pacific blennioid fishes. – Proc. R. Soc. B 268: 1931–1936.

Roberts, J. J. et al. 2010. Marine geospatial ecology tools: an integrated framework for ecological geoprocessing with ArcGIS, Python, R, MATLAB, and C++. – Environ. Model. Software 25: 1197–1207.

Robertson, D. R. 1998. Do coral-reef fish faunas have a distinctive taxonomic structure? – Coral Reefs 17: 179–186.

Robertson, D. R. 2008. Global biogeographical data bases on marine fishes: caveat emptor. – Divers. Distrib. 14: 891–892.

Rocha, L. A. et al. 2002. Adult habitat preferences, larval dispersal, and the comparative phylogeography of three Atlantic surgeonfishes (Teleostei: Acanthuridae). – Mol. Ecol. 11: 243–252.

Shanks, A. L. et al. 2003. Propagule dispersal distance and the size and spacing of marine reserves. – Ecol. Appl. 13: S159–S169.

Siegel, D. et al. 2003. Lagrangian descriptions of marine larval dispersion. – Mar. Ecol. Prog. Ser. 260: 83–96.

Smolarkiewicz, A. and Margolin, T. 1998. MPDATA: a finite-difference solver for geophysical flows. – J. Comput. Phys. 140: 459–480.

Stelkens, R. et al. 2010. The accumulation of reproductive incompatibilities in African Cichlid fish. – Evolution 64: 617–633.

Thresher, R. E. and Brothers, E. B. 1985. Reproductive ecology and biogeography of Indo-West Pacific angelfishes (Pisces: Pomacanthidae). – Evolution 23: 878–887.

Thresher, R. E. and Brothers, E. B. 1989. Evidence of intra- and inter-oceanic regional differences in the early life history of reef associated fishes. – Mar. Ecol. Prog. Ser. 57: 187–205.

Thresher, R. E. et al. 1989. Planktonic larval duration, distribution and population structure of western and central Pacific damselfishes (Pomacentridae). – Copeia 1989: 420–434.

Treml, E. A. et al. 2008. Modeling population connectivity by ocean currents, a graph-theoretic approach for marine conservation. – Landscape Ecol. 23: 19–36.

Victor, B. C. and Wellington, G. M. 2000. Endemism and the pelagic larval duration of reef fishes in the eastern Pacific Ocean. – Mar. Ecol. Prog. Ser. 205: 241–248.

Webb, T. J. and Gaston, K. J. 2000. Geographic range size and evolutionary age in birds. – Proc. R. Soc. B 267: 1843–1850.

Wellington, G. M. and Victor, B. C. 1989. Planktonic larval duration of one hundred species of Pacific and Atlantic damselfishes (Pomacentridae). – Mar. Biol. 101: 557–568.

Wessel, P. 2001. Global distribution of seamounts inferred from gridded Geosat/ERS-1 altimetry. – J. Geophys. Res. 106: 19431–19441.

Whitfield, P. E. et al. 2002. Biological invasion of the Indo-Pacific lionfish *Pterois volitans* along the Atlantic coast of North America. – Mar. Ecol. Prog. Ser. 235: 289–297.

Whitfield, P. E. et al. 2007. Abundance estimates of the Indo-Pacific lionfish *Pterois volitans/miles* complex in the western north atlantic. – Biol. Invasions 9: 53–64.

Yesson, C. et al. 2011. The global distribution of seamounts based on 30 arc seconds bathymetry data. – Deep Sea Res. Part 1 58: 442–453.

Zapata, F. A. and Herron, P. A. 2002. Pelagic larval duration and geographic distribution of tropical eastern Pacific snappers (Pisces: Lutjanidae). – Mar. Ecol. Prog. Ser. 230: 295–300.