

# UC Merced

## Frontiers of Biogeography

### Title

Population genetic and phylogeographic insights into the phyllosomal odyssey

### Permalink

<https://escholarship.org/uc/item/027657s1>

### Journal

Frontiers of Biogeography, 6(1)

### Author

Iacchei, Matthew

### Publication Date

2014

### DOI

10.21425/F5FBG19453

### Copyright Information

Copyright 2014 by the author(s). This work is made available under the terms of a Creative Commons Attribution License, available at

<https://creativecommons.org/licenses/by/4.0/>

thesis abstract

# Population genetic and phylogeographic insights into the phyllosomal odyssey

Matthew Iacchei<sup>1</sup>

*PhD Thesis:* Department of Biology, University of Hawai'i at Mānoa, 2538 McCarthy Mall, Honolulu, HI, 96822; *Current address:* Department of Oceanography, School of Ocean and Earth Science and Technology, University of Hawai'i at Mānoa, Honolulu, HI 96822; [iacchei@hawaii.edu](mailto:iacchei@hawaii.edu).

**Abstract.** The majority of marine species maintain genetic connectivity through pelagic propagules, with pelagic duration hypothesized to limit dispersal potential. This dissertation investigates the geographic scale of genetic connectivity when pelagic duration is likely not limiting. I analyzed mtDNA sequences and microsatellites to determine patterns of genetic structure across the geographic distributions of three lobster species: *Panulirus penicillatus* (Red Sea to the East Pacific Ocean), *P. interruptus* (sub-tropical East Pacific), and *P. marginatus* (Hawaiian endemic). At the broadest spatial scale, significant genetic discontinuities for *P. penicillatus* correspond to provincial biogeographic boundaries, including putative species-level disjunction across the East Pacific Barrier. On a smaller scale, novel kinship analyses combined with traditional *F*-statistics indicate that larval behavior and oceanographic processes result in localized recruitment for *P. interruptus*. Geographic scales of connectivity differ by location and species, even in Hawai'i, where *P. marginatus* and *P. penicillatus* co-occur. These findings indicate the combined effects of geography, ocean currents, and biology overcome extremely long pelagic periods and result in variable degrees of genetic connectivity.

**Keywords.** kinship, larval behavior, marine connectivity, pelagic larval dispersal, phylogeography, spiny lobster

## Introduction

Identifying the drivers of larval dispersal patterns and connectivity in marine populations is essential both to understand marine metapopulation dynamics and to successfully manage marine species and populations (Palumbi 2004, Kritzer and Sale 2006, Fogarty and Botsford 2007). The majority of marine taxa have a biphasic lifestyle, with sedentary adults, but a pelagic larval stage that persists in the water column from a few minutes to multiple years (Thorson 1950, Strathmann 1987, McEdward 1995). This larval phase enables individuals that may not move at all as adults to produce offspring that are capable of settling thousands of kilometers away. An intuitive expectation is the duration of the larvae in the water column will positively correlate with the distance larvae disperse, and in turn, the spatial scale at which popu-

lations are connected (Kinlan and Gaines 2003, Shanks et al. 2003). However, as the number of studies investigating correlations between pelagic larval duration (PLD), dispersal distance, and the genetic structure of populations has increased, the evidence has not supported these expectations, but instead has indicated a generally weak relationship between dispersal potential (PLD) and genetic structure (*F*-statistics) (reviewed in Bradbury et al. 2008, Shanks 2009, Weersing and Toonen 2009, Riginos et al. 2011, Selkoe and Toonen 2011).

When examined more closely, the PLDs across the 10s to 100s of studies in each of these meta-analyses generally fit a bimodal distribution, with propagules of some species in the water column for less than 10 hours, and the rest with PLD greater than 24 hours (Shanks et al. 2003, Shanks

<sup>1</sup> Recipient of the *International Biogeography Society's 2014 Doctoral Dissertation Award* for the best doctoral dissertation, as judged from thesis abstracts submitted to *Frontiers of Biogeography* by an Early Career Researcher (up to 2 years after graduation from a PhD program).

2009). Below the lower PLD threshold, the correlation between PLD, dispersal, and  $F_{ST}$  is actually strong: propagules in the water column for less than 10 hours tend rarely to disperse farther than 1 km, and in turn have higher levels of genetic structure.

Above the 24 hour threshold, the relationship is less clear: PLD can exceed four years (Strathmann and Strathmann 2007), dispersal distance varies from meters to 1000s of kilometers, and genetic structure ranges from low to high. The majority of propagules do not disperse as far as their PLD predicts, whether dispersal distance is estimated by a passive particle model (Shanks et al. 2003, Shanks 2009) or Lagrangian dispersal model (Siegel et al. 2003, Shanks 2009). However, newer biophysical models have successfully predicted dispersal patterns, often by incorporating environmental variables and/or larval behaviors hypothesized to reduce larval dispersal (Gilg and Hilbish 2003, Baums et al. 2006, Cowen et al. 2006, Galindo et al. 2006, White et al. 2010, Rivera et al. 2011, Foster et al. 2012). Furthermore, when factors such as geographic history and coalescence time can be controlled for by using synchronously diverging, co-distributed (SDC) taxa, the relationship between PLD and genetic structure are drastically improved for some species (Dawson 2012, 2014, Dawson et al. 2014).

Many factors may prevent larvae from realizing their full dispersal potential, including biogeographic barriers (Barber et al. 2002, Crandall et al. 2008, Gaither et al. 2010, but see Lessios and Robertson 2006, and review in Riginos et al. 2011), contemporary oceanographic currents (Shulman and Bermingham 1995, Baums et al. 2006, White et al. 2010), larval behavior (Jones et al. 1999, Leis 2006, Montgomery et al. 2006, Toonen and Tyre 2007), ecological barriers (Rocha et al. 2005, Selkoe et al. 2010), and even anthropogenic effects (Puritz and Toonen 2011). As Dawson's SDC approach (2012, 2014) suggests, confounding factors such as geographic distributions, recent bottlenecks or founder events, and historical population size fluctuations may obscure the relationship between PLD and dispersal distance. Similarly, PLD may act as confounding factor when

examining contemporary barriers to dispersal in specific regions. The majority of species studied to date, including those in the meta-analytical reviews, have PLDs less than ~60 days, allowing for the possibility that PLD may be a limiting or a confounding factor when evaluating the drivers of contemporary genetic patterns. What about species that have much longer PLDs (>180 days)? Is there an upper threshold PLD level, similar to the lower 24-hour threshold revealed by recent reviews, over which pelagic larvae will overcome any of the aforementioned barriers to dispersal and theoretically allow for effectively panmictic populations? Alternatively, can these species with long PLD be used to identify dispersal barriers and other factors shaping biogeographic distributions and influencing population connectivity without the confounding factor of PLD?

Scheltema (1971) named long-lived, pelagic larval dispersers "teleplanic": larvae that originate in the continental-shelf benthos, but are often found in the open ocean, providing a potential means for dispersal over very long distances. These larvae have been collected over 1500 km from coastal waters (Johnson 1956, 1960, Jeffs et al. 2005), and have been hypothesized not only to allow the colonization of new regions, but also to sustain gene flow across a full species distribution over ecological time scales (Scheltema 1971). Alternatively, Johnson (1971, 1974) proposed that the larvae found far offshore, past local entrainment features, had a very low probability of survival, and therefore represented a loss from their site of origin, rather than a potential recruit to a distant site. Further, Strathmann et al. (2002) hypothesize that the long PLD did not evolve in response to selection for the broad dispersal of larvae, but rather for the avoidance of predation during the larval phase (e.g., Morgan and Anastasia 2008), and that survivorship of larvae generally decreased with increasing distance from the natal site (Strathmann et al. 1981). In this case, the larvae found far offshore would be temporarily residing in an environment that is favorable to their survival (due to lower predation levels), but the majority would return to recruit proximate to their natal site.

For my dissertation, I use genetic data from three species of spiny lobsters within the genus *Panulirus*, each of which has a PLD exceeding 180 days (Phillips et al. 2006), to gain a more fundamental understanding of the role of the teleplanic larval phase in maintaining population connectivity and geographic range sizes in marine species: do teleplanic larvae sustain effectively panmictic populations across broad geographic expanses?

## Methods

I use a combination of mitochondrial DNA (mtDNA) sequence data and nuclear microsatellite markers to assess the scales of population genetic connectivity in three different *Panulirus* lobster species using standard genetic analysis techniques (e.g., diversity indices, AMOVA, pairwise  $F_{ST}/\Phi_{ST}/D_{est\_Chao}$ , median-joining networks). I first examine genetic connectivity with mtDNA sequence data (cytochrome *c* oxidase subunit I; COI) at the broadest spatial scale, using 751 samples from 32 sites throughout the distribution of *Panulirus penicillatus* (Olivier, 1791) from the Red Sea to the East Pacific Ocean (Iacchei 2013: Chapter 2). Next, I examine species distributions (Chapter 3, Iacchei and Toonen 2013) and patterns of genetic connectivity in mtDNA (Chapter 3, Iacchei and Toonen 2013; Chapter 4, Iacchei et al. 2014) of *P. penicillatus* at a smaller spatial scale (the Hawaiian Archipelago: 10 sites, 281 samples). I compare these data to those of a congeneric species, *Panulirus marginatus* (Quoy and Gaimard, 1825) from 13 sites (564 samples, COII genetic marker) in the Hawaiian Archipelago (Chapter 4, Iacchei et al. 2014). *Panulirus marginatus* is sympatric with *P. penicillatus* over this geographic extent, but is endemic to Hawai'i. Finally, I conduct a deeper investigation into the genetic structuring of a third species, *Panulirus interruptus* (Randall, 1840), across the majority of its species distribution along the West Coast of North America from Monterey Bay, CA to Bahía Magdalena, Mexico (17 sites, 1102 samples). I develop eight microsatellite markers to detect finer spatial genetic partitioning in *P. interruptus* (Chapter 5, Ben-Horin et al. 2009). I then combine mtDNA COI sequence data and seven of

the eight nuclear microsatellites (nDNA) to examine population connectivity in this species, and also propose a new analysis mechanism that uses microsatellite data to assess kinship, and gain a richer understanding of population genetic structuring in marine species (Chapter 6, Iacchei et al. 2013).

## Results and Discussion

*Is there an upper threshold PLD level over which pelagic larvae will overcome any barriers to dispersal and maintain effectively panmictic populations?*

Although each of the three lobster species has one or more haplotypes that are shared across most of the sampling sites within their species distributions, each species also has significant genetic differentiation across its species range. *Panulirus penicillatus* was significantly differentiated from the Red Sea to the East Pacific ( $\Phi_{ST} = 0.175$ ,  $P < 0.000005$ ; Chapter 2), despite a nine-month PLD (Matsuda et al. 2006). Global  $F_{ST}$  for *P. marginatus* across the Hawaiian Archipelago is low (0.0037) but statistically significant ( $P = 0.007$ ; Iacchei et al. 2014), despite an estimated 12-month PLD (Polovina and Moffitt 1995). Similarly, *P. interruptus*, with an estimated PLD of 8–11 months (Johnson 1956, 1960, Serfling and Ford 1975) has low, but statistically significant, genetic structure for both mtDNA ( $\Phi_{ST} = 0.006$ ,  $P = 0.001$ ), and seven nuclear microsatellite markers ( $F_{ST} = 0.004$ ,  $P < 0.0005$ ; Iacchei et al. 2013). These data refute the hypothesis that there is an upper threshold level PLD above which pelagic larvae will overcome any barriers to dispersal, unless that threshold is longer than 12 months. Other species with comparable PLDs have given mixed results. A number of genetic investigations of marine species have identified minimal population structuring across broad geographic scales, both for other lobsters (Ovenden et al. 1992, Silberman et al. 1994, Thompson et al. 1996, Tolley et al. 2005, Inoue et al. 2007, García-Rodríguez and Perez-Enriquez 2008) and for species with longer PLDs, such as moray eels with leptocephalus larvae and a PLD greater than 2-years (Reece et al.

2011). In other studies, genetic discontinuities have corresponded with known biogeographic barriers, or oceanographic transitions (Palero et al. 2008, Babbucci et al. 2010, Chow et al. 2011), but there has also been some evidence of local recruitment in species with greater than 180-day PLD (Silberman and Walsh 1994, Johnson and Wernham 1999).

Although few marine species have PLDs of this length, amphidromous species can have comparable PLDs (e.g., Radtke et al. 2001, Hoareau et al. 2007) and yield unique insights. Many amphidromous species show little to no genetic structure across their geographic ranges (cf., references in Crandall et al. 2010, Castelin et al. 2013), matching the expectation of their high dispersal potential. However, other species exhibit spatial genetic structure aligned with boundaries of biogeographic provinces (Briggs 1974, Briggs and Bowen 2012) that delimit species in taxa with shorter PLDs (Crandall et al. 2010, Lord et al. 2012, Castelin et al. 2013); and at least one amphidromous species has isolated populations within these biogeographic provinces (Minegishi et al. 2008). Even species that spend their whole lives in the plankton have genetically distinct populations isolated by large oceanographic features (Norton and Goetze 2013). These combined studies refute the hypothesis that there is a PLD threshold above which gene flow is maintained across all oceanographic barriers within a species range. Effective panmixia may occur within certain species, but those species cannot be predicted using a specific larval trait.

#### *What mechanisms are potentially driving population differentiation?*

The patterns of genetic differentiation varied across species and spatial scale, even in the Hawaiian Archipelago, where *P. marginatus* and *P. penicillatus* are sympatric (Iacchei et al. 2014), indicating that no single factor is driving genetic differentiation. All three patterns of differentiation identified in amphidromous species above were also observed in the spiny lobsters. At the broadest scale, *P. penicillatus* exhibits high levels of genetic differentiation corresponding with

known biogeographic barriers that often form species-level boundaries in other clades. For example, there is significant differentiation ( $\Phi_{CT} = 0.69$ ,  $P = 0.011$ ) across the three regions defined by the major Indo-Pacific biogeographic barriers (Western Indian Ocean, Western and Central Pacific, East Pacific). Of particular note, there has likely been no recent gene flow across the East Pacific Barrier, Darwin's (1872) 'impassable' barrier ( $\Phi_{CT} = 0.847$ ,  $P = 0.039$ ), in contrast to some species with significantly shorter pelagic durations (Lessios and Robertson 2006). Based on the high level of genetic differentiation and the sequence divergence between these regions, the East Pacific *P. penicillatus*, designated "*P. penicillatus* Red" by George (2006), deserves species-level recognition, distinct from the Indo-West Pacific *P. penicillatus*. Within the Western and Central Pacific, there are also significant genetic breaks between the Sino-Japanese Province and the rest of the tropical Indo-Pacific (Chapter 2). However, there is no differentiation across the Indo-Pacific biogeographic barrier ( $\Phi_{CT} = 0.00032$ ,  $P = 0.259$ ), which limits species distributions for many reef organisms and serves as a strong filter for others.

There is also regional isolation in Hawai'i, where *P. penicillatus* and *P. marginatus* have overlapping, though distinct distributions (Iacchei and Toonen 2013). Each species shows weak, but significant differentiation between the high islands in the main Hawaiian Islands and the northwestern Hawaiian Island atolls (*P. marginatus*  $F_{CT} = 0.002$ ,  $P = 0.047$ ; *P. penicillatus*  $F_{CT} = 0.008$ ,  $P = 0.0083$ ; Iacchei et al. 2014). There was not a signal of regional differentiation across the range of *P. interruptus*, despite its span of a known faunal boundary at Punta Eugenia, Mexico (Iacchei et al. 2013).

Notably, all three species show indications of site-specific drivers of genetic isolation particular to each species. In *P. penicillatus*, there is relative genetic isolation of a number of islands within the Indo-Polynesian province, while other sites within this province are well connected to locations throughout the species distribution (Chapter 2). Across Hawai'i, the genetic structure for *P. penicillatus* is weak, and mostly driven by isolation of two of the northernmost atolls (Iacchei et al.

2014). In contrast, *P. marginatus* sites in the Main Hawaiian Islands (Kaua'i and Maui) are significantly differentiated from the majority of other locations in the archipelago and drive the apparent regional pattern, while O'ahu, just over 100 and 150 km from Maui and Kaua'i respectively, is only distinct from Maui, and not any of the atolls located as far as 2000 km to the northwest (Iacchei et al. 2014). Similar patterns of site-specific differentiation are becoming more evident as multiple species are examined across the same locations (e.g., Kelly and Palumbi 2010, Selkoe et al. 2010, Toonen et al. 2011). However, given the identical oceanographic conditions that these lobsters encounter in Hawai'i, species-specific behaviors are likely driving genetic connectivity in this regime (e.g., Butler et al. 2011, Miller and Morgan 2013).

Similarly, for *P. interruptus*, there are four locations within Central and Northern Baja California, Mexico that are significantly differentiated from almost all other locations, while most sites throughout the range are genetically well connected. Kinship data for *P. interruptus* derived from multiple microsatellites provides evidence that the sites with the greatest level of differentiation from other sites also had the highest proportion of closely related individuals. The most closely related individuals (quarter to full-sibs) were almost exclusively found at the same location, rather than at different sites (Iacchei et al. 2013). The elevated levels of kinship at specific sites could be driven by localized recruitment, or by timed settlement of related individuals (i.e., Selkoe et al. 2006, Buston et al. 2009, Bernardi et al. 2012). Most of the isolated sites occurred within Baja California, Mexico, where there is a much stronger and more consistent upwelling regime, rather than in the Southern California Bight, where upwelling is almost non-existent. The proportion of kin at a site was positively correlated with the proximity of a site to an upwelling center: the closer to an upwelling center, the higher the proportion of kin. This evidence provides a potential mechanism driving the observed genetic cohesion within sites (Iacchei et al. 2013). This synthesis of population level  $F$ -statistics, individual-based

kinship analyses, and oceanographic data provides novel insight into a common scenario for marine species: low, but significant pairwise differentiation between locations, but with no particular regional separation or isolation-by-distance pattern, and without any known biogeographic explanation. With only one genetic marker per species, I was not able to assess kinship for *P. marginatus* or *P. penicillatus*. As more genetic markers become available through next-generation sequencing technology, and regional oceanographic models become more refined, this avenue of research should provide substantial insights into the patterns of genetic differentiation in marine taxa with a biphasic lifestyle.

The combined data from this dissertation lend some support to both the hypothesis of Scheltema (1971), and of Strathmann et al. (2002) on the role of teleplanic larvae in the maintenance of marine populations. These data do not speak to the specific function for which traits that enable teleplanic larval dispersal were selected. However, the data do provide evidence for both frequent long distance dispersal, as well as for the ability to recruit close to the natal site. As Iacchei et al. (2013) demonstrate, the coupling of  $F$ -statistics, individual-based kinship analyses, and oceanographic data yields substantially greater insight into drivers of genetic connectivity than  $F$ -statistics alone. This is an exciting time for the field because genetic, oceanographic, habitat, and environmental data are all increasing at exponential rates, and the computational power to analyze the data influx is more cheaply available. Forthcoming work on these species will incorporate coalescent simulations (Kingman 1982) using next-generation sequencing data to more accurately distinguish between ecological and evolutionary drivers of population differentiation, and to isolate the effects of population size ( $N_e$ ), migration, and demographic history that  $F$ -statistics summarize (cf., Marko and Hart 2011, 2012). In addition, I hope to relate migration results to oceanographic current simulations (e.g., Crandall et al. 2012) and assess the effects of habitat extent (e.g., Reece et al. 2011) and stability on patterns of genetic differentiation. I aim to compare these patterns with

other marine species with long PLDs, as well as amphidromous species across overlapping geographic ranges. These comparisons will provide a more robust picture of the shared drivers of genetic differentiation and the traits upon which these drivers act (e.g., Toonen et al. 2011, Dawson et al. 2014).

### Acknowledgements

Many thanks to my advisor, Robert Toonen, and to Brian Bowen for their support and encouragement throughout this dissertation, and for comments that greatly improved this manuscript. I am grateful to my additional committee members: Charles Birkeland, Megan Donahue, and Alison Rieser, for their assistance and insight. Thanks to my other co-authors on specific chapters for their input: Tal Ben-Horin, Christopher Bird, Michelle Gaither, Francisco García-Rodríguez, Thien Mai, Joseph O'Malley, and Kimberly Selkoe. Thanks also to those who collected lobster samples for these projects, assisted in the ToBo lab, and engaged in insightful discussions. Finally, I thank Chris Burridge, Mike Dawson, Pierre Feutry, Joaquín Hortal, and Ana Santos for very helpful commentary and assistance with earlier drafts. This work has been funded by the National Science Foundation (DEB#99-75287, OCE#04-54873, OCE#06-23678, OCE#09-29031, OCE#1260169); National Marine Fisheries Service; National Marine Sanctuaries NWHICRER-HIMB partnership (MOA-2005-008/6882); National Oceanic and Atmospheric Association (NOAA) Project R/HE-6, and Project E/ET-38, sponsored by the UH Sea Grant College Program, SOEST, under institutional grant NA09OAR4170060 from NOAA Office of Sea Grant, Department of Commerce; National Sea Grant, number NA06RG0142, project R/F-177; UC Coastal Environmental Quality Initiative; Offfield Family Foundation; Environmental Protection Agency's (EPA) STAR Fellowship; Watson T. Yoshimoto Foundation; Charles H. and Margaret B. Edmondson Research Fund; Jessie D. Kay Research Grant; UH Graduate Student Organization; and UH Ecology, Evolution, and Conservation Biology (EECB) program.

### References

- Babbucci, M., Buccoli, S., Cau, A., et al. (2010) Population structure, demographic history, and selective processes: contrasting evidences from mitochondrial and nuclear markers in the European spiny lobster *Panulirus elephas* (Fabricius, 1787). *Molecular Phylogenetics and Evolution*, 56, 1040–1050.
- Barber, P.H., Palumbi, S.R., Erdmann, M.V. & Moosa, M.K. (2002) Sharp genetic breaks among populations of *Haptosquilla pulchella* (Stomatopoda) indicate limits to larval transport: patterns, causes, and consequences. *Molecular Ecology*, 11, 659–674.
- Baums, I.B., Paris, C.B. & Cherubin, L.M. (2006) A bio-oceanographic filter to larval dispersal in a reef-building coral. *Limnology and Oceanography*, 51, 1969–1981.
- Ben-Horin, T., Iacchei, M., Selkoe, K.A., Mai, T.T. & Toonen, R.J. (2009) Characterization of eight polymorphic microsatellite loci for the California spiny lobster, *Panulirus interruptus* and cross-amplification in other achelate lobsters. *Conservation Genetics Resources*, 1, 193–197.
- Bernardi, G., Beldade, R., Holbrook, S.J. & Schmitt, R.J. (2012) Full-sibs in cohorts of newly settled coral reef fishes. *PLoS ONE*, 7, e44953.
- Bradbury, I.R., Laurel, B., Snelgrove, P.V.R., Bentzen, P. & Campana, S.E. (2008) Global patterns in marine dispersal estimates: the influence of geography, taxonomic category and life history. *Proceedings of the Royal Society of London Series B: Biological Sciences*, 275, 1803–1809.
- Briggs, J.C. (1974) *Marine zoogeography*. McGraw-Hill, New York, NY.
- Briggs, J.C. & Bowen, B.W. (2012) A realignment of marine biogeographic provinces with particular reference to fish distributions. *Journal of Biogeography*, 39, 12–30.
- Buston, P.M., Fauvelot, C., Wong, M.Y.L. & Planes, S. (2009) Genetic relatedness in groups of the humbug damselfish *Dascyllus aruanus*: small, similar-sized individuals may be close kin. *Molecular Ecology*, 18, 4707–4715.
- Butler, M.J., Paris, C.B., Goldstein, J.S., Matsuda, H. & Cowen, R.K. (2011) Behavior constrains the dispersal of long-lived spiny lobster larvae. *Marine Ecology Progress Series*, 422, 223–237.
- Castelin, M., Feutry, P., Hauteceur, M., Marquet, G., Wowor, D., Zimmermann, G. & Keith, P. (2013) New insight on population genetic connectivity of widespread amphidromous prawn *Macrobrachium lar* (Fabricius, 1798)(Crustacea: Decapoda: Palaemonidae). *Marine Biology*, 160, 1395–1406.
- Chow, S., Jeffs, A., Miyake, Y., et al. (2011) Genetic isolation between the Western and Eastern Pacific Populations of pronghorn spiny lobster *Panulirus penicillatus*. *PLoS ONE*, 6, e29280.
- Cowen, R.K., Paris, C.B. & Srinivasan, A. (2006) Scaling of connectivity in marine populations. *Science*, 311, 522–527.
- Crandall, E.D., Frey, M.A., Grosberg, R.K. & Barber, P.H. (2008) Contrasting demographic history and phylogeographical patterns in two Indo-Pacific gastropods. *Molecular Ecology*, 17, 611–626.

- Crandall, E., Taffel, J. & Barber, P. (2010) High gene flow due to pelagic larval dispersal among South Pacific archipelagos in two amphidromous gastropods (Neritimorpha: Neritidae). *Heredity*, 104, 563–572.
- Crandall, E.D., Treml, E.A. & Barber, P.H. (2012) Coalescent and biophysical models of stepping-stone gene flow in neritid snails. *Molecular Ecology*, 21, 5579–5598.
- Darwin, C. (1872) *The origin of species by means of natural selection*, 6<sup>th</sup> ed. Doubleday & Co., Garden City, NY.
- Dawson, M.N. (2012) Parallel phylogeographic structure in ecologically similar sympatric sister taxa. *Molecular Ecology*, 21, 987–1004.
- Dawson, M.N. (2014) Natural experiments and meta-analyses in comparative phylogeography. *Journal of Biogeography*, 41, 52–65, doi: 10.1111/jbi.12190
- Dawson, M.N., Hays, C.G., Grosberg, R.K. & Raimundi, P.K. (2014) Dispersal potential and population genetic structure in the marine intertidal of the eastern North Pacific. *Ecological Monographs*, doi: 10.1890/13-087.1
- Fogarty, M. & Botsford, L. (2007) Population connectivity and spatial management of marine fisheries. *Oceanography*, 20, 112–123.
- Foster, N.L., Paris, C.B., Kool, J.T., et al. (2012). Connectivity of Caribbean coral populations: complementary insights from empirical and modeled gene flow. *Molecular Ecology*, 21, 1143–1157.
- Gaither, M.R., Toonen, R.J., Robertson, D.R., Planes, S. & Bowen, B.W. (2010) Genetic evaluation of marine biogeographic barriers: perspectives from two widespread Indo-Pacific snappers (*Lutjanus kasmira* and *Lutjanus fulvus*). *Journal of Biogeography*, 37, 133–147.
- Galindo, H.M., Olson, D.B. & Palumbi, S.R. (2006) Seascape genetics: a coupled oceanographic-genetic model predicts population structure of Caribbean corals. *Current Biology*, 16, 1622–1626.
- García-Rodríguez, F.J. & Perez-Enriquez, R. (2008) Lack of genetic differentiation of blue spiny lobster *Panulirus inflatus* along the Pacific coast of Mexico inferred from mtDNA sequences. *Marine Ecology Progress Series*, 361, 203–212.
- George, R.W. (2006) Tethys sea fragmentation and speciation of *Panulirus* spiny lobsters. *Crustaceana*, 78, 1281–1309.
- Gilg, M.R. & Hilbish, T.J. (2003) Geography of marine larval dispersal: Coupling genetics with fine-scale physical oceanography. *Ecology*, 84, 2989–2998.
- Hoareau, T.B., Bosc, P., Valade, P. & Berrebi, P. (2007) Gene flow and genetic structure of *Sicyopterus lagocephalus* in the southwestern Indian Ocean, assessed by intron-length polymorphism. *Journal of Experimental Marine Biology and Ecology*, 349, 223–234.
- Iacchei, M. (2013) Population genetic and phylogeographic insights into the phyllosomal odyssey. Ph.D. dissertation, University of Hawai'i.
- Iacchei, M. & Toonen, R.J. (2013) Caverns, compressed air, and crustacean connectivity: insights into Hawaiian spiny lobster populations. In: Lang, M.A., and M.D.J. Sayer, eds. *Proceedings of the Curacao AAUS/ESDP Joint International Scientific Diving Symposium*. Dauphin Island: American Academy of Underwater Sciences, 115–124.
- Iacchei, M., Ben-Horin, T., Selkoe, K.A., Bird, C.E., García-Rodríguez, F.J. & Toonen, R.J. (2013) Combined analyses of kinship and  $F_{ST}$  suggest potential drivers of chaotic genetic patchiness in high gene flow populations. *Molecular Ecology*, 22, 3476–3494.
- Iacchei, M., O'Malley, J.M. & Toonen, R.J. (2014) After the gold rush: population structure of spiny lobsters in Hawai'i following a fishery closure and implications for contemporary spatial management. *Bulletin of Marine Science*, doi:10.5343/bms.2013.1042
- Inoue, N., Watanabe, H., Kojima, S. & Sekiguchi, H. (2007) Population structure of Japanese spiny lobster *Panulirus japonicus* inferred by nucleotide sequence analysis of mitochondrial COI gene. *Fisheries Science*, 73, 550–556.
- Jeffs, A.G., Montgomery, J.C. & Tindle, C.T. (2005) How do spiny lobster post-larvae find the coast? *New Zealand Journal of Marine and Freshwater Research*, 39, 605–617.
- Johnson, M.W. (1956) The larval development of the California spiny lobster *Panulirus interruptus* (Randall) with notes on *Panulirus gracilis* Streets. *Proceedings of the California Academy of Science*, 29, 1–19.
- Johnson, M.W. (1960) The offshore drift of larvae of the California spiny lobster *Panulirus interruptus*. *California Cooperative Oceanic Fisheries Investigations Reports*, 7, 147–161.
- Johnson, M.W. (1971) The palinurid and syllarid lobster larvae of the tropical eastern Pacific and their distribution as related to the prevailing hydrology. *Bulletin of the Scripps Institution of Oceanography*, 19, 1–36.
- Johnson, M.W. (1974) On the dispersal of larvae into the east Pacific barrier (Decapoda, Palinuridea). *Fisheries Bulletin*, 72, 639–647.
- Johnson, M.S. & Wernham, J. (1999) Temporal variation of recruits as a basis of ephemeral genetic heterogeneity in the western rock lobster *Panulirus cygnus*. *Marine Biology*, 135, 133–139.
- Jones, G.P., Milicich, M.J., Emslie, M.J. & Lunow, C. (1999) Self-recruitment in a coral reef fish population. *Nature*, 402, 802–804.
- Kelly, R.P. & Palumbi, S.R. (2010) Genetic structure among 50 species of the northeastern Pacific rocky intertidal community. *PLoS ONE*, 5, e8594.
- Kingman, J.F.C. (1982) *The coalescent. Stochastic Processes and their Applications*, 13, 235–248.
- Kinlan, B.P. & Gaines, S.D. (2003) Propagule dispersal in marine and terrestrial environments: a community perspective. *Ecology*, 84, 2007–2020.
- Kritzer, J.P. & Sale, P.F. (2006) *Marine metapopulations*. Academic Press, London.
- Leis, J.M. (2006) Are larvae of demersal fishes plankton or nekton? *Advances in Marine Biology*, 51, 59–141.
- Lessios, H.A. & Robertson, D.R. (2006) Crossing the impassable: genetic connections in 20 reef fishes across the eastern Pacific barrier. *Proceedings of the Royal Society of London Series B: Biological Sciences*, 273, 2201–2208.
- Lord, C., Lorion, J., Dettai, A., Watanabe, S., Tsukamoto, K., Cruaud, C. & Keith, P. (2012) From endemism to widespread distribution: phylogeography of three am-



- phidromous Sicyopterus species (Teleostei: Gobiodei: Sicydiinae). *Marine Ecology Progress Series*, 455, 269–285.
- Marko, P.B. & Hart, M.W. (2011) The complex analytical landscape of gene flow inference. *Trends in Ecology and Evolution*, 26, 448–456.
- Marko, P.B. & Hart, M.W. (2012) Retrospective coalescent methods and the reconstruction of metapopulation histories in the sea. *Evolutionary Ecology*, 26, 291–315.
- Matsuda, H., Takenouchi, T. & Goldstein, J.S. (2006) The complete larval development of the pronghorn spiny lobster *Panulirus penicillatus* (Decapoda: Palinuridae) in culture. *Journal of Crustacean Biology*, 26, 579–600.
- McEdward, L. (1995) *Ecology of marine invertebrate larvae*. CRC Press, Boca Raton, FL.
- Miller S.H. & Morgan, S.G. (2013) Interspecific differences in depth preference: regulation of larval transport in an upwelling system. *Marine Ecology Progress Series* 476, 301–306.
- Minegishi, Y., Aoyama, J. & Tsukamoto, K. (2008) Multiple population structure of the giant mottled eel, *Anguilla marmorata*. *Molecular Ecology*, 17, 3109–3122.
- Montgomery, J.C., Jeffs, A.G., Simpson, S.D., Meekan, M. & Tindle, C. (2006) Sound as an orientation cue for pelagic larvae of reef fishes and decapod crustaceans. *Advances in Marine Biology*, 51, 144–190.
- Morgan, S.G. & Anastasia, J.R. (2008) Behavioral tradeoff in estuarine larvae favors seaward migration over minimizing visibility to predators. *Proceedings of the National Academy of Science*, 105, 222–227.
- Norton, E.L. & Goetze, E. (2013) Equatorial dispersal barriers and limited connectivity among oceans in a planktonic copepod. *Limnology and Oceanography*, 58, 1581–1596.
- Ovenden, J.R., Brasher, D.J. & White, R.W.G. (1992) Mitochondrial DNA analyses of the red rock lobster *Jasus edwardsii* supports an apparent absence of population subdivision throughout Australasia. *Marine Biology*, 112, 319–326.
- Palero, F., Abelló, P., Macpherson, E., Gristina, M. & Pascual, M. (2008) Phylogeography of the European spiny lobster (*Palinurus elephas*): influence of current oceanographical features and historical processes. *Molecular Phylogenetics and Evolution*, 48, 708–717.
- Palumbi, S.R. (2004) Marine reserves and ocean neighborhoods: the spatial scale of marine populations and their management. *Annual Review of Environment and Resources*, 29, 31–68.
- Phillips, B.F., Booth, J.D., Cobb, J.S., Jeffs, A.G. & McWilliam, P. (2006) Larval and postlarval ecology. In: *Lobsters: biology, management, aquaculture and fisheries* (ed. by B.F. Phillips), pp. 231–262. Blackwell Scientific Press, Oxford, UK.
- Polovina, J.J. & Moffitt, R.B. (1995) Spatial and temporal distribution of the phyllosoma of the spiny lobster, *Panulirus marginatus*, in the Northwestern Hawaiian Islands. *Bulletin of Marine Science*, 56, 406–417.
- Puritz, J.B. & Toonen, R.J. (2011) Coastal pollution limits pelagic larval dispersal. *Nature Communications*, 2, 226.
- Radtke, R.L., Kinzie, R.A. & Shafer, D.J. (2001). Temporal and spatial variation in length of larval life and size at settlement of the Hawaiian amphidromous goby *Leptipes concolor*. *Journal of Fish Biology*, 59, 928–938.
- Reece, J.S., Bowen, B.W., Smith, D.G. & Larson, A. (2011) Comparative phylogeography of four Indo-Pacific moray eel species (Muraenidae) reveals comparable ocean-wide genetic connectivity despite five-fold differences in available adult habitat. *Marine Ecology Progress Series*, 437, 269–277.
- Riginos, C., Douglas, K.E., Jin, Y., Shanahan, D.F. & Tremblay, E.A. (2011) Effects of geography and life history traits on genetic differentiation in benthic marine fishes. *Ecography*, 34, 566–575.
- Rivera, M.A.J., Andrews, K.R., Kobayashi, D.R., Wren, J.L.K., Kelley, C., Roderick, G.K. & Toonen, R.J. (2011) Genetic analyses and simulations of larval dispersal reveal distinct populations and directional connectivity across the range of the Hawaiian Grouper (*Epinephelus quernus*). *Journal of Marine Biology*, # 765353, 11 pages.
- Rocha, L.A., Robertson, D.R., Roman, J. & Bowen, B.W. (2005) Ecological speciation in tropical reef fishes. *Proceedings of the Royal Society of London Series B: Biological Sciences*, 272, 573–579.
- Scheltema, R.S. (1971) The dispersal of the larvae of shoalwater benthic invertebrate species over long distances by ocean currents. In: *Fourth European Marine Biology Symposium* (ed. by D. Crisp). Cambridge University Press, London, UK.
- Selkoe, K.A. & Toonen, R.J. (2011) Marine connectivity: a new look at pelagic larval duration and genetic metrics of dispersal. *Marine Ecology Progress Series*, 436, 291–305.
- Selkoe, K.A., Gaines, S.D., Caselle, J.E. & Warner, R.R. (2006) Current shifts and kin aggregation explain genetic patchiness in fish recruits. *Ecology*, 87, 3082–3094.
- Selkoe, K.A., Watson, J.R., White, C., Ben-Horin, T., Iacchei, M., Mitarai, S., Siegel, D.A., Gaines, S.D. & Toonen, R.J. (2010) Taking the chaos out of genetic patchiness: seascape genetics reveals ecological and oceanographic drivers of genetic patterns in three temperate reef species. *Molecular Ecology*, 19, 3708–3726.
- Serfling, S.A. & Ford, R.F. (1975) Ecological studies of the puerulus larvae stages of the California spiny lobster, *Panulirus interruptus*. *Fishery Bulletin*, 73, 360–377.
- Shanks, A.L. (2009) Pelagic larval duration and dispersal distance revisited. *Biological Bulletin*, 216, 373–385.
- Shanks, A.L., Grantham, B. & Carr, M.H. (2003) Propagule dispersal distance and the size and spacing of marine reserves. *Ecological Applications*, 13, 159–169.
- Shulman, M.J. & Bermingham, E. (1995) Early life histories, ocean currents, and the population genetics of Caribbean reef fishes. *Evolution*, 49, 897–910.
- Siegel, D.A., Kinlan, B.P., Gaylord, B. & Gaines, S.D. (2003) Lagrangian descriptions of marine larval dispersion. *Marine Ecology Progress Series*, 260, 83–96.
- Silberman, J.D. & Walsh, P.J. (1994) Population genetics of the spiny lobster *Panulirus argus*. *Bulletin of Marine Science*, 54, 1084.
- Silberman, J.D., Sarver, S.K. & Walsh, P.J. (1994) Mitochondrial DNA variation and population structure in the spiny lobster *Panulirus argus*. *Marine Biology*, 120, 601–608.

- Strathmann, M.F. (1987) Reproduction and development of marine invertebrates of the northern Pacific Coast. University of Washington Press, Seattle, WA.
- Strathmann, M.F. & Strathmann, R.R. (2007) An extraordinarily long larval duration of 4.5 years from hatching to metamorphosis for teleplanic veligers of *Fusitriton oregonensis*. *Biological Bulletin*, 213, 152–159.
- Strathmann, R.R., Branscomb, E.S. & Vedder, K. (1981) Fatal errors in set as a cost of dispersal and the influence of intertidal flora on set of barnacles. *Oecologia*, 48(1), 13–18.
- Strathmann, M.F., Hughes, T.P., Kuris, A.M., Lindeman, K.C., Morgan, S.G., Pandolfi, J.M. & Warner, R.R. (2002) Evolution of local recruitment and its consequences for marine populations. *Bulletin of Marine Science*, 70, S377–S396.
- Thompson, A.P., Hanley, J.R. & Johnson, M.S. (1996) Genetic structure of the western rock lobster, *Panulirus cygnus*, with the benefit of hindsight. *Marine and Freshwater Research*, 47, 889–896.
- Thorson, G. (1950) Reproductive and larval ecology of marine bottom invertebrates. *Biological Reviews of the Cambridge Philosophical Society*, 25, 1–45.
- Tolley, K.A., Groeneveld, J.C., Gopal, K. & Matthee, C.A. 2005. Mitochondrial DNA panmixia in spiny lobster *Panulirus gilchristi* suggests a population expansion. *Marine Ecology Progress Series*, 297, 225–231.
- Toonen, R.J. & Tyre, A.J. (2007) If larvae were smart: a simple model for optimal settlement behavior of competent larvae. *Marine Ecology Progress Series*, 349, 43–61.
- Toonen, R.J., Andrews, K.R., Baums, I.B., et al. (2011) Defining boundaries for ecosystem-based management: A multispecies case study of marine connectivity across the Hawaiian Archipelago. *Journal of Marine Biology*. #460173, 13 pages.
- Weersing, K. & Toonen, R.J. (2009) Population genetics, larval dispersal, and connectivity in marine systems. *Marine Ecology Progress Series*, 393, 1–12.
- White, C., Watson, J., Siegel, D.A., Selkoe, K.A., Zacherl, D.C. & Toonen, R.J. (2010) Ocean currents help explain population genetic structure. *Proceedings of the Royal Society of London Series B: Biological Sciences*, 277, 1685–1694.

Submitted: 31 August 2013

Accepted: 20 February 2014

Edited by Ana M. C. Santos and Chris Burridge

You can find information about the **International Biogeography Society** at <http://www.biogeography.org/>, and contact with other biogeographers at the **IBS blog** (<http://biogeography.blogspot.com/>), the **IBS facebook group** (<http://www.facebook.com/group.php?gid=6908354463>) and the **IBS twitter channel** (<https://twitter.com/biogeography>).