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 that 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 populations 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

---

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 (subtropical 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

---

1 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).
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*$_{ST}$/*D*$_{est}$, *Chao*$_{2}$, 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, COI 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 Bahia 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 (*Φ*$_{ST}$ = 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 (*Φ*$_{ST}$ ≥ 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.
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 (*N₀*), 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 divers 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 Garcia-Rodriguez, 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; Offield 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


Matthew Iacchei — Patterns of genetic structure in Panulirus spp.
Matthew lacchei — Patterns of genetic structure in *Panulirus* spp.


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.


Submitted: 31 August 2013
Accepted: 20 February 2014
Edited by Ana M. C. Santos and Chris Burridge