

Measuring Connections in the Sea: Pushing the Boundaries of Seascape Genetics at Channel Islands National Park

Crow White

The challenge of analyzing dispersal in the seascape

THE EXCHANGE OF INDIVIDUALS AMONG POPULATIONS through dispersal, or population connectivity, can profoundly influence the abundance and persistence of local populations (Simberloff and Wilson 1969). Population connectivity is influenced by environmental factors such as mountains, rivers, and habitat corridors that mediate the movement of organisms and the probability of their successful dispersal from one location to another. Understanding population connectivity and the role of environmental factors is critical for effective wildlife conservation and management.

Monitoring and mark-recapture experiments have confirmed our intuition and improved our understanding of how landscape features affect the movement of individuals and the probabilities of dispersal between populations for terrestrial species (Wiens 2001). In marine systems, it is more difficult to directly monitor the exchange of individuals among populations. Marine fish and invertebrates are especially problematic due to their production of microscopic larvae that disperse with ocean currents for days to months before settling onto reefs or other habitat and growing into adults. Challenges to estimating population connectivity in marine systems are further exacerbated by our limited knowledge about how the marine seascape influences dispersal. Ocean currents have complex patterns and features that disperse marine larvae, much like wind and weather patterns disperse airborne seeds on land, but there is far less continuous monitoring and documentation of these patterns in the ocean. Because of the difficulty of tracking marine larvae, and our limited understanding of the environmental factors influencing dispersal in the sea, the question of where larvae disperse, and consequently, the degree of connectivity among populations, remains largely unanswered (Cowen et al. 2000). This creates a significant challenge for the management of nearly every marine species.

Many marine ecologists have turned to population genetics as a tool for indirectly estimating population connectivity. Unfortunately, the complex genetic patterns among popula-

The George Wright Forum, vol. 27, no. 3, pp. 280–291 (2010).

© 2010 The George Wright Society. All rights reserved.

(No copyright is claimed for previously published material reprinted herein.)

ISSN 0732-4715. Please direct all permission requests to info@georgewright.org.

tions typically observed in marine systems often complicate conclusions regarding connectivity (Bradbury and Bentzen 2007). For example, a common genetic analysis looks for a positive relationship between geographic distance and genetic distinctiveness between sampled populations, with the idea that populations further separated in space exchange genes less frequently. In many cases, however, no clear relationship is found. This may result from complex environmental forces affecting population connectivity in non-linear ways, such as by blocking gene flow between populations located near each other. Consequently, marine ecologists seeking to measure population connectivity and understand its underlying forces are moving beyond conventional genetic analyses based on geography and developing novel approaches for identifying the metaphorical mountains, valleys, and corridors of the sea that are influencing population connectivity among marine populations.

In the oceans, currents can be circuitous and oceanographic features like eddies and fronts can regulate dispersal of larvae. Two adjacent sites may rarely exchange larvae if located on different sides of an oceanographic front (Gill and Hilbish 2003), and two distant sites may be well connected by a strong current between them (Mitarai et al. 2009). A model of these oceanographic features may help explain genetic patterns across the seascape that would not be expected based on the geographical distribution of sites. On large spatial scales, incorporating oceanographic information into genetic analyses has proved fruitful for estimating connectivity (e.g., Galindo et al. 2006). The practice has been coined “seascape genetics,” and it borrows techniques from landscape genetics designed to test for environmental drivers of spatial genetic structure. Terrestrial landscape genetics has successfully quantified population connectivity at fine spatial scales as well, even when dispersal is high and genetic patterns are relatively uniform across populations (Clark et al. 2008). In contrast, seascape genetics has typically been limited to measuring population connectivity at coarse spatial scales and in association with prominent physical barriers (e.g., a narrow strait, deep channel, or prominent headland)—and only in species with low dispersal rates. Given the high dispersal potential in so many marine species, including most fishery species, a central challenge to generating useful estimates of marine population connectivity is to push the boundary of seascape genetics and uncover meaningful population genetic patterns that correspond with oceanographic conditions at spatial scales relevant to conservation and fisheries management.

Population connectivity in a marine national park

In this essay I highlight a recent study conducted by myself and others in Channel Islands National Park (CINP), offshore from Santa Barbara in southern California. This study substantially advances seascape genetics by using a model of oceanographic circulation to resolve fine-scale population connectivity from a seemingly chaotic pattern of genetic data (White et al. 2010). Involving an interdisciplinary team of marine ecologists, geneticists, and oceanographers, the study focused on a marine snail, Kelle’s whelk (*Kelletia kelletii*; Figure 1), whose geographic range is centered in the kelp forest reefs within CINP (Figure 2). Kelle’s whelk is an ecologically significant predator of other marine invertebrates (Halpern et al. 2006), and is preyed upon by octopus, sea stars, elasmobranches, and marine mammals. Although adult Kelle’s whelks travel no more than a couple hundred meters over many

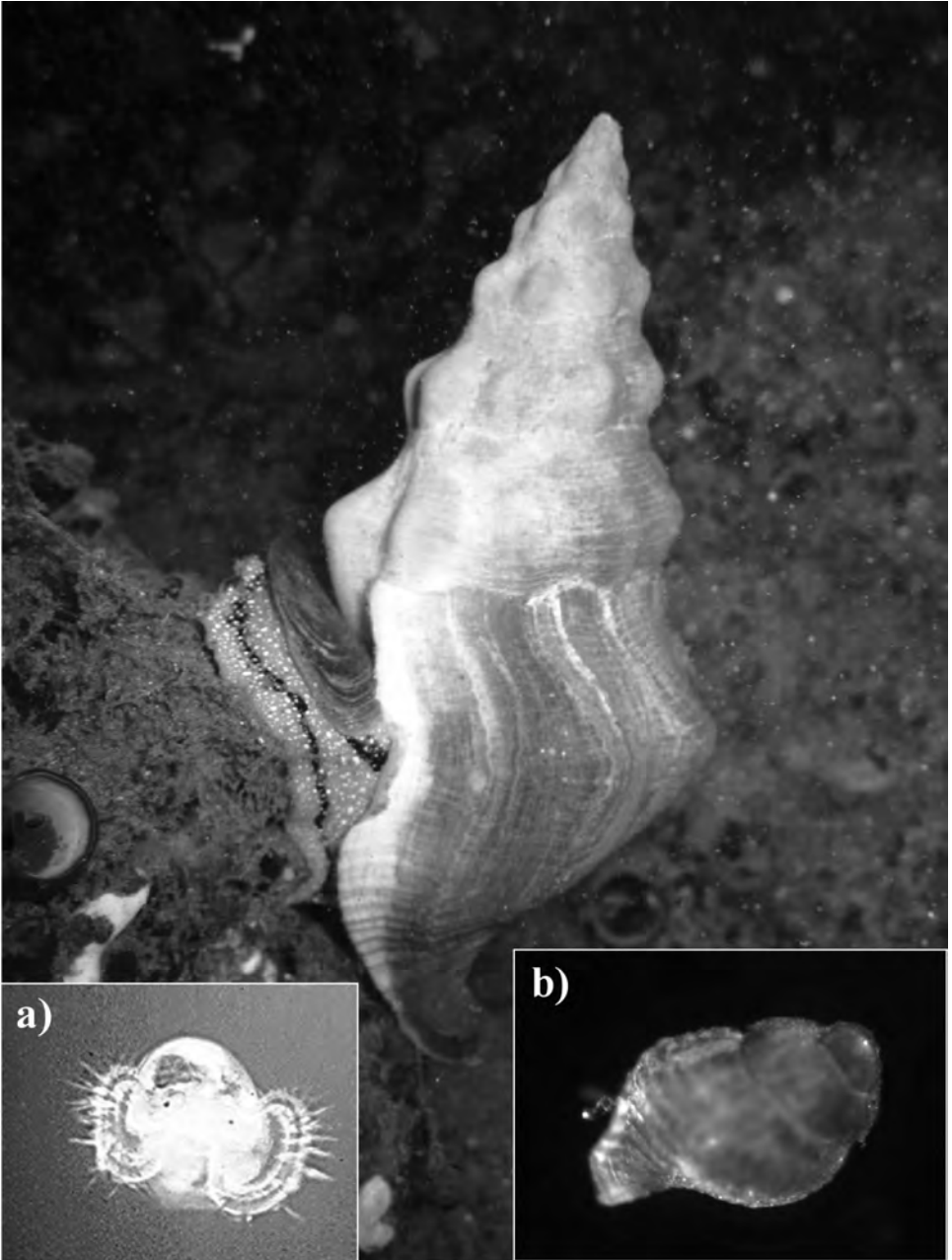


Figure 1. Adult Kelleys whelk with ~10-cm-long shell. Insets: (a) gastropod larva; (b) 3-month-old Kelleys whelk settler with ~1-mm-long protoconch shell. Photo credits: Ocean Institute Plankton Lab (a) and Sara Koch (b).

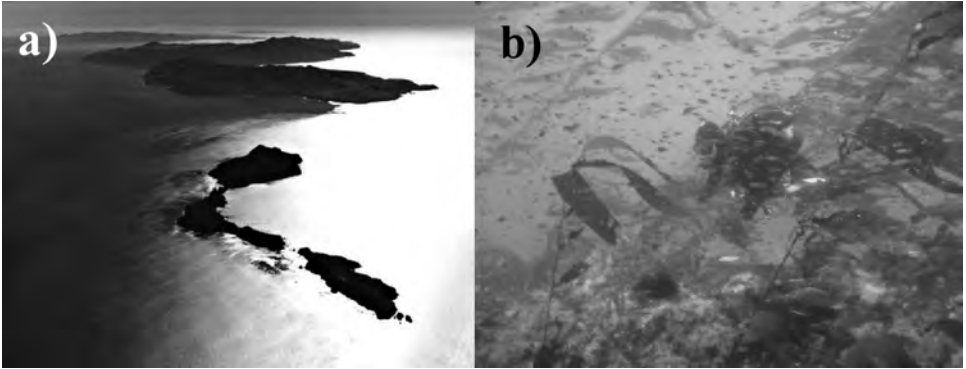


Figure 2. (a) Channel Islands National Park, looking West with Anacapa Island in the foreground . Channel Islands National Park is represented by five islands with ~300 km of coastline. (b) Research diver in a sub-tidal kelp forest. Photo credit: Channel Islands National Park (a).

years, the larvae they spawn every summer can travel great distances as they drift in the ocean for nearly two months before settling back onto reefs. Like most fish and invertebrate species, directly tracking the dispersal of these tiny larvae is logistically impossible.

Some Kellet's whelk populations are protected within no-take (i.e., no-fishing) marine reserves, which comprise approximately 23% of CINP's nearshore waters. Elsewhere in the park and in the surrounding Santa Barbara Channel region, commercial fishing of Kellet's whelk has increased exponentially over the last decade (Figure 3). Consequently, understanding the patterns of dispersal of Kellet's whelk larvae, and thus the degree of connectivity between Kellet's whelk populations in reserve and non-reserve areas, and between CINP and non-park waters, is important for guiding the conservation and management of this ecologically and economically significant species. More generally, patterns of population connectivity resolved for one species in CINP can help to guide the conservation and management of other, similar species. Lastly, demonstrating ocean circulation as an environmental factor driving larval dispersal and shaping population connectivity, especially at fine spatial scales, would provide a more general model for estimating connectivity in other regions and for other species.

For the Kellet's whelk seascape genetics research project, we analyzed DNA from whelks sampled at subtidal reefs in CINP and reefs along the adjacent Santa Barbara coastline (Figure 4). As is common among marine population genetic studies, we found the genetic differences among the sampled reef populations to be uniformly low and unrelated to geographic distance. That is, conventional spatial genetic analyses indicated no rhyme or reason to the observed genetic pattern. On their own, these results suggest that gene flow is high and random among the populations. However, we found a very different result after considering the genetic data in relation to ocean currents.

Using a model of ocean circulation produced from ocean temperature, salinity, current, and wind observations in the Santa Barbara Channel, we simulated dispersal pathways of virtual Kellet's whelk larvae, similar to tracking the movement of tiny particles in a simulated whirlpool. In the model, larvae were released along mainland and island nearshore waters

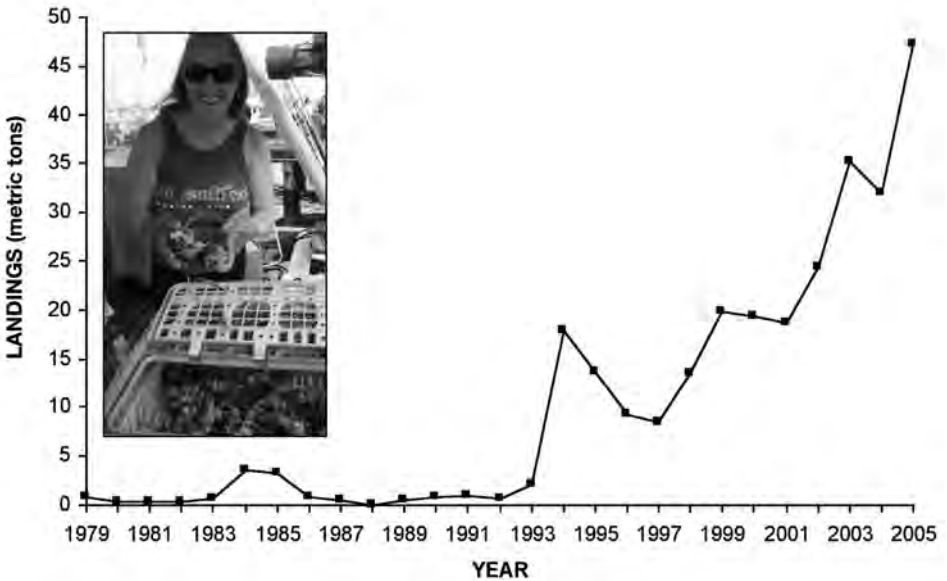


Figure 3. Southern California commercial landings of Kelle's whelk. Reproduced from Aseltine-Neilson et al. (2006). Inset: Vendor selling Kelle's whelk on the fishing pier in Santa Barbara.

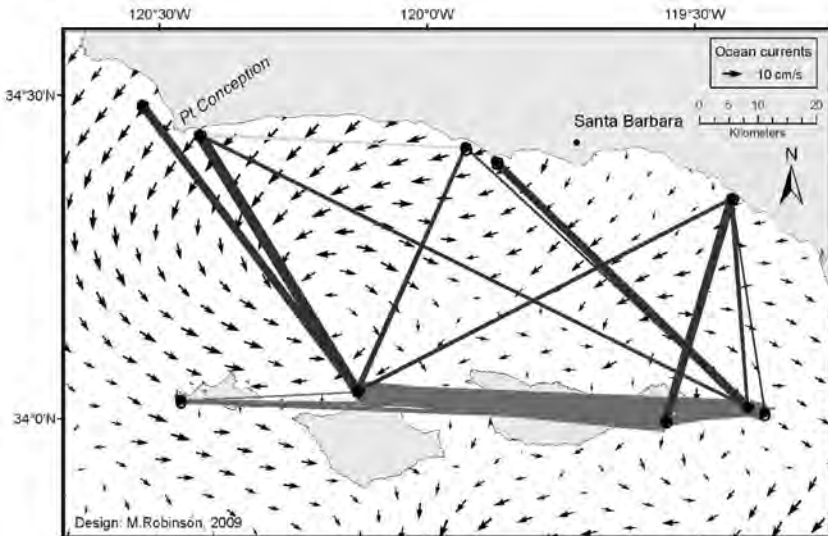


Figure 4. Map of Santa Barbara Channel region, overlaid with arrows indicating typical ocean circulation patterns, black dots ("nodes") indicating empirical genetic study locations, and straight lines ("spokes") indicating how likely, based on model simulations, Kelle's whelk larvae are to disperse between the different genetic study locations. Thicker lines indicate increased likelihood of dispersal between sites. Along the bottom half of the map, from left (west) to right (east), are Channel Islands National Park islands San Miguel, Santa Rosa, Santa Cruz, and Anacapa. Figure adapted from White et al. (2010).

where Kellet's whelk spawn, and the days of the year of their release and the number of days they were allowed to disperse in the model were set to match Kellet's whelks' natural spawning season and pelagic larval duration, respectively. Thus, the dispersal trajectories of the larvae were guided by their biological traits and the ocean currents carrying them (Figure 5). Based on the dispersal patterns exhibited by the simulated larvae, we calculated probabilities of larval exchange among the coastal locations in the model that matched the subtidal reef locations that we sampled in the field (Figure 4). We converted the probabilities of dispersal into relative oceanographic distances, and then compared these oceanographic distances with the observed pattern of genetic differences among Kellet's whelk populations. Unlike what was found in relation to geography, the comparison revealed a significant relationship between genetics and oceanography (Figure 6). Populations with the strongest

Figure 5. A "snapshot" of a simulation model of larval dispersal in the Santa Barbara Channel region. Land is indicated in gray, with Channel Islands National Park highlighted in light gray. In this illustrative example, larvae were released from the north shore of Santa Rosa Island, indicated by the star. Virtual larvae in the midst of dispersal and are represented by the dark circles; curved lines trace the dispersal path of each larva since their release. Note how most of the larvae were temporarily entrained in an oceanographic gyre (whirlpool) in the Santa Barbara Channel, then advected away by the southward-flowing California Current (see arrows in Figure 4). For visual clarity, only a fraction of the total larvae simulated in a formal analysis are shown here.

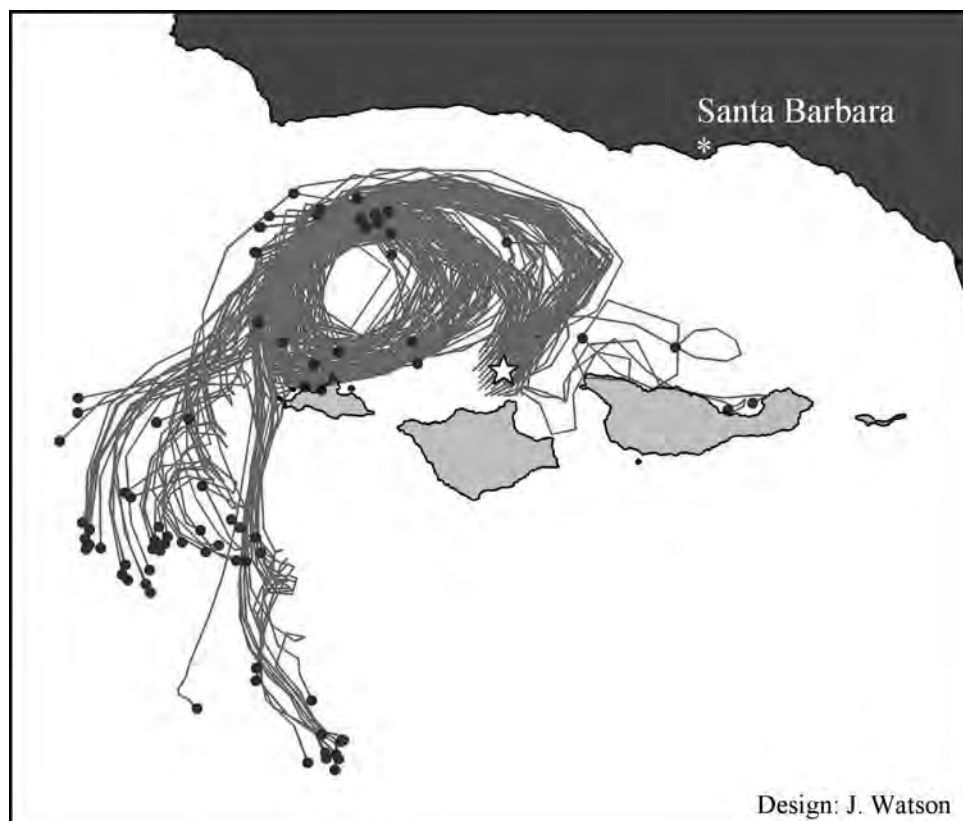




Figure 6. Genetic difference (pairwise F_{ST}) between sites in relation to the Euclidean distance between them based on (a) geography, and (b) oceanographic distance between them based on probabilities of simulated larval dispersal in a model of ocean currents. Figures adapted from White et al. (2010).

genetic differences had low probabilities of larval exchange and large oceanographic distances, and populations with the smallest genetic differences had high probabilities of larval exchange and small oceanographic distances. That is, the estimates of population connectivity based on genetics were nicely organized into a sensible pattern when viewed in relation to complex ocean currents.

Ecology and marine research implications

Sea- and landscape genetic analyses highlight the importance of considering dispersal from the perspective of the organism. In marine systems, the results from seascape genetic studies are developing into an increasingly clear message: that ocean circulation is an important environmental factor influencing dispersal, and thus population connectivity. Furthermore, ocean circulation patterns, thus larval dispersal trajectories, are far from well-mixed throughout a region. Consequently, in contrast to predictions based on conventional genetic analyses, neighboring populations are not necessarily genetically similar, nor are distant populations necessarily dramatically different. Instead, levels of connectivity between populations depend more on the currents than geographic distance between them. Marine mark-recapture studies have also already demonstrated that connectivity can be complex and not correlated with geographic distance for species with short (<2 weeks) larval dispersal periods (Planes et al. 2009), but these observations were not known to apply to the majority of marine species with long dispersal periods. The study on Kellet's whelk demonstrates that complex oceanographic conditions can generate such clear patterns of population connectivity even when marine larvae disperse for months.

A second, related message from seascape genetics studies is that oceanographic models, one of the few methods for simulating larval dispersal in marine systems, can be used for estimating population connectivity. The study on Kellet's whelk demonstrates the applicability of this message at fine spatial scales between populations less than tens of kilometers apart. This offers a useful shortcut for predicting connectivity. Population genetic studies require intensive field and laboratory work, are costly, and typically have to be repeated for every

species. And even after the work is complete, one is left with estimates of connectivity among only the locations where the researchers collected samples.

In contrast, using oceanography to estimate population connectivity requires large initial costs to gather data on oceanographic conditions and construct a circulation model; however, the ensuing costs of evaluating the dispersal trajectories of different species are relatively low, and estimates of connectivity can be generated among all coastal locations within the area represented by the model. The difference in research effort and cost associated with considering an additional site in a population genetic study (e.g., sampling individuals at the site, often using SCUBA, and analyzing their DNA in the laboratory), versus using oceanographic simulation (calculating frequency of larval exchange at that site in the model), is substantial. Consequently, there is great value in validating the use of oceanographic models for estimating patterns of larval dispersal at fine spatial scales in marine species with long pelagic larval dispersal periods, because it opens the door for marine ecologists to use this more cost-effective method for evaluating connectivity in countless marine species.

Implications for spatial management

Knowledge of population connectivity provides a fishery manager with the opportunity to strategically apply spatially explicit harvest regulations to further increase fishery returns (yields, profits) while still conserving high overall stock levels compared with those found under non-spatial management. Achieving such a win-win outcome can typically be achieved by following a simple rule of thumb characterizing harvest in relation to connectivity patterns among populations: locations that are larval sinks (i.e., areas of high larval settlement) are harvested more intensively, while locations that are larval sources (i.e., areas of high larval production and successful larval delivery to other locations) are protected from intense fishing. When an area is a particularly strong source of larvae, fishery returns may be maximized when it is closed to fishing entirely (Gaines et al. 2010). Identifying and conserving such high-output source areas not only requires an understanding by ecologists of larval dispersal and its effects on population connectivity, but also an appreciation by fishermen, managers, and policy-makers of the effect of population connectivity on population abundance and fishery yields.

California is in the midst of an intensive and controversial process to establish a series of no-fishing areas, called marine reserves, along its coastline. Guided by a state initiative, the Marine Life Protection Act (MLPA), the process engages scientists and stakeholders (e.g., fishermen) for designing a system of reserves that will rebuild and protect California's marine ecosystems, while minimizing the negative economic impact of the reserves on fisheries (or increase their benefit) (CDFG 2010). Marine reserve networks are inherently spatial management tools, and their design criteria (e.g., location, size, spacing, and configuration) determine their likely effectiveness. A core aspect of the MLPA is the establishment of multiple reserves along the coast that, due to larval dispersal, are anticipated to function as a connected network to conserve marine life and possibly enhance fishery returns more effectively than would individual reserves in isolation.

Achieving a "network effect" requires careful designing of the marine reserves in relation to the complicated source-sink pattern of larval dispersal in the region (Gaines et al.

2010). A key role of scientists in the MLPA is to evaluate the effectiveness of alternative marine reserve network proposals using bioeconomic models (CDFG 2010). In the models, reserve and non-reserve areas are all connected by larval dispersal, and larval dispersal patterns are estimated using oceanographic models of simulated larval dispersal, similar to what was done for the Kellet's whelk study. The models cover a variety of nearshore marine species; for most, there are no estimates of population connectivity using genetic or other empirical techniques, and for none are there empirical estimates of connectivity among all the populations along California's coast. Consequently, the MLPA scientists' ability to compare the effectiveness of the alternative marine reserve networks proposals hinges on the validity of using models of ocean circulation to simulate population connectivity. Furthermore, reserves proposed in the MLPA can be small (<1 km in length) and close together (<1 km from each other). Thus, confidence in projections of the effect of such a marine reserve network requires robust estimates of population connectivity at fine spatial scales. Results from previous seascape genetics studies, and in particular the Kellet's whelk study, represent substantial progress towards that goal.

In southern California, no new reserves will be placed in CINP; however, the location and characteristics of the thirteen existing marine reserve and conservation areas in the park are being explicitly accounted for in the design of reserves elsewhere. For example, low population connectivity between nearshore areas along the mainland in southern California and those around CINP's westernmost island, San Miguel (see Figure 4), indicates that conservation of fish stocks in the existing marine reserves around that island will contribute little to the network effect in southern California. In contrast, conservation of stocks in the reserves on CINP's more eastern Santa Rosa, Cruz and Anacapa islands, which exhibit high population connectivity with mainland nearshore areas, is expected to contribute substantially to the network effect in southern California. Moreover, we found Santa Cruz and Anacapa Islands to be most strongly connected to nearshore areas in the eastern half of the Santa Barbara Channel (e.g., near the city of Santa Barbara), suggesting that their network influence will be most apparent with reserves positioned along that stretch of coastline.

In marshalling validated and cost-effective oceanographic approaches to estimating connectivity, and explicitly incorporating the connectivity outputs into the evaluation of alternative spatial management policies, the MLPA models are maximizing our ability to accurately and effectively guide the design of California's marine reserve network. No other marine reserve design process has been so rigorous in this regard, setting an important precedent for analytical methods to guide marine spatial management and policy.

Moving forward

Despite the remarkable advances made recently in seascape genetics, the humble truth is that we have merely skimmed the surface in terms of generating precise and accurate estimates of population connectivity. Future progress will be marked by improved simulations of dispersal in relation to oceanography and larval biology, as well as improvements in our ability to identify and explicitly consider all of the major environmental factors driving gene flow among marine populations.

Larvae are not passive particles drifting aimlessly in the sea. They occupy all depths of the water column, and the larvae of many species actively maintain themselves at specific depths (e.g., near the bottom) or exhibit vertical migratory patterns by swimming among different depths periodically during dispersal. Ocean circulation is also a three-dimensional (3-D) process. Coastal upwelling and downwelling, and stratification in response to temperature and chemistry, cause velocity and direction of horizontal (two-dimensional) flow to vary with depth, making a column of water analogous to a stack of conveyor belts oriented in different directions and running at different speeds. From the perspective of a larva, where and when it positions itself on the stack of conveyor belts will influence its dispersal trajectory. Furthermore, larval survival while at sea varies depending on the availability of nutrients and the distribution of its predators, among other factors. Consequently, the dispersal path that a larva takes will influence its probability of survival and successful dispersal between locations. Improvements in our understanding of species-specific and spatially explicit vertical migratory swimming behaviors and mortality rates of larvae, and of the 3-D ocean circulation environment in which these dynamics occur, are necessary for more precise and accurate simulations of larval dispersal (Cowen et al. 2000; Marta-Almeida et al. 2006; Shanks 2009).

Unfortunately, recording swimming behaviors and daily survival rates of marine larvae in the wild over the course of their dispersal presents the same logistical challenges that prevent their direct tracking. Consequently, most estimates rely on laboratory observations. Measuring 3-D ocean flow, especially very close to shore, is also daunting, though progress on this front has been remarkable lately. Increases in computational power and algorithm efficiency are enabling oceanographers to estimate flow patterns at hourly intervals in relation to complex coastlines and bottom topography measured at the meter scale (Li et al. 2008). Consideration of such fine-scale model outputs of ocean circulation will vastly improve our ability to estimate population connectivity and the effectiveness of alternative management policies at the scale of individual reefs.

Even with perfect simulations of larval dispersal we are only left with an understanding of *potential* population connectivity. Actual, or realized, connectivity depends on the number of larvae spawned at each site, their condition (which affects their survival and swimming abilities), and the suitability of a settlement site for recruitment of larvae into juveniles (Watson et al. 2010). In Kellet's whelk, for example, average whelk size varies across the species range, and larger females produce more larvae. Also, in addition to ocean circulation, kelp cover has been found to help explain Kellet's whelk population genetic patterns, possibly regulating recruitment of settling larvae (Selkoe et al., in press). These biological and environmental factors were not considered in the Kellet's whelk seascape genetics study, thereby limiting its ability to tease apart their relative influence on realized population connectivity. Although some of these factors (e.g., habitat quality) are considered in the MLPA models, the underlying data (e.g., on bathymetry and substrate type) is spatially sparse and costly to obtain. Given limited resources, it is important to determine the value of gathering the data describing these factors. Such relative values of information can be quantified when these factors are explicitly compared with empirical patterns of genetic structure that reflect realized population connectivity. Identifying and focusing on the factors of greatest explana-

tory power will promote efficient construction and parameterization of models of connectivity for the most number of nearshore marine ecosystems.

Seascape genetics is a rapidly developing field that is substantially advancing our ability to measure population connectivity in relation to the marine environment. Marine larval dispersal—long considered the “black box” of marine ecology—is being unlocked by results and scientific tools arising out of seascape genetics. In opening this box, we are gaining an understanding of and appreciation for the complex patterns of population connectivity in the oceans, and contributing significantly to ongoing efforts to conserve and efficiently manage the ocean’s valuable biological resources.

References

- Aseltine-Neilson, D., B. Brady, M. Connell, P. Kalvass, L. Laughlin, B. Leos, J. Mello, G. Neillands, E. Roberts, I. Taniguchi, A. Vejar, R. Watanabe, and C. D.F. Game. 2006. Review of some California fisheries for 2005: Coastal pelagic finfish, market squid, Dungeness crab, sea urchin, abalone, Kellet’s whelk, groundfish, highly migratory species, ocean salmon, nearshore live-fish, Pacific herring, and white seabass. *California Cooperative Oceanic Fisheries Investigations Reports* 47, 9–29.
- Bradbury, I.R., and P. Bentzen. 2007. Non-linear genetic isolation by distance: Implications for dispersal estimation in anadromous and marine fish populations. *Marine Ecology–Progress Series* 340, 245–257.
- CDFG [California Department of Fish and Game]. 2010. Marine Life Protection Act Initiative. Online at www.dfg.ca.gov/mlpa.
- Clark, R.W., W.S. Brown, R. Stechert, and K.R. Zamudio. 2008. Integrating individual behaviour and landscape genetics: the population structure of timber rattlesnake hibernacula. *Molecular Ecology* 17, 719–730.
- Cowen, R.K., K.M.M. Lwiza, S. Sponaugle, C.B. Paris, and D.B. Olson. 2000. Connectivity of marine populations: Open or closed? *Science* 287, 857–859.
- Gaines, S.D., C. White, M.H. Carr, and S.R. Palumbi. 2010. Designing marine reserve networks for both conservation and fisheries management. *Proceedings of the National Academy of Sciences of the United States of America*. Online at www.pnas.org/content/107/43/18286.full.
- Galindo, H.M., D.B. Olson, and S.R. Palumbi. 2006. Seascape genetics: A coupled oceanographic-genetic model predicts population structure of Caribbean corals. *Current Biology* 16, 1622–1626.
- Gilg, M.R., and T.J. Hilbish. 2003. The geography of marine larval dispersal: Coupling genetics with fine-scale physical oceanography. *Ecology* 84, 2989–2998.
- Halpern, B.S., K. Cottenie, and B.R. Broitman. 2006. Strong top-down control in southern California kelp forest ecosystems. *Science* 312, 1230–1232.
- Li, Z.J., Y. Chao, J.C. McWilliams, and K. Ide. 2008. A three-dimensional variational data assimilation scheme for the regional ocean modeling system. *Journal of Atmospheric and Oceanic Technology* 25, 2074–2090.
- Marta-Almeida, M., J. Dubert, A. Peliz, and H. Queiroga. 2006. Influence of vertical migra-

- tion pattern on retention of crab larvae in a seasonal upwelling system. *Marine Ecology–Progress Series* 307, 1–19.
- Mitarai, S., D.A. Siegel, J.R. Watson, C. Dong, and J.C. McWilliams. 2009. Quantifying connectivity in the coastal ocean with application to the Southern California Bight. *Journal of Geophysical Research–Oceans* 114.
- Planes, S., G.P. Jones, and S.R. Thorrold. 2009. Larval dispersal connects fish populations in a network of marine protected areas. *Proceedings of the National Academy of Sciences of the United States of America* 106, 5693–5697.
- Selkoe, K.A., J.R. Watson, C. White, T. Ben-Horin, M. Iacchei, S. Mitarai, D.A. Siegel, S.D. Gaines, and R.J. Toonen. In press. Taking the chaos out of genetic patchiness: Seascape genetics reveals ecological and oceanographic drivers of genetic patterns in three temperate reef species. *Molecular Ecology*.
- Shanks, A.L. 2009. Pelagic larval duration and dispersal distance revisited. *Biological Bulletin* 216, 373–385.
- Simberloff, D.S., and E.O. Wilson. 1969. Experimental zoogeography of islands: The colonization of empty islands. *Ecology* 50:278–296.
- Watson, J.R., S. Mitarai, D.A. Siegel, J.E. Caselle, C. Dong, and J.C. McWilliams. 2010. Realized and potential larval connectivity in the Southern California Bight. *Marine Ecology–Progress Series* 401, 31–48.
- White, C., K.A. Selkoe, J. Watson, D.A. Siegel, D.C. Zacherl, and R.J. Toonen. 2010. Ocean currents help explain population genetic structure. *Proceedings of the Royal Society B–Biological Sciences* 277, 1685–1694.
- Wiens, J.A. 2001. The landscape context of dispersal. In *Dispersal*. J. Clobert, E. Danchin, A.A. Dhondt, and J.D. Nichols, eds. Oxford: Oxford University Press, 96–109.
- Crow White**, Marine Science Institute, University of California–Santa Barbara, Santa Barbara, California 93106; crowfeather@gmail.com