Seascape Genetics: Populations, Individuals, and Genes Marooned and Adrift

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Abstract

Seascape genetics is the study of how spatially variable structural and environmental features influence genetic patterns of marine organisms. Seascape genetics is conceptually linked to landscape genetics and this likeness frequently allows investigators to use similar theoretical and analytical methods for both seascape genetics and landscape genetics. But, the physical and environmental attributes of the ocean and biological attributes of organisms that live in the sea, especially the large spatial scales of seascape features and the high dispersal ability of many marine organisms, differ from those of terrestrial organisms that have typified landscape genetic studies. This paper reviews notable papers in the emerging field of seascape genetics, highlighting pervasive themes and biological attributes of species and seascape features that affect spatial genetic patterns in the sea. Similarities to, and differences from, (terrestrial) landscape genetics are discussed, and future directions are recommended.

Landscape and Seascape Genetics – Genetics in Spatially Heterogeneous Environments

The question of how spatially arrayed environmental and habitat features influence microevolutionary processes has a long history in population genetics (Epling & Dobzhansky 1942; Wright 1943). Recently there have been calls to explicitly integrate spatial ecological information with population genetic data, in an endeavor coined "landscape genetics" (Manel et al. 2003), where associations between specific landscape features and genetic variation can be statistically evaluated (Storfer et al. 2007). Thus, landscape genetics implicitly melds ecological and evolutionary outlooks in seeking to understand how spatial factors influence genetic changes over both space and time.

Although some authors have emphasized recent events as the primary focus of landscape genetics (Manel et al. 2003), we advocate a more flexible perspective whereby the relevant temporal scale will be determined by the spatial factor(s) of interest, the temporal stability of those spatial factors, and the dispersal ability of the organism(s). Different methods, of course, will be more suitable for some time scales than others (Balkenhol et al. 2009; Anderson et al. 2010; Bohonak & Vandergast 2011). Similarly, landscape genetics can encompass questions across a hierarchy of biological organization from specific genes or loci, to individuals, and populations. To date, most terrestrial and marine landscape genetic studies have focused on selectively neutral processes such as the identification of barriers or resistance to gene exchange, although spatial sources of selection fall within the scope of landscape genetics as well (Manel et al. 2003; Holderegger & Wagner 2006; Manel et al. 2010; Storfer et al. 2010).

In the last 10 years, there have been a profusion of papers in landscape genetics, with several marine examples (albeit in a much smaller proportion than for terrestrial studies: Storfer et al. 2010) and recognition that spatial processes could and should be investigated in marine "seascapes" (Galindo et al. 2006; Selkoe et al. 2008). Reviews have focused primarily on terrestrial examples (Manel et al. 2003; Storfer et al. 2007; Holderegger & Wagner 2008), with the exception of Selkoe et al. (2008) and a brief overview by Hansen and Hemmer-Hansen (2007) both of which emphasized the importance of oceanographic currents as a primary distinguishing feature between seascapes and (terrestrial) landscapes. Since those reviews, there have been an increasing number of studies that self-identify with "seascape" or "marine landscape" genetics; a search of the Web of Science (Dec. 2011) for the key words "seascape genetics" and "marine landscape genetics" yielded 48 studies (after removing non-marine and non-genetic hits), 37 of which were from 2008 onwards.

Thus, this review updates a quickly moving field from the earlier reviews. In addition, our definition of seascape genetics differs in emphasis. Whereas we agree that ocean currents are an important component of marine landscapes (as articulated by Galindo et al. 2006; Selkoe et al. 2008), we also contend that the relative influence of other spatial factors on marine genetic variation is little known and worthy of integrated investigation. Furthermore, full consideration of spatial structuring factors depends on the spatial and temporal scales of seascape features as well as the life history of the specific organism. For many marine organisms, their extensive dispersal ability may necessitate seascape genetic studies to encompass large geographic areas, yet some seascape attributes may also vary over short time periods. This juxtaposition of spatial and temporal scales creates challenges for the field. Although the terms "seascape genetics" and "marine landscape genetics" are relatively new, several older papers address similar issues, therefore, we attempt to refer both to new developments and classic studies in this field. In the companion paper to this review (Liggins et al. 2013) we discuss aspects of study design and genetic analysis relevant to seascape genetics, with an expanded description of biophysical models that are increasingly complementing genetic surveys.

A fluid lifestyle

Marine organisms live in a dense and viscous moving fluid, which transports nutrients, food, gametes, and/or individuals depending on species life history (Thorson 1971; Levinton & Haefner 2002; Carr et al. 2003; Dawson & Hamner 2008). Marine organisms have a wide diversity of life histories, and frequently different life stages make use of distinctly different environments. At the extremes, there are organisms with entirely benthic lifestyles and direct development of their young (including but not limited to seahorses, some gastropods, some echinoderms), whereas other organisms are entirely planktonic (many diatoms, dinoflagellates, copepods, krill) or entirely pelagic (including cetaceans and many fishes). Many life histories include both benthic and pelagic stages. For instance, seaweeds and kelp have benthic and floating stages: as adults they grow attached to the benthic substrate, but frequently fragment and floating pieces can drift large distances before attaching elsewhere or contributing gametes to other populations. Most animals which are benthic-associated as adults also have planktonic (pelagic) larvae, and these animals vary widely in their planktonic larval duration (PLD), ranging from minutes to months (Shanks 2009).

Complementing the wide variety of life histories and dispersal abilities of marine organisms, oceans and seas are spatially heterogeneous with respect to many important environmental variables (temperature, nutrients; Fig. 1), but these environmental conditions may change rapidly in relationship to relatively static features such as coastline configuration. Thus, for pelagic animals, static seascape features may appear to move relative to their frame of reference; they may track variable environmental features, for example, keeping themselves within a distinct water mass. In contrast, for relatively sedentary benthic organisms, their frame of reference will be the static benthos, but the environmental conditions in which they are immersed may shift rapidly due to water movements (i.e. considerable movement on an environmental axis, but no movement on a geographic axis).

Environmental factors and life history traits can interact synergistically to influence genetic patterns. For animals that are benthic as adults yet pelagic as larvae, the larval experience can potentially affect the adult population structure. For instance, PLD may be spatially variable within a species, because higher ambient temperatures are expected to raise metabolic rates and thus reduce the duration of the larval stage (O'Connor et al. 2007) perhaps affecting genetic structuring among locations (David et al. 2010). Similarly, the open water environment experienced by larvae can influence their survival (Shima & Swearer 2009) and even juvenile post-settlement survival (reviewed by Marshall & Morgan 2011), thus potentially affecting the genetic patterns formed across the seascape.

There has been much speculation regarding the consequences of high vagility, particularly planktonic larval movements, on genetic patterns of adult populations. For the many marine species that disperse extensively, population genetic theory predicts high genetic variability and low differentiation across large spatial scales (Waples 1998; Hellberg et al. 2002; Faurby & Barber 2012). Accordingly, many (but certainly not all) marine animals appear to be characterized by fairly low population genetic structure (Palumbi 1992; Ward et al. 1994; Kinlan & Gaines 2003). Therefore, population genetic structure may be very low and, as a consequence, difficult to detect empirically

	Patch size							Distance between patches							Temporal duration of patch								
	meters	tens of meters	hundreds of meters	kilometers	tens of kilometers	hundreds of kilometers	thousands of kilometers	meters	tens of meters	hundreds of meters	kilometers	tens of kilometers	hundreds of kilometers	thousands of kilometers	hours	days	months	years	decades	centuaries	thousands of years	tens of thousands of years	hundreds of thousands of years

Geologic features
Oceanic islands
Continental islands
Sea mounts
Continental shelves
Deep-sea trenches
Hydrothermal vents
Shoreline configuration *(bays, headlands)*
Configuration of abiotic substrate
Freshwater inputs

Oceanographic features
Oceanographic currents
Nearshore currents
Mean sea level *(by depth)*
Tidal amplitude
Wind force & direction
Wave energy
Depth stratified water masses
Primary productivity

Biotic structures
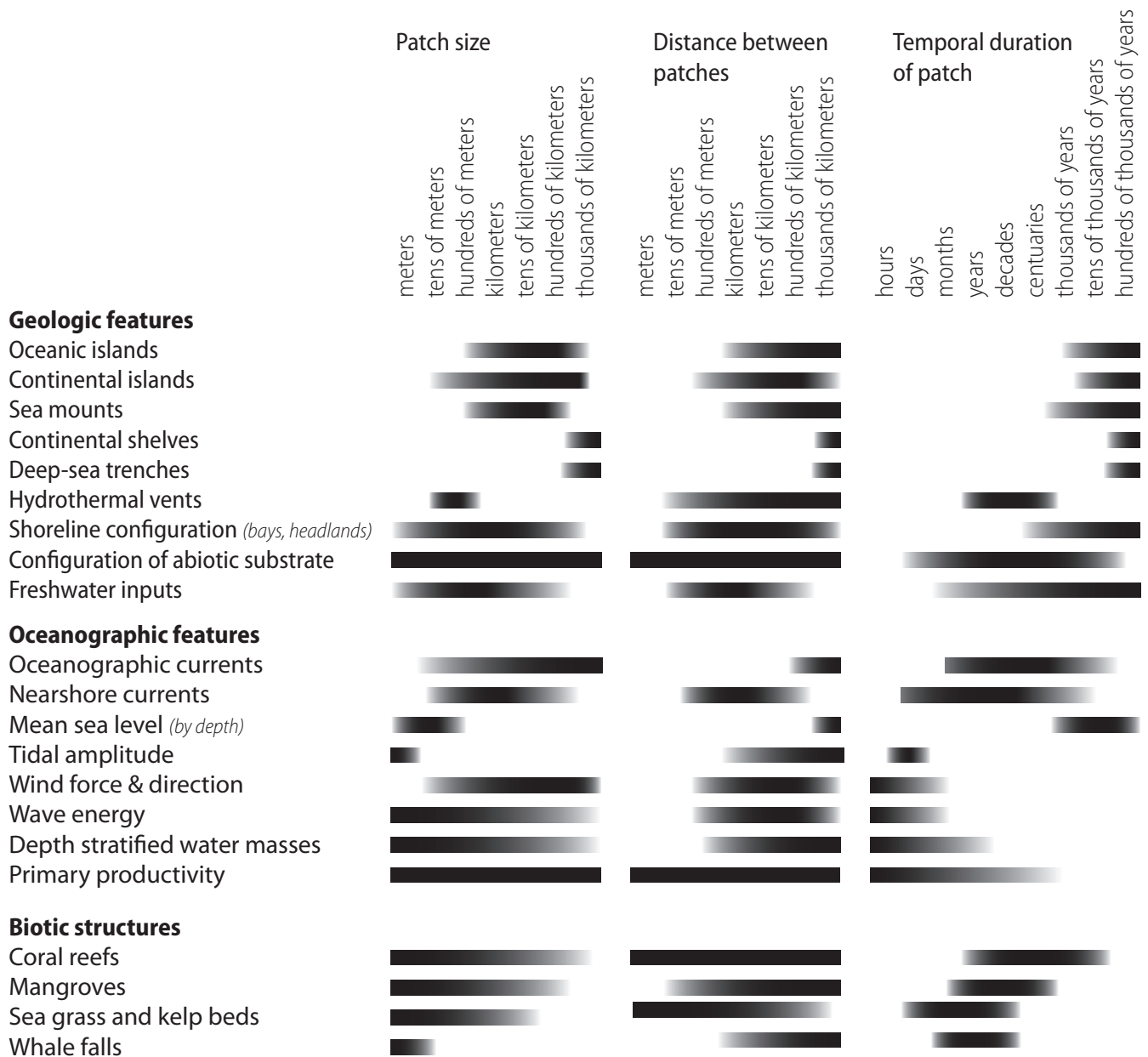Coral reefs
Mangroves
Sea grass and kelp beds
Whale falls

Fig. 1   Spatial and temporal variability of seascape features that may affect genetic differentiation. Patch size indicates the size of the feature. Patch size and distance between patches are aspects of environmental granularity. The temporal duration of a patch indicates the stability or permanence of a feature in a particular configuration. The intensity of shading is intended to convey the relative frequency of a particular size, distance, or duration. Relative frequencies were informed by soliciting expert opinions from geologists, oceanographers, evolutionary biologists, and ecologists.

(Waples 1998). Thus, geneticists may struggle to interpret weak and possibly unreliable genetic signals in a seascape context.

A related and prevailing hypothesis has been that higher levels of genetic differentiation should be found among populations of animals that have a short PLD, versus those that have a long PLD. Whereas recent analyses of published genetic data sets (invertebrate and fishes) have found PLD to be a weak or poor predictor of genetic differentiation (Weersing & Toonen 2009; Riginos et al. 2011; Selkoe & Toonen 2011), these post-hoc analyses ignore the effects of geographic location and evolutionary differences among species that may be correlated with other life history traits that affect

genetic structuring (Dawson 2012) and differences in effective population sizes among species that will also affect estimates of genetic differentiation (Faurby & Barber 2012). Indeed some studies of co-distributed taxa have found the expected relationship between PLD and genetic differentiation (Waples 1987; Doherty et al. 1995; Riginos & Victor 2001). The PLD - genetic differentiation relationship remains an area of active study and debate (see Weersing & Toonen 2009; Riginos et al. 2011; Selkoe & Toonen 2011; Dawson 2012 for more extensive discussions). A firm conclusion that emerges, however, is that species with direct development (PLD = 0) have high genetic structure (Weersing & Toonen 2009; Kelly & Palumbi 2010).

Another frequent observation that may arise from planktonic larval dispersal and temporally variable environments is that adult genetic patterns can fluctuate without obvious regard to space, in a phenomenon termed chaotic genetic patchiness (Johnson & Black 1982; and see Selkoe et al. 2008 for a comprehensive discussion). A number of explanations have been proposed to explain this phenomenon, including: high variability in reproductive success leading to differing parents contributing to distinct sets of larvae (Hedgecock 1994; Planes & Lenfant 2002) that may be transported in groups by temporally variable currents, selection on larvae during their pelagic stage (Johnson & Black 1984), and selection on juveniles after settlement to the benthos (Vigliola et al. 2007). Note that these competing explanations involve factors that are spatially variable, yet potentially predictable (see also discussion in Selkoe et al. 2008). Indeed Selkoe et al. (2006) showed that the location of a frontal boundary current for the two weeks prior to sampling influenced the genetic composition of kelp bass recruits. Hence, for kelp bass, an understanding of the temporally variable seascape can help explain genetic patterns.

In summary, the marine realm encompasses spatial elements whose temporal stabilities differ widely (Fig. 1), and marine organisms span a wide array of life histories and lifestyles (Carr et al. 2003). In many instances there are parallels between marine and terrestrial environments (Dawson & Hamner 2008), and some seascape genetic studies are similar in approach to those applied to terrestrial ecosystems, particularly when investigating effects of relatively static features on benthic organisms. Yet when temporarily variable features or highly dispersive organisms are the foci of study, then the application of methods developed from terrestrial landscape genetics may be inappropriate or require modification. The combined considerations of spatio-temporal instability and high dispersal are motivating creative approaches for studying spatial marine genetic patterns that are distinct from terrestrial landscape genetics.

Empirical investigations of seascape features

Seascape genetic studies have predominantly focused on how physical factors facilitate or restrict connections between populations or individuals, using genetic response variables such as F-statistics or estimates of gene flow. F-statistics (F_{ST} and related measures), estimate the proportion of genetic variation partitioned among populations relative to the total variation among all individuals and populations. Few studies have considered effects of seascape attributes on genetic variability (see Table 1 for some exceptions). Seascape factors that are likely to influence the genetic structure of marine species differ widely in their grain size and also in their permanence (Fig. 1). Both the relevant spatial and temporal scales for seascape variables should guide study design (see Liggins et al. 2013), and in general, studies emphasizing large spatial scales and relatively static landscape features have primarily used population-level sampling and associated methods, whereas studies interested in smaller spatial scales and temporally unstable variables have been more likely to employ individual-focused methods.

In the following subsections, we first describe studies that have investigated relatively stable factors such as geographic distance and topography (stable for thousands of years or more) followed by those that examine unstable factors, especially currents (varying by years, months, days, or hours), including attempts to summarize temporally variable factors as geo-referenced seascape attributes. Obviously these examples represent the tails of spatial and temporal continua (Fig. 1); designing studies that can estimate the effects arising from spatial and temporal processes that vary over many orders of magnitude is a challenge (see Liggins et al. 2012 for further discussion). In addition, the scale of investigation may determine the relevant stability; for example, major oceanographic currents and their boundaries may be present in the same location on the scale of 100-1000's of kilometers but at a

Table 1 Seascape genetic studies that have quantitatively tested for the effects of multiple factors

Seascape factors examined	Significant seascape factors[a]	Habitat configuration	Response variable(s)[b]	Type(s) of analysis	Loci	Common name	Scientific name	Reference
Only including relatively stable factors								
Habitat continuity, Euclidean distance	Habitat continuity, Euclidean distance	linear coastline	F_{ST}	multiple regression	Msat	Giant kelp	*Macrocystis pyrifera*	Alberto et al. 2010
Salinity, temperature (at spawning), Euclidean distance	salinity, temperature	enclosed basin (Baltic Sea)	F_{ST}	partial Mantel tests	Msat	herring	*Clupea harengus*	Jorgensen et al. 2005
Salinity, sand	salinity, sand	enclosed lagoon	first principal component (from PCA) based on genetic distance	linear models (GAM)	Pgi allozyme	cockle	*Cerastoderma galucum*	González-Wangüemert et al. 2009
Stormwater, wastewater, Euclidean distance	stormwater, wastewater	linear coastline	F_{ST}, D_{est}	single variate regressions, multivariate regressions, canonical redundancy analysis	mtDNA, Msat	bat star	*Patiria miniata*	Puritz & Toonen 2010
Sandy coastline, open water, biogeography, Euclidean distance	sandy coastline, open water, biogeography, Euclidean distance	semi enclosed basin (Gulf of California)	D	partial Mantel tests	mtDNA	Cortez triplefin	*Axoclinus nigircaudus*	Riginos & Nachman 2001
Including unstable factors								
Habitat continuity, minimal oceanographic transport time	habitat continuity, minimum oceanographic transport time	linear coastline	F_{ST}, D_{est}, assignment tests	multiple regression	Msat	Giant kelp	*Macrocystis pyrifera*	Alberto et al. 2011
SST[c] (mean and StDev), coastline topography, habitat area	SST StDev	linear coastline with two distant oceanic locations	Local genotypic autocorrelation	linear models	Msat	barrens forming urchin	*Centrostephanus rodgersii*	Banks et al. 2007
SST[c] (mean and StDev), coastline topography, area of recent range expansion	SST StDev, and coastline topography, area of recent range expansion	linear coastline including recent range expansion zone, with two distant oceanic locations	AR, H, F_{ST}, D, genotypic autocorrelation	partial Mantel tests, GESTE, modelling	Msat	barrens forming urchin	*Centrostephanus rodgersii*	Banks et al. 2010
Distance by habitat (depth), distance by current, Euclidean distance	distance by habitat (depth)	continental shelf, offshore banks	F_{ST}	partial Mantel tests	Msat	tusk fish	*Brosme brosme*	Knutsen et al. 2009

Table 1 Continued

Including unstable factors, continued.

Seascape factors examined	Significant seascape factors[a]	Habitat configuration	Response variable(s)[b]	Type(s) of analysis	Loci	Common name	Scientific name	Reference
Chlorophyll, turbidity, SST[c], Euclidean distance	Chlorophyll, turbidity, SST	linear coastline	F_{ST}	multiple Mantel tests, partial Mantel tests	mtDNA, Msat	franciscana dolphin	*Pontoporia blainvillei*	Mendez et al. 2010
Kelp cover, SST[c], flow centrality[d]	kelp cover, SST, flow centrality	linear coastline with nearshore islands	AR, H, local F_{ST}, G_{ST}'	multiple regression (modified linear mixed model)	Msat	Kellet's whelk	*Kelletia kelletii*	Selkoe et al. 2010
Kelp cover, SST[c], flow centrality[d]	kelp cover, SST, flow centrality	linear coastline with nearshore islands	AR, H, local F_{ST}, G_{ST}'	multiple regression (modified linear mixed model)	Msat	spiny lobster	*Panulirus interruptus*	Selkoe et al. 2010
Kelp cover, SST[c], flow centrality[d]	kelp cover, SST, flow centrality	linear coastline with nearshore islands	AR, H, local F_{ST}, G_{ST}'	multiple regression (modified linear mixed model)	Msat	kelp bass	*Paralabrax clathratus*	Selkoe et al. 2010
Oceanographic distance, Euclidean distance	Oceanographic distance	linear coastline with nearshore islands	F_{ST}, D_{est}	Mantel tests	Msat	Kellet's whelk	*Kelletia kelletii*	White et al. 2010

[a] Significant in at least some analyses
[b] AR, H, and D, represent Allelic richness, Heterozyosity, and genetic Distance; see original paper for specific methods of calculation and transformations. D_{est} and G_{ST}' are measures of differentiation that correct for allelic variability.
[c] SST = Sea Surface Temperature
[d] Flow centrality reflects the hub position in a network based on biophysical predicted connections.

finer sampling scale (10-100's km) their direction and magnitude of flow may shift over months and days.

The majority of seascape genetic studies to date have chosen to use genetic markers that are commonly assumed to be neutrally evolving (not subject to strong selection) such as microsatellites or mitochondrial (mt)DNA sequences. Because strong selection can alter allele frequencies for selected loci relatively rapidly (at least rapidly in an evolutionary sense), historical patterns (reflecting genetic drift and migration among populations) can be obscured. Thus, the ideal genetic markers for inferring demographic processes, such as isolation or migration among populations and changes in population size, are those that are neutral. For those investigators interested in non-neutral evolution, marine animals also are good study systems for investigating the effect of environmentally-mediated selection on genetic variation (Schmidt et al. 2008; Nielsen et al. 2009a), whereby the biological units of interest are not individuals or populations, but rather are the genetic loci themselves. We also review some of these gene focused studies in a following section.

STABLE CONFIGURATIONS – DISTANCE AND TOPOGRAPHY

Just as on land, geographic distance, barriers, and habitat isolation in the sea can reduce genetic exchanges and, through the action of genetic drift and sometimes selection, lead to divergence between populations and individuals. If, i) populations are evenly spaced, as in a lattice formation, ii) gene exchange is inversely proportional to geographic distance between populations or individuals, that is, migration occurs in a stepping-stone manner, and iii) sufficient time has elapsed for an equilibrium between migration and genetic drift to be established, then an isolation-by-distance (IBD) pattern is expected (Slatkin 1993; Rousset 2000) and often found for marine species (Selkoe & Toonen 2011). Although IBD analyses traditionally use straight-line (Euclidean) geographic distances, other ecologically relevant distance measures, such as shortest over-water distance, shortest habitat path, and oceanographic distance (derived from an ocean circulation model that may or may not be parameterized with biological attributes of the organism, i.e. a biophysical model) may capture physical and/or biological processes affecting gene exchange and, therefore, be better predictors of genetic differentiation than Euclidean geographic distance. Thus, in seascape studies, Euclidean distance can form a simple model against which more sophisticated models can be compared, or Euclidean distance can be included as a covariate along with other predictive variables so that the independent contributions of each variable are estimated (see Table 1 for examples).

Distance in and of itself can modify gene exchange, but other types of barriers or habitat discontinuities can also obstruct movement. Obviously landmasses form barriers and, depending on their configuration, landmasses may be complete barriers to movement. More complex cases are permeable barriers that reduce but might not preclude gene exchange. For coastal or reef species, large stretches of open water can contribute to greater divergence relative to comparisons along coastlines (Doherty et al. 1995; Ayre & Hughes 2004). Features along coastlines can also influence genetic patterns, as found for the large freshwater outflow of the Amazon River on some reef dwelling surgeonfishes (Rocha et al. 2002), upwelling locations for rockfish (Johansson et al. 2008), large stretches of sand for some rocky reef fishes (Riginos & Nachman 2001; Johansson et al. 2008) and invertebrates (Ayre et al. 2009), and even hotspots of wastewater and stormwater pollution for a bat star (Puritz & Toonen 2011). For a fish restricted to deep continental shelves (100-1000 m), deep trenches (>1000 m) were similarly found to significantly contribute to genetic differentiation (Knutsen et al. 2009).

In some cases, the effect of partial barriers is modulated by the size of that barrier. For example, for the rock-associated Cortez triplefin, the IBD slope (Euclidean geographic distance vs. F_{ST}) for populations separated by sand was steeper than the slope for populations separated by rock reef (Riginos & Nachman 2001). Similarly, the degree of habitat discontinuity (estimated using satellite image analysis in a GIS - geographic information system) in combination with geographic distance were better predictors of genetic differentiation between giant kelp populations than either factor alone (Alberto et al. 2010). For golden jellyfish living in land-surrounded marine lakes, the genetic distance between lake and reef lagoon populations was correlated with geographic distance between each lake and its nearest lagoon (Dawson 2005). The effect of distance can also vary with spatial scale; for example, IBD was found within Pacific archipelagos, but no linear relationship with distance was found among archipelagos for a surgeonfish (Planes et al. 1996). Conversely, for the crown-of-thorns

starfish, IBD was found among Pacific locations (spanning large stretches of open ocean) but not within the more continuous reefs of Japan and the Philippines (Yasuda et al. 2009). The potential for interactions between distance and other spatial variables highlights the utility of considering multivariate approaches (Table 1) that can evaluate the relative importance of differing variables and their interactions.

UNSTABLE CONFIGURATIONS – CURRENTS

Advances in remote sensing and oceanographic modeling have greatly enhanced the resolution with which currents, particularly nearshore currents relevant to coastal larvae, can be inferred in both space and time. Knowledge of water movements can be combined with species-specific biology to create complex biophysical models that yield spatially explicit dispersal probabilities (see Liggins et al. 2013). Earlier examinations of major (offshore) oceanographic currents and genetic patterns found modest correlation (Palumbi et al. 1997) or highlighted disparities (Benzie 1999), whereas some recent investigations, especially using more precise biophysical models to predict genetic patterns, have been compelling and are discussed below.

Most studies with oceanographically-informed predictions attempt to correlate the simulated movement of individuals or water masses against empirical genetic data, often using qualitative comparisons. For example, Cowen et al.'s (2006) biophysical model of larval dispersal for reef fish defined four largely distinct regions of population connectivity within the Caribbean that qualitatively matched genetic patterns previously described for a goby (Taylor & Hellberg 2003) and a coral (Baums et al. 2005). Similarly, Baums et al. (2006) found that simulated coral larvae could not disperse across an ocean passage between the eastern and western Caribbean, which coincided with a genetic break revealed using empirical genetic data.

Some investigators have taken the connectivity matrices produced by biophysical models and used them to project the development of population genetic structure forward through time, allowing simulated genetic patterns and empirical genetic patterns to be compared directly. The first application of this method found that simulated genetic patterns for a broadcast spawning coral, *Acropora cervicornis*, in the Caribbean were in agreement with the broadscale observed genetic patterns (Galindo et al. 2006). Similarly, Kool and co-workers found that biophysically-predicted genetic structure in coral reef populations in the Caribbean (Kool et al. 2010) and coral reef communities in the Indo-West Pacific (Kool et al. 2011) matched observations of genetic structure qualitatively assessed across many species and specifically for the coral *Montastraea annularis* (Foster et al. 2012). Discordances between modeled data (either coupled or uncoupled to genetic simulations) and observed genetic data can highlight regions where dispersal alone does not capture connectivity (such as when post-settlement processes are important) and shortcomings in the model (Galindo et al. 2011; Foster et al. 2012), but discordances also may reflect the inherently differing time scales between modeled biophysical data and empirical genetic patterns of real organisms.

Other studies have sought to quantify the relationships between different oceanographic predictors and empirical data. For instance, connections based on oceanographic models were found to better predict F_{ST} values between population pairs as compared to Euclidean distances in linear regression analyses for a whelk (White et al. 2010) and a giant kelp (Alberto et al. 2011). For the whelk, an oceanographic distance, indicating the likely distance that larvae would travel, was the better predictor of pairwise F_{ST} values (White et al. 2010). In the case of the giant kelp, the best explanatory model was one that combined minimum transport time and habitat continuity (Alberto et al. 2011). Rather than inferring genetic metrics independently for each set of population pairs, Crandall et al. (2012) derived coalescent estimates of gene flow simultaneously among all sampled populations and demonstrated that biophysically-based stepping-stone models of gene flow were a better fit to the data than a series of other migration models. (Coalescent analyses are based on computationally intensive simulations whereby the observed data are compared against the parameter space that could produce such data; see Hey and Machado 2003 for a general review).

A key aspect of predictions derived from oceanographic measurements is that if currents are important for transporting propagules and influencing genetic patterns, then genetic exchange should be asymmetric (Wares et al. 2001), and genetic methods that can detect asymmetric migration (Marko & Hart 2011) should outperform genetic response variables that provide a single bidirectional value between populations such as F_{ST}. For instance, Wares et al. (2001) developed a test based on

genealogical patterns of mtDNA haplotypes and demonstrated statistically significant north to south dispersal for two barnacle species and an urchin, matching the prevailing southward current. Similarly, dispersal inferred from assignment tests using nuclear microsatellites was in the same direction that sea beet seeds were expected to float (Fievet et al. 2007), and coalescent estimates of directional gene flow for Antarctic icefishes (Matschiner et al. 2009; Papetti et al. 2012) and neritid snails (Crandall et al. 2012) matched the Antarctic circumpolar current flow and dispersal predicted by biophysical models, respectively. Other studies, however, have not found matching asymmetries between currents and genetic estimates of migration, as was the case for the kelp *Laminaria digitata* (Billot et al. 2003) and for the giant kelp *Macrocystis pyrifera*, where oceanographic models predicted F_{ST} better than a response variable based on assignment tests (Alberto et al. 2011). Oceanographic predictions of movement are averaged over time, typically over many years; if dispersal is highly variable in the short-term, as appears likely, short time windows assessed by assignment tests that use patterns of linkage disequilibria to identify migrants from the present or previous 1-2 generations may be mismatched with time-averaged predictions. Aside from assignment tests, most genetic statistics are based on allele frequency differences among populations that arise over evolutionary time frames (tens to hundreds of thousands of years or more). Thus, it is equally surprising that biophysical models based on present-day models of currents (rather than Pleistocene averages) and empirical genetic patterns are concordant in many instances.

SPATIALLY EXPLICIT SUMMARIES OF TEMPORALLY VARIABLE CONDITIONS

Because the transitory nature of currents precludes associating single values to specific geo-referenced locations, several studies have taken summary values, such as mean sea surface temperature (SST), mean or maximum current speed and direction, chlorophyll, and turbidity (Mendez et al. 2010; White et al. 2010; Alberto et al. 2011; Knutsen et al. 2011). For example, Mendez et al. (2010) examined the predictive power of regional (time averaged) differences in SST, chlorophyll, and turbidity for Franciscana dolphins and found these environmental differences to be better predictors than Euclidean geographic distances for microsatellites, but not mtDNA.

Others have summarized variability as a landscape attribute. For example, in a study of the barrens-forming urchin, Banks and co-workers estimated the "protectedness" of embayments, as measured by the amount of coastline within 20 km of a site, and found that within protected sites there was greater genotypic autocorrelation (similarity) among individuals (Banks et al. 2007) and greater differentiation between sites (Banks et al. 2010), consistent with larvae being retained in protected bays. Banks et al. (2007) also showed that genotypic autocorrelation among local individuals was positively associated with variability in SST. SST variance should be correlated with variance in currents because the region in question is one where eddies are periodically shed from a major oceanic current; thus, the positive association between SST variance and within population genetic autocorrelation was consistent with fewer cohorts recruiting to locations with highly variable currents (Banks et al. 2007). In another example, Selkoe et al. (2010) took biophysically-derived migration probabilities and rated populations of whelks, lobsters, and kelp bass based on the centrality of their position relative to an inferred network of oceanographic connections, with the prediction that central populations would be more diverse and less genetically differentiated than peripheral populations. However, support for this hypothesis was modest and mixed across species, with the best evidence found in kelp bass.

Although currents have received the greatest consideration, other spatial attributes are also dynamic. For instance, in the deep sea, hydrothermal vent communities are only stable for years to decades, with vent longevity reduced by high rates of tectonic spreading. Coykendall et al. (2011) found that genetic diversity of rift tubeworms was inversely correlated with tectonic spreading rates, as would be expected if young vents have been more recently settled or received fewer colonizing settlers over the life of the local vent than older vent tubeworm populations. These studies of urchins, whelks, lobsters, kelp bass, and rift tubeworms illustrate innovative ways in which temporally dynamic properties of the seascape can be summarized as predictive variables.

COMPARISONS AMONG SPECIES

Comparisons among species can reveal the relative importance of biological traits on genetic patterns and also identify spatial commonalities among species. Yet, comparative landscape genetic

studies are rare (Storfer et al. 2010), presumably because the difficulty of working with a single species is compounded with the inclusion of multiple species. Species differing in dispersal-related traits have been evaluated in a landscape context only in a few studies. For instance, in a comparison of corals across the same reef systems, the neighborhood distance (reflecting dispersal) was greater for the broadcast spawning *Acropora tenuous* as compared to brooding *Seriotopora hystrix* (Underwood et al. 2009). For ten species of co-distributed intertidal invertebrates, an extensive (300 km) sandy coastline was found to be a persistent barrier to gene flow for most species with planktonic developing larvae, but not for two of the species with direct developing larvae, with the conclusion that habitat generalists are less affected by this barrier (Ayre et al. 2009). The idea of accounting for shared landscape features can be scaled up to include many species, but including many species may necessitate spatially-implicit rather than spatially-explicit evaluations if species are not co-distributed. For instance, several analyses of published datasets have examined the effect of PLD in an IBD framework (Kinlan & Gaines 2003; Selkoe & Toonen 2011). This type of approach was expanded for reef fishes whereby spatially implicit factors included both biogeographic boundaries and Euclidean over water distance to show that the dispersal-related trait of egg type (benthic vs. pelagic) was an additional contributor to species level F_{ST} (with biogeographic boundaries and over water distance significant as well: Riginos et al. 2011).

Although the aforementioned studies made explicit contrasts among species traits, one could similarly ask whether specific seascape features or locations contributed to common spatial genetic patterns among species. This type of question is well established in the instance of assessing specific features such as biogeographic boundaries (as in Lessios et al. 1998; Ayre et al. 2009), but less so for identifying emergent commonalities across species. An exception is the approach used by Selkoe et al. (2010), where they tested for spatially consistent patterns among three species along the California coast and found correlations between site-specific heterozygosity and between site differentiation (Table 1). In the future, the identification of specific geographic areas that are associated with either greater or less than expected genetic differentiation across multiple species could inspire testable hypotheses regarding the general influence of specific features in marine landscapes.

ADAPTIVE DIFFERENTIATION, SEASCAPE GENOMICS, AND FITNESS

The high dispersal lifestyle typified by many marine organisms is frequently cited as a challenge for the evolution of local adaptation (Slatkin 1985; Lenormand 2002), because locally adapted variants may be swamped by migration and individuals may fail to disperse to an environment that best suits their genetic makeup. Yet, empirical examples of allele frequency shifts in response to environmental gradients are well documented (reviewed by Schmidt et al. 2008), including the classic example of selection induced by salinity on the *Lap* locus in mussels, whereby the *Lap94* allele diminished in frequency during summer months among new settlers in low salinity Long Island Sound (across tens of kilometers, Koehn et al. 1980b). Because the biochemical properties of the Lap94 protein are physiologically disadvantageous in low salinity conditions relative to protein products of other *Lap* alleles (Koehn et al. 1980a; Koehn & Siebenaller 1981), there is a clear functional link between the Lap locus, fitness of individual mussels, and spatial genetic patterns. Not only was selection on *Lap* found to vary spatially with salinity, selection was also seasonally dependent, highlighting the importance of time and seasonality, as well as dispersal, for understanding spatial patterns induced by selection.

Another example of locus-specific selection tied to environmental variables comes from cod and the *Pan I* locus. Patterns of nucleotide variation indicated that selection has affected *Pan I* evolution (Pogson 2001; Pogson & Mesa 2004) and subsequent surveys have revealed geographically complex patterns of *Pan I* polymorphism. In the northeastern Atlantic, mean June SST was a significant predictor of *Pan I* allele frequencies among adults when controlling for Euclidean distance in partial Mantel tests (Case et al. 2005), whereas water depth was a strong predictor of *Pan I* allele frequencies among Icelandic populations (Pampoulie et al. 2006). For juvenile cod within a Norwegian fjord, the strongest predictors of *Pan I* allele frequencies were temperature, salinity, and depth (Case et al. 2005). Genome scans in cod have also identified additional loci that show correlations in their allele frequencies with temperature, salinity, latitude, and longitude among Atlantic locations (Moen et al. 2008; Nielsen et al. 2009b).

As is the case with all spatial genetic studies, correlations between landscape or seascape features and genetic loci (such as *Pan I* and depth, temperature, salinity etc.) identify candidate loci for

environmental mediated selection. That is, correlations are identified but causation cannot be inferred. For instance, the surveyed marker may be physically linked to the target of selection or statistical associations among loci could arise as a consequence of demographic history. A convincing case for causation would require demonstrating a mechanistic link (Feder & Mitchell-Olds 2003; Lowry 2010). For *Lap* in mussels, the biochemical properties of the proteins resulting from different alleles are well resolved providing a functional explanation for the spatial genetic patterns. For *Pan I* in cod, the patterns of nucleotide variation of that locus corroborate selection, but further understanding of the function of the Pan I gene product would be necessary to link selection at this locus to a specific environmental attribute.

On a small spatial scale (tens of meters), several recent studies have highlighted strong genetic discontinuities between adjacent populations segregating by intertidal height (periwinkles: Johannesson et al. 2010) or by depth (gorgonians: Mokhtar-Jamai et al. 2010 and Prada et al. 2008; bird's nest coral: Bongaerts et al. 2010). In addition to the caveats about correlation mentioned above, even if genotype-by-environment fitness differences can be demonstrated (as in Bongaerts et al. 2011), it will be important to consider whether endogenous reproductive incompatibilities also maintain genetic divergence, with multiple loci segregating with environmental features indicative of such a situation. If the adjacent populations have some degree of inherent reproductive isolation, then for a given locus or linkage group, distinguishing between seascape (depth) induced selection and endogenous selection will be difficult (Bierne et al. 2011). In such situations, a seascape feature such as depth may be detectably contributing to spatial segregation between adjacent ecotypes, but identifying which loci may be specifically under selection due to local adaptation will be extremely challenging.

Despite the many interesting and spatially replicated gradients that occur in the marine environment (see Schmidt et al. 2008), studies investigating selection in a seascape genetic framework are relatively uncommon. Expansion of seascape genetics to a genomic perspective (Nielsen et al. 2009a) will open up avenues of investigation. Increasingly, genomic methods and next generation sequencing are facilitating population genomics of non-model organisms (Luikart et al. 2003; Hohenlohe et al. 2010) and extensions into "landscape genomics" (Joost et al. 2007; Nielsen et al. 2009a; Manel et al. 2010). Population genomic methods could reveal candidate genes for selection associated with seascape features, as with cod (see previous and Nielsen et al. 2009b), and thus provide hypotheses which could be verified experimentally and functionally.

Future directions: competing seascape factors and analytical challenges

A fundamental challenge for seascape genetics is to develop predictive models that adequately describe both (relatively) static and dynamic seascape features. A consequence of this challenge has been an emphasis on simple landscape attributes such as geographic distance between sites (i.e. spatially implicit features) and less attention to precise geo-referenced spatial data (Alberto et al. 2010). Certainly several recent studies have made use of geo-referenced data and GIS type approaches (Banks et al. 2007; Alberto et al. 2010; Alberto et al. 2011; Puritz & Toonen 2011), but many approaches familiar to terrestrial landscape ecologists are often less useful to seascape ecologists due to the high temporal variability of many seascape features (currents, SST, salinity; Fig. 1); the dynamic nature of currents and associated seascape features are difficult to summarize in a spatially explicit manner. In particular, concepts of landscape resistance used for least cost path and isolation by resistance analyses (McRae 2006) are not easily translatable to flowing aqueous habitats and fail to accommodate the likely asymmetries in migration. Connectivity models assuming symmetric migration can make misleading predictions if migration is asymmetric (Vuilleumier & Possingham 2006). Similarly, when symmetric metrics of population genetics (such as F_{ST}) are applied to situations with asymmetric gene flow, estimates of gene flow can be highly inaccurate (Wilkinson-Herbots & Ettridge 2004; Marko & Hart 2011). Not surprisingly, then, seascape genetics has seen strong development and usage of biophysical models that incorporate asymmetric movements (Galindo et al. 2006; Treml et al. 2008; Kool et al. 2010; Selkoe et al. 2010; White et al. 2010; Kool et al. 2011; Foster et al. 2012), with published models for the Caribbean, the California coast, and parts of the Pacific and Indian Oceans. This usage and formulation of biophysical models will certainly continue and expand in geographic coverage.

At present biophysical models generate estimates of potential dispersal, whereas realized genetic connectivity depends on larvae reaching their destination and surviving to reproduce. The larval and

settlement periods are characterized by high daily mortality (Almany & Webster 2006), some of which undoubtedly results in natural selection. Also, emerging research in marine biology indicates that larval environments influence both planktonic larval dispersal (O'Connor et al. 2007; Shima & Swearer 2009) and juvenile survival (reviewed by Marshall & Morgan 2011). Note that such fitness consequences are not necessarily due to selection on heritable traits (natural selection). Thus, for benthic animals with pelagic larvae, the effects of the open water and post-settlement environments on individuals as well as genotypes and allele frequencies are likely to be far more complex than predicted by physical impediments to larval movement. Better functional understanding of how larval experiences shape lifetime fitness may inspire hypotheses, including those formulated by biophysical models, that account for larval or post-settlement deaths resulting from relevant environmental characteristics. Such hypotheses, informed by larval biology, will be well-suited for testing using a seascape genetics approach. Therefore seascape genetics can contribute to a fuller understanding of which factors influence realized connectivity.

Clearly the challenges of understanding dispersal through water sets seascape genetics apart from terrestrial landscape genetics. Another contrast between the two fields is that terrestrial landscape genetics has embraced individual level sampling and analyses, whereas seascape genetic studies have primarily used population-level sampling (that is, collecting many individuals from each sampling location with typically <15 locations total). The geographic scale over which marine organisms are likely to disperse combined with the spatial scales of seascape features (Fig. 1) make sampling hundreds of individuals evenly (or at random intervals) along thousands of kilometers logistically challenging. We only know of one seascape genetic study that can truly be described as using individual-based sampling over large geographic distances: a survey of harbour porpoises in Europe where sampling was fairly even with respect to the Atlantic coastline (Fontaine et al. 2007). But individual approaches have resolved sources of variation across relatively small scales for low dispersal organisms (as in Underwood et al. 2009; David et al. 2010), and individual-based methods have successfully been applied to studies with population level sampling (Jones et al. 2005; Selkoe et al. 2006; Banks et al. 2007; Buston et al. 2009; Banks et al. 2010; Saenz-Agudelo et al. 2011). Where logistically feasible, seascape genetics as a field could benefit by incorporating more individual-level approaches, both in sampling and analyses. In particular, a situation in which individual approaches would be highly informative would be locus-specific investigations of selection over steep environmental clines, such as depth, intertidal exposure, or salinity.

An aspiration for all areas of landscape genetics is to move beyond exploratory studies and embrace experimental designs aimed at testing *a priori* hypotheses (Storfer et al. 2010). This necessitates planning the sampling strategy and analyses such that competing factors can be statistically evaluated (Selkoe et al. 2008, Liggins et al. 2013). In reviewing studies that were self-identified as seascape or marine landscape genetic, we found many studies that qualitatively evaluated factors (typically "barriers" of one kind or another). Studies that quantitatively evaluated multiple seascape features, however, were rare (and summarized in Table 1). In our opinion, greater utilization of multivariate approaches and model testing (see Balkenhol et al. 2009 for a recent review) would enhance our understanding of which factors influence genetic variation in marine species.

Conclusions

Seascape genetics is a rapidly developing field of inference. Although many advances from (terrestrial) landscape genetics are relevant and should be embraced by marine-focused investigators, the dynamic fluid medium of seas and oceans also necessitates novel approaches and methods of analysis that will continue bringing together investigatory teams with expertise in both genetics and oceanography. Whereas the ability to predict water movements at levels of resolution relevant to the dispersal of populations and individuals is very exciting, additional seascape factors are likely to also impact spatial genetic patterns. Because genetic differentiation and variability depend on survival to reproductive age and not just dispersal, investigations of factors influencing survival (whether selection on specific traits or effects of larval exposures) will complement dissections of dispersal-affecting seascape features. Finally, we encourage investigators using spatial outlooks to design their studies such that competing seascape features can be quantitatively assessed.

Short Biographies

Cynthia Riginos has a long-standing interest in the ecological and evolutionary implications of planktonic larval dispersal. She is currently a Senior Lecturer at the University of Queensland in the School of Biological Sciences. She teaches first year Genetics, second year Ecology, and a senior undergraduate class in Ecological and Evolutionary Genetics. She and her research group work on a wide array of organisms, including reef fishes, cartilaginous fishes, mollusks, echinoderms, ascidians, and even insects. Current topics of interest include applying spatially explicit considerations to marine population genetics and using genomic tools to measure post-settlement selection. Cynthia received her MS and PhD from the University of Arizona in Ecology and Evolutionary Biology and was a post-doctoral fellow for several years at Duke University in the Department of Biology.

Libby Liggins is a PhD candidate at the University of Queensland within the School of Biological Sciences. Her current research takes a phylogeographic and population genetic approach to understanding connectivity among coral reef populations in several species common to the Austral-West-Pacific region. Specifically, she is interested in understanding the drivers of spatial genetic patterns across this region and shifts in the genetic composition of populations across life history stages and through time. Libby completed her BSc in Ecology and Environmental Science and MSc in Conservation Biology within the School of Biological Sciences at Victoria University of Wellington.

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