FEATURE ARTICLE: REVIEW

A decade of seascape genetics: contributions to basic and applied marine connectivity

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ABSTRACT: Seascape genetics, a term coined in 2006, is a fast growing area of population genetics that draws on ecology, oceanography and geography to address challenges in basic understanding of marine connectivity and applications to management. We provide an accessible overview of the latest developments in seascape genetics that merge exciting new ideas from the field of marine population connectivity with statistical and technical advances in population genetics. After summarizing the historical context leading to the emergence of seascape genetics, we detail questions and methodological approaches that are evolving the discipline, highlight applications to conservation and management, and conclude with a summary of the field's transition to seascape genomics. From 100 seascape genetic studies, we assess trends in taxonomic and geographic coverage, sampling and statistical design, and dominant seascape drivers. Notably, temperature, oceanography and geography show equal prevalence of influence on spatial genetic patterns, and tests of over 20 other seascape factors suggest that a variety of forces impact connectivity at distinct spatio-temporal scales. A new level of rigor in statistical analysis is critical for disentangling multiple drivers and spurious effects. Coupled with GIS data and genomic scale sequencing methods, this rigor is taking seascape genetics beyond an initial focus on identifying correlations to hypothesis-driven insights into patterns and processes of population

An underwater seascape from the top of Steve's Bommie in the Great Barrier Reef, Australia.

Photo by Jonathan B. Puritz

connectivity and adaptation. The latest studies are illuminating differences between demographic, functional and neutral genetic connectivity, and informing applications to marine reserve design, fisheries science and strategies to assess resilience to climate change and other anthropogenic impacts.

KEY WORDS: Seascape genetics · Genomics · Connectivity · Marine population genetics · Gene flow · Dispersal · Landscape genetics

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INTRODUCTION

In 2013, the field of landscape genetics turned 10 years old (Manel & Holderegger 2013). Seascape genetics could be viewed as a younger sibling, recently passing its own 10 years mark and showing an accelerating rate of publication, enabled in part by rapid growth in GIS data and advances in statistical methods (Fig. 1) (Galindo et al. 2006, Fontaine et al. 2007, Hansen & Hemmer-Hansen 2007). A major emphasis for landscape and seascape genetics has been taking an organismal perspective of the dispersal process, creating a need for new models and methods (Manel et al. 2003, Storfer et al. 2007, Holderegger & Wagner 2008, Balkenhol et al. 2015). Many foundational population genetic and ecological models assume that spatial heterogeneity is either lacking or highly ordered and predictable. The rise of landscape and seascape genetics as named disciplines reflects interest in overcoming these simplifying assumptions to understand how movement of an organism through the landscape or seascape impacts realized dispersal and gene flow. These subdisciplines distinguish themselves within the field of population genetics by their focus on spatially explicit processes and statistics (Dyer 2015), and a focus on the linkages between environment, ecology and genetics. The topic resonates widely, in part because identifying landscape features critical to the persistence and adaptation of populations is central to effective strategies for conservation and resource management (Wagner & Fortin 2013).

Our focus here is on detailing the approaches and findings of seascape genetics for a wide audience interested in the field of marine connectivity. While
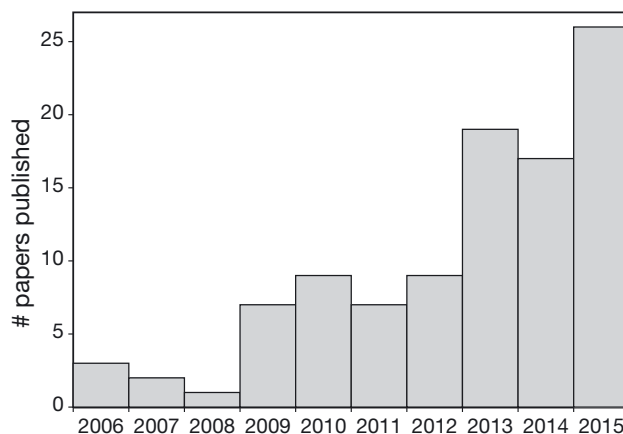

Fig. 1. Seascape genetic papers published between 2006 and 2015. See the Supplement at www.int-res.com/articles/suppl/m554p001_supp.pdf for details on paper collection and the full reference list

many concepts and analyses are shared between seascape and landscape versions of this discipline, seascape genetics has unique challenges that stem from the biology of marine taxa and the fluid medium in which they disperse (Riginos & Liggins 2013, Selkoe et al. 2015). For a majority of marine species, dispersal is undertaken during a larval phase, and trajectories of individual larvae, as well as long-term patterns of dispersal, are difficult to predict (Siegel et al. 2008). The seascape's heterogeneity (e.g. in bathymetry, current speeds and water chemistry) is largely hidden from our view; little is known about marine organisms' behavior and ecological interactions during the dispersive phase; and even the most complex oceanographic models are limited to coarse scales relative to a larva's perspective (Levin 2006, Woodson & McManus 2007, Cowen & Sponaugle 2009, Morgan et al. 2014, Mazzuco et al. 2015, Nickols et al. 2015). Consequently, the organism's view of the dispersal process is easier to understand and quantify in terrestrial settings compared to marine systems (Marshall & Morgan 2011, Burgess et al. 2015). In some ways, these challenges and unknowns of the marine environment increase the potential contribution of seascape genetics to our understanding of marine population connectivity.

THE RISE OF A SEASCAPE PERSPECTIVE

Genetic tools have long played an instrumental role in the study of marine connectivity (e.g. Berger 1973, Waples 1987, Hellberg 1994, Palumbi 1996) because they promise insights into the scale of marine larval dispersal that are simply not possible with other natural or artificial tags (Berumen et al. 2010). While this promise has not always been realized (Waples 1998), population genetic approaches have enabled tests of specific hypotheses about spatial patterns of exchange (e.g. hierarchical or continuous) and drivers of exchange (e.g. whether a biogeographic boundary serves as a boundary to gene flow). Trends in hypotheses and study designs have been shaped by recent changes in our understanding of marine connectivity, as well as an increasing abundance and variety of genetic and environmental data.

At the turn of the century, the paradigm of open populations and uniform larval pools was beginning to erode (Jones et al. 1999, Swearer et al. 1999, Kinlan & Gaines 2003, Palumbi 2003). Diverse evidence solidified a new focus on complex dispersal kernels (Siegel et al. 2003), local retention (Swearer et al. 2002) and quantifying genetic variation across larval

cohorts (Hedgecock 1994, Selkoe et al. 2006). These seminal works supported the emergence of seascape genetics by motivating the exploration of the patterns and drivers of nuanced spatial genetic variation across populations, recruits and larval samples.

Following the first published use of the term in 2006, an early priority of seascape genetics was to test the role of ocean currents in generating spatial genetic patterns (e.g. Baums et al. 2006, Galindo et al. 2006, reviewed in Liggins et al. 2013). More recently, seascape genetics has expanded to embrace a rich suite of potential ecological and genetic forces discernable by spatial analysis of genetic data when used in analytical frameworks borrowed from landscape genetics (Fig. 2). This more holistic approach will aid the field of marine connectivity in continued efforts to disentangle the relative effects of ocean currents, larval behavior and processes occurring at settlement and recruitment in driving patterns of population exchange. Current genetic technology enables a range of spatio-temporal scales of inference on marine connectivity, including estimates of single dispersal events, recent and historical migration rates, hybridization and speciation (see Box 1). The multifaceted perspective on spatial genetic structure summarized in Fig. 2 has helped the field of marine population genetics overcome a few key pitfalls. For example, some studies were misleading because they interpreted genetic metrics to solely indicate differences in dispersal when other processes may contribute to spatial patterns of allele frequencies (e.g. range expansions, see Hart & Marko 2010, Marko & Hart 2011). Others mistakenly assumed very high rates of larval exchange and long-distance dispersal because of insufficient statistical power to detect spatial genetic structure, or methods that are inappropriate for the data (as discussed in Meirmans 2014, Richardson et al. 2016). Although genome sequencing advances are helping to address low power by increasing locus sample size (Gagnaire et al. 2015), simply adding more genetic loci will not necessarily improve inference of connectivity without a change in analytical philosophy (Ryman et al. 2006, Larsson et al. 2009, Bowen et al. 2014).

Landscape and seascape genetics have catalyzed a shift from describing patterns of genetic structure in a null-hypothesis testing framework to distinguishing the many forces contributing to observed spatial patterns, including interactions between ecology and genetics, in a formal model selection framework (Manel & Holderegger 2013, Wagner & Fortin 2013). While many studies related seascape features to population genetic data before the term 'seascape genetics' was coined (e.g. Johnson & Black 1991, Riginos & Nachman 2001, Gilg & Hilbish 2003), there are a variety of new and newly popularized multivariate statistical approaches to integrating diverse data types that are rapidly bringing the field of empirical population genetics beyond an exploratory era (reviewed by Balkenhol et al. 2015, Rellstab et al. 2015). At the same time, evolutionary geneticists have uncovered strong linkages between rates of selection, drift and gene flow that likely impact connectivity inference, and demonstrated how selection can strongly affect neutral genomic regions (reviewed by Nosil et al. 2009, Orsini et al. 2013). The rising number of seascape genetic studies using single nucleotide polymorphisms (SNPs) sampled across the genome is improving our ability to explore these linkages (Fig. 3). Compared to seascape genetics, seascape genomics creates even greater imperative for grounding analyses in model selection to minimize spurious effects and ensure interpretability of findings (Meirmans 2015, Riginos et al. 2016).
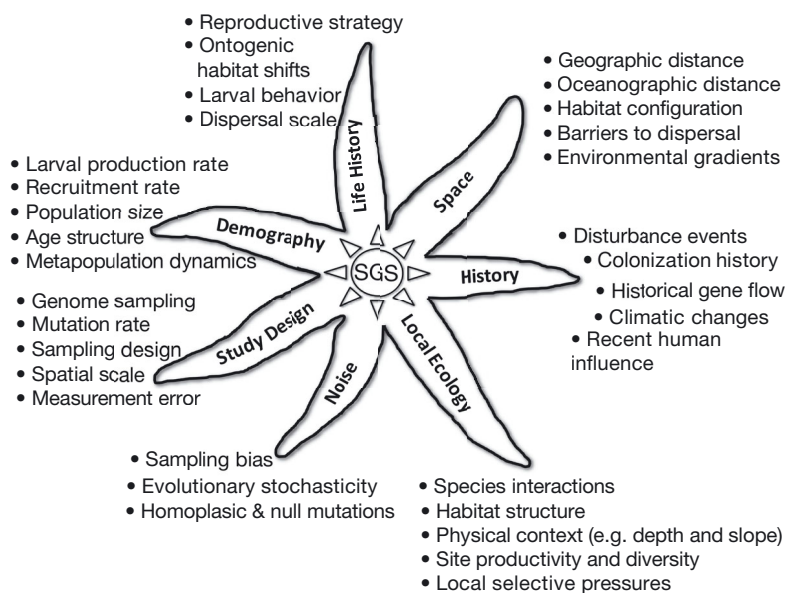

Fig. 2. Spatial genetic structure (SGS) of marine populations is the combined result of a suite of interacting forces and traits that can be categorized into topics (listed on sea star). These forces include demography, species' life history traits, rates of migration influenced by spatial factors, lingering signals of history, influences of local ecology and/or local adaptation, some degree of noise and study design factors. Seascape genetics focuses on uncovering support for effects of these forces on SGS. Examples of possible predictors of these varied effects are listed adjacent to each ray

Box 1. Defining marine connectivity across spatial and temporal scales. A variety of terms distinguish key agents, time-scales and viewpoints of marine connectivity, and collectively contribute to a holistic understanding of connectivity

Alternative definitions of connectivity

In its broadest sense, 'connectivity' refers to any relationship between spatially or temporally distinct entities (Kool et al. 2013). The field of marine connectivity largely focuses on the materials and processes that connect ecological communities across space and those that disrupt or bound connectivity.

Structural connectivity quantifies the physical relationships of landscape elements, including spatial positioning of habitat (e.g. Kool et al. 2013), geo-morphological features of the seafloor and/or hydrodynamic flow features impacting movements, pathways and boundaries. Structural connectivity creates potential for biological connectivity.

Functional connectivity is a product of the organism interacting with the landscape. It concerns the patterns and rates of dispersal that result from the response of individuals to the structural matrix, mediated by behavioral traits and dispersal success. Questions of functional connectivity focus on whether landscape elements impede or facilitate dispersal, given the species' traits. Biophysical oceanographic modeling of larval dispersal is commonly used to predict functional connectivity (e.g. Treml et al. 2008, 2015, Kool et al. 2011).

Demographic connectivity relates the dispersal of individuals to their cumulative effects on population-level processes such as population growth, extinction or recolonization. Thus, measures require estimates of demographic rates and the relative contributions of self-recruitment and immigration to these rates (see Lowe & Allendorf 2010).

Genetic connectivity tracks the dispersal of genes (and genomes), which only accounts for those individuals that successfully reproduce after dispersing. Genetic connectivity is the opposite of reproductive isolation. Like demographic connectivity, genetic connectivity is inherently a population-level metric that reflects the cumulative impact of functional connectivity on allele frequencies in a population over one or more generations.

Adaptive genetic connectivity measures movement of alleles with consequence to individual fitness. It can diverge greatly from neutral genetic connectivity and relates to the adaptive potential of a population.

Neutral genetic connectivity measures movement of alleles that have no consequence to fitness. Neutral connectivity estimates can be related to the long-term outcome of demographic connectivity (Funk et al. 2012).

Relating genetics to connectivity

Typically, seascape genetic studies estimate metrics of genetic connectivity; however, some methods may enable the measurement of demographic connectivity (see Box 2) (Lowe & Allendorf 2010). 'Genetic tagging' studies that distinguish individuals and kin using genetic markers are used to discover dispersal events. Most other uses of genetic markers use indirect inference to estimate genetic connectivity. Indirect inference depends on theoretical population genetic models with simplifying assumptions about possible effects of mutation, selection and drift on genetic patterns to be able to infer migration (Waples & Gaggiotti 2006). Estimators based on Wright's fixation index (F_{ST}) integrate over longer time-scales, possibly representing historical connectivity more than present day because of response lags dependent on rates of marker mutation and drift (Epps & Keyghobadi 2015). Landscape and seascape genetic studies commonly aim to estimate the correlations among variables representing different types of connectivity. This strategy can identify important physical features that influence multiple types of connectivity, or important ways that the types of connectivity diverge.

APPROACHES AND STUDY DESIGNS

There are almost always multiple potential causes of genetic discontinuities (i.e. spatial shifts in allele frequencies or diversity). These alternative factors have often been treated in a post hoc or qualitative way. Seascape genetics provides the tools and perspective needed to design a study *a priori* to identify the drivers of genetic discontinuities, with a suite of complementary methodologies (see Box 2). All seascape genetic study designs should assess spatial co-variation of seascape factors of interest, so that sites for genetic sampling are chosen to maximally represent the full range of these gradients with minimal confounding (Wang & Bradburd 2014, Riginos et al. 2016). Individual-based sampling designs may better capture these gradients compared to highly clustered 'population-based' sampling, especially when many loci are used (Prunier et al. 2013, Wang & Bradburd

2014). Choice of genetic metrics should be guided by hypotheses about mechanisms generating the correlative patterns tested, including effects on genetic links, nodes, boundaries and neighborhoods, as described in Wagner & Fortin (2013). These 4 terms are defined below in sections that expand on their distinct value and applications in marine settings.

Links: parsing drivers of genetic exchange

Link-based designs, which make up the majority of empirical studies, focus on pairwise genetic distance and address how seascape features either create discontinuities or promote gene flow between sites. Within a rigorous alternative hypothesis testing framework, multiple coincident or competing factors, e.g. habitat patchiness, environmental gradients and/or oceanographic flow fields, can be disentangled. Mar-
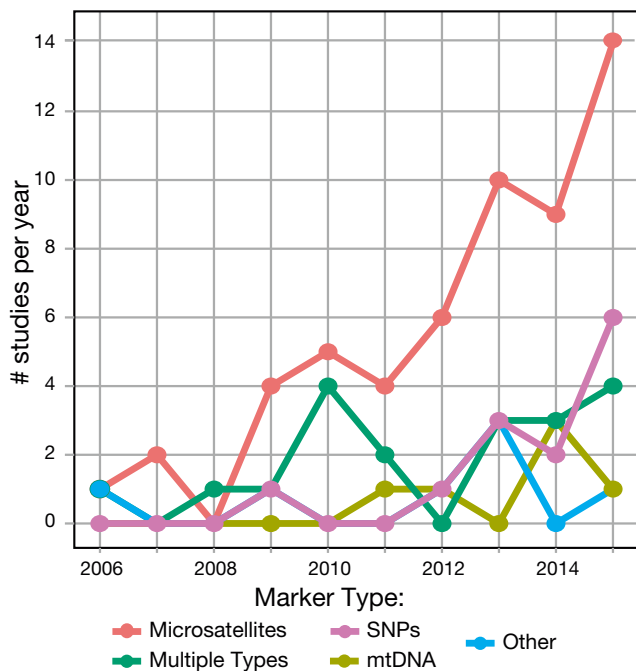
Fig. 3. Trends in marker usage over time. Microsatellites are the most common marker type used, but single nucleotide polymorphism (SNP) studies are rising. Multiple Types: studies that use more than one marker type, with the most common combination being microsatellites + mtDNA. Other: marker types used infrequently in seascape genetic studies (e.g. inter simple sequence repeats, allozymes, single nuclear sequences)

ine populations often have large effective population sizes and relatively high rates of gene flow, resulting in greater difficulty to assess population structure than in terrestrial systems due to low genetic differentiation between populations (Mills & Allendorf 1996, Waples 1998). Sometimes, low differentiation is actually caused or enhanced by high mutation rates and extreme marker heterozygosity that mask genetic distinction among populations, so interpreting levels of differentiation requires careful contextualization (Hellberg 2007, Bird et al. 2011, Gagnaire et al. 2015). Importantly, recent seascape genetics studies demonstrate that despite genetic estimates and 'isolation by distance' (IBD) tests that are not statistically distinguishable from zero, significant spatial patterning in differentiation is uncovered when seascape features are used (1) to inform appropriate null hypotheses, (2) as parameters in a Bayesian framework, or (3) as predictors in model testing. For example, Crandall et al. (2012) showed that despite very low genetic structure for 4 neritid snails sampled throughout the Pacific, incorporating gene flow predictions from oceanography into a Bayesian coales-

cent model revealed the effects of stepping-stone versus long-distance dispersal in generating high gene flow. Liggins et al. (2016) used a multiple-regression model-testing approach to show that spatial genetic patterns of different species could be attributed to the same seascape features despite little congruence in spatial genetic patterns across species. These and other studies provide important tests of existing theories, such as the role of upwelling, headlands and embayments in local retention of larvae (e.g. Mace & Morgan 2006, Banks et al. 2007, Lotterhos & Markel 2012, Iacchei et al. 2013, Pfaff et al. 2015). In sum, seascape studies are increasingly able to overcome the obstacle of weak genetic signal to help push forward concepts about the possible mechanisms influencing larval production, emigration, dispersal and settlement.

Exploring the relationship between ocean currents and link-based genetic data has been a cornerstone of seascape genetics since its inception (see Liggins et al. 2013 for an overview). Estimates of larval exchange from biophysical transport models can be directly compared to observed genetic patterns, or first incorporated into population genetic simulations that are then compared to empirical genetic data. The latter is especially valuable for illuminating how multi-generational, often asymmetrical stepping-stone dispersal can lead to high genetic connectivity despite a lack of direct larval exchange (Treml et al. 2008, Kool et al. 2010, White et al. 2010, Crandall et al. 2012, Foster et al. 2012, Munguia-Vega et al. 2014). These simulations can also explore the effects of spawning, life history and behavioral traits on genetic connectivity and source−sink metapopulation dynamics (Galindo et al. 2006, Lee et al. 2013, Young et al. 2015, Selkoe et al. 2016). Continued expansion of oceanographically informed genetic simulations will help elucidate why and when gene flow patterns are expected to diverge from transport patterns. They can also uncover the limitations of available oceanographic data (e.g. coarse spatial resolution, short time series, missing nearshore features) that interfere with comparisons between empirical genetic data and biophysical dispersal estimates (Pineda et al. 2007, Pringle & Wares 2007).

Nodes: local effects on spatial genetic patterns

Node-based studies use metrics that characterize a location, rather than pairwise differences between locations. Node-based genetic metrics typically describe how allele frequencies or diversity of a site

Box 2. Advances in methodology. We highlight select techniques that are bringing rigor and creativity to hypothesis formation and data analysis

Kinship analyses: relating dispersal to gene flow

Kinship analyses generate direct estimates of dispersal distances, in contrast to indirect inference based on population-level genetic data (see Box 1). Dispersal distances can be reconstructed by linking individuals' multi-locus genotypes to natal populations (Hogan et al. 2012), parents (Christie 2010) or sibling groups (Schunter et al. 2014). The most popular kinship approach is parentage analysis in which pools of potential parents and offspring are genotyped to assign offspring to parents (Christie 2013, D'Aloia et al. 2015). Assuming minimal post-settlement movement, the distance between parent and offspring is the net dispersal distance. Parentage studies can describe the magnitude and direction of dispersal between sites (Jones et al. 2005, Planes et al. 2009, Harrison et al. 2012), and with intense sampling can estimate dispersal kernels (Almany et al. 2013, D'Aloia et al. 2015). The emerging theme is that most marine larvae disperse shorter distances than inferred from estimates of genetic structure, supporting a conclusion from the larval biology literature that long-distance marine dispersal may be maladaptive (e.g. Strathmann et al. 1981, Burgess et al. 2012). Importantly, the discrepancy between direct and indirect dispersal estimates may result from the fact that genetic structure is affected by multiple generations of gene flow, and is influenced by rare long-distance gene flow events that parentage methods do not capture. Comparison of kinship-derived dispersal kernels to genetic structure estimates will hone our conceptual understanding of how to relate dispersal to various connectivity metrics, given their distinct temporal and spatial scales.

Coalescent techniques: explicit treatment of history

Coalescent approaches consider demography and metapopulation history separately (Rosenberg & Nordborg 2002), and thus can overcome the simplifying assumptions necessary for estimating gene flow from F-statistics (Whitlock & McCauley 1999). Coalescent models can specify directional and asymmetric gene flow, distinct population sizes and the timing of population divergence (Hey & Machado 2003). By estimating effective population size and proportion of migrants per generation separately, coalescent models are able to estimate rates of gene flow at much higher levels than F-statistics, and with appropriate estimates of uncertainty. Coalescent samplers such as Migrate or BEAST calculate a marginal likelihood for any specified coalescent model, which may then be compared to other modeled hypotheses using standard information theoretic methods (Beerli & Palczewski 2010, Baele et al. 2012). These methods have been used to test hypotheses generated from biogeography (Teske et al. 2011), biophysical dispersal models (Crandall et al. 2012) and mark–recapture data (Jue et al. 2015). Approximate Bayesian computation (ABC) methods applied to coalescent modeling can handle hierarchical models, wherein parameter estimates for individual species are nested within hyperparameters based on summary statistics of the species' valaues (Hickerson et al. 2006, Hickerson & Meyer 2008). Coalescent approaches offer new opportunities for community-level seascape genetics, but their application requires considerable computing resources, informed model design and careful investigation of outputs. With these caveats, coalescent analyses provide the opportunity to wring far more information from hard won data than traditional population genetic statistics.

Analysis of pairwise data: moving beyond Mantel

Given the prevalence of link-based studies, a key statistical issue is the treatment of non-independence for pairwise data. After decades of widespread use, the Mantel test was recently shown to be an inappropriate way to address non-independence for most population genetic data (Legendre et al. 2015). We estimated that 63% of seascape genetic studies have used Mantel tests, begging for an assessment of how our understanding of isolation by distance in the sea may be biased. Importantly, extensions of the Mantel, such as multiple regression on distance matrices, may also be prone to biased model selection (Goldberg & Waits 2010, van Strien et al. 2012, Guillot & Rousset 2013). In a recent review, Rellstab et al. (2015) suggested that valid inference can still be obtained within the Mantel framework if effect sizes are used to interpret results, or if a rank-based partial Mantel test is utilized, as in Bayenv2 (Günther & Coop 2013). Alternatively, instead of using summary statistics like F_{ST}, populations' allele frequencies can be modeled as a linear function of environmental factors in a multiple linear regression framework, or with multivariate frameworks like canonical correspondence analysis (CCA) or redundancy analysis (RDA) (Legendre & Legendre 2012).

Future directions for increasingly complex datasets

Mixed models, such as maximum-likelihood population-effects (MLPE) models, may offer a robust way to evaluate predictors of pairwise population genetic data (van Strien et al. 2012, Row et al. 2015, reviewed in Rellstab et al. 2015). Mixed models treat sampling location as a random effect, and they can isolate neutral genetic structure when testing for the influence of environmental factors on allele frequencies (e.g. latent factor mixed models, Frichot et al. 2013) New techniques based on Bayesian modeling of allele covariance structures, eigenvector mapping and others are also gaining traction (reviewed in Wang & Bradburd 2014, Gautier 2015). Whether you use well-known or cutting-edge statistics, we urge researchers to carefully consider model assumptions before applying them to seascape genetic data sets, to test multiple approaches for concordant results and to clearly describe the methods they adopt.

differs from the mean of all sites, and node-based seascape metrics assign values to each sampling site. When the seascape is hypothesized to have effects on current population size, rates of drift, local selection and historical events, node-based studies may be most appropriate and effective for analysis. So far, node-based studies are less common, but arguably they can be more powerful and reliable, as node-based genetic metrics often have less sampling error than most link-based metrics, and statistical testing is comparatively unproblematic. A rigorous method for node-based analyses is a Bayesian approach to associating local (i.e. site-specific) estimates of F_{ST} with node-based predictors in the software GESTE (Foll & Gaggiotti 2006). Arizmendi-Mejía et al. (2015) used local F_{ST} and other node-based metrics to test the interplay between ecological and evolutionary factors in a Mediterranean gorgonian and define conservation units. The results showed genetic drift linked to partial mortality to be a primary driver of genetic structuring. Describing seascape effects on patterns of local genetic diversity also fits a node-based design. For example, Liggins et al. (2015) assessed distributions of shared and private haplotypes using measures of nestedness and partitioned beta-diversity to support the hypothesis that the southern limit of a damselfish's range is a demographic 'sink.'

Boundaries: uncovering lines in the sea

Boundary-based studies define genetic groups across space and relate boundaries between groups to seascape features. Understanding the forces creating genetic boundaries informs fundamental questions in biogeography, evolution and population dynamics as well as marine management. The long history of statistical approaches to boundary detection has resulted in a range of user-friendly software (e.g. ARLEQUIN, STRUCTURE and BARRIER), but relatively few studies have taken the next step in statistically testing for the relationship between boundaries and relevant seascape features. These few studies report temperature, salinity, irradiance, turbidity, depth and sediment type as significant drivers (e.g. González-Wangüemert et al. 2009, Roy et al. 2012, Viricel & Rosel 2014, Johansson et al. 2015). For example, a study of white hake in the Northwest Atlantic found that depth was the only significant environmental predictor of genetic group membership in a highly fished population across time, so the authors recommended a depth-based approach to

defining fisheries management units (Roy et al. 2012). An important study design issue for boundary-level analyses is determining whether spatial gradients in genetic patterns occur in tandem with boundaries in genetic patterns, as gradients can affect the output of barrier detection and clustering algorithms (Manni et al. 2004, Meirmans 2012).

Neighborhoods: defining local scales

Neighborhood-based studies focus on how the local seascape and habitat array influence the scale of connectivity or, more generally, the scale of covariation in genetic metrics across samples or patches (Wagner & Fortin 2013). Investigations can take a variety of formats and use an assortment of metrics. For example, D'Aloia et al. (2015) compared kinship-derived dispersal kernels to microhabitat characteristics (e.g. depth) and local context (e.g. directionality, latitude) to determine whether local features predicted the spatial scale of dispersal for a coral reef goby within a 41 km neighborhood. Munguia-Vega et al. (2014) explored a variety of network metrics derived from a biophysical dispersal model for leopard grouper in the Gulf of California and found that the topographic relationships of sites (i.e. the neighborhood layout) is more critical than the rate of exchange among sites for explaining genetic patterns. Employing biophysical models or simulated gene flow outputs is a critical means of understanding the influence of the spatial configuration of habitat patches, spawning aggregations or marine reserves on connectivity to inform marine management and parameterize metapopulation models (e.g. Crandall et al. 2012, Wood et al. 2014, Davies et al. 2015).

Multi-approach studies: relating pattern and process

Including more than one type of analysis is often required for robust interpretation of correlative studies. Ecologically, feedbacks exist between processes that take place at nodes, neighborhoods, links and boundaries. For example, Dawson et al. (2014) found that differences in population genetic structure among intertidal species of the eastern North Pacific were due to the combination of 2 node-based metrics—census size and fecundity of populations—and species' pelagic larval duration, a link-based metric representing relative rates of migration. Importantly, pairwise genetic differentiation will be amplified if there are large differences in the genetic diversities

of the focal populations, thus intertwining node-based effects into a link-based analysis. Selkoe et al. (2010) found that differences in local genetic diversity primarily drove pairwise genetic structuring for temperate reef species in Southern California. In both these study systems, recolonization following disturbance likely impacts standing genetic diversity (although with distinct mechanisms and time-scales). Because recolonization is influenced by life history adaptations to environmental regimes, we can posit that local selection may indirectly contribute to these putatively neutral genetic patterns.

Selection is often considered separately from genetic drift and gene flow. Importantly, however, the 3 forces are linked: strong selection can enhance rates of drift by disrupting gene flow and increasing isolation (Nosil et al. 2008, Bird et al. 2012). The large effective population sizes typical of many marine species generally allow selection to have a large influence on the genome relative to drift, yet the role of selection has historically been underappreciated in marine genetic studies (Allendorf et al. 2010). One example of how selection indirectly affects neutral genetics is termed monopolization. Namely, a positive feedback between priority effects and local adaptation during colonization events disrupts the influence of oceanographic connectivity on neutral population genetic structure by reducing the success of later immigrants (De Meester et al. 2002, Waters et al. 2013, Fraser et al. 2015). Drawing from the previous example, Selkoe et al. (2010) found that genetic diversity of territorial predators like kelp bass and lobster scaled inversely to kelp forest size. These species cannibalize and exclude new recruits, and their territory size expands as they age and grow. With recolonization of a reef following storm disturbance, the expanding size of territories and rate of cannibalism may contribute to a winnowing of genetic diversity in the site's population, even as the kelp bed itself expands and adds new habitat (Selkoe et al. 2010). Thus, an ecological process connected to life history and recolonization may indirectly influence neutral genetic diversity.

Many studies focus on detecting direct effects of selection by assessing 'isolation by environment' (IBE), a pattern of positive correlation between genetic metrics and environmental factors, both abiotic and biotic (reviewed by Wang & Bradburd 2014). Related conceptualizations of IBE that focus on process include 'isolation by adaptation' (i.e. due to adaptive phenotypic divergence) and 'isolation by ecology' (i.e. due to selective reduction in gene flow resulting from fitness differentials) (Nosil et al. 2008,

Shafer & Wolf 2013, Wang & Bradburd 2014). Comparative analyses with neutral and non-neutral panels of SNPs can elucidate the processes driving IBE patterns. For instance, Tepolt & Palumbi (2015) compared SNPs from the neutral genome and the cardiac transcriptome to address questions about the roles of colonization bottlenecks and local temperature adaptation in both the native and expanding ranges of an invasive green crab. Marine populations may commonly harbor unique adaptations associated with oceanographic features, temperature, productivity or more subtle features like sand inundation (Teske et al. 2011, Hecht et al. 2015, Young et al. 2015). Increasingly, evidence is accumulating for genetic impacts of anthropogenic threats to marine systems (Puritz & Toonen 2011). Seascape genetic approaches can elucidate these spatial patterns and drivers of adaptation, which in turn can have important implications for marine conservation (see Box 3 for example applications to marine management efforts).

SURVEY OF SEASCAPE GENETIC STUDIES

As the number of seascape genetic studies has grown, we are gaining insight into the most common drivers of genetic structuring. To foster a synoptic perspective on the direction that the field has taken so far and its potential insights, we conducted a literature search and retained 100 empirical studies from 2006 to 2015 that self-identified with 'seascape' or 'marine landscape' genetics (see the Supplement at www.int-res.com/articles/suppl/m554p001_supp.pdf for details). From this survey, we assessed the taxonomic and geographic coverage in the first generation of seascape genetic studies. The vast majority of studies focused on chordates (primarily fishes) (48%) and invertebrates (38%) as study organisms (Fig. 4a). Far less attention has been paid to the seascape genetics of algae (9%), marine angiosperms (5%) and other marine phyla over the past 10 yr. A bias towards temperate waters (68%) is partly driven by intense study of temperate diadromous fishery species (despite likely underrepresentation of diadromous studies with our search terms) (Fig. 4b). Tropical studies (26%) concentrated on coral reef seascapes, and polar studies are still rare (6%). Most studies were subtidal (65%) (Fig. 4c); fewer studies focused on intertidal (15%) or estuarine (14%) environments, and the fewest focused on pelagic ecosystems (5%), perhaps due to the mobile lifestyle of many pelagic species. Although seascape genetic studies have occurred in most of the world's major

Box 3. Applied seascape genetics: building roadmaps for conservation and management. We highlight 3 arenas where seascape genetics brings unique value to conservation and management of marine populations and communities

Species-based management

Demographic parameter estimates such as lifetime fecundity, self-recruitment and age-specific survival rates can all be generated from neutral genetic data, and are critical to marine reserve success (Mace & Morgan 2006, Burgess et al. 2014, Bonin et al. 2016). Seascape genetics can specifically identify ecological and biophysical attributes associated with high spill-over from marine reserves, asymmetries in source–sink dynamics within reserve networks (Harrison et al. 2012, Young et al. 2015), and the potential positive and negative effects of altered gene flow (Richardson et al. 2016). Locations can be characterized by key attributes such as high centrality or high outgoing connectivity in prioritization algorithms for network design (Beger et al. 2014, Mendez et al. 2014). Understanding the spatial distribution of genomic variation and drivers of local adaptation is critical to the protection of genetic resources and population resilience of fisheries (e.g. Limborg et al. 2012). Pinsky & Palumbi (2014) showed a decline in genetic diversity for numerous exploited marine fishes, attributed to over-harvesting. These trends imply widespread fisheries-induced evolution, and underscore the idea that spatial patterns of human impacts on seascapes can strongly influence genetic diversity and long-term resilience.

Biodiversity conservation

When the target of management is protecting intact habitats and biodiverse areas, a community genetics approach to integrate genetic data across species is key. Bayesian modeling can leverage multiple studies to assess regional patterns in genetic diversity across many taxa by accounting for spatial effects, species traits and disparate sampling designs (Pope et al. 2015). Over the long term, marine managers must consider how to maintain ecological resilience in an uncertain future. Identifying seascape features that promote persistence and diversity can inform this goal. Neutral genetic diversity indicates a population's potential to resist inbreeding depression, recover from disturbances and preserve adaptive potential (Young et al. 1996, Hughes & Stachowicz 2004, Reusch et al. 2005). In

Hawai'i, an analysis of mitochondrial genetic diversity in approximately 40 reef species identified large reef size and high coral cover as key predictors of high diversity, and these features could be used to select areas for long-term protection (Selkoe et al. 2016). Genetic diversity and species diversity often co-vary, indicating that ecological resilience and genetic resilience are linked (Messmer et al. 2012, Wright et al. 2015, Selkoe et al. 2016). Syntheses of genomic data across multiple species have the potential to identify suites of species with similar local adaptations that could lead to more nuanced delineation of conservation units and habitat restoration plans (Funk et al. 2012). In the future, using genetic tools to monitor biodiversity and measure resilience holds promise to rapidly advance marine conservation and restoration (e.g. Port et al. 2016).

Climate adaptation

Climate-induced range shifts of individual species and communities are becoming well documented (Beaugrand 2009). Studies are starting to investigate how these shifts impact connectivity between populations (Andrello et al. 2015, Young et al. 2015) and reshape the overall genetic structuring of species (Cossu et al. 2015), thereby impacting conservation features (McLeod et al. 2009). Seascape genetics can identify climate variables with the greatest influence on both neutral and functional regions of the genome. For example, an apparent negative correlation between temperature stress and mean genetic diversity of Hawaiian reef species highlights the potential for global warming to compromise the genetic resilience of entire communities (Selkoe et al. 2016). A seascape genetics perspective can inform strategies for genotype-based coral restoration using trans-generation acclimatization, selection of either host or symbiont genotypes (van Oppen et al. 2015), and targeted gene flow that aims to increase adaptive variation and fitness in populations (Kelly & Phillips 2016). As genomic data become more widely available, incorporating ecological niche models and projections of climate-induced environmental extremes into genetic studies will help identify marine populations most likely to persist under future conditions (Sgrò et al. 2011, Fitzpatrick & Keller 2015, Razgour 2015).

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oceans and seas (Fig. 4d), a bias exists towards the Northern Hemisphere, and underrepresented regions remain (e.g. the Southern Atlantic).

Emerging patterns in seascape effects

Using a sub-sample of 53 studies that tested for multiple seascape predictors of spatial genetic patterns (see the Supplement), we examined which study designs and seascape factors have received the most attention by the field. This sample size was insufficient to comment on how seascape drivers differ by

taxon, life history, geography and scale. Nevertheless, these studies provide a striking suggestion that seascape effects on genetics are varied and ubiquitous. Link-based study designs were most prevalent. A total of 43 studies with link-based designs tested the influence of 2 to 9 seascape factors against pairwise genetic distance metrics. Considering each unique combination of species, marker type, spatial scale, statistical test and genetic response variable, these 43 studies included 66 tests. Nearly two-thirds of these tests were partial Mantel or multiple regression on distance matrices, which recent work has shown to lead to inflated false positives (Legendre et
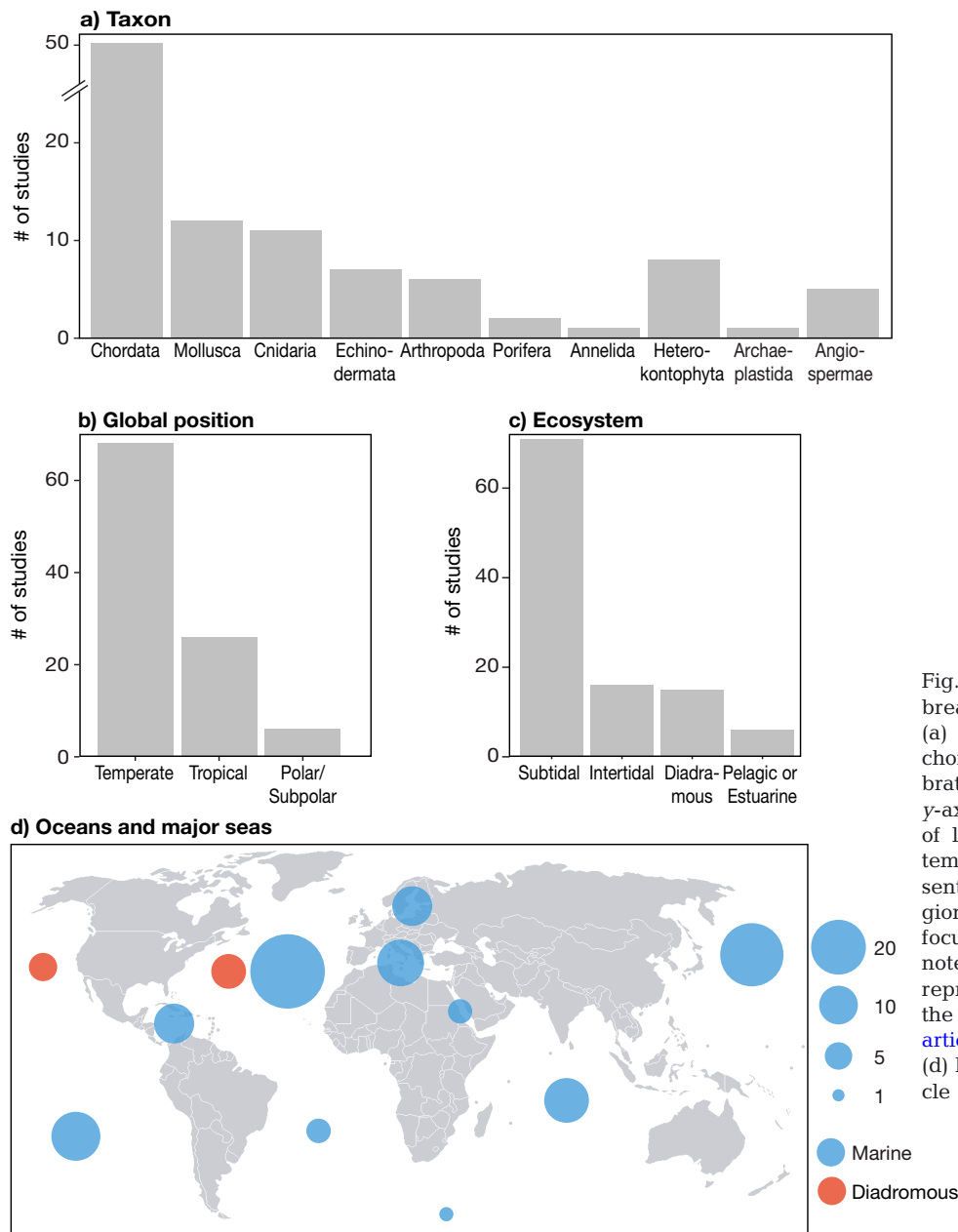
Fig. 4. Taxonomic and geographic breadth of seascape genetic studies. (a) Taxonomy reveals a focus on chordates (mainly fish) and invertebrate phyla. Note the break in the *y*-axis. (b) Global position in terms of latitude reveals a bias towards temperate regions and underrepresentation of polar and subpolar regions. (c) Ecosystem type reveals a focus on subtidal ecosystems (but note our search terms may underrepresent diadromous studies; see the Supplement at www.int-res.com/articles/suppl/m554p001_supp.pdf). (d) Major oceans and seas, with circle size proportional to number of studies in each body of water

al. 2015). With this caveat in mind, we report that for 25 types of seascape predictors, 20 were found to be a significant driver in at least one test. This sample is far from random—bias towards positive results is expected from informed choice of important seascape drivers, but biased reporting and false positives are also possible. We note that most studies focused on abiotic predictors; only a handful of biotic factors were apparent in the literature survey (e.g. 'chlorophyll *a*' and 'presence of vegetation'). A vast array of ecological interactions likely also play a role in shaping marine species distributions and deserve greater focus.

Nearly all link-based studies included geographic distance as a predictor and nearly one-half of these reported significance. For comparison, a previous review of IBD in marine studies found that one-third of sampled studies showed significant IBD; however, study selection criteria differed (Selkoe & Toonen 2011). Several software programs such as Bayenv (Coop et al. 2010) assume and adjust for IBD before testing effects of other factors. Given that only half of seascape studies find significant spatial autocorrelation in the genetic response variable, careful choice and appropriate use of software is critical (i.e. only adjust for IBD if it is present). For the 32 link-based stud-

ies in our survey that lacked evidence of geographical influence, half reported a significant influence of at least one other seascape factor. Arguably, this indicates that seascape effects may account for a substantial number of cases of what is commonly called 'chaotic genetic heterogeneity'—a lack of genetic spatial autocorrelation despite significant genetic structuring (Johnson & Black 1982, Toonen & Grosberg 2011). The flipside of this view is that the cause of spatial genetic structure in roughly one-quarter of marine studies was unresolved, suggesting that there is still much to be learned about the drivers of genetic structuring in the sea. Addressing the role of time alongside space may be key to gains in this arena. For instance, by analyzing 3 successive years and over 2000 fish, R. Henriques et al. (unpubl.) show that anomalous low oxygen water events contribute to chaotic genetic patchiness of hake in the southern Benguela system. Most seascape studies encompass only 1 sampling event and so cannot illuminate how natural fluctuations in seascape drivers and genetic patterns may result in unexplained spatial genetic variance.

A study's selection of seascape predictors and interpretation of findings depends on consideration of how life history, ecology and environment influence gene flow. Our sample of multi-factor studies showed that the most common seascape factors tested were metrics of temperature and ocean transport; 43% of tests of temperature were reported to be significant, while only 31% of ocean transport metrics were significant (Table 1). These results suggest that temperature may be as influential as geography on regional scale population genetics of marine species, and more so than ocean currents. However, it may also be either easier or more common to design effective sampling arrays across temperature gradients than across ocean transport gradients. A half-dozen other categories of seascape factors were tested 10 to 25 times across the sample of studies, and all showed significant results in 40 to 80% of the tests (Table 1). In light of these trends, the idea of using patterns of potential connectivity based on ocean flows as an informed null model may be no more defensible than using geography, depth or temperature. Some of the driver metrics, such as habitat

Table 1. Number and outcome of tests that evaluated each type of driver studied, taken from 53 studies that statistically tested correlation of genetic metrics with at least 2 seascape drivers

Predictor	All studies		Link-based		Node-based	
	Tests	Significant (%)	Tests	Significant (%)	Tests	Significant (%)
Geography	86	40	62	48	22	18
Temperature	47	43	26	54	21	29
Ocean transport	35	31	26	27	9	44
Habitat patch size	25	48	10	60	15	40
Depth	23	65	15	73	8	50
Other climatic variables	18	50	10	70	8	25
Salinity	16	69	13	69	3	67
Precipitation	15	80	7	100	8	63
Biogeographic breaks/ecoregions	14	43	12	50	0	0
Chlorophyll *a*	11	45	10	50	1	0
Habitat continuity	9	89	9	89	0	0
Turbidity	8	75	6	67	2	100
Nutrients	7	25	6	33	2	0
Sediment type	7	86	4	100	3	67
Hydrodynamic regime	6	33	3	33	3	33
Habitat exploitation	5	20	1	0	4	25
Dissolved matter	4	50	3	67	1	0
Other hydrodynamic variables	4	100	3	100	1	100
Geological history (e.g. glaciation)	3	33	1	100	2	0
Oxygen	3	67	3	67	0	0
Solar irradiance	3	67	2	50	1	100
Tidal flux	3	67	3	67	0	0
pH	2	50	1	0	1	100
Coastal pollution	1	50	1	0	1	100
Presence of vegetation	1	0	0	0	1	0
Wave energy	1	0	1	0	0	0

patch size, wave energy and sediment type, may be more obviously related to mechanisms affecting populations within sites than dispersal and gene flow between sites, meaning that study designs focused on node-based analyses may be more appropriate than link-based analyses (Wagner & Fortin 2013).

Fewer significant drivers were identified in node-based studies than in link-based studies, consistent with the finding that the non-independence of link-based data can lead to biased model selection and spurious predictor variables (Wagner & Fortin 2015). Alternatively, the seascape may influence migration more strongly than drift and local adaptation, although this is unlikely. Node-based studies showed that geography was a significant predictor only 18% of the time, and temperature 29% (Table 1). Ocean transport metrics were more commonly significant in node-based studies, at a 44% rate of significance.

Study design effects

Considering all multi-factor studies, an average of 3.6 drivers were tested, with statistical support for 1 or 2 of them. Interestingly, we found that when a larger number of potential drivers was tested against a single response variable, a smaller fraction of drivers was found to be significant. This trend suggests that only 1 or a few drivers tend to dominate genetic structuring, or that variables are sometimes added without strong rationale. Studies using nuclear markers found larger fractions of tested drivers to be significant than those using mtDNA, with no difference in apparent power for SNP versus microsatellite studies. Of course, these trends depend on choices of study design, statistical testing and which drivers and taxa are easily sampled in the marine environment. Nevertheless, they lend insight into the range of seascape predictors reported in recent studies and the effects of study design (see Fig. 2), and highlight underrepresented predictors that deserve future study.

THE ADVENT OF SEASCAPE GENOMICS

Genomic studies of non-model organisms are becoming more accessible thanks to techniques that cheaply and randomly sub-sample the genome, such as restriction site associated DNA sequencing (RAD-seq) (Miller et al. 2007, Baird et al. 2008, Toonen et al. 2013, Puritz et al. 2014a, Andrews et al. 2016). Bioinformatic pipelines specifically designed to handle data from marine organisms are also improving (Puritz et al. 2014b). Consequently, SNP-based seascape genetic analyses are growing rapidly (Fig. 3). Below we highlight examples demonstrating how genomic sampling has 2 distinct benefits for seascape analyses: (1) increased power and likelihood to detect gene–environment interactions, and (2) the ability to simultaneously investigate the roles of drift, migration and selection in shaping genetic structure.

Power through replication

In the majority of seascape genetic studies, the amount of sampled genetic variation is relatively low compared to the potential number of seascape drivers. Consequently, investigators are required to test only a small number of seascape factors or to collapse them down into coordinate axes to balance Type I and II error. Scaling up to genomic data adds response variation that can be parsed among additional factors and lead to more detailed interpretation. For example, 2 studies recently examined population discontinuities in clownfish *Amphiprion bicinctus* over a similar region in the Red Sea. Nanninga et al. (2014) used 38 microsatellite loci and Saenz-Agudelo et al. (2015) used 4559 SNPs with partially overlapping population samples, and both detected a pattern of IBE between clownfish populations above and below an oligotrophic–eutrophic transition zone, but no additional drivers of genetic differentiation among the populations within each sample regime. Nanninga et al. (2014) chose chlorophyll *a* concentrations as the best representative for environmental distance and were able to evaluate a hypothesis of IBE versus IBD using partial Mantel tests and multiple matrix regressions with randomization. With an order of magnitude increase in genetic variance, Saenz-Agudelo et al. (2015) used a different powerful statistical approach including an information theoretic model selection framework and the evaluation of 49 different linear models of seascape drivers including the presence of genetic breaks. This approach greatly improved the overall model fit, and revealed a new dimension (presence of genetic discontinuities) that a simple IBD/IBE analysis would have overlooked.

Parsing neutral and adaptive genetics

One of the key benefits of genome-level analyses on populations is sampling more unlinked (i.e. inde-

pendently sorting) portions of the genome. This allows more robust characterization of a species' demography that overcomes idiosyncratic gene histories (i.e. differentiation between responses to environmental selection, migration, drift, etc.). For example, in a recent study on bonnethead sharks, Portnoy et al. (2015) isolated the entire mtDNA control region, and used RADseq to produce 5914 SNPs; 49 SNPs were outliers in their level of spatial genetic structure compared to the other loci. Outlier SNPs exhibited signatures of latitude-driven selection while the mtDNA data, in conjunction with the rest of the SNPs, showed a signature of female philopatry and male-mediated gene flow among the sampled populations. The non-outlier SNPs also supported a classic biogeographic separation between the Gulf of Mexico and the western Atlantic Ocean populations. Importantly, the combination of multiple individual unlinked gene genealogies enabled the characterization of population dynamics and historical biogeography of bonnethead sharks.

Outlier loci, especially those that are associated with the environment, have special utility for seascape analyses, but theory predicts that extreme outlier loci should be rare. Importantly, complex landscapes can lead to high rates of false positives when studies are not properly designed (Lotterhos & Whitlock 2014, 2015, Forester et al. 2016). In general, false positives are a major challenge for seascape genomics, given the deluge of genetic and environmental data (De Mita et al. 2013, de Villemereuil et al. 2014, Lotterhos & Whitlock 2014). New analyses coupling outlier detection with environmental gradients reduce false positives (de Villemereuil & Gaggiotti 2015). Furthermore, a focus on extreme outliers misses more common selective actions that should be distributed as small selective effects at multiple genomic regions responding to similar environmental forcing in concert (Schwartz et al. 2010). These polygenic effects would not likely be detected via outlier analyses. For example, Laporte et al. (2016) surveyed 23 659 and 14 755 SNPs in North Atlantic eels across 'polluted' and control environments. Outlier detection revealed only 2 outlier loci; however, a machine learning technique (random forest algorithm) coupled with a distance-based redundancy analysis detected over 140 loci under polygenic selection. Whether disentangling the effects of demography, life history and migration, or detecting the subtle genetic effects of environmental polygenic selection, genomic-scale data sets will enhance the scope and power of seascape analysis.

Future directions

The next challenge for seascape genomics is to progress from pattern to process, i.e. from seascape correlates of spatial genetic patterns to specific mechanisms of population differentiation (reviewed in Riginos et al. 2016). New analytical frameworks will play a key role in uncovering selective forces. For instance, linking shifts in allele frequencies to adaptive phenotypes will require creative approaches that draw on gene ontology databases and experimental tests of fitness advantage (reviewed in de Villemereuil et al. 2015, Pardo-Diaz et al. 2015, Rellstab et al. 2015). Research on responses of a sea urchin model system to ocean acidification (e.g. Kelly et al. 2013, Pespeni & Palumbi 2013, Pespeni et al. 2013, Evans et al. 2015) provides a glimpse of how ecological experiments and genomic and transcriptomic data together illuminate adaptive evolutionary response across a seascape.

CONCLUSIONS

Fueled by GIS data, genomics and statistical advances, the first wave of seascape genetic studies has changed our conceptual understanding of the multiple historical and contemporary processes shaping dispersal and gene flow in the sea. Importantly, it can be tempting to overlook potential false positives, and over-interpret nuanced spatial patterns and slight but significant explanatory power (Meirmans 2015, Richardson et al. 2016), but not all spatial genetic structure has ecological meaning (Hedrick 1999). At present, we still largely lack the tools and perspective needed to gauge where to limit inference on the meaning of subtle effects. Complementing empirical studies with simulations holds promise to illuminate these boundaries.

In many ways, the rise of landscape and seascape genetics represents the maturation of population genetics, with a stronger emphasis on spatial ecological predictors (Dyer 2015). Perhaps unsurprisingly, we found that many seascape genetic studies have been oriented towards the population genetic literature, as evidenced by the strong bias in journal publication (Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m554p001_supp.pdf). We propose that broadening the audience of seascape genetic studies is a critical step in improving their utility and value across disciplinary lines.

As the field of seascape genetics progresses, we anticipate that the most exciting advances will come

from a stronger integration with biological oceanography, metapopulation ecology, biogeography, larval ecology, physiology, evolution and other disciplines. Finally, we emphasize that as marine ecosystems around the globe face anthropogenic impacts on unprecedented levels, seascape genetics can play a unique and powerful role in understanding effective long-term conservation and management strategies.

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