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Using large scale natural experiments to better understand the distribution of genetic variation in eastern North Pacific intertidal invertebrates

A dissertation submitted in partial satisfaction of the requirements
for the degree Doctor of Philosophy

in

Environmental Systems

by

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To my family — lifelong and picked up along the way

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LIST OF ABBREVIATIONS

CI	Confidence Interval
COI	Cytochrome Oxidase
ddRAD	Double Digest Restriction-site Associated DNA
d.f.	Degrees of Freedom
DNA	Deoxyribonucleic Acid
EF1A	Elongation Factor 1-α
F	Fecundity
KZ	Area affected by multispecies mortality event, a.k.a 'kill zone'
LDD	Long-Distance Dispersal
mtDNA	Mitochondrial DNA
nMDS	Non-Metric Multidimensional Scaling
PD	Pelagic Duration
PERMANOVA	Permutational Multivariate Analysis of Variance
RADseq	Restriction-site Associated DNA Sequencing
SDC	Synchronously Diverging Co-distributed
SDM	Species Distribution Model
SNP	Single Nucleotide Polymorphism
SSWD	Sea Star Wasting Disease
USA	United States of America

LIST OF SYMBOLS

F_{ST}	Measure of population genetic differentiation, also used to refer to analogs here
N_C	Census population size
Nm	Number of migrants per generation
${}^{P}Nm_c$	Predicted contrast of number of migrants per generation
${}^{E}Nm_c$	Empirical contrast of number of migrants per generation
ϕ_{ST}	Measure of population genetic differentiation based on sequence distance
tMRCA	Time to most recent common ancestor
χ^2	Chi-squared

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ABSTRACT

Using large scale natural experiments to better understand the distribution of genetic variation in eastern North Pacific intertidal invertebrates

by

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Environmental Systems
University of California, Merced, 2017
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Identifying patterns, and ascertaining causes, of the current distribution of genetic variation is often difficult in natural systems. Historical legacies and complex interactions among multiple abiotic and biotic processes lead to sometimes weak inference. One way to tackle this complexity is to study systems that allow for control or constraint of some variables. My thesis employs multiple natural experiments to carefully study the influence of dispersal and selection on population genetic structure through three focal studies. First, I use a meta-analysis of paired taxa (controlling for species age and environment) to identify correlates of gene flow. I found broad support for a positive relationship between dispersal potential and gene flow and in the exceptions find results that suggest the influence of genetic drift and natural selection. Second, I track the multi-year ecological and genetic recovery of three species from a die-off along the central coast of California to reveal how dispersal potential relates to rates of larval recruitment and spatial genetics. Species with higher dispersal potential re-colonized a broader extent of the impacted range, and did so more quickly, than species with lower dispersal potential, suggesting species' attributes (e.g. fecundity, pelagic duration, and population size) can influenced realized dispersal. Third, I capture the genetic consequences of a high mortality (83% loss) marine epizootic in an intertidal keystone predator by comparing specimens collected the year before the outbreak with survivors after the outbreak, and comparing these each to newly recruited juveniles during the outbreak. Patterns in changing allele frequencies in candidate loci suggest natural selection is the main driver contributing to changes observed in this system, rather than genetic drift or gene flow. This series of natural experiments uses a framework aimed at predicting the influence of a suite of life-history traits — e.g. fecundity, pelagic duration, and population size — on population genetic differentiation, including how patterns of recruitment (spatial and genetic) are shaped by dispersal and its interaction with the filtering effects of natural selection.

Chapter 1. A case for deconstructing dispersal potential

Conceptions of the processes shaping life in the seas have changed in recent decades, with a shift from attention on dispersal to recognizing the importance of selection. Yet, despite these decades of studies, understanding how population genetic variation is shaped by the interplay between dispersal and selection remains one of the "Grand Challenges" in biology (Lindsay 2012); and genetic drift remains largely unaddressed. Correlations between dispersal potential and gene flow (Bohonak 1999) have suggested a relationship between life-history and population genetic structure, consistent with longstanding theory that predicts that geographic genetic structure should emerge from interactions among life-history, environment, and species' age (Marko & Hart 2011). However, there is an ever-growing list of exceptions (Selkoe et al. 2010; Weersing & Toonen 2009).

In the pursuit of uncovering generalities amid seemingly chaotic genetic patterns, hundreds of studies have aimed to test the relationship between pelagic duration (*PD*; usually the pelagic larval duration, *PLD*) and population genetic structure. The idea is simple — the length of time an organism spends drifting in the sea, i.e. the *PD*, could be a convenient proxy for dispersal potential, i.e. current * time = distance. However, a variety of studies, time and time again, have concluded that there is no relationship between pelagic duration (*PD*) and population genetic structure (e.g. Bay et al. 2006; Bowen et al. 2006; Weersing & Toonen 2009; Selkoe et al. 2010). Relationships found between *PD* and F_{ST} have largely been driven by species lacking a pelagic larval phase (*PD* = 0) (Kelly & Palumbi 2010; Riginos et al. 2011). Using *PD* as a proxy for dispersal potential seems to fall short in terms of predicting genetic outcomes.

The lack of agreement has led recently to increased attention on other traits, such as larval behavior (Shanks 2009). Others have begun to emphasize the importance of looking at alternative life-history traits to account for differences in population genetic patterns (Bradbury et al. 2008; Riginos et al. 2011; Selkoe & Toonen 2011; Faurby & Barber 2012). Kelly & Palumbi (2010) point out that the unexpected high gene flow in *Tegula funebralis* (*PD* = 5 days) could possibly be accounted for by its extremely high abundance. Environment and oceanography also are considerations (Cowen & Sponaugle 2009). Perhaps a more nuanced conclusion would suggest a single life-history trait is only as important as its role relative to other traits, and the environment.

Rather than employing *post hoc* explanations to account for unexpected findings based on single traits, an alternative approach would be to incorporate knowledge about variation in life-history traits, environment, time, etcetera, *a priori*. Integrating adult abundances and fecundity with *PD* can improve estimates of dispersal potential and lead to a clear relationship between *PD* and population connectivity (Treml et al. 2012; Dawson et al. 2014). Rather than conclude that *PD* by itself is a poor predictor of population genetic structure, it could be incorporated as one of multiple life-history traits contributing to dispersal potential (e.g. dispersal 'syndromes', Dawson 2014a). A lack of relationship between a single trait and genetic structure or a relationship with another trait does not negate the influence of any particular trait on population genetic structure (Figure 1.1). Moreover, a positive relationship between a single trait and population genetic structure does not mean it is necessarily the causal factor (Figure 1.1).

My dissertation aims to take a synthetic approach. I seek to integrate ecological and evolutionary approaches to address the influence of a suite of life-history traits — e.g. population size, fecundity, and *PD* — on population genetic differentiation, including how patterns of recruitment (spatial and genetic) are shaped by dispersal and its interaction with the filtering effects of natural selection.

To identify whether there are discernable generalities between dispersal potential and population genetic structure, in Chapter 2 I first look at the global scale using a meta-analysis of pairs of species that are co-distributed and of similar age, which is intended to control for potential sources of environmental and temporal variance (Dawson 2014b). This allows for clearer comparison of the factors in question, i.e. dispersal-linked life-history traits, and their impact on population genetic structure.

On a regional scale, in Chapter 3, I use both ecological and genetic approaches (Reitzel et al. 2013) to examine the role of combinatorial dispersal potential in influencing realized dispersal and population genetic structure. Specifically, I use a multi-species mortality event to reveal whether differences in dispersal potential (estimated from life-history characteristics) are congruent with differences in population genetic structure, ecological recruitment in the area of extirpation, and genetic assignment of recruits to adult populations.

Finally, in Chapter 4, I explore the effects of a rare pandemic event on the standing stock of genetic variation in a sea star. This study provides opportunity to disentangle the dynamic interaction between natural selection, dispersal, and extreme conditions as it unfolds. In human history we have seen how disease has sculpted population patterns (e.g. black plague, small pox, and HIV), but we know virtually nothing of these disease dynamics in marine taxa.

My thesis employs a series of natural experiments that provide the framework to clarify how a suite of life-history traits influence the distribution of genetic variation by deconstructing dispersal potential and integrating ecological and evolutionary approaches.

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1.2 Figures

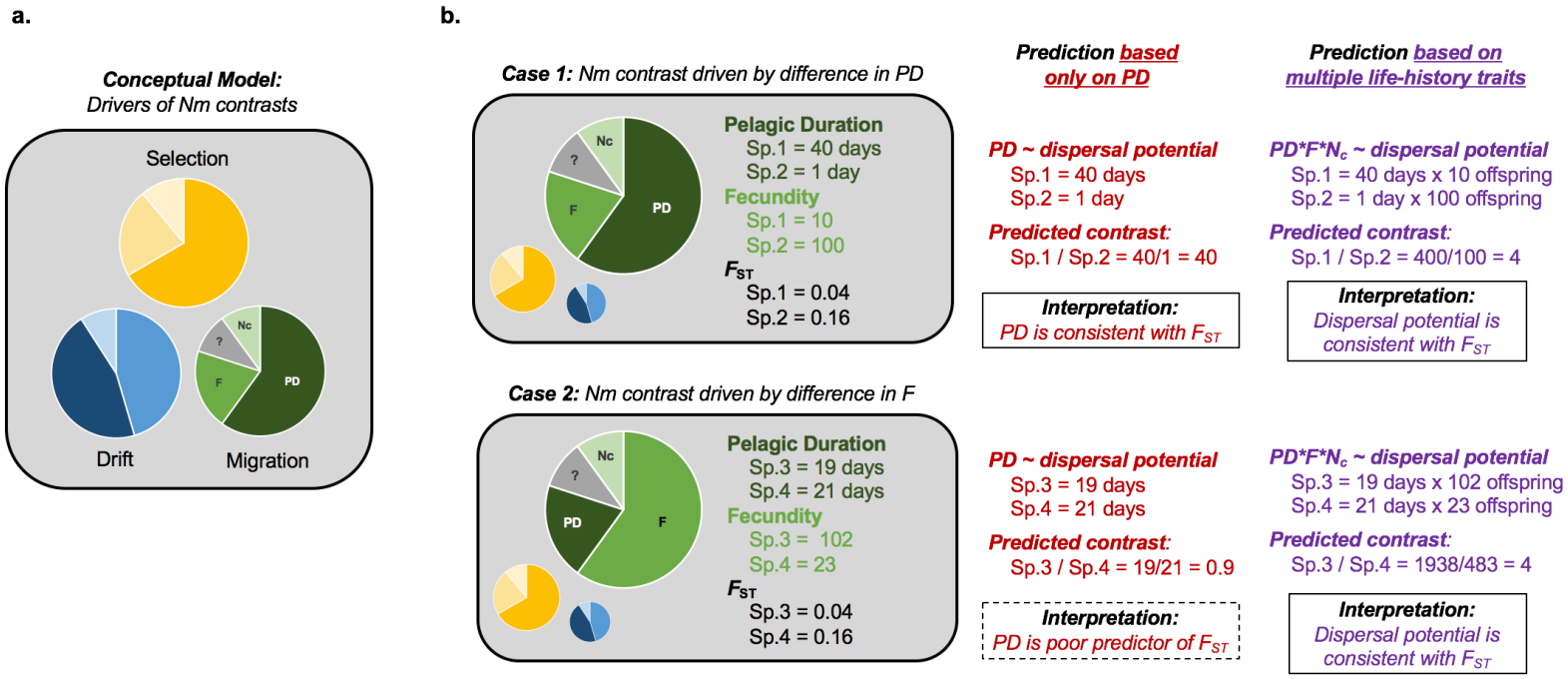

Figure 1.1 Conceptual example illustrating contrasts between two species in dispersal potential and F_{ST}. (a) A conceptual framework highlighting the relative roles of the principle micro-evolutionary mechanisms. The grey box represents a common evolutionary age and environment shared by the species being compared. The size of each pie-chart represents the relative role of each mechanism in driving the difference in predictions of the number of migrants per generation (*Nm*). The size of each pie slice corresponds to the relative importance of a particular trait in driving contrasts in *Nm*. For migration, slices represent *PD* = pelagic duration, *F* = fecundity, N_c = census population size, and ? = a potential explanatory trait that has not been identified or stochastic variation. (b) A conceptual example using two cases to illustrate how considering single versus multiple life-history traits might lead to different interpretations about the link between a particular trait and F_{ST}. In each of the cases presented, the predicted contrast in dispersal potential is equal when multiple factors are considered (purple) and congruent with empirical estimates of gene flow (e.g. F_{ST}), where the species with higher dispersal potential should have lower F_{ST}. However, when only a single life-history trait is considered (red) and compared directly to F_{ST}, different inferences are made depending on the relative importance of the chosen trait. N_c is equivalent in this example and so contrast is 1 and therefore not shown in calculations. Note, this example is meant to be illustrative only; detailed discussions of *Nm* contrasts are handled in Chapter 2 and Chapter 3.

Chapter 2. Correlates of gene flow in marine and terrestrial environments

2.1 Abstract

Theory predicts that differences in phylogeographic structure between species should be related to differences in life-history, environment, and evolutionary time. Contrasts of life-history traits and gene flow between synchronously diverging co-distributed (SDC) taxa control for effects of environment and time, offering opportunity to test whether traits favoring greater dispersal lead to higher gene flow. We conducted a meta-analysis using SDC taxa, in marine and in terrestrial settings, to test whether increased gene flow is related to higher fecundity (F), larger census population size (N_c), and other traits linked to dispersal. Overall, we find a strong relationship consistent with predictions. SDC taxa with similar dispersal potential show similar gene flow; those with higher dispersal potential have higher gene flow. While the relationship is stronger on land than in the sea, many factors influence population genetic structure; deviations in measured versus predicted gene flow may indicate drift or selection.

2.2 Introduction

Genetic variation is pervasive, yet distributed heterogeneously within and among species and geographically. Understanding how population genetic structure is shaped by the interplay between dispersal and selection remains one of the "Grand Challenges" in biology (Lindsay 2012) despite decades of study. For example, longstanding theory predicts that phylogeographic structure should be shaped by life-history, environment, and coalescent age (Marko & Hart 2011). However, reviews of empirical studies have suggested sometimes complex interactions (Bohonak 1999) and possibly a preponderance of exceptions (Weersing & Toonen 2009; Selkoe et al. 2010) to the intuitive generalization that increasing dispersal potential should lead to reduced population genetic differentiation (Waples 1987; Stevens et al. 2013).

The lack of consensus may have several explanations. There could be epistemological problems: theory could be wrong or unrepresentative of natural situations, and expectations for simple relationships could be unrealistic. Alternatively, interpretation may be confounded by differences between taxa — e.g. in life-history, ecology, population size — as well as by differences in history that influence the contemporary distribution of genetic variation (Marko et al. 2010); moreover, complex traits may alter how species interact with their environment (Shanks 2009) in different circumstances. Additionally, emphases may have been on subsets of mechanisms rather than on their interplay and may have been studied to differing extents in different environments (Bohonak 1999). For example, in the marine realm, migration has been credited as the main driver in structuring populations, although only recently have studies started paying equal attention to the influence of other mechanisms of evolution (Sanford & Kelly 2011). In terrestrial systems, much attention has been focused on the influence of natural selection (e.g. Endler 1986), but genetic drift and gene flow can still have a marked influence on the distribution of genetic variation among populations (Farkas et al. 2015).

A fourth explanation for the lack of consensus may be that methods used to address this question have been insufficient. Identifying the causal relationships between traits, mechanisms of evolution, and phylogeographic patterns is difficult in natural systems, due to multiple complex levels of interlinked processes. Consequently, some studies may be suggestive but inconclusive. To reduce complexity and strengthen inference, simplified study systems that allow for control or constraint of some variables have been sought out. One such approach is comparison of sister species (Lynch 1989; Hickerson et al. 2010), but sympatric sister species are relatively rare in nature. An alternative approach, one that should be more abundant in nature, may be contrasts of life-history traits and gene flow between taxa that are synchronously diverging and co-distributed (SDC). These SDC species comparisons should, like sympatric sister species comparisons, control for effects of environment and time, offering the opportunity to test whether traits favoring greater dispersal (e.g. higher fecundity, larger population size, and differences in other dispersal-linked traits) lead to higher gene flow (Dawson 2014a). Like sister species comparisons (Dawson et al. 2002), recent studies have found that SDC contrasts in gene flow can be explained largely

by contrasts in fecundity (*F*), census population size (N_c), and other dispersal-linked traits and/or co-correlates (Dawson 2014a; Dawson et al. 2014). Empirical contrasts found to deviate from predicted contrasts indicate that genetic drift and selection also can play important roles in shaping population genetic structure. The SDC approach also enables meta-analyses of effect sizes, an opportunity that has not yet been explored.

Here we explore the generality of the predicted relationship between dispersal and gene flow by conducting a meta-analysis of SDC taxa in marine and terrestrial/freshwater settings. We test the hypothesis that: increased gene flow is proportional to traits including fecundity (*F*), census population size (N_c), and others linked to dispersal (such as pelagic duration in the marine realm).

2.3 Materials and methods

We conducted a meta-analysis of data describing SDC pairs in the peer-reviewed published literature. We discovered articles by searching Web of Science using the following terms: "comparative phylogeograph*" plus ("co-distributed" or "codistributed" or "sympatr*") plus ("time to most recent common ancestor" or "tMRCA" or "divergence time" or "coalescen*"). To broaden coverage of the literature, including identifying appropriate articles not recovered by the Web of Science search we also randomly searched approximately one third of articles returned by Google Scholar using the same search terms except "coalescen*" (which yielded an unmanageable number of articles). The Web of Science search yielded zero marine SDC pairs, although we know from our own publications that some exist, so we also filtered the full Google Scholar results to extract all marine studies. Duplicates and non-peer-reviewed reports or conference abstracts that were misclassified as Journal Articles by Google Scholar were manually removed when compiling the final list of articles for analysis.

All articles included in the final analysis contained at least one pair of taxa that were (i) synchronously diverging, i.e. the coalescent of each fell within the 95% credibility interval of the other (or, if only a range was provided, the median of the range fell within the range of the paired taxon), and (ii) co-distributed, i.e. at least 70% of their ranges overlap as a rule of thumb (Dawson 2012). Additionally, articles were included only if sufficient information was available to compare measures of population genetic structure and dispersal potential. The article itself had to contain (iii) estimated F_{ST}, ϕ_{ST} or analogous descriptors of population differentiation (either global or mean pairwise with 95% CI) using the same locus, and provide (iv) information on fecundity (*F)*, census population size (N_c), or other dispersal-linked traits, or such information had to be available or estimatable from other literature. In cases where three species met the SDC criteria in a single study, two of the three possible pairs were randomly selected to be included in the meta-analysis to avoid the statistical problem of non-independence of comparisons.

We tested whether gene flow is influenced by traits including fecundity (*F*), census population size (N_c), dispersal duration (e.g. pelagic duration in the marine realm [*PD*]), and/or co-correlates — i.e. other life-history, behavioral, physiological, or morphological traits contributing to 'dispersal syndromes' (Clobert et al. 2009; Dawson 2014b) — for all SDC pairs and then for terrestrial/freshwater and marine taxa separately. We ranked each species within each SDC pair as having higher, lower, or equal dispersal potential based on life-history traits (Table 2.1). SDC pairs were then categorized as 'supporting' or 'refuting' the relationship between dispersal potential and F_{ST} based on whether F_{ST} was congruent with predictions (Table 2.1). We used χ^2 tests against a null hypothesis of no relationship — i.e. the expectation that dispersal potential and F_{ST} will have an equal chance of congruence or non-congruence if random. Achieved power was calculated using G* Power 3 (Faul et al. 2007). Effect sizes were calculated for SDC pairs for which dispersal potential could be estimated quantitatively (Dawson et al. 2014).

For species that had quantitative estimates of life-history traits — e.g. *PD*, *F*, or N_c — predicted contrasts in the number of migrants per generation ($^{P}Nm_c$) were calculated and compared to empirical contrasts, $^{E}Nm_c$, inferred from measured F_{ST} for SDC taxa (Dawson et al. 2014). We use *Nm* in our analysis because it is readily estimated from both dispersal potential and F_{ST} and acts as a common comparator, although we acknowledge potential non-linear

relationships among these variables can complicate interpretation. Fecundity (*F*) and census population size (N_c) were taken from the literature when available. When N_c was unavailable, study sample sizes were used as a proxy since we were primarily interested in relative abundances of the two species in the SDC pair, i.e. we made the assumption that approximately equal effort was applied to collecting both species and took differences in sample sizes as indication of one species being generally more common than the other. For each SDC pair, *F* and N_c were used as direct proportional estimates of *Nm*, calculated as a factor of the lower disperser following Dawson et al. (2014), and pelagic duration (*PD*) was converted using the regression of Doherty et al. (1995) $\log F_{ST} = -0.043$ (no. of days) – 0.315 followed by $Nm = (1/F_{ST} - 1)/4$. Overall predicted *Nm* per species was calculated as the product of *Nm* taken from *F*, N_c, and *PD*, or whichever subset of these quantitative traits was available (see table 2.1). The same quantitative traits were used within each SDC pair. The predicted contrast (${}^{P}Nm_c$) factoring in all available quantitative life-history traits for pairs of SDC taxa was represented as the ratio of the higher dispersing species' ${}^{P}Nm_1$ over the lower dispersing species' ${}^{P}Nm_2$, and therefore always yielded a contrast of ≥ 1. Empirical contrasts (${}^{E}Nm_c$), the ratio from measured estimates of F_{ST} using $Nm = (1/F_{ST} - 1)/4$, also were calculated as a ratio of the species with higher predicted dispersal divided by the species with lower predicted dispersal. Here, values could be ${}^{E}Nm_1 / {}^{E}Nm_2 \geq 1$, indicating general support for the relationship between dispersal potential and gene flow, but values also could be ≤ 1 indicating a lack of support for the predicted relationship. The logarithm was then plotted for each of the two ratios. The theoretical expectation that contrasts in overall dispersal potential predict contrasts in empirically inferred *Nm* is represented by ${}^{P}Nm_1 / {}^{P}Nm_2 \approx {}^{E}Nm_1 / {}^{E}Nm_2$. Thus, we draw conclusions from two aspects of the *Nm* contrasts: (1) the quadrant to which the SDC pair plots and (2) the position of the pair within the positive quadrant — the upper left triangle (${}^{E}Nm_c > {}^{P}Nm_c$) or the lower right triangle (${}^{E}Nm_c < {}^{P}Nm_c$).

2.4 Results

The literature survey returned a total of 507 papers, 65 of which were from Web of Science and 442 from Google Scholar. We read a total of 274 papers including all 65 from Web of Science, 159 (36%) selected randomly from Google Scholar, and all 50 remaining marine papers from the Google Scholar search. The survey yielded 21 papers containing 30 species pairs — 14 marine and 16 terrestrial/freshwater — that met the criteria for SDC comparisons and had sufficient information available to make an estimate of dispersal potential (Table 2.1 and data sources therein). SDC-appropriate papers were more common in 2014 than previous years and appeared more frequently in *Molecular Ecology* than any other journal. Many of the main animal phyla were represented, though vertebrates had greatest representation (Fig. 2.1). Terrestrial pairs were distributed across 5 continents and marine pairs came from the Pacific Ocean and Indian Ocean (Fig. 2.2).

Overall, SDC taxa with similar dispersal potential usually show similar gene flow (6 of 8 pairs), and those with higher dispersal potential usually have higher gene flow (18 of 22 pairs), consistent with predictions (Fig. 2.3.; Table 2.1). We found a positive relationship between gene flow and *F*, N_c, and other dispersal-linked traits (Table 2.1) with the full dataset of SDC pairs (n = 30, α = 0.05, $\chi^2 = 10.800$, critical value = 3.841, d.f. = 1, power = 0.91). The relationship between gene flow and dispersal potential is also supported in the terrestrial dataset alone (n = 16, α = 0.05, $\chi^2 = 9.0$, critical value = 3.841, d.f. = 1, power = 0.85). However, although the majority (10 v. 4) of marine pairs support the prediction and the mean effect size is positive, the χ^2-test lacks statistical power in the marine dataset alone (n = 14, α = 0.05, $\chi^2 = 2.571$, d.f. = 1, critical value = 3.841, power = 0.36).

Quantitative descriptions of one or more dispersal-related traits existed for two-thirds of the SDC species pairs. In 10 cases, a single trait (*F* or *PD*) could be used to estimate predicted gene flow (Table 2.1), of which 6 cases showed that the species with higher ${}^{P}Nm$ also had higher ${}^{E}Nm$ and so reduced population genetic structure (Fig. 2.4). However, it is the cumulative effect of multiple life-history traits that should provide the best estimate of realized dispersal. Two additional cases allowed analysis of the combined effect of two traits (Table 2.1): comparison of

New Zealand limpets, based on *F* and *PD*, contradicted the hypothesis that the contrast in ${}^{P}Nm$ predicts the direction of the contrast in ${}^{E}Nm$; comparison of a barnacle and limpet in southeastern Australia, based on N_c and *PD*, supported the hypothesis that ${}^{P}Nm_c$ predicts ${}^{E}Nm_c$. None of the SDC species pairs in our literature search had quantitative data for more than two dispersal-related traits.

When contrasts in the number of migrants per generation are compared per SDC pair, ${}^{E}Nm_c$ is positively associated with ${}^{P}Nm_c$ (i.e. points occur in the positive quadrant in Fig. 2.5), consistent with the hypothesis that gene flow is generally a function of dispersal potential. The majority of terrestrial SDC species pairs fall in the upper left triangle of the positive quadrant (i.e. ${}^{E}Nm_c > {}^{P}Nm_c$) indicating that the estimated difference in dispersal potential explains only a portion of the measured difference in gene flow (Fig. 2.5). This same pattern is not seen in marine taxa, in which contrasts in ${}^{P}Nm$ better correspond with contrasts in ${}^{E}Nm$ (Fig. 2.5). Of the five pairs of taxa that refute the relationship between dispersal potential and gene flow (Fig. 2.5; Table 2.1), two showed no difference when one was expected (No. 11 & 16; Table 2.1), two showed the higher dispersing species had greater population genetic structure (No. 3 & 29; Table 2.1), and one showed a slight difference when none was expected (i.e. the species shared the same *PD* [the only life-history trait with available data]; No. 13; Table 2.1).

2.5 Discussion

As a general rule, phylogeographic structure is inversely related to dispersal potential. Species with higher dispersal potential — in terms of *PD*, *F*, N_c, a co-correlate, or 'dispersal syndrome' — generally have higher gene flow than lower dispersal species; and species with similar dispersal potential generally have similar gene flow. For SDC species pairs with quantitative estimates of *PD*, *F*, or N_c, contrasts in ${}^{P}Nm$ predict the direction of contrasts in ${}^{E}Nm$ the large majority of the time (Fig. 2.5). Deviations from the prediction may be a consequence of incomplete estimates of ${}^{P}Nm$ or ${}^{E}Nm$ — e.g. data on life-history and ecology generally were scarce, mathematical underpinnings are non-linear — or suggest other mechanisms of evolution also play an interacting role in shaping population genetic structure. Below, we discuss select pairs of SDC taxa in more detail to explore the relationship between life-history traits, dispersal potential, and gene flow, as well as potential interactions with natural selection and genetic drift. Additionally, we highlight the need for more life-history and ecological information as these are, more often than not, the limiting factors in analyses.

2.5.1 Exceptions to 'the rule'

Eighty percent of SDC species pairs support the relationship between dispersal potential and gene flow based on the ecological data available in the literature. The twenty percent that are 'exceptions to 'the rule'' fall into two categories: (1) cases that probably can be explained with available data, and (2) cases that cannot be explained with currently available data.

In the first category, of the six pairs reported as "refuting" the pattern, two were from islands (No. 3 & 29, Table 2.1). In island situations, genetic drift and selection are known to be important drivers of patterns of genetic variation (Losos & Ricklefs 2009) and may overwhelm dispersal which is expected to be sporadic. Concomitantly, in both island studies, the predicted difference in dispersal did not manifest in empirical estimates of gene flow; rather, the species with higher ${}^{P}Nm$ had lower ${}^{E}Nm$. Moreover, quantitative differences in *F* and N_c of bird lice (No. 29, Table 2.1) may be overcome by traits reported qualitatively: *Icosta nigra* is volant and vagile and so may have higher relative dispersal ability than *Colpocephalum turbinatum* which is transmitted via body to body contact between hosts (Whiteman et al. 2007).

In the second category are the remaining four of the six SDC pairs reported as refuting the pattern. Two pairs — of brittlestars (*Ophiarachnella gorgonia L1* and *Ophiopeza fallax L1*; No. 7, Table 2.1) and eels (*Gymnothorax undulatus* and *Echidna nebulosa*; No. 13, Table 2.1) — were predicted to have no difference in ${}^{P}Nm$; however, F_{ST} was -0.057 v. 0.106 for the brittlestars and 0.034 (95% CI 0.007–0.064) v. 0.002 (95% CI 0.000–0.007) for the eels, which translates into large differences in ${}^{E}Nm$. Two other pairs — a marine snail versus fish (*Rapana venosa* and

Engraulis japonicas; No. 11, Table 2.1) and a frog versus lizard (*Proceratophrys boiei* and *Ischnocnema gr. ramagii*; No. 16, Table 2.1) — were predicted to differ significantly but no clear distinction was observed in ${}^{E}Nm$. But, in all four cases, life-history data were limited (Table 2.1) and it is conceivable that variation in other traits could explain the observed differences. For example, the two eels' *PD*s are similar (60–80 days; Reece 2010) and, while the measured F_{ST} appears to refute 'the rule' (mean [95%CI]: 0.034 [0.007–0.064] versus 0.002 [0.000–0.007]), both are clearly high dispersal species in theory and in reality; modest differences in F, N_c, or other traits could account for the modest differences observed in F_{ST} (Fig. 2.3). Additionally, precise estimation of Nm from F_{ST} is difficult in species with high gene flow given (in addition to concerns about non-equilibrium) the inverse relationship between F_{ST} and Nm, meaning a small error in F_{ST} translates into a much larger error in Nm (Waples 1998). Likewise, the prediction for *R. venosa* and *E. japonicas* based on *PD* might be changed by a modest difference in other life-history traits, as seen in Ayre et al. (2009) (No. 1, Table 2.1).

Of course, one might argue that cases which currently support the hypothesized 'rule' based on a single trait might change to refute the hypothesis when based on additional traits. This is a possibility; however, notwithstanding the 'file drawer problem' of publication bias (Rosenthal 1979), our approach to the literature survey should have yielded representative studies. We consider it unlikely that there is a sufficiently large systematic bias in our dataset that it would reverse the majority support for the hypothesis that increasing dispersal potential leads to reduced population genetic differentiation.

2.5.2 Contrasts between regions within realms

A proposed advantage of meta-analyses of SDC pairs is the ability to explore both general trends, such as the relationship between dispersal potential and gene flow, and how such generalities are modified by interactions specific to locations or taxa (Dawson 2014a). While the current dearth of life-history data for most species limits the scope of current analyses, two examples enable us to briefly and cautiously explore the utility of contrasts between regions within realms. These examples build on the idea that habitat discontinuity is expected to reduce gene flow (Riginos & Nachman 2001), in which case — all other things being equal — we might expect to see a smaller effect size of dispersal potential (${}^{P}Nm_c$) on realized gene flow (${}^{E}Nm_c$) due to a stronger effect of selection and/or drift.

Contrasting two pairs of marine SDC taxa — whose ${}^{P}Nm_c$ is within an order of magnitude but one occupying coastal regions, one occupying hydrothermal vent regions — we find ${}^{P}Nm_c$ accounts for ${}^{E}Nm_c$ in the pair with greater habitat connectivity, whereas ${}^{P}Nm_c$ overestimates ${}^{E}Nm_c$ in the pair with limited habitat connectivity. The first pair, a snail and limpet (*Nucella emarginata* – *Lottia austrodigitalis*, Dawson et al. 2014), occupy relatively continuous intertidal habitat along the west coast of the USA (Table 1 in Dawson et al. 2014), while the other pair, a mussel and limpet (*Bathymodiolus thermophilus* and *Eulepetopsis vitrea*, No. 12, Table 2.1), occupy patchily distributed deep-sea hydrothermal vents (Tunnicliffe et al. 1998; Vrijenhoek 2009). For the coastal pair, the ratio of empirical Nm falls within the range of predicted Nm (range of ${}^{P}Nm_c$ = 16.8–3440 [median 1728], ${}^{E}Nm_c$ = 144; ${}^{P}Nm_c \approx {}^{E}Nm_c$), whereas for the hydrothermal vent pair, the ratio of empirical Nm is three orders of magnitude less than predicted Nm (${}^{P}Nm_c$ = 5000, ${}^{E}Nm_c$ = 4; ${}^{P}Nm_c >> {}^{E}Nm_c$), suggesting the lack of habitat continuity influences the interaction between dispersal potential and gene flow. Despite a large difference in fecundity for the vent SDC pair (Table 2.1), patchiness in vent v. coastal habitats may contribute to dispersal dynamics and influence the realized rate of migration (Cowen & Sponaugle 2009).

Similar to the marine example, we compare two pairs of terrestrial SDC beetles — one occupying the Sierra Nevada mountains and the other occupying subterranean aquifers — that appear to have similar ${}^{P}Nm_c$ but differ in their degree of habitat continuity, and find that ${}^{E}Nm_c$ deviates more from ${}^{P}Nm_c$ for the pair associated with habitat that is more discontinuous. The first pair (*Nebria ingens* – *Nebria spatulata*, No. 27, Table 2.1) occupy habitat that is more continuous in the Sierra Nevada mountains in the US, relative to the second pair (*Paroster microsturtensis* – *Paroster macrosturtensis*, No. 18, Table 2.1) that occupy aquifers described as 'islands under the desert' (Cooper et al. 2002) in central Western Australia. For the Sierra Nevada pair, the ratio of

empirical *Nm* is very similar to predicted *Nm* ($^{P}Nm_c$ = 1.3, $^{E}Nm_c$ = 1.8; $^{P}Nm_c \approx {}^{E}Nm_c$), whereas for the desert aquifer pair, the ratio of empirical *Nm* is two orders of magnitude greater than predicted *Nm* ($^{P}Nm_c$ = 1.3, $^{E}Nm_c$ = 149; $^{P}Nm_c << {}^{E}Nm_c$), suggesting the difference in environment or life-history-environment interactions may contribute to the difference in observed gene flow.

For these two SDC examples we see markedly different responses to what appears to be a similar difference in habitat connectivity. The taxon pairs occupying relatively continuous habitats meet the expectation of $^{P}Nm_c \approx {}^{E}Nm_c$, whereas the two pairs occupying relatively discontinuous habitats deviate from this expectation, but in different ways. Though we do not have the sample sizes to adequately explore this relationship, it seems likely SDC meta-analyses should be able to pull out important regional signals, but more and better quality data are needed for discerning subtle differences.

2.5.3 Contrasts between marine and terrestrial SDC taxa

Among the longest-standing contrasts amongst regions of the world are those made between marine and non-marine systems (Mayr 1954; Steele 1985; Smetacek & Pollehne 1986; Paulay & Meyer 2002; Vermeij & Grosberg 2010; Vega & Wiens 2012). Particularly, dispersal and gene flow are generally thought to be pervasively higher in marine versus terrestrial systems (e.g. Neigel 1997; Carr et al. 2003). Consistent with the idea that there may be statistical differences between the two realms — but not fundamental differences, i.e. gene flow, selection, and drift operate to produce, low, intermediate, and high population structure in both realms (Dawson & Hamner 2008) — we find the majority of terrestrial species have $^{E}Nm_c > {}^{P}Nm_c$ (i.e. in the upper left triangle of positive quadrant, Fig. 2.5) whereas marine species tend to have $^{E}Nm_c \leq {}^{P}Nm_c$ (lower right triangle, Fig. 2.5), suggesting that SDC contrasts provide a mechanism for exploring factors influencing the degrees of genetic differentiation in terrestrial and marine environments.

Terrestrial SDC species pairs had *Nm* ratios that suggest differences in observed gene flow exceed differences predicted by dispersal potential alone (Fig. 2.5). Such mismatch between dispersal potential and gene flow suggests selection and/or drift may be important; disequilibrium among dispersal, mutation, and drift also may be distributed heterogeneously across the landscape or between realms (Grosberg & Cunningham 2001) and thus may variously accentuate or diminish contrasts. Coalescent age does not seem to explain this pattern as we see a range of ages in both realms (Table 2.1). Considering the effect of geographically varying selection, species with reduced gene flow should exhibit more local adaptation than those with elevated gene flow (Holt & Gaines 1992). Indeed, isolation by environment (IBE) is common in terrestrial taxa, whereas unrestricted gene flow is nearly twice as common in the marine realm (Sexton et al. 2014). Thus, reduced gene flow may tend to allow disproportionately greater local adaptation in the lower dispersal species of an SDC pair and thus accentuate the contrast in observed $^{E}Nm_c$. Likewise, terrestrial taxa persist at generally lower densities than marine taxa, putatively due to selective advantages of lower costs of mobility (Vermeij & Grosberg 2010). For species that are less abundant (and less mobile), environmental stochasticity can have more pronounced effects on metapopulation dynamics (Watson et al. 2012). Greater isolation may then act to elevate the roles of selection and/or drift in the terrestrial versus marine realm, commensurately affecting $^{E}Nm_c$.

However, such things might also occur to some extent in marine systems. Some stochastic processes may be more likely to occur in marine animals than in terrestrial animals: e.g. fecundity and population size are often larger in the marine environment (Strathmann 1990) favoring unpredictable Lagrangian transport of large plumes of larvae and ‘sweepstakes’ recruitment (*sensu* Hedgecock 1994). Reproductive traits that influence population genetic structure may be more similar in terrestrial plants and marine invertebrates than either is with terrestrial animals (Palumbi 1992). Exceptionally isolated habitats and populations do exist in the marine realm as in the terrestrial realm (Dawson & Hamner 2005; Gillespie & Clague 2009; Dawson et al. 2016). Both realms possess the full range from restricted to high gene flow and from small to large $^{E}Nm_c$ (Fig. 2.3). While we recognize exceptions to the general rule that ‘gene flow $\propto$ dispersal potential’ may be reasonably common (~20%), we argue it is the exceptions from which we have the most to gain in terms of furthering our understanding of patterns of

population genetic structure — if studied in an appropriate framework. The previously discussed mountain v. aquifer and coastal v. vent examples suggest the SDC framework could provide the context to rigorously test the relative influence of habitat continuity and whether discontinuity acts to amplify differences in ${}^{E}Nm_c$ in the terrestrial realm relative to that predicted by ${}^{P}Nm_c$, while diminishing differences in ${}^{E}Nm_c$ in the marine realm.

2.5.4 Considerations for future studies

Using the SDC framework to test hypotheses relating life-history traits that influence dispersal potential to gene flow minimizes confounding factors that otherwise cloud inference (e.g. demonstrated in Fig. 2.6) (Dawson 2014a). The origins of the approach are rooted in sympatric sister species comparisons (Dawson et al. 2002; Hickerson et al. 2010; Dawson 2012) and expanded to include species that are, like sister species, synchronously diverging (Dawson 2014a; Dawson et al. 2014). However, SDC analyses still can be improved in several ways: by incorporating species distribution models and paleodistributions, exploring the mathematical non-linearities associated with dispersal potential and empirical estimates of gene flow, and by collecting more and better quality ecological data.

On the first count, integrating species distribution models (SDMs) and paleodistributions allows one to independently corroborate (or refute) modern distributional, and historical demographic, inferences about the degree of co-distribution between species in the past and present (Dawson 2014a). Better quantifying the duration of co-distribution is important because species' histories can shape current distributions of genetic variation and can be complex (Knowles 2009). Few of the studies reviewed here incorporated such analyses (but see Schoville et al. 2012; Kuo et al. 2014), and although such studies are rapidly increasing in number (Gavin et al. 2014) they remain much under-employed (Riddle 2016).

Second, while a generally desirable property of *Nm* contrasts is that they reflect the *relative* magnitudes of differences in predicted and observed migration, different combinations of predicted and empirical *Nm* can lead to similar ratios of ${}^{E}Nm_c$ and ${}^{P}Nm_c$. Moreover, the relationship between life-history traits and population genetic structure may be non-linear. Interpreting SDC contrasts therefore can be challenging if appropriate contextual information is lacking. The conceptual appeal of contrasting sympatric synchronously diverging taxon-pairs within a multiple regression framework to estimate causes and effects (Hickerson et al. 2010) may mask multiple analytical complexities that likely require formulation and evaluation of multiple competing models (Hickerson et al. 2010). Nonetheless, our initial comparison provides a useful starting place to explore additional questions. For example, we do find terrestrial SDC taxa exhibit ${}^{E}Nm_c > {}^{P}Nm_c$ more often than marine SDC taxa; what (if anything) is the biological significance?

Finally, and perhaps most importantly, more and better trait data are required. Only a single trait could be estimated in many of the cases we considered here (Table 2.1), whereas it is the cumulative influence of multiple traits that determine gene flow (Clobert et al. 2009; Dawson et al. 2014; Dawson 2014b). For SDC pairs for which at least three traits were quantitatively assessed, *Nm* contrasts between dispersal potential and F_{ST} may adequately account for the relative magnitudes of differences in observed gene flow (Dawson et al. 2014). With multi-trait data in hand, we might better understand how life-history traits interact in dispersal syndromes, and identify emergent properties of complex traits such as dispersal potential. Though, comparison between realms will remain difficult as long as marine studies are under-represented in the literature (Dawson et al. 2013; Whittaker 2014). In our opinion, the major roadblock for understanding dispersal and population genetic structure is no longer the cost or logistics of large-scale genetic analyses, nor available methods, the epistemological framework, nor theory, but rather a dearth of high quality comprehensive ecological data across multiple species, habitats, and realms.

A carefully designed study is one component of rigorous statistical analysis (Wasserstein et al. 2016). SDC comparisons provide a rigorous method for disentangling the factors driving patterns of genetic variation in the marine and non-marine realms. The current lack of ecological data and studies employing SDC species prevented us from exploring effect sizes further, however we found broad support for a relationship between dispersal potential and gene flow, i.e.

that higher dispersal potential is associated with higher gene flow (irrespective of modifying interactions with drift and selection).

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2.7 Tables

Table 2.1 Synchronously diverging co-distributed (SDC) species by realm. The predicted relative F_{ST} is reported for each pair and is based on how known life-history traits relate to dispersal potential; F_{ST} (or analog) is reported and whether a positive relationship between dispersal potential and gene flow is supported.

Realm	SDC pair ID	SDC reference (additional life history references)	Geographic region	DNA locus	SDC pairs	Divergence time (confidence interval)	Dispersal potential: population size (N_C), fecundity, and other dispersal related traits	Prediction	Genetic differentiation: F_{ST}, Φ_{ST}, or G_{ST}†	Result
Marine	**1**	Ayre *et al* ., 2009 (Stewart *et al.,* 2007)	Southeast Australian coast	COI	*Cellana tramoserica*	185–633 (104–1160) Ka	broadcast spawn; Nc>*C. polymerus*; pelagic duration 48 hours	**lower F_{ST}**	0.335*	**Supported**
					Catomerus polymerus	209–463 (167–576) Ka	eggs brooded; Nc< *C. tramoserica* ; pelagic duration 16 days	**higher F_{ST}**	0.91*	
	2	Baums *et al* ., 2014	Central Pacific	COI	*Calcinus haigae*	0.83 (0.55–1.14) Ma	long pelagic duration; Nc not significantly different	**similar F_{ST}**	0.004	**Supported**
					Calcinus laevimanus	0.69 (0.48–0.94) Ma	long pelagic duration; Nc not significantly different	**similar F_{ST}**	0.006*	
	3	Goldstien, 2005 (Goldstien *et al* ., 2006; Dunmore & Schiel, 2000; Creese & Ballantine, 1983)	New Zealand	cyt*b*	*Cellana ornata*	0.200–0.300 Ma	pelagic duration 3–11 days; fecundity = 230000	**lower F_{ST}**	0.829*	Refuted
					Cellana radians	0.200–0.300 Ma	pelagic duration 3–11 days; fecundity = 105000	**higher F_{ST}**	0.142*	
	4	Hoareau *et al* ., 2013	Southwest Indian Ocean	COI	*Ophiocoma brevipes*	0.1371 (0.07124–0.2149) Ma	planktotrophic larvae	**similar F_{ST}**	0.01847	**Supported**
					Ophiocoma erinaceus	0.1620 (0.0922–0.2498) Ma	planktotrophic larvae	**similar F_{ST}**	0.07006	
	5	Hoareau *et al* ., 2013	Southwest Indian Ocean	COI	*Ophiocoma cynthiae*	0.3293 (0.1699–0.5238) Ma	planktotrophic larvae	**similar F_{ST}**	0.14020*	**Supported**
					Ophiocoma scolopendrina	0.3148 (0.1648–0.4993) Ma	planktotrophic larvae	**similar F_{ST}**	0.10851*	
	6	Hoareau *et al* ., 2013	Southwest Indian Ocean	COI	*Ophiocoma erinaceus*	0.1620 (0.0922–0.2498) Ma	planktotrophic larvae	**lower F_{ST}**	0.07006	**Supported**
					Ophioplocus imbricatus	0.1288 (0.0626–0.2142) Ma	lecithotrophic larvae	**higher F_{ST}**	0.31463*	

	7	Hoareau *et al* ., 2013	Southwest Indian Ocean	COI	*Ophiarachnella gorgonia L1*	0.3384 (0.0995–0.6739) Ma	lecithotrophic larvae	**similar F_{ST}**	-0.05653	Refuted
					Ophiopeza fallax L1	0.2974 (0.0888–0.6079) Ma	lecithotrophic larvae	**similar F_{ST}**	0.10647	
	8	Marko *et al* ., 2010	Northeast Pacific	COI	*Katharina tunicata*	0.425 (0.398–0.452) Ma population expansion	planktonic larvae	**lower F_{ST}**	-0.037	**Supported**
				mtCR	*Xiphister atropurpureus*	0.437 (0.374–0.499) Ma population expansion	benthic larvae	**higher F_{ST}**	0.296*	
	9	Ni *et al* ., 2014	Western Pacific	cyt*b*	*Larimichthys polyactis*	78.8 (59–248) Ka	pelagic duration 30 days	**lower F_{ST}**	0	**Supported**
				COI	*Octopus ocellatus*	91.0 (14.5–154) Ka	pelagic duration 0 days	**higher F_{ST}**	0.87*	
	10	Ni *et al* ., 2014	Western Pacific	cyt*b*	*Pampus argenteus*	63.5 (41.4–96.2) Ka	pelagic duration 30 days	**lower F_{ST}**	0	**Supported**
				COI	*Octopus ocellatus*	91.0 (14.5–154) Ka	pelagic duration 0 days	**higher F_{ST}**	0.87*	
	11	Ni *et al* ., 2014	Western Pacific	16S	*Rapana venosa*	311 (43–1465) Ka	pelagic duration 21–42 days	**lower F_{ST}**	0.01	Refuted
				COI	*Engraulis japonicus*	140 (36.5–577) Ka	pelagic duration 14 days	**higher F_{ST}**	0.02	
	12	Plouviez *et al* ., 2009	East Pacific Rise & Galapagos Rift	COI	*Bathymodiolus thermophilus*	1.6 Ma	planktotrophic larvae; fecundity = 1000000	**lower F_{ST}**	0.255*	**Supported**
					Eulepetopsis vitrea	1.6 Ma	lecithotrophic larvae; fecundity = 200	**higher F_{ST}**	0.578*	
	13	Reece, 2010 (Reece *et al.,* 2011)	Indo-Pacific	cyt*b*, COI	*Gymnothorax undulatus*	6.05 (3.5–8.6) Ma	pelagic duration 60–80 days	**similar F_{ST}**	0.034 (95% CI 0.007–0.064)	Refuted
					Echidna nebulosa	6.65 (4.2–9.1) Ma	pelagic duration 60–80 days	**similar F_{ST}**	0.002 (95% CI 0.000–0.007)	
	14	Teske *et al* ., 2011	Southeast Aftrica	COI	*Siphonaria concinna*	0.36 ±0.01 (0.06–3.87) Ma	planktonic disperser	**lower F_{ST}**	0.07 (95% CI 0.03–0.10)	**Supported**
					Siphonaria nigerrima	0.26 ±0.01 (0.21–0.45) Ma	direct developer	**higher F_{ST}**	0.30 (95% CI 0.22– 0.39)	
Terrestrial	**15**	Bagley & Johnson, 2014 (Lucinda, 2003; Froese & Binohlan, 2000; Bussing, 1998; Baensch & Riehl, 1985)	Central America	cyt*b*	*Alfaro cultratus*	1.398 (0.460–4.272) Ma	lifetime reproductive output 244–7314; relatively larger Nc	**lower F_{ST}**	0.73-0.80*	**Supported**
					Xenophallus umbratilis	1.842 (0.656–5.605) Ma	lifetime reproductive output 224–748; relatively smaller Nc	**higher F_{ST}**	0.99*	

16	Carnaval *et al* ., 2007 (Giaretta *et al.,* 2008)	Eastern Brazil	cyt*b*, ND2	*Proceratophrys boiei*	132.898 (65.593–299.448) Ka	larval phase; fecundity = 1296	**lower F_{ST}**	0.72 (95% CI 0.60–0.85)	Refuted
				Ischnocnema gr. ramagii	77.394 (24.497–412.987) Ka	direct developing; fecundity = 21.5	**higher F_{ST}**	0.8 (95% CI 0.69–0.91)	
17	Cook *et al* ., 2014 (Juan-Jordá *et al* ., 2013; Allen *et al*., 2002; Winemiller & Rose, 1992; Allen, 1989)	Northern Australia	ATPase 6/8	*Pseudomugil gertrudae*	1.073 (0.502–1.645) Ma	length 3.8 cm (size ∝ fecundity)	**similar F_{ST}**	0.815*	**Supported**
				Denariusa australis	1.140 (0.452–1.827) Ma	length 4.5 cm, commonly 3.5 cm (size ∝ fecundity)	**similar F_{ST}**	0.826*	
18	Guzik *et al* ., 2009	Central Western Australia	COI	*Paroster microsturtensis*	0.95 (0.83–1.07) Ma	relatively larger Nc; body size 1.8 mm (favorable for dispersal given environment)	**lower F_{ST}**	0.01	**Supported**
				Paroster macrosturtensis	0.93 (0.66–1.19) Ma	relatively smaller Nc; body size 4 mm (less favorable for dispersal given environment)	**higher F_{ST}**	0.6*	
19	Hosner *et al* ., 2014 (Fishpool & Tobias, 2016; Cheke *et al.,* 2001)	Philippines	ND2	*Prionochilus olivaceus*	1.1 (0.6–1.6) Ma	fecundity = 1–4	**similar F_{ST}**	0.92*	**Supported**
				Pycnonotus urostictus	0.95 (0.6–1.3) Ma	fecundity = 3	**similar F_{ST}**	0.90*	
20	Kirchman & Franklin, 2007 (Speakman, 2005)	Vanuatu	Domain I mtCR	*Chalcophaps indica*	11.790 (4.740–21.410) Ka	lifetime reproductive output 36–176	**lower F_{ST}**	-0.025 (pairwise range -0.096–0.042)	**Supported**
				Rhipidura spilodera	13.100 (4.100–26.470) Ka	lifetime reproductive output 15–31	**higher F_{ST}**	0.336 (pairwise range 0.181–0.545)	
21	Kirchman & Franklin, 2007 (Taylor, 2010; Speakman, 2005)	Vanuatu	Domain I mtCR	*Gallirallus philippensis*	16.660 (4.980–32.150) Ka	lifetime reproductive output 104–574	**lower F_{ST}**	0.026 (pairwise range -0.087–0.046)	**Supported**
				Rhipidura spilodera	13.100 (4.100–26.470) Ka	lifetime reproductive output 14–29	**higher F_{ST}**	0.336 (pairwise range 0.181–0.545)	
22	Kuo *et al* ., 2014	Taiwan	cyt*b*	*Murina gracilis*	558 (346–822) Ka	extreme site fidelity and limited natal dispersal	**similar F_{ST}**	0.05*	**Supported**
				Murina recondita	469 (279–699) Ka	extreme site fidelity and limited natal dispersal	**similar F_{ST}**	0.06*	
23	Qu & Lei, 2009	Tibetan plateau	COI	*Onychostruthus taczanowskii*	56–160 (52–220) Ka	strong flight ability and a tendency to seasonal altitudinal movements	**lower F_{ST}**	0.02725	**Supported**
				Pseudopodoces humilis	56–153 (34– 200) Ka	very active on the ground, but flies only rarely and weakly	**higher F_{ST}**	0.21938*	

24	Qu *et al* ., 2010	Tibetan plateau	cyt*b*, COI, ND2	*Pyrgilauda blanfordi*	0.22 (0.11–0.34) Ma	strong flight and a tendency to altitudinal migration	**lower F_{ST}**	0.0314	**Supported**
				Eremophila alpestris	0.249 (0.17–0.348) Ma	habitat specific and have restricted dispersal ability	**higher F_{ST}**	0.1133*	
25	Qu *et al* ., 2010	Tibetan plateau	cyt*b*, COI, ND2	*Pyrgilauda blanfordi*	0.22 (0.11–0.34) Ma	strong flight and a tendency to altitudinal migration	**lower F_{ST}**	0.0314	**Supported**
				Montifringilla adamsi	0.16 (0.089–0.25) Ma	habitat specific and have restricted dispersal ability	**higher F_{ST}**	0.1302*	
26	Schoville *et al* ., 2012 (Honěk 1993)	Sierra Nevada, US	COI	*Nebria ingens*	48.544 (28.415–74.353) Ka	length 12–15 mm (size ∝ fecundity)	**lower F_{ST}**	0.676*	**Supported**
				Nebria ovipennis	37.246 (20.518–59.600) Ka	length 9.5–12 mm (size ∝ fecundity)	**higher F_{ST}**	0.811*	
27	Schoville *et al* ., 2012 (Honěk, 1993)	Sierra Nevada, US	COI	*Nebria ingens*	48.544 (28.415–74.353) Ka	length 12–15 mm (size ∝ fecundity)	**lower F_{ST}**	0.676*	**Supported**
				Nebria spatulata	51.817 (34.974–72.997) Ka	length 9.5–12 mm (size ∝ fecundity)	**higher F_{ST}**	0.788*	
28	Whiteman *et al* ., 2007	Galapagos Islands	COI	*Colpocephalum turbinatum*	126 (51–254) Ka	moderate relative dispersal ability (horizontal transmission); mean abundance 74.59 (58–89.98)	**lower F_{ST}**	0.73*	**Supported**
				Degeeriella regalis	126 (51–254) Ka	low relative dispersal ability (vertical transmission during brooding); mean abundance 14.36 (11.05–17.51)	**higher F_{ST}**	0.85*	
29	Whiteman *et al* ., 2007	Galapagos Islands	COI	*Icosta nigra*	126 (51–254) Ka	high relative dispersal ability (volant & vagile); mean abundance 1.49; lower fecundity	**higher F_{ST}**	0.63*	Refuted
				Colpocephalum turbinatum	126 (51–254) Ka	moderate relative dispersal ability (horizontal transmission); mean abundance 74.59 (58–89.98); higher fecundity	**lower F_{ST}**	0.73*	
30	Zhang *et al* ., 2013	Subtropical China	ndhJ-trnF & atpI-atpH	*Fagus lucida*	6.38 (2.29–13.25) Ma	Similar life history; relatively larger Nc	**lower F_{ST}**	0.705 ± 0.067†	**Supported**
				Fagus longipetiolata	6.38 (2.29–13.25) Ma	Similar life history; relatively smaller Nc	**higher F_{ST}**	0.936 ± 0.036†	

* Genetic differentiation significant at $P < 0.05$.

Notes: Four additional SDC pairs were excluded from the meta-analysis for lack of independence (*i.e.* when three species were SDC, one of the three possible pairs were randomly selected for exclusion). Had these additional pairs — *Ophiocoma brevipes* & *Ophioplocus imbricatus* (*O.b.-O.i.*) (Hoareau *et al.,* 2013); *Nebria ovipenni*s & *Nebria spatulata* (*N.o.-N.*s.) (Scholville *et al.,* 2012); *Chalcophaps indica* & *Gallirallus philippensis* (*C.i.-G.p.*) (Kirchman & Franklin, 2007); *Degeeriella regalis* & *Icosta nigra* (*D.r.-I.n.*) (Whiteman *et al.,* 2007) — been included, three would support (*O.b.-O.i.*, *N.o.-N.p.*, *C.i.-G.p.*) and one would refute (*D.r.-I.n.*) the relationship between dispersal potential and gene flow.

2.8 Figures

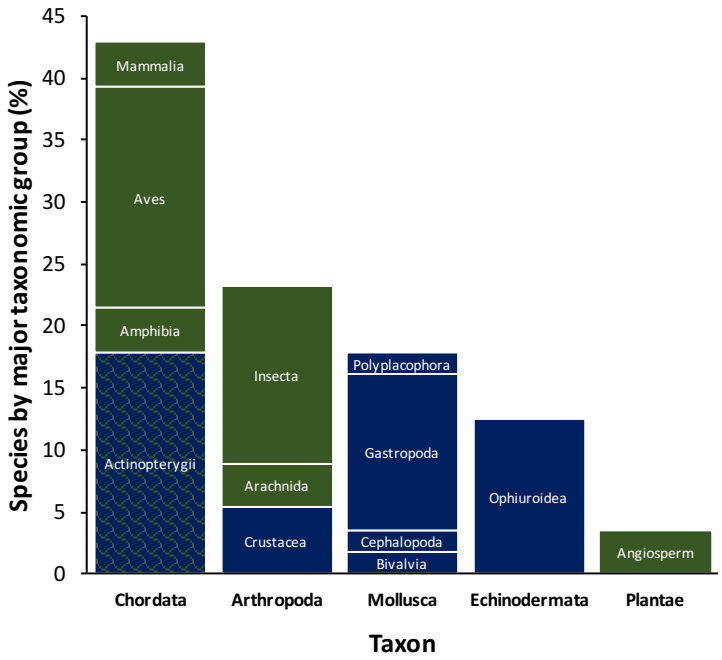

Figure 2.1 Summary of literature survey results satisfying synchronously diverging and co-distributed (SDC) criteria showing the proportion of species representing major taxonomic groups by realm (blue = marine, green = terrestrial or freshwater).

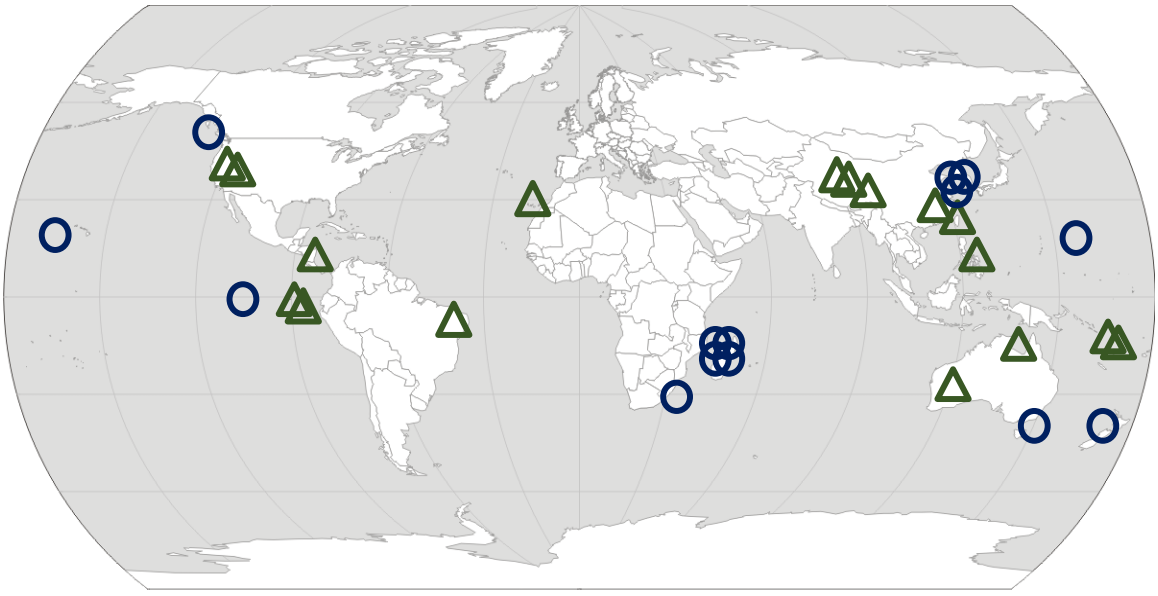

Figure 2.2 Geographic locations of synchronously diverging and co-distributed (SDC) species pairs. Blue circles correspond to marine pairs and green triangles correspond to terrestrial or freshwater pairs.

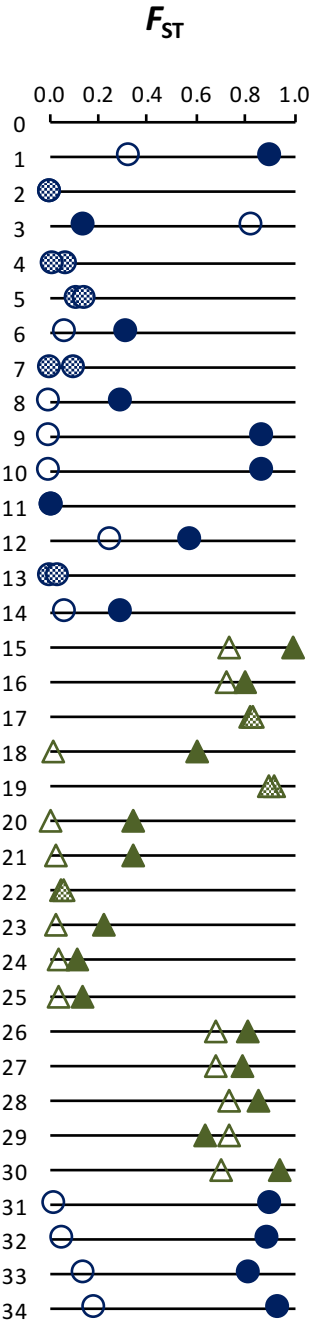

Figure 2.3 F_{ST} values for each synchronously diverging and co-distributed (SDC) species pair (circles = marine, triangles = terrestrial/freshwater). Numbers 1–30 correspond to SDC pairs described in Table 2.1. Numbers 31–34 correspond to additional SDC pairs from Dawson et al. (2002, 2014) included for subsequent comparison. Open shapes represent the taxon in each SDC pair with higher predicted dispersal based on life-history traits (and expected to correspond to lower F_{ST}); solid shapes correspond to the taxon with lower predicted dispersal (and expected higher F_{ST}). Patterned shapes represent pairs of taxa that are expected to have the same dispersal potential (and F_{ST}) based on known life-history traits.

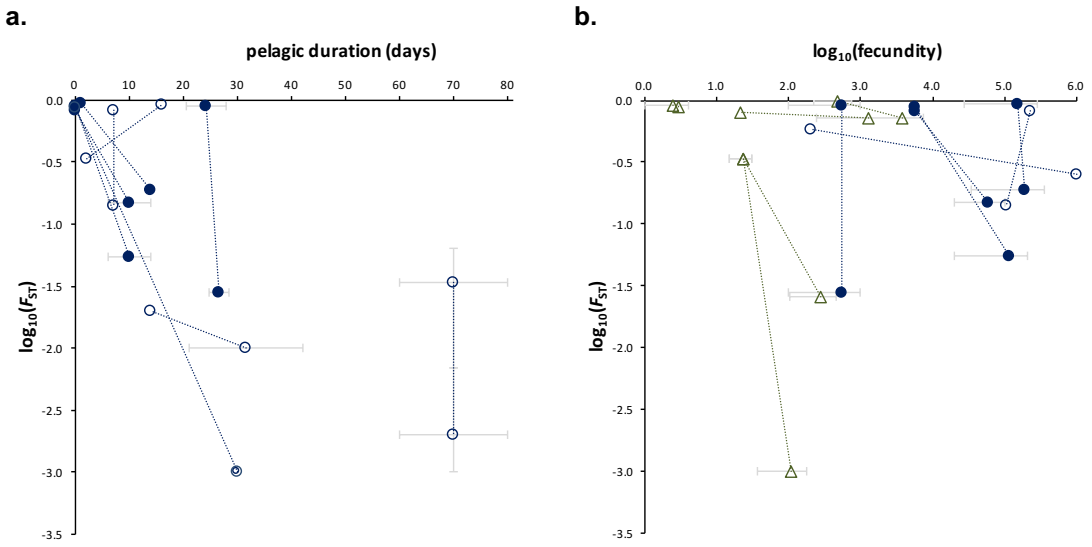

Figure 2.4 The relationship between select life-history traits — (a) pelagic duration, *PD*, and (b) fecundity, *F* — and population genetic structure, F_{ST}, for synchronously diverging and co-distributed (SDC) species pairs from this meta-analysis (open symbols) and for 4 additional SDC pairs from Dawson (2012) and Dawson et al. (2014) (closed symbols). For fecundity, lifetime reproductive output is used when available, otherwise annual fecundity is reported; the metric used is consistent within SDC pairs. Each pair of points connected by a dotted line represents an SDC pair (marine = blue circles; terrestrial = green triangles). Horizontal error bars represent the range of recorded values for pelagic duration or fecundity for each species and vertical error bars are 95% confidence intervals for F_{ST}, if this information was available.

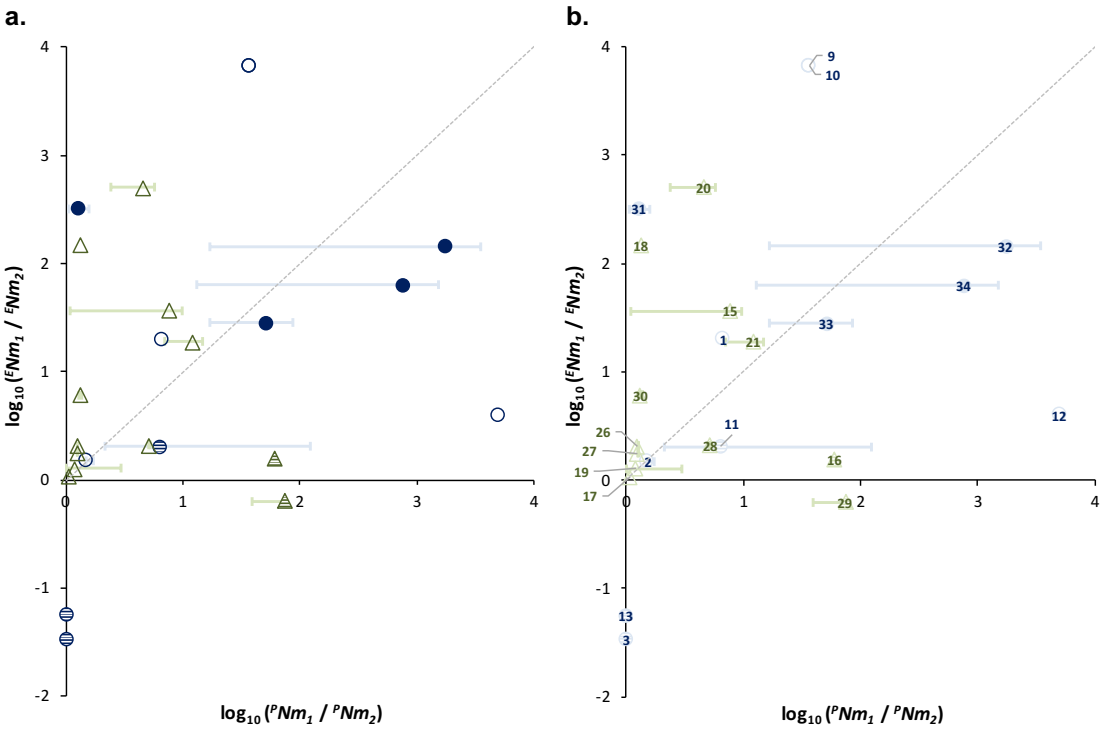

Figure 2.5 (a) Comparison of the relative estimated numbers of migrants per generation (*Nm*) predicted from dispersal potential (x-axis) and inferred empirically from F_{ST} or an F_{ST}-analog (y-axis) for pairs of synchronously diverging and co-distributed (SDC) species. Blue circle = marine; green triangle = terrestrial/freshwater. Striping indicates SDC pairs classified as refuting the predicted relationship (Table 2.1). In most cases, only a single trait could be assessed, except for two pairs for which two traits could be assessed. The dashed gray line represents the relationship ${}^{P}Nm_1 / {}^{P}Nm_2 \approx {}^{E}Nm_1 / {}^{E}Nm_2$ and is the simple theoretical expectation that differences in dispersal potential lead to corresponding differences in population genetic structure. The four solid-filled marine points represent SDC species contrasts from Dawson et al. (2002) (using *F* and *PD* [Spies & Steele 2016]) and Dawson et al. (2014) (using *F*, N_c, and *PD*) to calculate *Nm* contrasts. (b) Replicate of (a) identifying specific synchronously diverging and co-distributed species pairs that correspond with Figure 3 and Table 2.1. The four solid-filled marine points represent SDC species not recovered in our literature search, but included here for comparison: No. 31 (*Clevelandia ios* – *Eucyclogobius newberryi*) from Dawson et al. (2002) using *F* and *PD* (Spies & Steele 2016) and No. 32–34 (*Nucella emarginata* – *Lottia austrodigitalis*, *Nucella ostrina* – *Lottia digitalis*, *Silvetia compressa* – *Lottia scabra*) in Dawson et al. (2014) using *F*, N_c, and *PD* to calculate *Nm* contrasts.

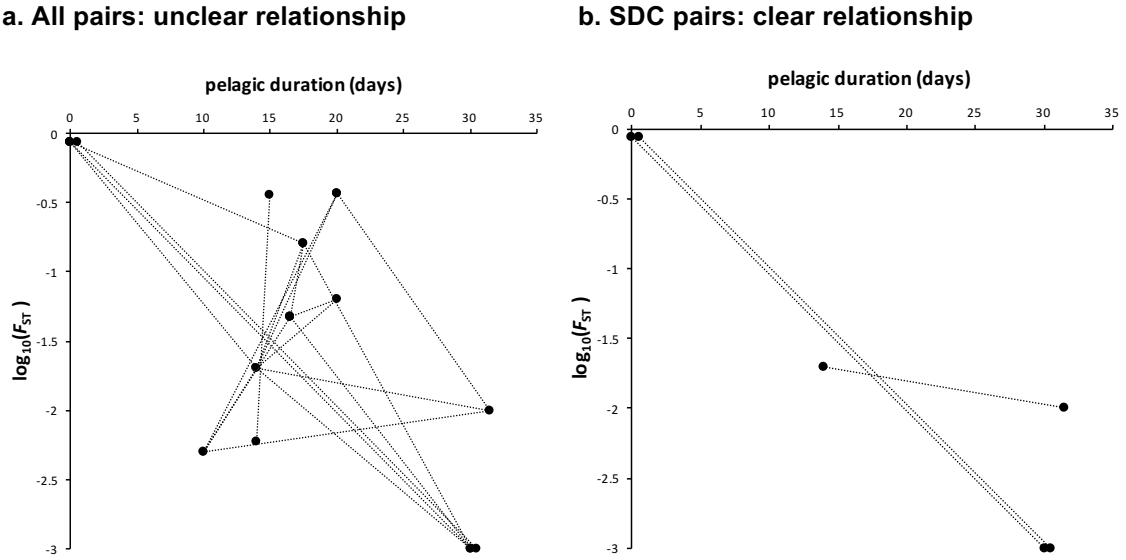

Figure 2.6 An illustration of the different outcomes when dispersal potential, in this case pelagic duration, and population genetic differentiation are interpreted using (a) all pairs of taxa, regardless of evolutionary duration of spatial distribution, and (b) pairs of synchronously diverging and co-distributed (SDC) taxa; n.b. three SDC pairs are present, of which two are slightly offset because they have the same values. Each taxon pair is represented by two points connected by a dotted line. The hypothesis is that as dispersal potential increases, F_{ST} will decrease (i.e. gene flow will increase). Plotted using data from Ni et al. (2014).

Chapter 3. Ecological and evolutionary evidence for a relationship between potential and realized dispersal

3.1 Abstract

Dispersal potential should influence gene flow but studies of pelagic duration, a common proxy for marine dispersal potential, have often reported poor correlation with F_{ST}. Explanations for this discrepancy may include poor study design or inadequate information in complex settings. To overcome these limitations, we used a multi-species mortality event as a large-scale (100km) natural experiment to test the hypothesis that species with life-history characteristics favoring greater dispersal potential — e.g. longer pelagic duration and higher fecundity — have greater realized dispersal. Three species of differing dispersal potential were surveyed annually across a 'kill zone' and adjacent coastline to quantify abundance and distribution of recruits and assign these recruits to likely parental sources; the significant reduction of adult populations within the kill zone simplified this usually challenging problem. We found high dispersal taxa showed higher gene flow than low dispersal taxa. Species with higher dispersal potential re-colonized a broader extent of the impacted range, and did so more quickly, than species with lower dispersal potential. Moreover, taxa with higher dispersal potential exhibited more immigration (80–85%), with predominant north to south dispersal of immigrants. The low dispersal species showed high local recruitment (78–95%) with low immigration. Our estimates of dispersal potential reconcile with estimates of population structure because they link ecological with evolutionary perspectives and in that context demonstrate that a suite of interacting species' attributes (e.g. pelagic duration, fecundity, and population size) influence realized dispersal. An integrative eco-evolutionary approach is needed to further develop a more explicit predictive framework to test hypotheses of the effect of dispersal-linked life-history traits on realized dispersal and population genetic differentiation.

3.2 Introduction

The range of physical and biological attributes that influence connectivity in coastal marine systems is becoming clearer (e.g. Sponaugle et al. 2002; Pineda et al. 2007; Cowen & Sponaugle 2009; Morgan et al. 2009a); however, the ways in which they interact to shape patterns of genetic structure remains enigmatic. Reconciling geographic and temporal patterns of variation is particularly challenging conceptually and practically, though Bohonak (1999) identified a positive relationship between dispersal potential and gene flow across diverse taxa. More recently, attempts to link ecological scales to evolutionary scales raise questions about the generality of, for example, the expected link between pelagic duration, dispersal potential, and population genetic structure within species (D'Aloia et al. 2015) and across species (e.g. Shanks 2009). Phylogeographic studies, which integrate migration, selection, and drift over millennia or more, can provide rigorous comparative evidence of the predicted influence of dispersal potential on population genetic structure (e.g. Dawson et al. 2002, 2014; Dawson 2012) but their direct relationship to ecological dispersal is remote. Therefore, it could be that focusing only on spatio-temporal snapshots of patterns of population genetics and recruitment can be misleading due to high variance between years (Sun & Hedgecock 2017).

On ecological scales, multi-year studies find recruitment rates vary substantially across space, time, and species (Broitman et al. 2008; Toonen & Grosberg 2011) and that source populations can vary depending on spawning season or currents (Kordos & Burton 1993). The result, unexplained patterns of recruitment where cohorts of larvae are genetically distinct both from nearby adult populations and other larval cohorts, termed chaotic genetic patchiness (Johnson & Black 1982, 1984), is a common feature of meroplanktonic species (Eldon et al. 2016). While chaotic genetic patchiness may be pervasive, it is the outcome of a finite set of factors (Eldon et al. 2016) and can hold ecological significance (Selkoe et al. 2010). Additionally, sweepstakes reproductive success (Hedgecock 1994) is common in a variety of marine taxa, potentially elevating the role of genetic drift (Hedgecock & Pudovkin 2011). Despite the extensive list of interacting physical and biological attributes acting to complicate the system, the lack of

short-term concordance between dispersal potential, direct (e.g. genetic assignment tests of recruits) and indirect (e.g. F_{ST} of adult population) measures of connectivity does not preclude a significant long-term relationship (Hedgecock 2010).

While predicting the specific trajectory and ultimate fate of dispersing larvae at a particular time is currently impossible, it is necessarily the accumulation of such recruitment events that determines the genetic similarity between locations and connectivity of populations. As such, an integrated mechanistic eco-evolutionary approach for predicting recruitment is needed, as no single predictor can account for the full dispersal potential of a species — e.g. pelagic duration (Shanks 2009; Riginos 2011) — and failing to include particular traits — e.g. fecundity (Castorani et al. 2017) — can lead to over- (or under-) estimation of potential connectivity. Dispersal potential itself is likely comprised of multiple complex traits — e.g. *PD* within species is normally distributed (D'Aloia et al. 2015) suggesting it is multilocus — potentially in 'dispersal syndromes' (Dawson 2014a). By taking into account multiple life-history traits, e.g. pelagic duration, census population size, and fecundity, it is possible to bracket long-term successful larval dispersal and subsequent gene flow (Dawson et al. 2014). Our understanding of recruitment has been advanced by genetic studies of single species (e.g. Johnson & Black 1984; Kordos & Burton 1993; D'Aloia et al. 2015; Puritz et al. 2016) and ecological studies across multiple species and years (e.g. Broitman et al. 2008; Morgan et al. 2009a). However, to clarify how dispersal potential translates to realized dispersal and genetic connectivity and determine whether generalities exist additional genetic studies that incorporate multiple species (D'Aloia et al. 2015), multiple years (Hellberg et al. 2002) and multiple approaches (e.g. direct and indirect genetic measures) are needed (Hedgecock 2010) to bridge the eco-evolutionary gap.

An opportunity simplifying nature's usual complexity, which can mask relationships, occurred in 2011, when a massive multi-species invertebrate die-off provided a virtual 'blank slate' on which to examine ecological and genetic consequences of dispersal in multiple taxa. Species with various dispersal potentials were affected (Table 3.1), including: *Strongylocentrotus purpuratus*, *Pisaster ochraceus*, and *Leptasterias* sp. (Jurgens et al. 2015). This natural removal experiment — along ~100 km of coast in north central California — provided a clear comparison of larval dispersal and recruitment as well as documenting the likely source of propagules. By integrating ecological and evolutionary approaches we explore the relationship between life-history characteristics, dispersal, and the distribution of genetic variation in the years immediately following the mass mortality event. The reduction in the adult population in the affected region simplifies this system and allows us to track more easily annual recruitment from outside into the blank slate. To test the hypothesis that species with life-history characteristics favoring greater dispersal potential — e.g. longer pelagic duration and higher fecundity (Table 3.1) — have greater realized dispersal we use (1) the rate of recolonization of the affected region over three years (Figure 3.1) and (2) genetic assignment tests of new recruits to likely source populations over two years.

3.3. Materials and methods

3.3.1 Estimating dispersal potential

Relative dispersal potential for *S. purpuratus*, *P. ochraceus*, and *Leptasterias* sp. was estimated by converting quantitative life-history traits — pelagic duration (*PD*), fecundity (*F*), and census population size (N_c) (Table 3.1) — into predicted number of migrants (*Nm*) following Dawson et al. (2014). *PD* was converted to *Nm* by way of the regression $\log(F_{ST}) = -0.043$ (no. of days) – 0.315 from Doherty et al. (1995), followed by $Nm = (1/F_{ST} - 1)/4$. *F* and N_c were each used as proportional estimates of *Nm*. The product of relative *Nm* taken from *PD*, *F*, and N_c for each pair of species was used to estimate overall relative difference in overall dispersal potential between each pair of taxa — *S. purpuratus–P. ochraceus*, *P. ochraceus–Leptasterias* sp., *S. purpuratus–Leptasterias* sp. — in terms of the lower disperser.

3.3.2 Ecological surveys

We surveyed 17 sites annually starting in 2012, the first recruitment season following the mortality event (Table 3.2). At each location, we sampled two rocky intertidal areas, usually one on either side of a beach or headland and separated by approximately 100 meters. To estimate abundance we used quadrats to target juveniles and small sea stars and transects to target larger adult *P. ochraceus* and *S. purpuratus*. Size was recorded per individual: radius for *P. ochraceus* (center to arm tip), diameter for *Leptasterias* sp. (arm tip to opposite arm tip), and diameter of the test for *S. purpuratus*. All specimens were georeferenced using a Garmin C60X GPS (±3 m precision). Five additional reference sites to the north and south of the mortality zone were sampled less frequently (Table 3.2). Data were reported as the number of individuals per square meter.

Quadrats: We exhaustively searched 32–40 one-meter square quadrats (composed of four contiguous 0.25x0.25 m quadrats) per site (i.e. 16–20 per each of 2 areas, depending on sea conditions, tidal height, etcetera), recording GPS waypoint, time, percent cover of major substrate and macrophytes, and abundances and sizes of each target species for each quadrat. Quadrat locations were selected by first finding one of the target habitat types (based on preliminary surveys of recruit distributions) — surf grass, low-zone red algae, coralline turf, cobble or boulder field, or urchin pools with pits either empty or occupied — selecting a starting point haphazardly, and then using a random numbers table (range of 1-10 meters) to choose remaining quadrat locations.

Transects. To provide more thorough estimates of site-specific density for the large, conspicuous *P. ochraceus* and *S. purpuratus*, we conducted timed, GPS-tracked, 2m or 4m wide swath transects nested in each of two areas at each site. From a distance, an approximate starting point and orientation (with landmarks) for the starting transect was selected. Transects ran from the most shoreward to the most seaward possible suitable habitat at approximately 10m intervals along shore, particularly targeting the low intertidal zone when the tide was maximally receded, with as many transects being done as permitted by the tide. The GPS was set to auto-record a trackpoint every 6 seconds. To reduce error in estimates of the length and position of swathes (commonly ±3 m for civilian GPS), we smoothed tracks by averaging across windows of two consecutive trackpoints, and removed outlying trackpoints that led to a Euclidean distance ≥ 8 meters, since these were likely due to temporary drop-outs in satellite signal. We calculated total transect search area by multiplying the adjusted transect length by swath width.

Statistical analyses of recruitment. Given the high number of zero densities and right skew in the data, densities were fourth-root transformed (Anderson et al. 2008). We tested for differences in recruitment between species within the 'kill zone' using non-parametric permutational multivariate analysis of variance (PERMANOVA, Anderson 2001) given the distribution of recruit densities were heavily right skewed. Analyses were executed using the PERMANOVA+ add-on for PRIMER7 (Anderson et al. 2008). Study design included 3 factors: species (fixed, three levels—*S. purpuratus*, *P. ochraceus*, and *Leptasterias* sp. [as a proxy for dispersal potential: high, intermediate, low]), site (random, 9 levels), and area (random, nested in site, 18 levels). The Euclidean distance measure, Type III sums of squares, and 999 permutations of the residuals under a reduced model were used to calculate the pseudo-*F* statistic. Significance was assessed at alpha = 0.05. In PERMANOVA the test statistic (pseudo-*F*) and *P* (perm) are analogous to the *F*-value and *P* of an ANOVA and can be interpreted in a similar manner. We conducted *a posteriori* pair-wise comparisons among species when significant main effects were found.

We also used PERMANOVA to test for differences in recruitment by year for each species. Study design included 3 factors: year (fixed, three levels—year 1, year 2, and year 3), site (random, 9 levels), and area (random, nested in site, 18 levels). The Euclidean distance measure, Type III sums of squares, and 999 permutations were used. Significance was assessed at alpha = 0.05. We conducted *a posteriori* pair-wise comparisons among years when significant main effects were found.

Non-metric multidimensional scaling (nMDS) of the Euclidean distance matrix was used to visualize relationships among samples. Multiple plots were constructed to show the differences in recruitment between species and the differences in recruitment between years.

3.3.3 Sample processing for genetic analyses

We used as minimally invasive sampling techniques as possible, taking spine tissue for urchins and tube feet or 2–3mm of arm tip for sea stars. Samples were immediately preserved in 95% ethanol for downstream genetic analyses (Table 3.2). DNA was extracted using a silica based filter plate (PALL Corp., Cat#5053; Ivanova, et al. 2006). 50–100 ng of DNA in 25 ul for each specimen was submitted to the Genomic Sequencing and Analysis Facility at the University of Texas at Austin (GSAF) for quantitation, normalization, double-digestion with the *EcoRI* and *MspI* restriction enzyme pair following Peterson et al. (2012), size selection for 300±50bp using custom bead prep (GSAF), adaptor ligation, purification, and 2x150 paired-end sequencing on an Illumina HiSeq 4000.

Sequences were demultiplexed using process_radtags from STACKS v.1.35 (Catchen et al. 2011) allowing a maximum of 2 mismatches in the barcode. Raw sequences will be deposited in the Short Read Archive of NCBI.

DDOCENT v.2.2.13 (Puritz et al. 2014) was used to trim, assemble, and map reads to available genomes (except for *Leptasterias* sp. *de novo* assembly), and genotype SNPs. *S. purpuratus* and *P. ochraceus* reads were trimmed and then directly mapped to either the *S. purpuratus* (GenBank assembly accession: GCA_000002235.3) or *P. ochraceus* (in prep) genomes, respectively. For *Leptasterias* sp. assembly, three individuals with a minimum of 1 million reads were randomly selected from each of the ten total sites (Table 3.2) for *de novo* reference assembly across multiple assembly parameter combinations (k1=2–8:k2=2–8); k1=2, k2=3, and 90% clustering similarity were selected for the final assembly; remaining reads were then mapped to the reference assembly. For all species, SNPs were genotyped by DDOCENT using default parameters (Table 3.3).

SNPs underwent additional filtering, modified from Puritz et al. (2016). Sequences were filtered using VCFTOOLS v.0.1.15 (https://vcftools.github.io/index.html; Danecek et al. 2011) and custom scripts (https://github.com/jpuritz/dDocent/tree/master/scripts; Puritz et al. 2016). Final filtered vcf files for all species had a 95% genotype call rate across all individuals, minor allele frequency of at least 0.01, and minimum read depth of 20. To achieve this level of coverage, 5–45 individuals per species had to be dropped and excluded from subsequent genetic analyses (Table 3.3). Files were recoded to plink format in VCFTOOLS v.0.1.15 (Danecek et al. 2011) to include only biallelic SNPs in subsequent analyses.

3.3.4 Population genetics of adults

The distribution of genetic variation in adult populations of *S. purpuratus*, *P. ochraceus*, and *Leptasterias* sp. was quantified and visualized using F_{ST} and minimum spanning trees. F_{ST} was calculated across all loci for each species using **`basic.stats`** in the *HierFstat* package (Goudet & Jombart 2015) in R (R Core Team, 2016). 95% confidence intervals were calculated. F_{ST} was then converted to *Nm* using $Nm = (1/F_{ST} - 1)/4$ for comparison with estimated dispersal potential. Although there is some concern regarding the effects of nonequilibrium dynamics on estimation of *Nm* from F_{ST}, we consider it a useful first approximation (Meirmans & Hedrick 2011). Minimum spanning trees (MSTs) were constructed following Prim's Algorithm in the R package *netview p* (Steinig et al. 2016) with a mutual *k*-nearest neighbors (mk-NN) value of 15 — to balance fine- and large-scale structure in the network (Steinig et al. 2016) — and genetic distance matrices calculated using biallelic SNPs in PLINK v.1.07 (Purcell et al. 2007).

3.3.5 Genetic assignment of recruits

The likely source of new recruits for each species was determined with a discriminant analysis of principal components (DAPC) using all biallelic SNPs. The DAPC was implemented first on the adult populations using **`dapc`** in the *adegenet v.2.0.2* package in R (Jombart & Ahmed 2011). Geographic location was used for discrimination *a priori*. Enough principal components

were retained to account for 80% of the variance observed in each species. After performing DAPC on the adults, recruits were assigned by transformation using the centering and scaling of the adult data and projected onto the predicted position using the same discriminant coefficients as the adults (Jombart & Collins 2015). Recruit assignment was evaluated using posterior membership probabilities generated with the **`predict.dapc`** function in *adegenet v.2.0.2*. Membership assignment was visualized by constructing stacked bar graphs of posterior membership probabilities for all recruits.

Dispersal was evaluated for each species by plotting a frequency histogram summarizing the direction (north v. south) and distance (in terms of number of sub-regions) to the most likely source sub-region of each recruit. We used χ^2 tests against a null hypothesis of equal dispersal from the north and from the south. Achieved power was calculated using G* Power 3 (Faul *et al*., 2007). In addition to using all recruit assignments, sensitivity of the result was evaluated using a posterior membership probability threshold of 0.5 and 0.8.

3.4 Results

3.4.1 Estimates of dispersal potential

Quantitative life-history traits (Table 3.1) converted to *Nm* reveal *S. purpuratus* (Sp) has the greatest dispersal potential, followed by *P. ochraceus* (Po), and then *Leptasterias* sp. (Lsp). For relative *Nm* estimated from *PD*, *S. purpuratus* has 7–1,682 times higher *Nm* than *P. ochraceus* and 898–832,712 times higher *Nm* than *Leptasterias* sp, while *P. ochraceus* has 123–495 times higher *Nm* than *Leptasterias* sp. For relative annual *F*, *P. ochraceus* was 1.18 times greater than *S. purpuratus*, *P. ochraceus* was 6,436–30,189 times greater than *Leptasterias* sp., and *S. purpuratus* was 5,471–25,660 times greater than *Leptasterias* sp. For relative N_c, *S. purpuratus* was 1.04 times greater than *P. ochraceus*, *P. ochraceus* was 52 times greater than *Leptasterias* sp., and *S. purpuratus* was 54 times greater than *Leptasterias* sp. Therefore, the ranges of overall estimated potential differences in *Nm* for each pair of taxa were: *S. purpuratus* was 6–1,485 times greater than *P. ochraceus*, *P. ochraceus* was $1.7x10^8$–$1.9x10^8$ times greater than *Leptasterias* sp., and *S. purpuratus* was $1.2x10^9$–$2.5x10^{11}$ times greater than *Leptasterias* sp.

3.4.2 Ecological pattern of recruitment

Taxa with higher dispersal potential — *S. purpuratus* and *P. ochraceus* — had higher recruitment in the 'kill zone' relative to the low dispersal potential *Leptasterias*. By the second year following the mortality event new *S. purpuratus* recruits were detected at all surveyed sites in the 'kill zone', and *P. ochraceus* was detected at all surveyed sites by year 3 (Figure 3.1). PERMANOVA analyses and nMDS reveal significant differences in recruitment between the three species and between the three collection years (Table 3.4, Figure 3.1, Figure 3.2). Interactions revealed significant variability in recruitment between areas (nested within sites) by species in all years studied and variability between sites by species in years 2 and 3 ($P < 0.05$,Table 3.4a). Recruitment differed significantly among species in all three years ($P < 0.05$, Table 3.4a); pair-wise tests reveal significant differences ($P < 0.05$) in recruitment between species by year as follows: Yr 1 & Yr 2, *S. purpuratus* > *P. ochraceus* & *Leptasterias* sp.; and Yr 3, *S. purpuratus* & *P. ochraceus* > *Leptasterias* sp.

Additional species-specific PERMANOVA and nMDS analyses also revealed significant differences in annual recruitment (Table 3.4, Figure 3.1 and Figure 3.2) and interactions revealed significant variability in recruitment between areas (nested within sites) or sites by year for *S. purpuratus* and *P. ochraceus* ($P < 0.05$, Table 3.4a). Recruitment differed significantly among years for *S. purpuratus* and *P. ochraceus* ($P < 0.05$, Table 3.4b); pair-wise tests reveal significant differences ($P < 0.05$) in recruitment between years as follows: *S. purpuratus* recruitment was greater in Yr 2 and Yr 3 relative to Yr 1, *P. ochraceus* recruitment was greater in Yr 3 relative to Yr 1 and Yr 2; *Leptasterias* sp. had zero recruitment detected in surveys in all years (1–3). Generally, recruitment increased in each subsequent year for *S. purpuratus* and *P. ochraceus*.

3.4.3 Samples for genetic analyses

A total of 1,211 samples — 591 *S. purpuratus*, 310 *P. ochraceus*, and 310 *Leptasterias* sp. (Table 3.2) — were retained after bioinformatic filtering and used in subsequent analyses. *S. purpuratus* had a final set of 8,447 biallelic SNPs, *P. ochraceus* had 11,578, and *Leptasterias* sp. had 14,862 (Figure 3.3).

3.4.4 Patterns of population genetic structure in adults

Leptasterias sp., the species with the lowest dispersal potential, shows the most population genetic structure (F_{ST} = 0.172; Figure 3.3), relative to *P. ochraceus* (F_{ST} = 0.002) and *S. purpuratus* (F_{ST} = 0.000), which show well-mixed gene pools over broad geographic scales (Figure 3.3). These results are largely congruent with dispersal potential outlined in section 3.4.1. Empirically estimated *Nm* is 125 for *P. ochraceus* and 1.2 for *Leptasterias* sp., a difference of 102x, which tends toward, albeit is 6 orders of magnitude less than, predictions based solely on life-history characteristics. *S. purpuratus* F_{ST} was 0.000 and therefore could not be converted to *Nm*.

3.4.5 Genetic assignment of recruits

New recruits in taxa with higher dispersal potential — *S. purpuratus* and *P. ochraceus* — showed signals of dispersal to more distant non-natal sites than shown by recruits in the species with low dispersal, *Leptasterias* sp.

Genetic assignment tests reveal *Leptasterias* had high local recruitment at sub-regional levels in both years (78–95%, Figure 3.4, 3.5) as well as the site-specific level (72–74%, Figure 3.4), while low local recruitment was evident at the sub-region level in *P. ochraceus* (15–25%) and *S. purpuratus* (17–20%) with most recruits having dispersed from other sub-regions (Figure 3.5, 3.6). The predominant direction of dispersal was from north to south across both sampling years (Figure 3.5) for *S. purpuratus* (Year 1: n = 78, α = 0.01, χ^2 = 32.051, critical value = 6.635, d.f. = 1, power = 1.00; Year 2: n = 339, α = 0.01, χ^2 = 219.850, critical value = 6.635, d.f. = 1, power = 1.00) and *P. ochraceus* (Year 1: n = 3, α = 0.01, χ^2 = 3.000, critical value = 6.635, d.f. = 1, n.s. [low sample size, but all samples dispersing southward]; Year 2: n = 110, α = 0.01, χ^2 = 44.545, critical value = 6.635, d.f. = 1, power = 1.00). High local recruitment in *Leptasterias* sp. precludes sufficient statistical power to determine a difference in the direction of dispersal of immigrants, but there were approximately 1.5 times more immigrants coming from the north (Figure 3.5). All samples were used to construct recruit membership graphs in Figure 3.6 based on DAPC posterior membership probabilities; sensitivity tests at posterior membership probabilities of 0.5 and 0.8 reveal no qualitative change in the trend, i.e. high local recruitment in *Leptasterias* sp. and high immigration from north to south in other taxa; χ^2 significance outcome also did not change (data not shown).

3.5 Discussion

Although recent studies have called into question the relationship between pelagic duration and population genetic structure (e.g. Bowen et al. 2006; Selkoe et al. 2010) others have found a significant relationship when pelagic duration is considered in the context of a suite of other dispersal-relevant life-history traits (e.g. fecundity and census population size) (Dawson 2014a; Dawson et al. 2014). This suggests, intuitively, no single life-history trait will account for the full magnitude of differences observed in population genetic structure between two species.

Ecological surveys across multiple sites and years, and genetic analyses of hundreds of recruits using thousands of SNPs, reveal differences in dispersal potential (estimated from life-history characteristics — Table 3.1) are congruent with differences in population genetic structure, ecological recruitment, and genetic assignment of recruits across *S. purpuratus*, *P. ochraceus*, and *Leptasterias* sp. The strongest evidence provided here is in the comparison of *S. purpuratus* and *Leptasterias* sp. because these species underwent total extirpation in the 'kill-zone'. However, the pattern is also evident in comparisons with *P. ochraceus*, which did not suffer

complete mortality. Given *S. purpuratus* and *P. ochraceus* are ostensibly both high dispersers, the fact that *P. ochraceus* persisted in the 'kill zone' provides additional evidence for higher dispersal potential in *S. purpuratus* (i.e. higher recruitment in the 'kill-zone' in *S. purpuratus*).

3.5.1 Insight from incomplete mortality in Pisaster ochraceus

This study revealed the dominance of upstream populations of adults contributing to downstream recruitment in *S. purpuratus* and *P. ochraceus* (Figure 3.5, Figure 3.6). Though substantial *P. ochraceus* mortality was observed in the 'kill zone' (Jurgens et al. 2015: Fig.1), densities did not differ significantly from surveys conducted before the mortality event (Jurgens et al. 2015: Fig.7). Perhaps consequently, in the large pulse of *P. ochraceus* recruitment in sub-region S1 (Point Reyes) (Figure 3.1, Table 3.2), the vast majority (75%) were assigned to adult survivors in the 'kill zone'; only 11% of recruits were assigned to adults in sub-regions N1 or N2; (Figure 3.6). For comparative purposes, excluding *P. ochraceus* recruits that were assigned to adult survivors in the 'kill zone' and collected in sub-region S1 reveal consistent recruit abundances in *S. purpuratus* (n = 13) and *P. ochraceus* (n = 12) in sub-region S1. As *S. purpuratus* numbers recovered in the 'kill zone' we would expect to see an increase in recruitment in sub-region S1, which is indeed what happened. Surveys conducted in year 4 — after which two years of *S. purpuratus* recruits (Table 3.2) in the 'kill zone' would have reached reproductive maturity — we observed an order of magnitude increase in *S. purpuratus* recruit abundance (n = 151; L. Schiebelhut, unpublished data), suggesting an emerging contribution of adult *S. purpuratus* in the 'kill zone' to recruitment in Point Reyes (S1).

Variation in *P. ochraceus* recruitment across the study region is broadly consistent with oceanographic patterns during times of seasonal reproduction and larval transport with southward flow during the upwelling season (Largier et al. 1993; Wing et al. 1995; Table 3.1). Waters immediately downstream and upstream of Point Reyes are known to persist during upwelling events potentially restricting advection offshore (Largier et al. 2006); we find the highest *P. ochraceus* recruitment corresponds to this region.

3.5.2 Potential for recovery in Leptasterias

Given the low dispersal potential of *Leptasterias*, recovery in the 'kill zone' would seem to depend largely on incremental expansion from adjacent populations to the north and south. However, the presence of two distinct genetic clusters of adults present across sites north of the 'kill zone' as well as adults collected from S1 clustering with adults from N1 and N2 (Figure 3.3) suggest long-distance dispersal (LDD) may play an important role in this species. Despite no detection of *Leptasterias* in quadrat and transect surveys in the 'kill zone', independent observations captured *Leptasterias* rafting in kelp holdfasts washed up on shore (J. Sones, personal observation). Three rafting individuals were observed, two of which assigned with high confidence to adults sampled north of the 'kill zone', while the third fails to match closely any genetic cluster of adults surveyed in our study (Figure 3.7). Rafting in this species is not uncommon and has been observed elsewhere (Highsmith 1985), suggesting LDD may play an important role in recolonization of *Leptasterias* in the 'kill zone'.

3.5.3 Variation in contrasts between predicted and empirical dispersal

Relative dispersal potential estimated using a suite of quantitative life-history characteristics accounted for the observed relative differences in empirical estimates of dispersal: *S. purpuratus* had the highest dispersal potential, followed by *P. ochraceus* and then *Leptasterias*. Moreover, these observed empirical differences were consistent across ecological, ecological-genetic, and population genetic measures of recruitment in the 'kill zone' (Figure 3.1), genetic assignment of recruits (Figure 3.4; Figure 3.5), and adult population genetic structure (Figure 3.3). However, contrasts in predicted *Nm* (*P. ochraceus* = 1.7×10^8 to 1.9×10^8 times *Leptasterias* sp., section 3.4.1) and empirical estimates of *Nm* (*P. ochraceus* = 102 times *L*eptasterias sp., section 3.4.4) differ by 6 orders of magnitude between *Leptasterias* and *P. ochraceus* (and by logical extension, the contrast in *Nm* between *S. purpuratus* and *Leptasterias* sp. is even greater).

The analytical landscape for inferring gene flow is complex (Marko & Hart 2011). Population genetic structure can be influenced by life-history traits that can influence dispersal, abiotic and biotic factors, and eco-evolutionary interactions. Different coalescent ages among species can contribute to noise in estimates of *Nm* taken from F_{ST} of adults (Dawson 2014b), but in this study is unlikely to account for six orders of magnitude difference between *P. ochraceus* (which had a population expansion after the last glacial maximum [Marko et al. 2010]) and *Leptasterias* sp. (with a coalescent that dates back to the Pleistocene [Foltz et al. 2008]). Other possible explanations include estimates of predicted *Nm* fail to account for important dispersal-relevant life-history characteristics, or selection or drift may play a more prominent role.

While *PD*, *F*, and N_c might reasonably account for differences in taxa with a pelagic larval phase (Dawson et al. 2014), existing frameworks may fall short in taxa for which pelagic dispersal is accomplished via phoretic dispersal of adults. Although the frequency of dispersal via rafting is unknown, documentation of such events in this study and in previous work on *Leptasterias* sp. (e.g. Highsmith 1985) finding multiple individuals on a single kelp holdfast suggest phoretic dispersal is not uncommon. If phoretic dispersal were included in estimates of potential dispersal, it may act to substantially decrease estimates of predicted F_{ST} in *Leptasterias* sp.

Another potential source of variation is introduced by differences in recruit survivorship. For species with similar survivorship curves, *Nm* contrasts based on mean annual fecundity are largely comparable, e.g. *S. purpuratus* and *P. ochraceus* both have Type III survivorship curves meaning that the vast majority of offspring die and realized recruitment can only be a tiny fraction of fecundity in both cases. However, comparison with a species with different survivorship, e.g. *Leptasterias*, which has a Type II survivorship curve, is clearly non-linear because the relative proportion of offspring recruiting back to shore is no longer proportional to fecundity. *Leptasterias* sp. has 5 orders of magnitude higher juvenile survivorship than *P. ochraceus* (Menge 1975), clearly diminishing the difference observed in annual fecundity (Table 3.1). Indeed, adjusting the 6 orders of magnitude difference in fecundity for the five orders of magnitude difference in survivorship brings the estimated predictions of now one order-of-magnitude difference in recruitment far more in line with the observed 102-fold difference between *P. ochraceus* and *Leptasterias* sp. Recruit survival rates are useful in describing population persistence (Burgess et al. 2014), as such, their integration may improve estimates of migration potential.

An additional consideration is that quantitative estimates of individual life-history characteristics used to estimate dispersal potential can be imprecise if they are based on snapshots of a single year or over only a few sites. While, in principle, other things being equal, measures of population genetic structure in stable populations should reflect mean annual fecundity; other things may not always be even approximately equal. Fecundity, for example, can itself be highly variable, fluctuating with mean body mass of reproductive adults, food availability, or other environmental factors and ignoring this variation can lead to over- or under-estimation of genetic connectivity (Castorani et al. 2017). There also can be considerable between-individual variation in dispersal (D'aloia et al. 2015) which could be trait-based. Such deviations may contribute to non-predicted outcomes in SDC contrasts (Chapter 2).

The greatest promise in describing the relationship between dispersal, recruitment, and genetic structure, lies in the integration of a variety of ecological data including functional life-history traits, genetic analyses on comparable scales, along with oceanographic modelling (Selkoe et al. 2010; Dawson et al. 2014). Although we cannot yet predict a particular recruitment event, maybe we could predict general outcomes after the accumulation of multiple events with similar tendencies, and forecast the relative probabilities of outcomes for different taxa based on differing life-history characteristics. Reflecting on the search for the ecological significance among a number of interacting factors, Dawson et al. (2010) recast chaotic genetic patchiness instead as 'eurymixis', trying to re-emphasize the importance of purposefully seeking understanding of mechanisms and interactions determining short- through long-term relationships. A major limiting factor to obtaining good estimates of dispersal potential is the paucity of life-history data for many species (Chapter 2); others include understanding of behavior (Morgan et al. 2009b; Gaylord et al. 2013), and near-shore oceanography (Sponaugle 2002; Largier 2003; Largier et al. 2006; Nickols et al. 2012).

In a time when mass mortality events are on the rise in a variety of taxa (Fey et al. 2015) and increased emphasis on (and criticism of) networks of marine protected areas (Toonen et al. 2013; Ballantine 2014; Devillers et al. 2015), understanding marine connectivity remains an essential goal, a.k.a. "Grand Challenges" *sensu* Lindsay (2012). Further developing the theory and quantitative relationships for forecasting species' potential for recovery using a suite of life-history characteristics, possibly in part based on 'dispersal syndromes' (Dawson 2014a) would be valuable for management purposes. This may not seem out of reach, given the emerging relationship between relative dispersal potential and empirical estimates of connectivity (Haye et al. 2014; Weber et al. 2015; Young et al. 2015).

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3.7 Tables

Table 3.1 Life-history characteristics of study species.

	S. purpuratus	*P. ochraceus*	*Leptasterias* sp.
Density·m^{-2} (N_c proxy)	0.054	0.052	0.001
Pelagic duration	9–19 weeks[1]	6–8 weeks[2]	0 weeks; brooder[3]
Annual fecundity	6.8 million[4]	8.0 million[5]	265–1243 ($\propto$size)[6]
Longevity	10–50 years[7]	34.1 years[8]	10.2 years[8]
Age at first reproduction	2 years[9]	5 years[8]	2 years[8]
Reproductive season	Jan.–Mar.[3]	Apr.–May[3]	Nov.–Apr.[3]

Notes: Adult densities were quantified in this study and averaged across sites outside the 'kill zone' to be used as a proxy for relative N_c across species.

Sources: 1, Strathmann (1978); 2, Strathmann (1987); 3, Morris et al. (1980); 4, Leahy et al. (1981); 5, Fraser et al. (1981); 6, Menge (1974); 7, Ebert (1967) 8, Menge (1975); 9, Gonor (1972).

Table 3.2 List of sites surveyed organized north to south (see map in Figure 3.4) and sample sizes used in genetic analyses.

						S. purpuratus			***P. ochraceus***			***Leptasterias* sp.**		
						2012		2013	2012		2013	2012		2013
Site	County	Regional Code	Site Code	Latitude	Longitude	Adults	Yr 1 Recruits	Yr 2 Recruits	Adults	Yr 1 Recruits	Yr 2 Recruits	Adults	Yr 1 Recruits	Yr 2 Recruits
Van Damme	Mendocino	N1	VDM	39.279	-123.804	10[⌘]	**ns**	5	4[⌘]	**ns**	·	10[⌘]	**ns**	6
Stornetta	Mendocino	N1	STO	38.937	-123.727	10[⌘]	**ns**	9	··	**ns**	·	10[⌘]	**ns**	25
Arena Cove	Mendocino	N1	ACM	38.918	-123.721	8	8	16	9	·	·	10	7	64
Moat Creek	Mendocino	N2	MCM	38.880	-123.675	9	2	10	10	·	·	10	13	64
Iversen Point	Mendocino	N2	IPM	38.848	-123.647	9	8	12	10	·	·	10*	3	12
Serenisea	Mendocino	N2	SSM	38.798	-123.573	·	·	31	10	·	·	·	·	·
Del Mar	Sonoma	N2/KZ1[†]	DMS	38.741	-123.508	9	18	39	10	·	··	·	·	·
Sculpture Point	Sonoma	KZ1	SPS	38.700	-123.443	·	1	100	10	·	·	·	·	·
Fisk Mill Cove	Sonoma	KZ1	FMS	38.597	-123.351	·	5	43	5	·	6	·	·	·
Phillips Gulch	Sonoma	KZ1	PGS	38.587	-123.342	·	8	63	10	·	·	·	·	·
Windermere Point	Sonoma	KZ2	WPS	38.525	-123.268	·	2	9	10	·	·	·	·	·
Twin Coves	Sonoma	KZ2	TCS	38.459	-123.146	·	1	25	10	·	·	·	·	·
Shell Beach	Sonoma	KZ2	SBS	38.418	-123.108	·	2	1	·	·	·	·	·	·
Bodega Reserve	Sonoma	KZ2	BRS	38.317	-123.073	·	2	26	10*	·	27	·	·	·
Bodega Head	Sonoma	KZ2	BHS	38.303	-123.053	·	1	15	10	·	·	·	·	·
McClures Beach	Marin	S1	CCM	38.182	-122.966	·	1	3	10	2	76	·	·	·
Lifeboat House	Marin	S1	LHM	37.997	-122.979	·	··	·	9	··	21	·	·	·
Palomarin	Marin	S1	PMM	37.931	-122.750	2	1	1	10	·	·	10*	1	2
Duxbury Reef	Marin	S1	DRM	37.893	-122.707	9	6	1	7	·	·	8	3	1
Pigeon Point	San Mateo	S2	PIS	37.183	-122.389	·	·	·	4	·	·	10	6	·
Scott Creek	Santa Cruz	S2	SCC	37.044	-122.235	9	15	·	10	·	·	10*	3	·
Andrew Molera	Montery	S2	AMM	36.281	-121.863	10	16	·	8	2	·	9	3	·
					Totals	85	97	409	176	4	130	97	39	174

Notes:

[⌘] Samples collected in second sampling year (2013), but reported in adult column for simplicity since 2012 was not sampled for these sites.

ns Site not sampled/surveyed

[†] Given the heterogeneous northern limit of the 'kill zone', *S. purpuratus* adults were included in the N2 region for genetic analysis.

* Additional adults collected in subsequent years to increase sample sizes. *P. ochraceus*: BHS 7 in 2013; *Leptasterias* sp.: IPM 6 in 2013, PMM 2 in 2013 & 7 in 2014, SCC 4 in 2014.

· Site surveyed but no specimens found to collect for genetic analysis.

·· Site surveyed and specimens found, but dropped after filtering.

Table 3.3 Summary of genetic data by species at multiple points of the data processing pipeline.

	Variable sites post-dDocent	**Sites retained after filtering**	**Individuals dropped**	**Total biallelic sites**	**Mean depth per site**	**Total loci/ scaffolds**
S. purpuratus	11,583,550	9,079	45	8,447	34.6	1,340 scaffolds
P. ochraceus	2,136,713	12,480	20	11,578	84.5	202 scaffolds
Leptasterias sp.	573,990	16,039	5	14,862	70.7	2,547 loci

Table 3.4 Summary of PERMANOVA results and pairwise tests on Euclidean distances of fourth root transformed density of recruits in the 'kill zone' for (a) all species by each year, with factors species, site, and area and (b) all years for *S. purpuratus* and *P. ochraceus*, with factors year, site, and area. *Leptasterias* sp. had zero detectable recruitment in the 'kill zone' in any of the three years studied. Number of permutations = 999. * = *P* (perm) significant at < 0.05; ** = *P* (perm) significant at < 0.01.

a.

PERMANOVA								***PAIR-WISE TESTS (species)***				
Source of variation	*df*	SS	MS	Pseudo-F	*P* (perm)	Signif	Unique perms	Groups	*t*	*P* (perm)	Signif	Unique perms
Recruitment across all species in Year 1												
Species	2	1.447	0.723	10.611	0.001	**	998	Sp, Po	3.257	0.018	*	991
Site	8	0.594	0.074	1.536	0.278		999	Sp, L	3.257	0.017	*	988
Area (Site)	9	0.437	0.049	1.786	0.061		999	Po, L	Denominator is 0			
Species x Site	16	1.189	0.074	1.536	0.193		998					
Species x Area (Site)	18	0.874	0.049	1.786	0.030	*	999					
Res	885	24.066	0.027									
Total	938	28.168										
Recruitment across all species in Year 2												
Species	2	34.342	17.171	23.192	0.001	**	999	Sp, Po	4.382	0.003	**	998
Site	8	5.921	0.740	1.465	0.276		999	Sp, L	5.687	0.002	**	998
Area (Site)	9	4.553	0.506	3.739	0.002	**	999	Po, L	1.808	0.102		886
Species x Site	16	12.009	0.751	2.733	0.020	*	999					
Species x Area (Site)	18	4.949	0.275	2.032	0.006	**	999					
Res	876	118.520	0.135									
Total	929	179.490										
Recruitment across all species in Year 3												
Species	2	41.692	20.846	11.254	0.001	**	999	Sp, Po	2.141	0.071		994
Site	8	11.770	1.471	1.489	0.293		999	Sp, L	4.846	0.002	**	997
Area (Site)	9	8.907	0.990	5.303	0.001	**	999	Po, L	3.028	0.016	*	997
Species x Site	16	29.935	1.871	3.452	0.006	**	998					
Species x Area (Site)	18	9.767	0.543	2.908	0.001	**	999					
Res	885	165.160	0.187									
Total	938	263.360										

b.

PERMANOVA								***PAIR-WISE TESTS (years)***				
Source of variation	*df*	SS	MS	Pseudo-F	*P* (perm)		Unique perms	Groups	*t*	*P* (perm)		Unique perms
Recruitment in *S. purpuratus* across all years												
Year	2	29.113	14.556	15.411	0.002	**	998	1, 2	5.092	0.004	**	996
Site	8	31.714	3.964	3.610	0.042	*	999	1, 3	4.249	0.004	**	996
Area (Site)	9	9.910	1.101	3.873	0.001	**	999	2, 3	1.176	0.264		995
Year x Site	16	15.629	0.977	3.758	0.010	*	998					
Year x Area (Site)	18	4.677	0.260	0.914	0.566		998					
Res	882	250.770	0.284									
Total	935	344.870										
Recruitment in *P. ochraceus* across all years												
Year	2	7.539	3.769	8.051	0.004	**	998	1, 2	2.076	0.054		964
Site	8	7.108	0.888	1.471	0.206		999	1, 3	3.090	0.016	*	996
Area (Site)	9	5.454	0.606	9.381	0.001	**	998	2, 3	2.533	0.045	*	997
Year x Site	16	7.807	0.488	1.589	0.135		999					
Year x Area (Site)	18	5.545	0.308	4.769	0.001	**	998					
Res	882	56.974	0.065									
Total	935	89.936										

3.8 Figures

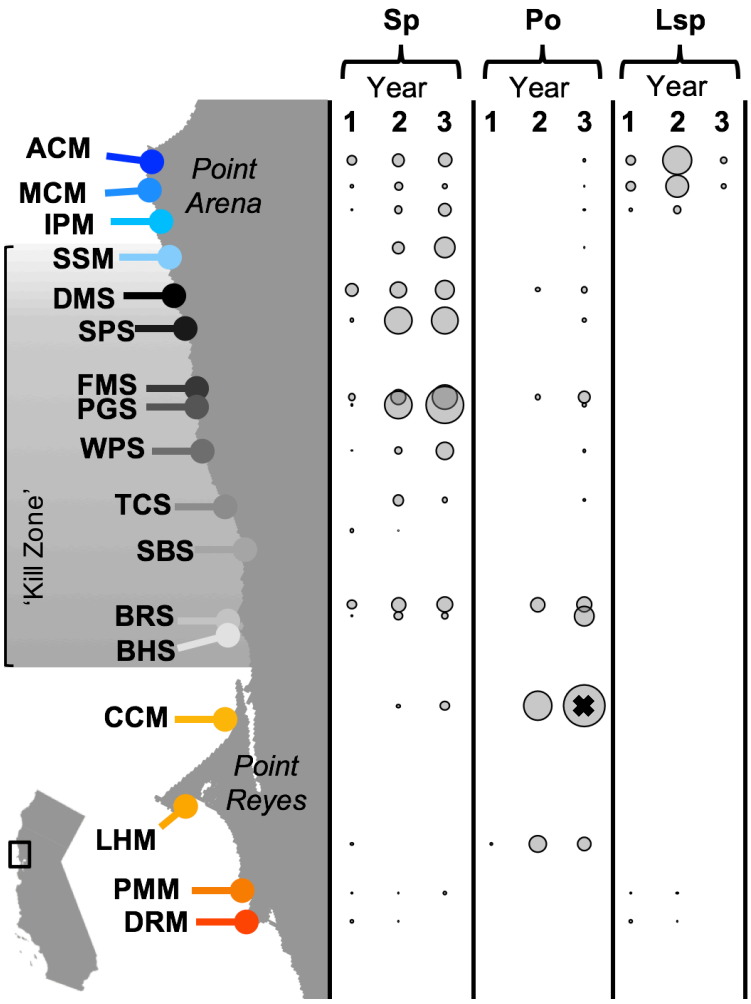

Figure 3.1 Map of 'kill zone' with adjacent reference sites and bubble plot showing new recruit densities by year. Sp = *S. purpuratus*, Po = *P. ochraceus*, Lsp = *Leptasterias* sp. Area of circle proportional to density and relative to highest density circle (denoted with '**X**'; 7.61 recruits·m^{-2}). The first column for each species represents the first wave of recruitment in the winter following the die-off and subsequent columns represent subsequent years of recruitment. Sites labelled on map correspond to adjacent bubble plots.

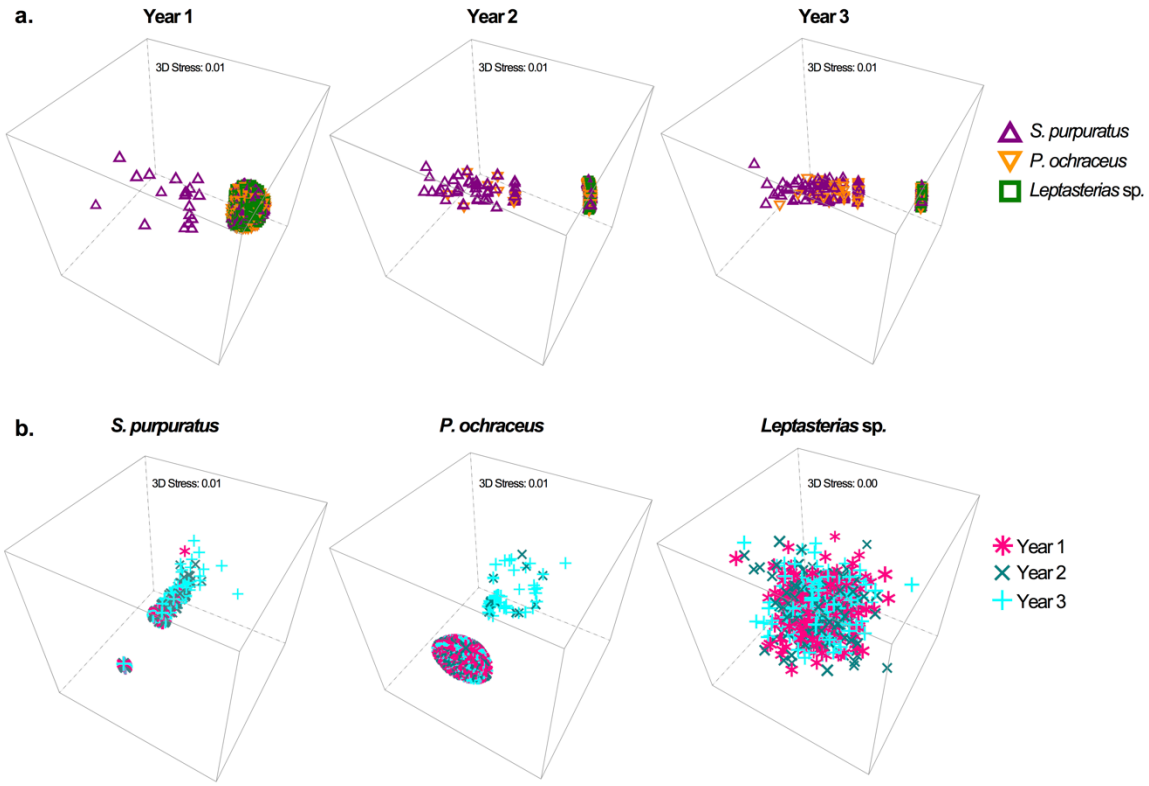

Figure 3.2 Patterns of recruitment across species and years (see also Table 3.4). 3D nMDS plots showing differences in recruitment (a) between *S. purpuratus*, *P. ochraceus*, and *Leptasterias* sp. in the first three years following the die-off and (b) between years for each species. Recruit densities for all species were fourth root transformed and converted to a resemblance matrix using Euclidean distance. The data set was dominated by zeros which manifests as tight clusters of data points in these plots. N.B. *Leptasterias* sp. plot (b) is zoomed relative to other plots. Recruitment is highest in *S. purpuratus* and increases in *S. purpuratus* and *P. ochraceus* in subsequent years. *Leptasterias* sp. does not recruit to the 'kill zone'. Dense data points represent distances between 0-density quadrats.

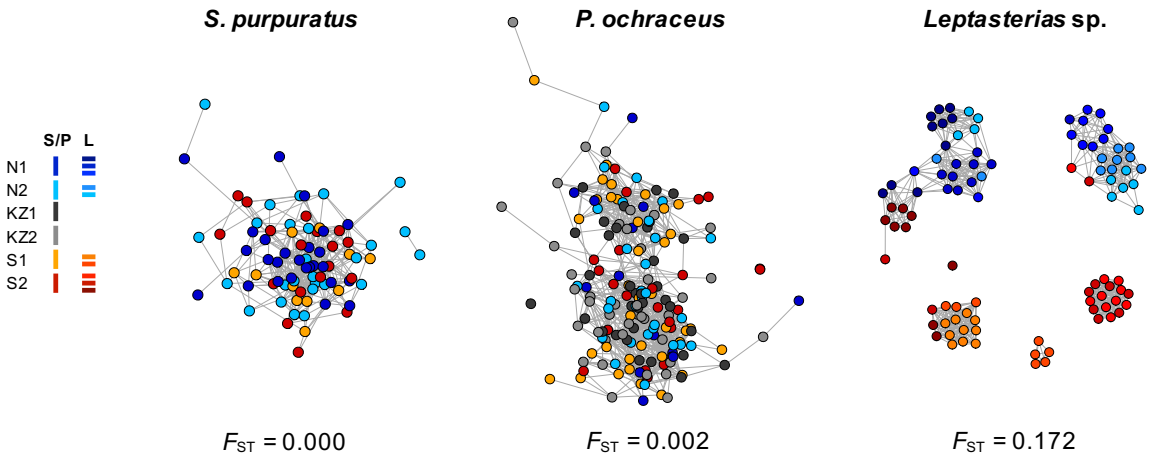

Figure 3.3 Minimum spanning trees and F_{ST} across all loci for adults from each species. Each circle represents an individual. Colors correspond to geographic locations in key (left) and map in Figure 3.4. S = *S. purpuratus*, P = *P. ochraceus*, L = *Leptasterias* sp. Sample sizes listed in Table 3.2. Graphical representation in this figure space may contain superimposition of individuals.

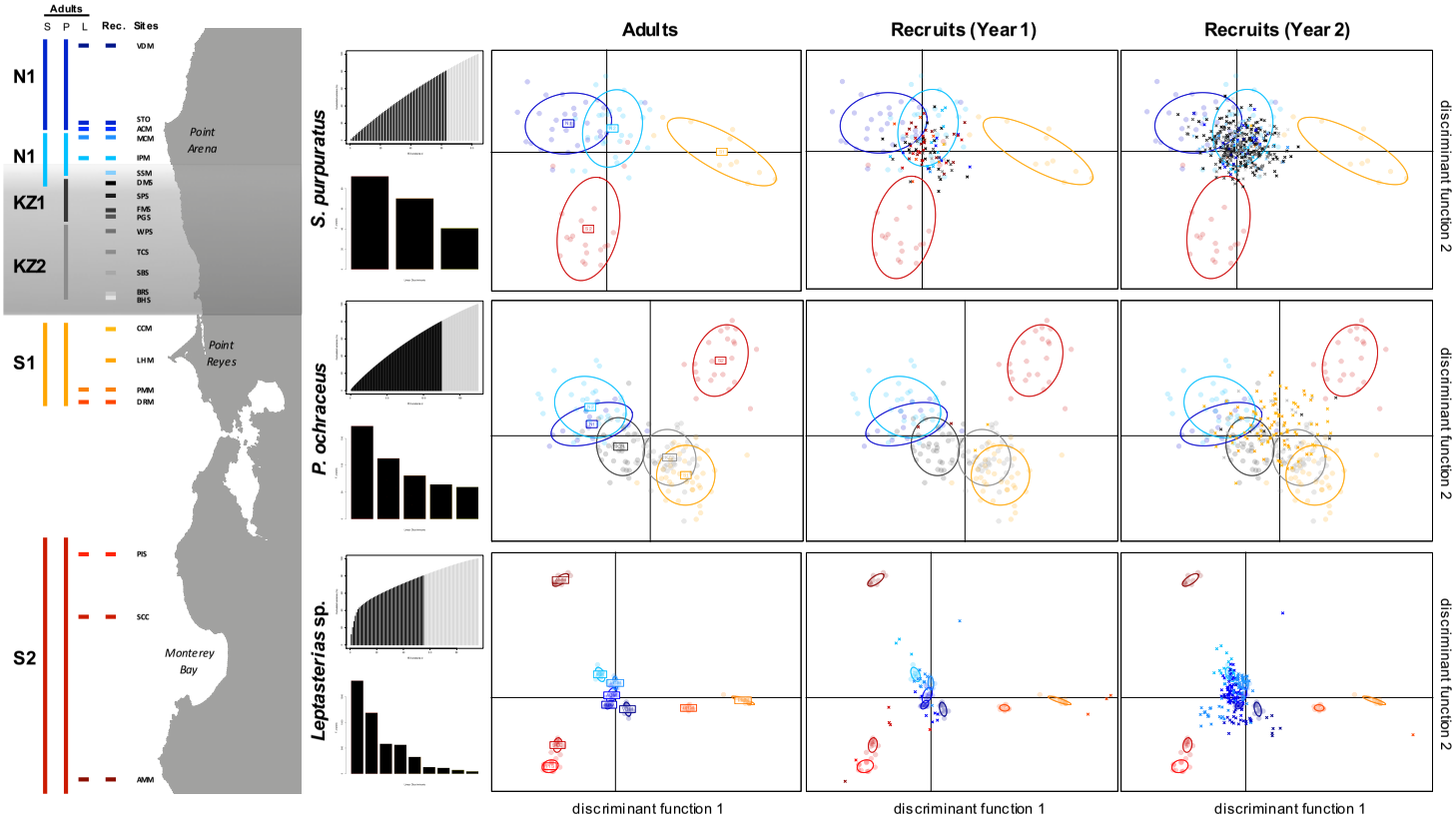

Figure 3.4 Discriminant analysis of principal components (DAPC) using all filtered SNPs from mature *S. purpuratus* (top), *P. ochraceus* (middle), and *Leptasterias* sp. (bottom) plotting the first two discriminant functions. Colors indicate geographic location of collection and correspond to adjacent map. From north to south regions are broken into sub-regions: north of the 'kill zone' (N1, N2), in the 'kill zone' (KZ1, KZ2), and south (S1, S2). *Leptasterias* sp. is further broken down by specific site within sub-region. For each species the pair of bar graphs represent (1, top) the number of principal components retained to explain 80% of the cumulative variance (black bars) and (2, bottom) the discriminant functions used in the DAPC with corresponding F-statistic. New recruits collected in year 1 (2012-13) and year 2 (2013-14) were assigned to adult groups and plotted. The gray shaded region on the map delimits the geographic extent of elevated mortality ('kill zone') (Jurgens et al. 2015); the northern limit was heterogeneous, as indicated by the shading gradient (e.g. there was complete mortality of *S. purpuratus* at site SSM, but a small group of adults were found at DMS (Table 3.2) and therefore included with the other northern sites, whereas *P. ochraceus* from DMS were included in KZ1 to maintain sample balance for the DAPC). "Rec" means recruits from any species.

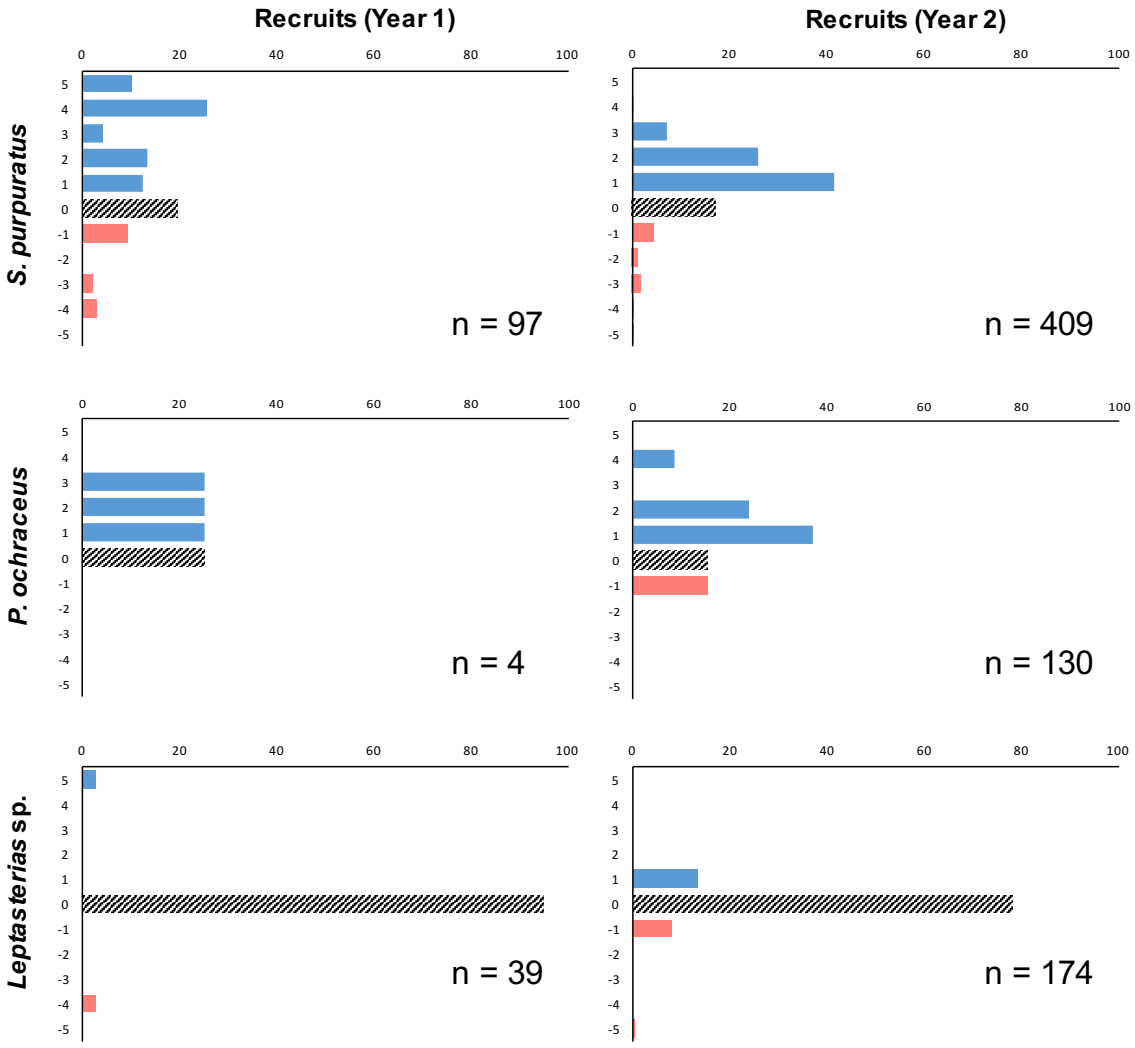

Figure 3.5 Estimated dispersal direction and dispersal distance of new recruits. Frequency histogram showing assignment of recruits to source sub-regions relative to the sub-region at which they were collected. Striped bars represent recruits assigned to the sub-region from which they were collected (Figure 3.4, 3.6). Blue represents genetic assignment of recruits to adults north of collection sub-region (i.e. southward dispersal) and salmon represents assignment of recruits to adults south of collection sub-region (i.e. northward dispersal). Sub-regional sites correspond to N1, N2, KZ1, KZ2, S1, and S2 as defined in Figure 3.4 and Table 3.2; the y-axis corresponds to the number of sub-regions from site of collection to sub-region of genetic assignment. Assignment is based on posterior membership probabilities from DAPC analysis (Figure 3.4, 3.6). For consistency with other taxa, *Leptasterias* sp. is presented here in terms of sub-regions rather than specific sites, although variation and structure are sufficient that assignments could be made with site-by-site resolution in *Leptasterias* sp only. *Leptasterias* sp. shows high local recruitment (78–95%), while *P. ochraceus* and *S. purpuratus* show high rates of immigration (80–85%). All species primarily show migration from north to south.

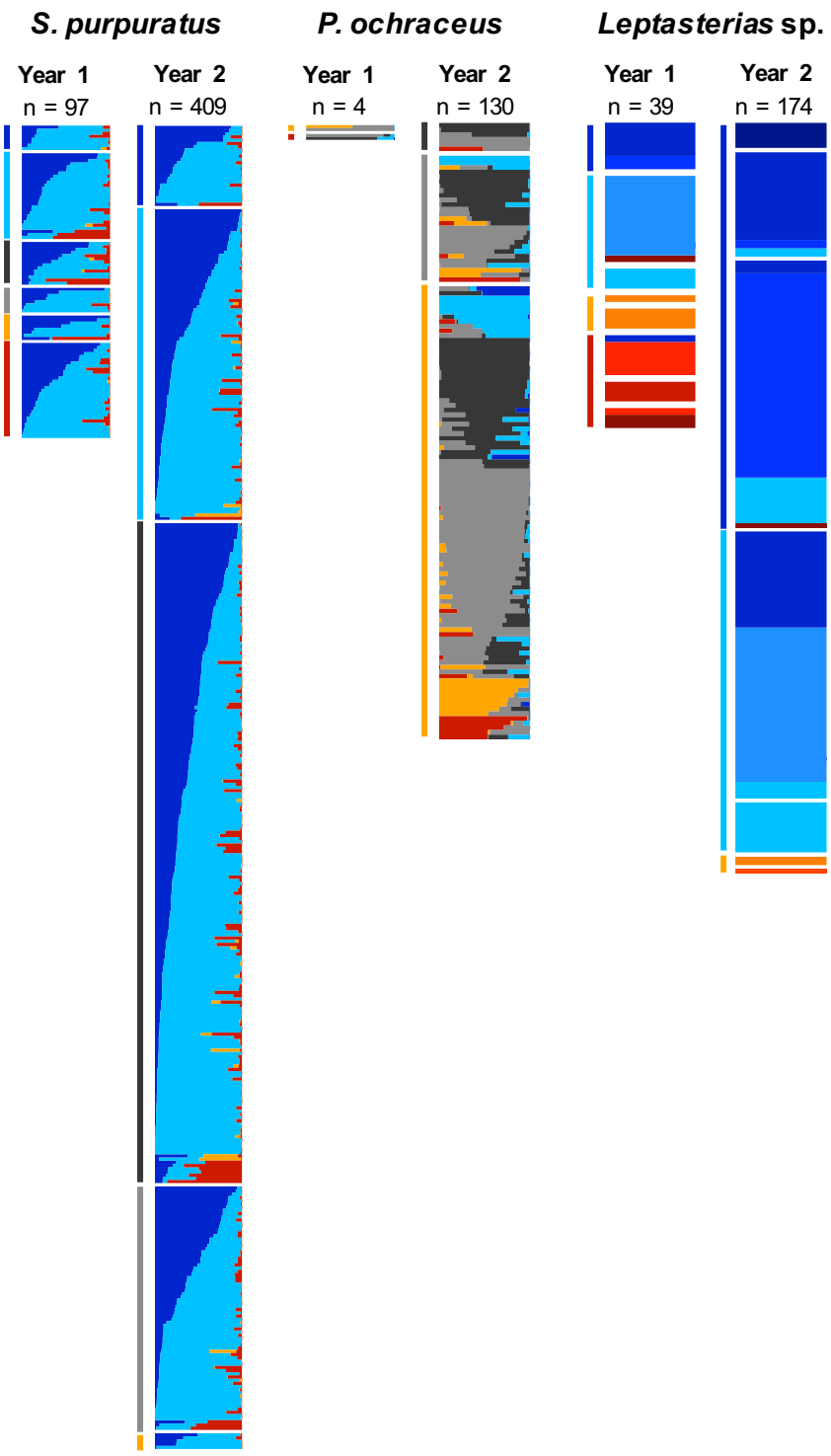

Figure 3.6 Posterior membership probability for each new recruit by species and recruitment year. Each column within a bar graph represents a single individual and the posterior membership probability of that individual to each adult group (shown in Figure 3.4). Colors in the bar chart correspond to assignment locations. Colored lines to the left of each bar graph correspond to the geographic location the recruits were collected.

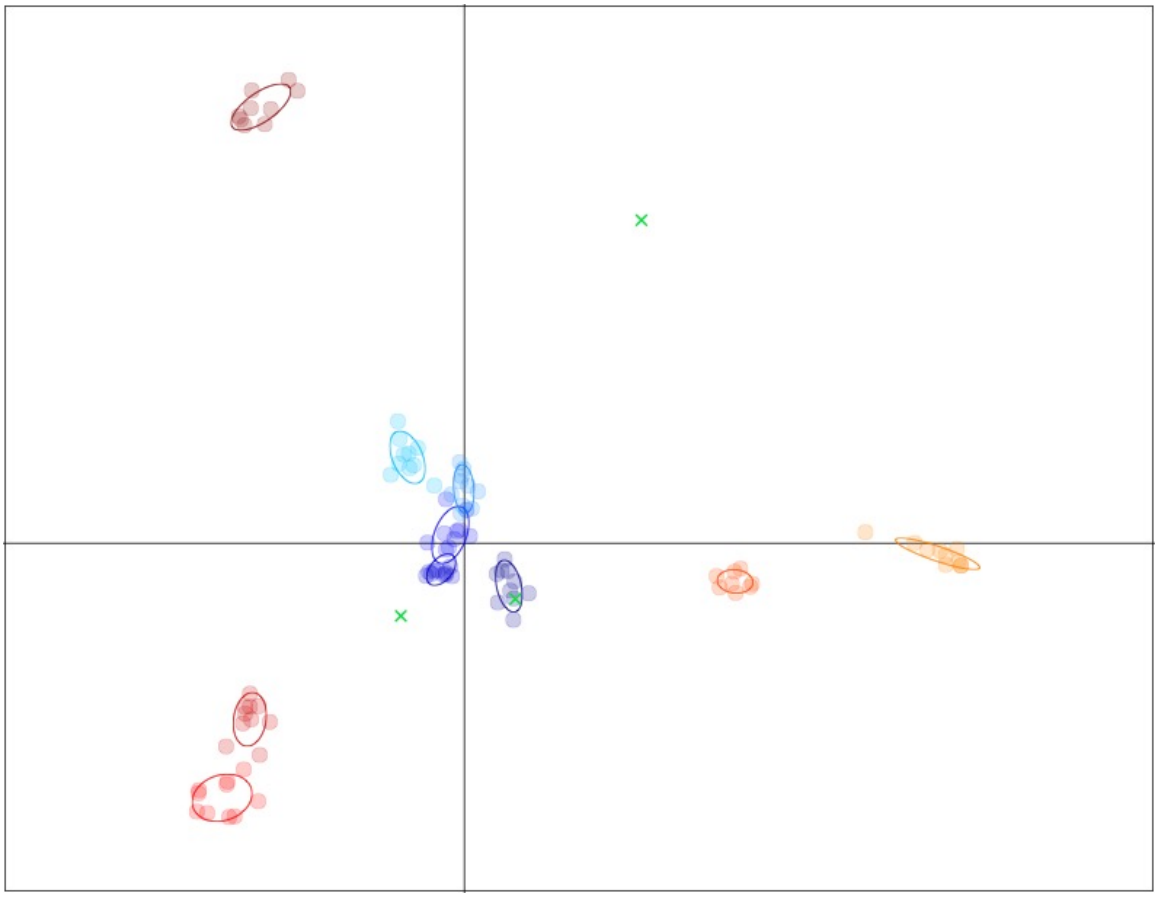

Figure 3.7 *Leptasterias* sp. found rafting in beach cast kelp holdfasts in 'kill zone' assigned to potential source populations following the same DAPC procedure used in Figure 3.4. Three green 'X's denote rafters. Colors of potential sources populations correspond to Figure 3.4.

Chapter 4. Tracking genetic changes in *Pisaster ochraceus* during decimation by sea star wasting disease

4.1 Abstract

Standing genetic variation enables or restricts populations' adaptation to changing environments, including the extreme disturbances that are expected to increase in frequency and intensity with continuing anthropogenic climate change. However, we know little about what determines resilience or susceptibility to extreme events, or how population dynamics may influence and be influenced by population genomic change. We use a range-wide epizootic sea star wasting disease (SSWD) that caused mass mortality in *Pisaster ochraceus* to explore how a familiar marine species — with large population size, broad range size, high gene flow, and high fecundity — responded to an extreme perturbation. We integrated quantitative field surveys with RADSeq data to (1) describe the population dynamics of mortality and recovery, (2) compare allele frequencies in mature *P. ochraceus* before and after the onset of the disease outbreak, and (3) compare allele frequencies in new recruits to both pre- and post-outbreak adult samples. We aimed to answer two questions: (i) did selection occur and how strong was it relative to genetic drift, and (ii) were new juvenile *P. ochraceus* recruits the progeny of pre-outbreak adults or of the post-outbreak surviving adult *P. ochraceus* population? We found *P. ochraceus* suffered 83% mortality in the study region, and coincidentally a 93-fold increase in recruitment, following onset of the sea star wasting epizootic in 2013. Direct comparison of pre- and post-outbreak adults revealed potential signals of selection in the post-SSWD *P. ochraceus* population, though power was weak due to small sample sizes. Newly recruited *P. ochraceus* were genetically most similar to the pre-SSWD adult population; however, 95 of the 100 largest allele frequency shifts between pre- and recruit samples paralleled allele frequency changes between pre- and post-SSWD adult samples, suggesting these SNPs may be under selection. These data suggest detectable signals of selection in a typical high gene flow marine species, and highlight the potential for maintenance of this signature of selection in future generations, potentially contributing to increased resilience to future environmental change.

4.2 Introduction

Species are being adversely affected by chronic and acute environmental changes (Parmesan 2006), the effects mediated via physiological tolerances and life-history traits, which may reflect underlying genetic differences (Munday et al. 2013). Such genetic differences may amplify or mute a species' sensitivity to change (Foo et al. 2012; Kelly et al. 2012). Known consequences of environmental change include suppressed fisheries, increased disease outbreaks, and mass mortality of marine taxa (Diaz & Rosenberg 2008; Keller et al. 2010). Species' capacity to respond on short time scales will become increasingly important as rapid environmental change intensifies (Palumbi 2001) and extreme disturbances potentially increase in both frequency and intensity (Kharin et al. 2007; Jentsch et al. 2007); standing genetic variation will be essential in enabling rapid adaptation to a changing environment (Colosimo et al. 2005; Steiner et al. 2007; Tishkoff et al. 2007). However, we know little about what determines which species or individuals are resilient or susceptible, whether or how impacted populations may recover, and if recovery increases resilience to future perturbations.

Detecting selection in wild populations is challenging due to demographic processes in contemporary populations — such as range expansions, growth, and asymmetric migration resulting in complex spatial genetic patterns (Riginos et al. 2016) — leading to potentially false conclusions about selective sweeps that are simply artifacts (Barrett & Schluter 2008). A strategy to sidestep this problem involves identifying adaptive alleles in the ancestral population that have increased frequency in derived populations, however it is not always possible to know if a beneficial allele was secondarily introduced to the ancestral population (Barrett & Schluter 2008). Additionally, selection can manifest in different ways in the genome, for example, a selected trait can be controlled by few genes of large effect or many genes of small effect; in the latter case the intensity of selection is diluted over many genes, resulting in only small changes in allele

frequency (Gagnaire & Gaggiotti 2016). Marine taxa can pose particular challenges due to a suite of common traits — high fecundity, large population size, and high dispersal potential — acting to homogenize the gene pool and consequently restricting signals of selection to very small genomic regions (Gagnaire et al. 2015).

We have identified a study system that ameliorates many of these challenges because individuals with different functional responses can be identified easily, and ancestral and derived (sub)populations differing in those functional responses are known. In 2013, a range-wide sea star wasting disease (SSWD) epizootic leading to mass mortality across the range of *Pisaster ochraceus* (Hewson et al. 2014) created a rare opportunity to explore the genetic landscape in which selection acts, and to directly identify alleles that responded to the event through changes in frequency. Genetic differences between symptomatic and asymptomatic individuals during the outbreak were documented (Wares & Schiebelhut 2016). In addition, a study of *Pisaster ochraceus* by Jurgens et al. (2015) immediately preceding the outbreak was available to be coupled with samples following the disease outbreak, at multiple locations, along with quantitative surveys of mortality, to capture both the initial standing genetic variation and the aftermath of the largest documented non-commercial marine pandemic (Eisenlord et al. 2016). Additionally, this mortality event offered the opportunity to explore how newly recruited *P. ochraceus* did or did not reflect the same genetic signature of the event as the adult population. Thus, we are able to capture the literal change from the original standing genetic stock and potentially distinguish between selection and genetic drift.

We aim to identify the genetic consequences of a mass mortality event on the standing stock of genetic variation using comparisons of pre- and post-SSWD samples of adult *P. ochraceus* and newly recruited juveniles. Our goals are to ascertain whether selection occurred and determine its importance relative to genetic drift in the surviving population of *P. ochraceus*. Additionally, we test whether juvenile *P. ochraceus* recruiting in the first year following the mortality event are most likely progeny of the original or surviving *P. ochraceus* population (possible scenarios outlined in Figure 4.1). In doing so we aim to shed light on how this species, which in many ways is a typical marine species — large population size, broad range size, high gene flow, high fecundity, high dispersal potential (see Table 3.1 in Chapter 3) — responds to an extreme event and what signature this may leave on the subsequent generation.

4.3 Materials and methods

4.3.1 Ecological surveys

Quantitative surveys of *P. ochraceus* were conducted at fifteen sites (Figure 4.2) the year preceding and following the 2013 SSWD outbreak. Detailed methods are described in section 3.3.2 in Chapter 3. At each site, we sampled two rocky intertidal areas, using quadrats to estimate juvenile abundance and transects to target larger adult *P. ochraceus* (N.B. one of the fifteen sites [Figure 4.2] only had quadrat surveys). All specimens were georeferenced using a Garmin C60X GPS (±3 m precision). Data were reported as the number of individuals per square meter.

Quadrats: We exhaustively searched 32–40 one-meter square quadrats per site (i.e. 16–20 per each of 2 areas), recording GPS waypoint, time, percent cover of major substrate and macrophytes, and abundances and sizes of *P. ochraceus* for each quadrat. Quadrat locations were selected by first finding one of the target habitat types (based on preliminary surveys of recruit distributions) — surf grass, low-zone red algae, coralline turf, cobble or boulder field, or urchin pools with pits either empty or occupied — selecting a starting point haphazardly, and then using a random numbers table (range of 1-10 meters) to choose remaining quadrat locations.

Transects. To quantify changes in mature *P. ochraceus* density, we conducted timed, GPS-tracked, 2m or 4m wide swath transects nested in each of two areas at each site. From a distance, an approximate starting point and orientation (with landmarks) for the starting transect was selected. Transects ran from the most shoreward to the most seaward possible suitable habitat at approximately 10m intervals along shore, particularly targeting the low intertidal zone

when the tide was maximally receded, with as many transects being done as permitted by the tide. The GPS was set to auto-record a trackpoint every 6 seconds. To reduce error (commonly ±3 m for civilian GPS), we smoothed tracks by averaging across windows of two consecutive trackpoints, and removed outlying trackpoints that led to a Euclidean distance ≥ 8 meters, since these were likely due to temporary drop-outs in satellite signal. We calculated total transect search area by multiplying the adjusted transect length by swath width.

Statistical analyses. Normality was tested in adult and recruit data sets using the Shapiro-Wilk Normality Test in the *stats v3.3.2* package in R (R Core Team, 2016). Given normality was rejected in adults and recruits (Shapiro-Wilk normality test, adults: $W = 0.553$, $p = 1.584 \times 10^{-5}$; recruits: $W = 0.284$, $p = 9.834 \times 10^{-8}$) the non-parametric Wilcox rank-sum test was used to test for a change in density between pre- and post-SSWD outbreak samples using the *stats v3.3.2* package in R (R Core Team, 2016).

4.3.2 Sample processing for genetic analyses

Tissue samples were collected from *P. ochraceus* of reproductive size before the onset of the sea star wasting disease outbreak from each of two locations in 2012 (Table 4.1; map in Figure 4.2). Complementary samples of mature adults and new recruits (< 1 year) were collect in 2014, after the onset of SSWD in 2013. Tissue collection consisted of approximately a half dozen tube feet or 2–3mm of arm tip. Samples were immediately preserved in 95% ethanol for downstream genetic analyses (Table 4.1). DNA was extracted using a silica based filter plate (PALL Corp., Cat#5053; Ivanova, et al. 2006). 50–100 ng of DNA in 25 ul for each specimen was submitted to the Genomic Sequencing and Analysis Facility at the University of Texas at Austin (GSAF) for quantitation, normalization, double-digestion with the *EcoRI* and *MspI* restriction enzyme pair following Peterson et al. (2012), size selection for 300±50bp using custom bead prep (GSAF), adaptor ligation, purification, and 2x150 paired-end sequencing on an Illumina HiSeq 4000.

Sequences were demultiplexed and processed with the sequences from chapter 3, using process_radtags from STACKS v.1.35 (Catchen et al. 2011) allowing a maximum of 2 mismatches in the barcode. Raw sequences will be deposited in the Short Read Archive of NCBI. DDOCENT v.2.2.13 (Puritz et al. 2014) was used to trim and map reads, and genotype SNPs using default parameters. Trimmed reads were directly mapped to the *P. ochraceus* draft genome (in prep).

Genotyped SNPs underwent additional filtering, modified from Puritz et al. (2016). Sequences were filtered using VCFTOOLS v.0.1.15 (https://vcftools.github.io/index.html; Danecek et al. 2011) and custom scripts (https://github.com/jpuritz/dDocent/tree/master/scripts; Puritz et al. 2016). The final filtered vcf file had a 95% genotype call rate across all individuals, minimum depth of 20, and a minor allele frequency of at least 0.01. The final filtered vcf file was recoded to multiple formats for subsequent analyses: first, converted to plink format in VCFTOOLS v.0.1.15 (Danecek et al. 2011) to include only biallelic SNPs, and then converted to BayeScan format using PGDSPIDER v.2.1.0.3 (Lischer & Excoffier 2012).

4.3.3 Tests for selection in adult P. ochraceus

Two main approaches were used to test for signals of selection: (1) an F_{ST}-based outlier method implemented in BayeScan (Foll & Gaggiotti 2008) and (2) a discriminant analysis of principal components (DAPC) (Jombart & Ahmed 2011). In both approaches, pre- and post-SSWD adult *P. ochraceus* were treated as separate samples and allele frequencies were compared for top candidate SNPs.

BAYESCAN v.2.1 (Foll & Gaggiotti 2008) was used to test for candidate loci under selection by using the difference in allele frequencies between samples (i.e. pre- and post-SSWD adults). This method will have weak power at small sample sizes (as we have here), but should not have any particular risk of bias given it is Bayesian (Foll 2012). Default parameters were employed: thinning interval of 10 and 20 pilot runs for 5,000 iterations, with an additional burn in of 50,000; prior odds for neutral model was 10. The *q*-value was calculated for each SNP and a false discovery rate (FDR) of 0.1, an analog of the *p*-value, was used to determine significance of outlier SNPs.

The DAPC was performed first on adult *P. ochraceus* using **`dapc`** in the *adegenet v.2.0.2* package in R (Jombart & Ahmed 2011). The first DAPC was performed using four groups split by collection site and collection year *a priori* to determine whether there was a general split between pre- and post-SSWD samples, not driven by site differences. Twenty-six principal components were retained (proportion of conserved variance: 79%) with three discriminant functions (n groups – 1). After evaluation of the four-group DAPC, a two-group DAPC was performed for adults defined *a priori* by strictly pre- or post-SSWD (Table 4.1) using 26 principal components (proportion of conserved variance: 79%) and 1 discriminant function (n groups – 1). Allele frequencies were calculated for the top 100 discriminatory SNPs identified in the DAPC analysis for pre- and post-SSWD adults using the *PopGenReport v.3.0.0* package in R (Adamack & Gruber 2014). Allele frequencies were converted into a heat map for visualization.

4.3.4 Estimating genetic affinity of new recruits

After performing both DAPCs on the adults, recruits were assigned by transformation using the centering and scaling of the adult data and projected onto the predicted position using the same discriminant coefficients as the adults (Jombart & Collins 2015). For the two-group DAPC recruit assignment was evaluated using posterior membership probabilities of at least 0.8 generated with the **`predict.dapc`** function in *adegenet v.2.0.2*. We used separate χ^2 tests against a null hypothesis of (1) equal probability the recruits came from the pre- and post-SSWD adult samples and (2) equal probability recruit allele frequencies will be in the same or different direction of change as the post-SSWD adult sample, relative to the original population. Achieved power was calculated using G* Power 3 (Faul *et al*., 2007). Specific allele frequencies for the top 100 discriminatory SNPs identified in the two-group DAPC analysis were calculated using the *PopGenReport v.3.0.0* and added to the heat map generated in section 4.3.3 for comparison with adult samples.

4.4 Results

4.4.1 Mortality and recruitment in P. ochraceus

Following the outbreak of sea star wasting disease in 2013, median density of *P. ochraceus* adults in 2014 ($0.005 \cdot m^{-2}$; Q1 = $0.003 \cdot m^{-2}$, Q3 = $0.012 \cdot m^{-2}$) was 83% lower than densities in 2012 ($0.028 \cdot m^{-2}$; Q1 = $0.013 \cdot m^{-2}$, Q3 = $0.047 \cdot m^{-2}$; Wilcoxon rank-sum test, V = 91, d.f. = 1, p = 8.281×10^{-4}; Figure 4.2). For recruits, though a statistically significant difference in density could not be computed due to high heterogeneity and an abundance of zeros, there was a 93-fold increase in mean density driven by a subset of sites ($0.005 \cdot m^{-2}$ in 2012 and $0.428 \cdot m^{-2}$ in 2013–14, following the initial SSWD outbreak; Figure 4.2).

4.4.2. Samples for genetic analyses

A total of 108 samples were used in the genetic analyses (Table 4.1). dDOCENT identified a total of 2,136,713 variable sites, of which 12,480 were retained after filtering. The final data set contained 11,578 biallelic SNPs, which were used in all genetic analyses.

4.4.3 Tests for selection in adult P. ochraceus

The BayeScan test for F_{ST} outliers between pre- and post-SSWD *P. ochraceus* yielded zero outlier SNPs at an FDR of 0.1 (Figure 4.3). For SNPs to be identified as outliers, the FDR would have to be raised to 0.33. However, the top 100 discriminatory SNPs identified in the DAPC analysis have a mean change in allele frequency of 0.28 (SD = 0.06) discriminating pre- and post- *P. ochraceus* samples following the epizootic (Figure 4.5, Figure 4.6).

4.4.4 Estimating genetic affinity of new recruits

DAPC results show 90% of the new recruits collected following the outbreak of SSWD assign primarily to pre-outbreak adult samples of *P. ochraceus* (Figure 4.4) (n = 72 [9 individuals dropped with posterior probability < 0.80], $\alpha = 0.01$, $\chi^2 = 38.111$, critical value = 6.635, d.f. = 1,

power = 1.00). Comparisons of the top 100 discriminant SNPs also reveal the magnitude of difference between recruits and adult samples of (pre- and post-SSWD) *P. ochraceus* for these SNPs: pre-SSWD adults compared to recruits, mean 0.11 ± 0.01 95% CI difference in frequency; post-SSWD adults compared to recruits, mean 0.17 ± 0.01 95% CI (Figure 4.5, Figure 4.6). Post-SSWD adult and recruit allele frequencies differ from pre-SSWD adult samples, however the direction of change (i.e. increasing or decreasing) is consistent in 95% of SNPs (n = 100, α = 0.01, χ^2 = 81, critical value = 6.635, d.f. = 1, power = 1.00) and 94% of recruit allele frequencies in top candidate SNPs represent an intermediate frequency between pre- and post-SSWD adults (Figure 4.5).

4.5 Discussion

The evolution of marine species that have high fecundity and large population size is expected to be shaped less by genetic drift and more by natural selection (Gagnaire & Gaggiotti 2016). Though, marine species with high dispersal potential also may be characterized by high levels of gene flow that lead to genetic homogenization, making signals of selection difficult to detect. High gene flow marine species with large population size also are challenging because they commonly have low linkage disequilibrium (Gagnaire & Gaggiotti 2016), so even genome-wide association studies using emerging tools such as RADSeq may not detect signals of selection unless sweeps have been hard and recent; genome scans often miss many loci that are either under selection or linked with loci under selection, particularly when linkage disequilibrium is low (Lowry et al. 2017a,b). However, multiple studies have detected evidence of selection in such 'typical' species (Sanford and Kelly 2011; Pespeni & Palumbi 2013) and tools amenable to studying selection in non-model marine invertebrates, such as RADSeq, can offer the potential to identify signals of selection (Catchen et al. 2017). Linkage disequilibrium appears not to be a limiting factor in many empirical cases (McKinney et al. 2017), notwithstanding the 'file drawer problem' of publication bias (Rosenthal, 1979).

This study has the benefit of not relying on sophisticated methods to deconstruct signals of population growth, range expansion, or on linkage mapping to infer the landscape of the rest of the genome to detect potential signals of selection. Samples of the *P. ochraceus* population immediately before the putative selection event are compared to samples collected shortly after the event, allowing meaningful direct comparison of allele frequencies. In north central California, we found *P. ochraceus* suffered elevated mortality, and a coincident pulse of recruitment, during the sea star wasting epizootic (Figure 4.2). Direct comparisons of RADSeq data revealed potential signals of selection on the post-SSWD adult *P. ochraceus* samples (Figure 4.3, Figure 4.5), though power was weak due to small sample sizes. Newly recruited *P. ochraceus* were genetically most similar to the pre-SSWD adult sample (Figure 4.4); however, shifts in allele frequencies in top candidate SNPs occur in the same direction in the recruits as in the post-SSWD sample, relative to the pre-SSWD sample (Figure 4.5), suggesting natural selection is the predominant driver of evolution in this system.

4.5.1 Natural selection v. genetic drift

In the decimation of the highly abundant and fecund *P. ochraceus* by an epizootic disease epidemic, theory would predict that selection would drive differentiation rather than genetic drift or gene flow (Gagnaire & Gaggiotti 2016). However, a traditional test using F_{ST} outliers (BayeScan) did not yield any significant outlier loci in our data set. Other studies have found high gene flow led to allele frequencies that are similar between sites across a broad geographic range, though also identified loci (not detected as outliers) that had non-random higher F_{ST} relative to other loci, suggesting potential hidden signals of selection (Pespeni et al. 2012) perhaps associated with multi-genic traits, weak selection on or near the locus. Methods of outlier detection of candidate loci may then depend on high numbers of SNPs and large sample sizes if the loci are of weak effect (Gagnaire & Gaggiotti 2016). Currently, our data set is small (Table 4.1), likely contributing to weak power to detect outliers. Moreover, polygenic selection is likely common in natural populations, but often undetected with conventional methods for

detecting selection (Pritchard & Di Rienzo 2010). Given BayeScan relies on extreme F_{ST} values between samples, it may fail to capture polygenic selection because of weak statistical power due to the small effect size of each locus (Villemereuil et al. 2014).

The nature of our data set — i.e. paired temporal samples — made it amenable to direct comparison of allele frequencies between the pre- and post-SSWD samples of *P. ochraceus*. SNPs of largest effect in our data set, identified by the discriminant analysis of principal components, were directly compared for changes in allele frequency between the original *P. ochraceus* population and sea star wasting survivors and new recruits (Figure 4.5). Importantly, the DAPC was conducted using the groups pre- and post-SSWD for discrimination; recruits were subsequently mapped using the already constructed discriminant function and thus did not influence which loci were identified as having the largest difference. When compared among all three groups (pre-, post-SSWD adults, and recruits) the discriminating loci reveal consistent, i.e. non-random, changes in allele frequencies between the original population and survivors and recruits (Figure 4.5b), suggesting selective forces drove shifts in allele frequencies rather than drift.

Undoubtedly, selection and genetic drift are always operating, and drifts' influence relative to selection and gene flow is expected to increase at smaller population sizes (Futuyma 1998, p.392). In the aftermath of a massive reduction in population size (decrease by 83%) of *P. ochraceus*, did genetic drift play a major role in shaping patterns of genetic change? The relative importance of drift in driving observed differences in pre- and post-SSWD samples of *P. ochraceus* does not appear to have been discernibly elevated. Theoretically, while reduction in population size was significant, the post-outbreak population size of *P. ochraceus* still was large in population genetic terms (we estimate no less than a quarter-million individuals). In such cases, even a tiny coefficient of selection often exceeded in natural situations (Charlesworth 2009), would numerically overwhelm $1/4N_e$ and so the expected magnitude of the effect of drift. It can be difficult to distinguish between selection and drift using changes in allele frequencies between time series samples (Feder et al. 2014). However, empirically, it is statistically improbable that drift leads to random allele frequency shifts in the same direction in post-SSWD adults and new recruits more than, for example 60% of the time in a sample size of 100 (χ^2 test, $\alpha = 0.05$, d.f. = 1) and we see it in 95% of SNPs ($\alpha = 0.05$, Section 4.4.4; Figure 4.5). As such, we infer the primary mechanism driving apparent differences between the original population of *P. ochraceus* and survivors and new recruits is natural selection. This will be further tested with an expanded data set using comparisons between geographic sites to identify whether there are consistent independent shifts in allele frequencies.

4.5.2 Gene Flow

Having samples from only two locations (Figure 4.2) restricts detailed exploration of the potential influence gene flow has on new recruits. There is some evidence of self-recruitment (Chapter 3, Figure 3.6) and asymmetric dispersal (Chapter 3, Figure 3.5, Figure 3.6) in this region. Additionally, gene flow in *P. ochraceus* is high (Chapter 3; Harley et al. 2006) and the disease outbreak was range-wide (http://seastarwasting.org). A more thorough discussion of this will require additional samples from additional locations.

4.5.3 The case for new recruits being progeny of pre-SSWD P. ochraceus

Despite the apparent correlation in shifts in allele frequencies observed in new *P. ochraceus* recruits and post-SSWD adults (Figure 4.5) the majority of evidence points toward pre-SSWD adults as the likely source population of new recruits. DAPC results assign 90% of recruits to the pre-SSWD population and allele frequencies — despite being correlated in the direction of change with post-SSWD adults — are closer to pre-SSWD frequencies. Additionally, the timeline of reproduction, mortality, and recruitment (Figure 4.7) fit most closely with the hypothesis that pre-SSWD adults were the source for new recruits in 2014. *P. ochraceus* spawn from April–May (Morris et al. 1980) and have a pelagic duration of 6–8 weeks (Strathmann 1987), which would lead to intertidal settlement in approximately June–August. Recruits for this study were collected in Jan–May 2014 and therefore likely were spawned in the previous year. Observations of sea

star wasting disease were first documented in this region in late summer 2013 (http://seastarwasting.org). The timeline suggests the recruits used in this study could have been exposed to SSWD for approximately 4–8 months in the intertidal.

4.5.4 The future of P. ochraceus

P. ochraceus suffered major mortality between 2013-2014 associated with SSWD epizootic (Figure 4.2; Menge et al. 2016), but also experienced record recruitment rates up to 300 times previous records (Menge et al. 2016). Sea star wasting disease is still present in *P. ochraceus* populations (http://seastarwasting.org; pers. obs.) and likely still exerting selection on susceptible individuals in otherwise seemingly somewhat resilient populations. Despite recently elevated recruitment rates, these new recruits will not contribute to reproduction for some time; *P. ochraceus* do not reach maturity until approximately 5 years of age (Menge 1975), although maturation time could be shorter if *P. ochraceus* feed to satiation (Monaco et al. 2014). This lag time makes predictions about recovery difficult, given continued persistence of the disease in *P. ochraceus*.

After a period of very low recruitment in *P. ochraceus* (Figure 4.2; Menge et al. 2016), elevated pulses of recruitment have continued through at least 2016 (Chapter 3 and L. Schiebelhut unpublished data). All years of recruitment after the event documented in this study would be spawned by the post-SSWD population, suggesting the shift in allele frequency should be maintained in future generations (e.g. see scenario 1 in Figure 4.1). However, a number of factors could influence the trajectory of change in future populations. For example, elevated recruitment could bring with it the dispersal of deleterious alleles from other locations given heterogeneity in mortality and counteract allele frequency changes caused by selection (Lenormand 2002). Additionally, sweepstakes reproduction is thought to be common in taxa with high fecundity and high larval mortality, whereby only a subset of adults contribute to successful cohorts of juveniles (Hedgecock 1994), potentially reducing the genetic pool on which selection can act in cohorts of new recruits. An intriguing possibility of unknown effect includes the potential for planktonic larval cloning increasing recruitment from the originally spawned cohort (Bosch et al. 1989; Rogers-Bennett 2007). While we have shown that juvenile sea stars recruiting the first year following the wasting disease outbreak were likely spawned by adults before the onset of mass mortality, subsequent pulses of recruitment would have likely been spawned by survivors (i.e. only 13% of the original population). Genotyping of subsequent pulses of recruitment needs to be done to determine genetic relationships between adults and juveniles, and to help us better understand the range of possible futures for *P. ochraceus* in the aftermath of this outbreak of sea star wasting disease.

A major concern in species affected by environmental change is that adaptation is outpaced by environmental change (van Oppen et al. 2015). If observed shifts in allele frequency in *P. ochraceus* are linked with increased survivorship leading to reproductive success, perhaps *P. ochraceus* has the potential to be pre-adapted to future outbreaks of sea star wasting if caused by the same pathogen. However, the dynamics of how the virus implicated in SSWD (SSaDV) interacts with the environment to influence susceptibility in *P. ochraceus* and SSWD prevalence are still unknown. For example, temperature is perceived to play a role in exacerbating SSWD, but whether the role is in elevated temperature (Eisenlord et al. 2016; Kohl et al. 2016) or reduced temperature (Menge et al. 2016) remains unresolved. It also is unclear whether the current outbreak of SSWD and prior geographically restricted outbreaks (Eckert et al. 1999; Becker 2006; Bates et al. 2009) are attributable to the same causes, and so whether adaptation in the current outbreak will convey resistance in future outbreaks.

Nonetheless, *P. ochraceus* seems to have the propensity to persist and adapt to perturbation given its large population size, extensive gene flow (Chapter 3), and high standing stock of genetic variation on which selection can act (Lynch 2010). Future work will expand analyses to samples from the full geographic range of sampling (Figure 4.2 plus 4 additional site outside this region) and beyond using archived samples (Harley et al. 2006), to examine the consistency in allele frequency shifts across sites and whether there is a correlation with site-

specific mortality rate, other environmental factors, and better understand the circumstances under which tension may exist between genetic drift, migration, and selection.

4.6 References

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4.7 Tables

Table 4.1 List of sites and sample sizes used in genetic analyses.

	Site	County	Latitude	Longitude	Adults Pre-SSWD	Adults Post-SSWD	Recruits <1yr
1	Bodega Head	Sonoma	38.32	-123.07	13*	7	27
2	Lifeboat House	Marin	38.00	-122.98	9	7	45
				Totals	22	14	72

Notes:

* Adults taken from two different sites on Bodega Head (n = 3 and 10).

4.8 Figures

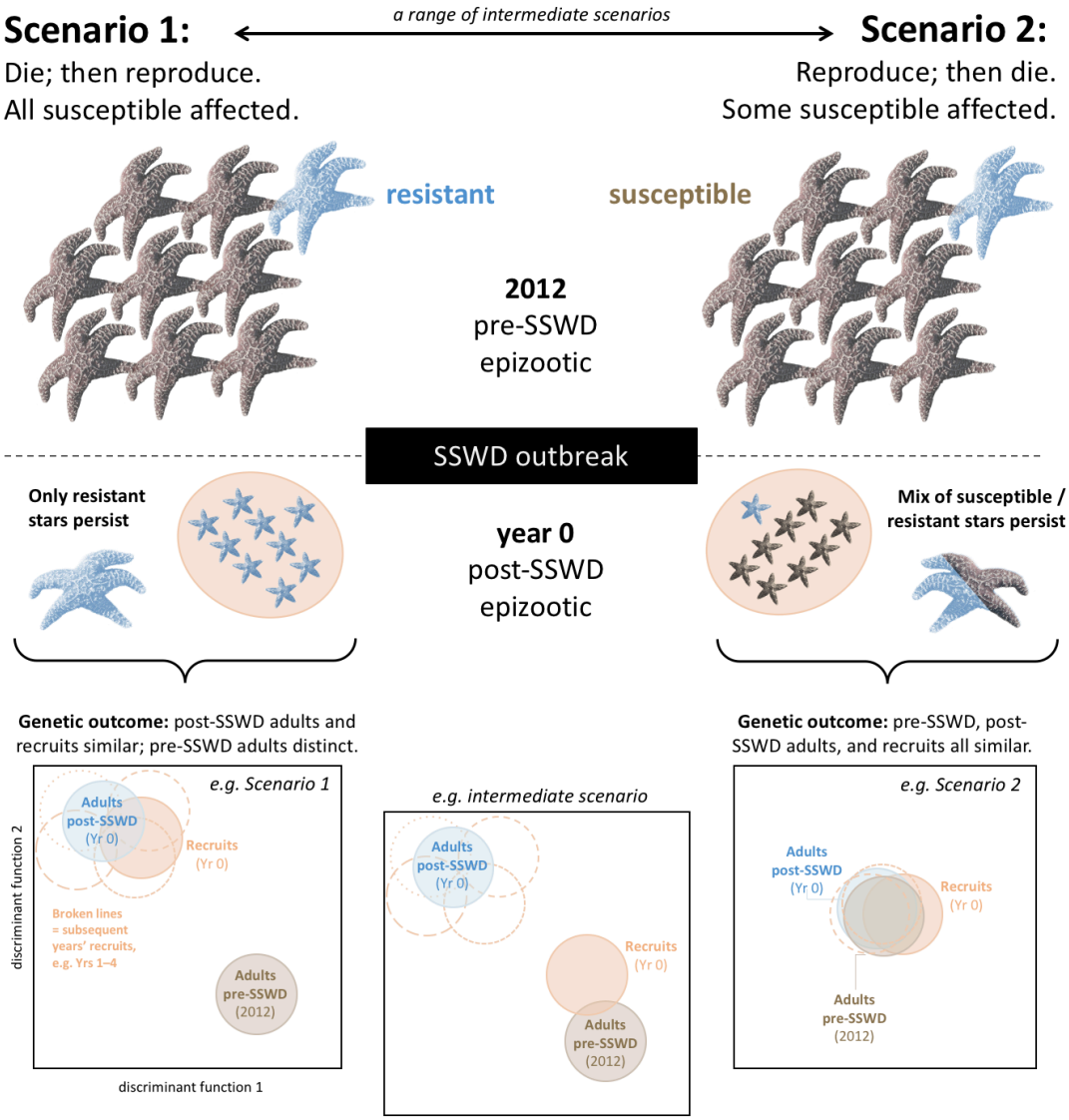

Figure 4.1 Schematic showing the range of population genomic changes in *P. ochraceus* that could be caused by a SSWD pandemic. ***Scenario 1:*** If all susceptible (brown) sea stars died before reproduction (spawning time in spring), all new recruits (i.e. <1 year-old) will be spawned by and genetically similar to the surviving resistant adults (blue). SSWD would lead to a substantial long-term shift to resistant forms, as illustrated in the discriminant analysis plot at bottom left. ***Scenario 2:*** If SSWD was geographically patchy or insufficiently prevalent to eliminate most susceptible genotypes from the reproductive and recruitment pools, there could be no substantial short- or long-term effect on allele frequencies, as illustrated in the plot at bottom right. Many ***intermediate scenarios*** are possible, of which one is shown (bottom, center): if reproduction preceded mass mortality of the majority of susceptible individuals (i.e. a mix of Scenarios 2 & 1) the surviving adults would be resistant but the new recruits would, like their pre-outbreak parental population, be susceptible to SSWD. However, new recruits in subsequent years would be spawned by the surviving resistant adult sea stars. The frequencies of adults and recruits in the schematic are illustrative only; the half-brown/blue star is used to illustrate a small population with both resistant and susceptible alleles (i.e. it does not represent a heterozygote).

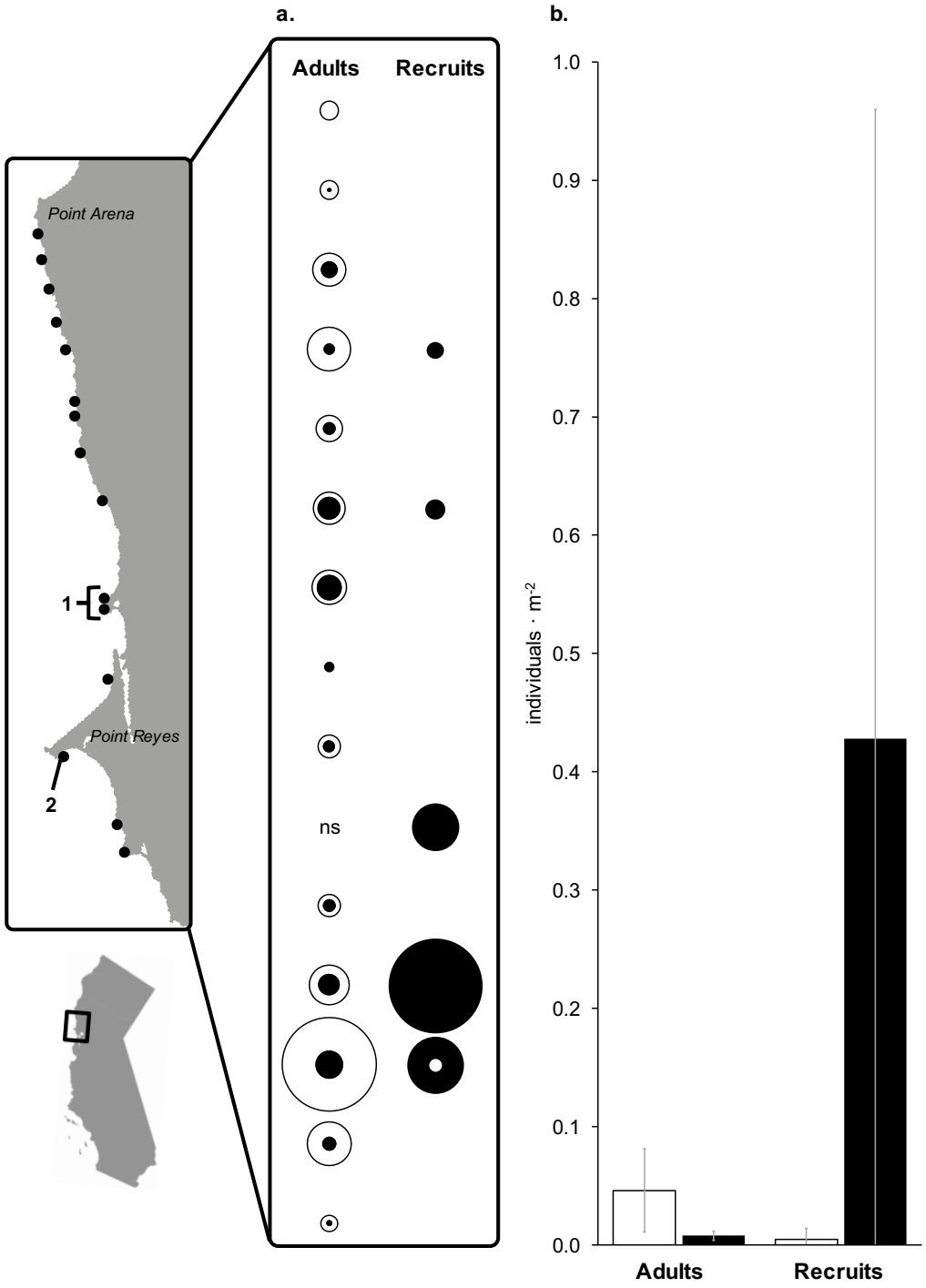

Figure 4.2 Spatial and temporal variation in abundance of *P. ochraceus* before (white) and after (black) the 2013 SSWD outbreak that killed mean 83% of *P. ochraceus* in this region. (a) Change in adult and recruit densities is represented by concentric bubbles; area of bubbles is proportional to density (adults: max area = $0.27 \cdot m^{-2}$; recruits: max area = $3.78 \cdot m^{-2}$). (b) Mean density per square meter and 95% CI across surveyed sites. ns = quantitative survey not conducted (though DNA samples were collected here). Sites labelled 1 and 2 denote sites with specimens used in genetic analyses.

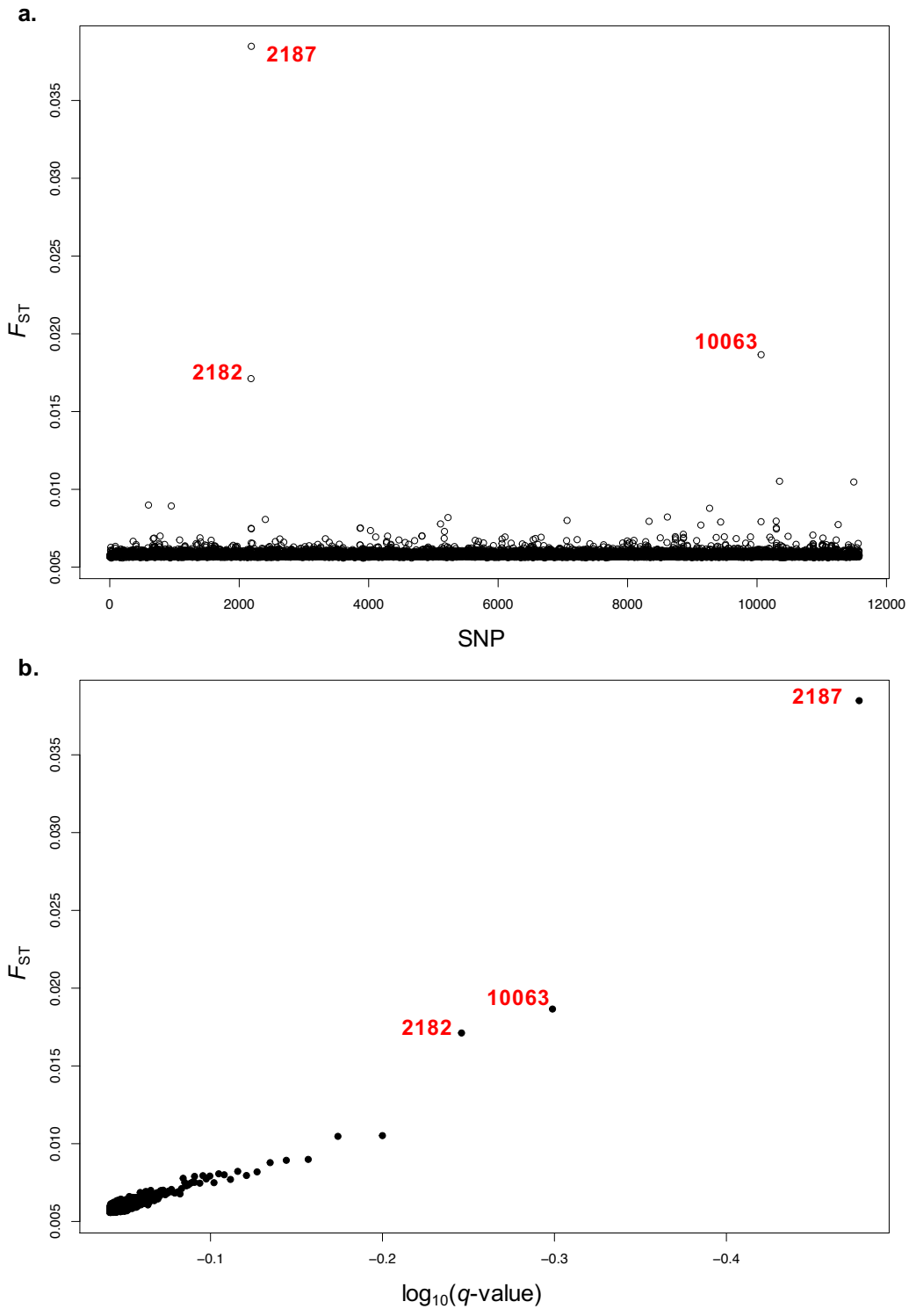

Figure 4.3 Results from the BayeScan test for SNP outliers comparing *P. ochraceus* adults collected before and after the SSWD outbreak. (a) F_{ST} values by SNP and (b) F_{ST} values by corresponding *q*-value. N.B. no SNPs were detected as outliers at an FDR = 0.1. The most extreme SNPs are labeled red and cross-identified in Figure 4.5.

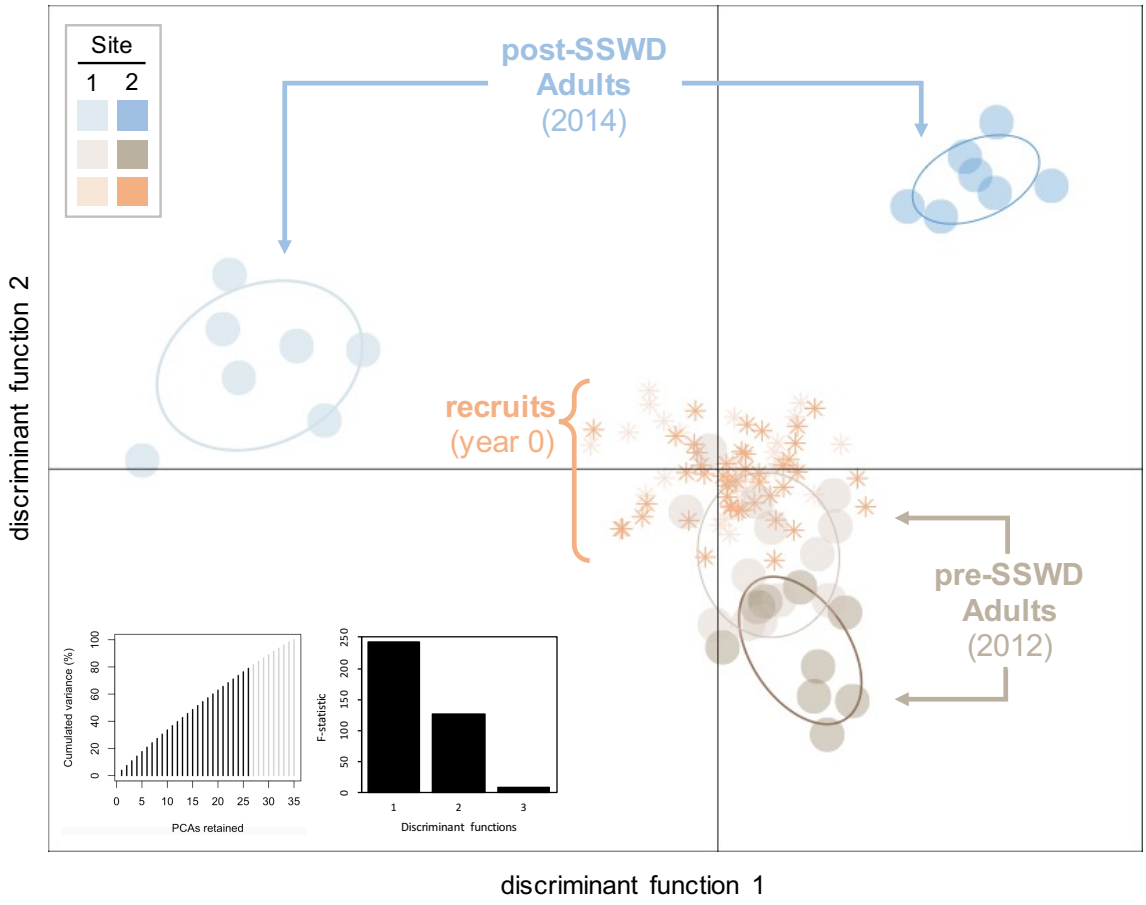

Figure 4.4 Discriminant analysis of principal components (DAPC) of 11,578 ddRAD generated SNPs comparing pre- (2012) and post-SSWD outbreak populations of adult *P. ochraceus* and <1 year-old recruits collected in 2014. These preliminary analyses are based on samples from only two sites (Lifeboat House in Point Reyes and Bodega Head; sites 1 and 2 in Figure 4.2). The two inset bar graphs represent the number of principal components retained (black bars) to explain 79% of the cumulative variance (left) and the discriminant functions used (n groups – 1) in the DAPC with corresponding F-statistic (right).

a.

SNP	Pre-SSWD Adults	Recruits	Post-SSWD Adults
8615	0.262	0.612	0.786
4021	0.286	0.398	0.679
1080	0.364	0.516	0.607
768	0.405	0.698	0.857
10296	0.409	0.576	0.679
10298	0.409	0.576	0.679
763	0.409	0.507	0.75
10297	0.409	0.563	0.786
4347	0.409	0.563	0.786
689	0.409	0.563	0.786
4028	0.432	0.629	0.679
9102	0.432	0.679	0.714
10062	0.432	0.589	0.75
3391	0.432	0.589	0.75
4367	0.432	0.667	0.75
3873	0.455	0.553	0.714
6107	0.477	0.582	0.75
11221	0.477	0.676	0.821
11210	0.5	0.664	0.75
10031	0.5	0.592	0.786
767	0.5	0.653	0.821
4022	0.5	0.656	0.929
7111	0.523	0.581	0.214
4581	0.523	0.589	0.214
5519	0.523	0.574	0.714
6374	0.523	0.574	0.714
10304	0.523	0.574	0.714
5536	0.523	0.583	0.714
8609	0.523	0.597	0.786
10302	0.523	0.579	0.821
691	0.523	0.587	0.821
5736	0.523	0.595	0.821
5927	0.524	0.617	0.786
10863	0.568	0.656	0.846
5171	0.591	0.567	0.286
2197	0.591	0.523	0.357
8414	0.591	0.538	0.357
8410	0.591	0.636	0.821
5673	0.591	0.804	0.857
5674	0.591	0.804	0.857
7112	0.595	0.819	0.929
7114	0.595	0.81	0.929
3141	0.614	0.524	0.357
5218	0.614	0.758	0.821
7992	0.614	0.698	0.875
2184	0.614	0.698	0.875
2188	0.614	0.698	0.875
8532	0.614	0.698	0.875
3867	0.614	0.698	0.875
665	0.625	0.551	0.286

Continued.

769	0.636	0.821	0.857
2182	0.636	0.707	0.893
5774	0.636	0.788	0.893
6899	0.643	0.515	0.321
8197	0.659	0.568	0.429
3780	0.659	0.788	0.893
482	0.675	0.81	0.964
10334	0.682	0.54	0.357
10063	0.682	0.636	0.393
764	0.682	0.619	0.393
1508	0.682	0.659	0.429
951	0.682	0.825	0.929
3776	0.705	0.563	0.321
9274	0.705	0.556	0.393
8280	0.705	0.652	0.429
733	0.705	0.592	0.429
7571	0.705	0.817	0.929
3036	0.705	0.825	0.929
848	0.727	0.632	0.357
5167	0.727	0.686	0.429
7110	0.727	0.566	0.464
1507	0.727	0.549	0.464
11212	0.727	0.614	0.5
11213	0.727	0.614	0.5
4348	0.727	0.702	0.5
10261	0.727	0.702	0.5
8535	0.727	0.702	0.5
8536	0.727	0.686	0.5
8537	0.727	0.702	0.5
8548	0.727	0.625	0.5
8279	0.75	0.649	0.429
1501	0.75	0.718	0.429
732	0.75	0.716	0.464
2187	0.75	0.708	0.5
11337	0.75	0.79	0.5
11206	0.75	0.75	0.5
4346	0.75	0.742	0.5
8538	0.773	0.635	0.464
8030	0.773	0.466	0.5
11211	0.795	0.68	0.5
700	0.795	0.73	0.571
5699	0.864	0.731	0.5
2482	0.864	0.833	0.607
4343	0.864	0.804	0.607
4344	0.864	0.804	0.607
1500	0.864	0.792	0.607
10299	0.886	0.89	0.571
8200	0.886	0.762	0.643
1630	0.932	0.726	0.643
8004	0.932	0.726	0.643

b.

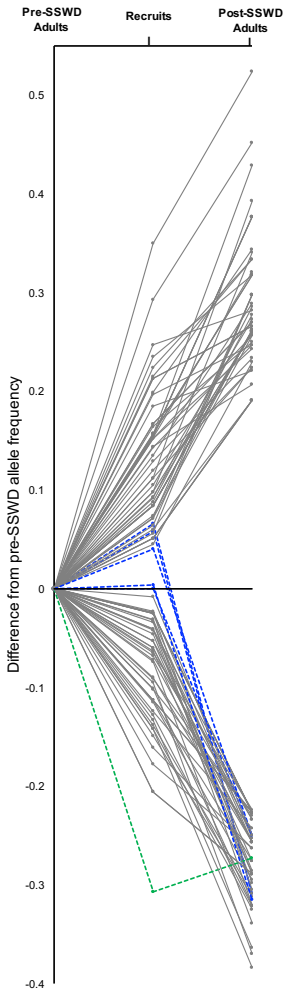

Figure 4.5 Frequencies of the top 100 biallelic discriminatory SNPs identified in the DAPC analysis for pre-SSWD, recruits, and post-SSWD adults shown by (a) a heat map (yellow = low frequency; purple = high frequency), with SNPs organized in order of increasing frequency for the pre-SSWD adults and (b) a line plot showing the difference in allele frequency between the original *P. ochraceus* population and new recruits and post-SSWD population; the horizontal black line represents no change and dashed lines represent the 6 (of 100) SNPs for which recruit allele frequencies are not intermediate to pre- and post-SSWD adult allele frequencies (blue = change in frequency in opposite direction for recruit and 'post' adult; green = change in same direction, but recruit greater change than 'post' adult). N.B. the connecting lines are meant to highlight trends, not suggest succession. The recruits are most similar to the pre-SSWD adult population (Pre–v–Recruit: mean 0.11 ± 0.01 95% CI difference in frequency; Post–v–Recruit: mean 0.17 ± 0.01 95% CI; Figure 4.6), however, the direction of allele frequency change is generally consistent in the post- and recruit populations; 94% of recruit allele frequencies represent an intermediate frequency between pre- and post-SSWD adults. Red boxes highlight potential outlier SNPs from BayeScan (Figure 4.3).

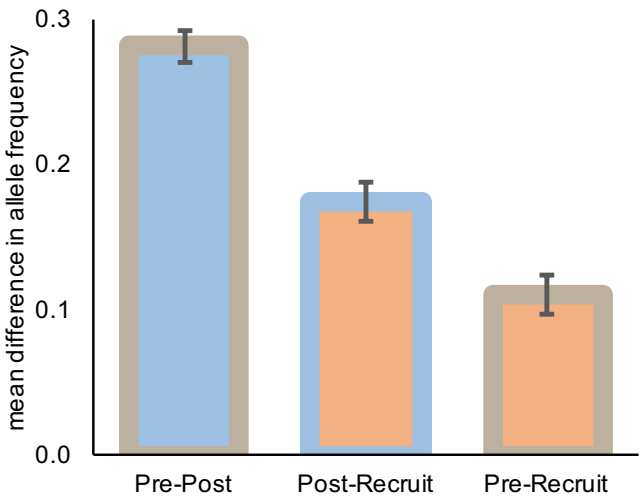

Figure 4.6 Mean change in allele frequency for top 100 biallelic discriminatory SNPs (Figure 4.3) between *P. ochraceus* adults collected before (Pre, brown) and after (Post, blue) the SSWD outbreak and between the 'Pre' and 'Post' adult samples versus new 2014 recruits (orange). Colors indicate comparison and match labels on x-axis. Error bars are 95% confidence intervals.

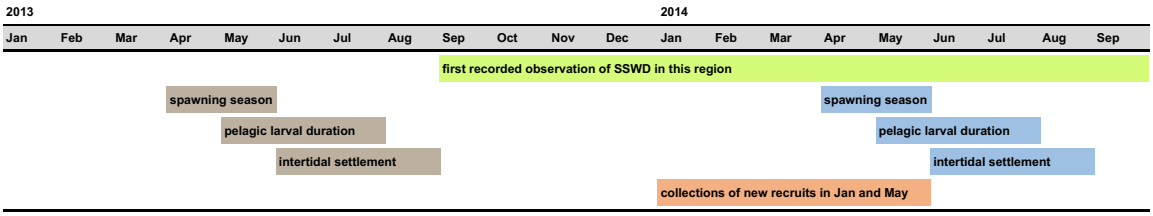

Figure 4.7 Timeline of main reproductive stages for the 'pre' and 'post' sea star wasting disease adults and onset of SSWD for *P. ochraceus*. Recruits would have been spawned by the 'pre' outbreak population of *P. ochraceus*.

Chapter 5. The confluence of ecological meandering and evolutionary trends points toward predictable patterns

Ecological time and evolutionary time often have been considered, probably incorrectly, as distinct units for study (Schoener 2011). However, it is at their fuzzy interface that populations are shaped and reshaped by ecological processes and evolutionary mechanisms (Thompson 1998, 1999; Schoener 2011). Through a series of studies spanning these timelines I have aimed to integrate process in 'natural experiments' to disentangle some of the complexities found in the natural systems where population genetic factors interact to shape drift, migration, and selection.

On the shortest time-scales, I studied a temporally rare, extreme event (in Chapter 4) which led to high mortality in a species with high dispersal potential (i.e. large population size, high fecundity, and long pelagic duration). I found that rare events can have large impacts and these impacts can leave detectable signals in future generations. But this study leaves open the question of how long these detectable signals will persist. Chapter 3 provided an additional perspective on temporal heterogeneity: that it may vary chronologically, from year to year to year. What drives the heterogeneity in recruitment between years? For *Pisaster ochraceus*, recruitment increased from nearly nonexistent to highest on record in the span of a few years (chapters 3, 4; Menge et al. 2016). Temporally highly variable recruitment is not uncommon and can be an effective strategy for avoiding predation (Yang et al. 2010) similar to masting in trees linked with favorable environmental conditions in terrestrial systems (Koenig et al. 2015). How might life-history strategies in marine species interact with oceanographic conditions to explain observed differences in *P. ochraceus*, *Strongylocentrotus purpuratus*, and *Leptasterias* sp. and other taxa?

I also explored spatial heterogeneity. I found that, intermeshed within inter-annual variability, recruitment also was spatially variable across the study region (Chapter 3). Our ecological surveys now extend over five years across the same geographic sites and one thing is clear: recruitment is variable. A second thing is also clear: recruitment rates and distances vary predictably with life-history traits. These two observations suggest, despite the complexities, that there are underlying processes at work leading to predictable patterns. Understanding the interaction of biological (and physical) processes over multiple spatial and temporal scales is one of the main challenges in ecology (Thompson et al. 2001).

One important consideration, not explored in great detail in my thesis, is that the environment is not static. Large scale patterns (e.g. El Niño / La Niña), overlaid on millennial climate change, and modified by seasonal or shorter timescale (and thus spatial scale) interact to form the environmental landscape in which populations live, respond, and evolve. Ecological meandering thus can be driven by a number of factors, for which few are accounted given the short period of studies typical in many marine systems. For example, the tidal epoch (every 18 years) can create peaks in risk for heat extremes in the intertidal (Mislan et al. 2009), which could be exacerbated if coupled with El Niño. How does such a scenario impact populations? How does this change the pattern of recruitment or the genetic source of recruits? Do different combinations of environmental factors lead to different dispersal kernels? How long do signals of this inter-annual variability persist and how do they translate into population genetic patterns? And are there predictable outcomes to these ecological meanderings (e.g. Figure 5.1)?

My dissertation highlights how the integration of life-history traits in estimates of dispersal potential, when effects of the environment are controlled for, can lead to predictable outcomes across ecological and evolutionary timescales. However, it is important to remember that traits may not be static, though my studies handle each species' trait values as having a meaningful central tendency. Quantitative estimates of traits are taken from field or laboratory studies, often across only a small subset of individuals, conditions, or time points. Trait values in the literature may only represent a small fraction of the variation present in wild populations, variation which is itself shaped by ecological and evolutionary processes. Fecundity, for example, can be highly variable, fluctuating with mean body mass of reproductive adults, food availability, or other environmental factors (Castorani et al. 2017). Nevertheless, estimates of dispersal potential seem to account for differences in empirical estimates of population genetic structure in many cases (Chapter 2). Is this a lucky coincidence? Or do the vagaries of space and time which display as

ecological meanderings tend to manifest as evolutionary trends? My results suggest yes, there is a causal predictive relationship, not just an emergent pattern that we discern (or imagine) when looking back through the mists of time; these are tales of real events and their consequences (Chapters 2–4), not retrospective 'just so' stories (Shanks & Eckert 2005).

As global meta-analyses in Chapter 2 illustrate, despite the complexity in natural systems, heterogeneous patterns of recruitment, and paucity of ecological data, a general relationship between dispersal potential and population genetic structure is nevertheless detectable. In most cases enough of the variation in dispersal potential is captured by available ecological data to account for relative differences in gene flow between species. However, exceptions do exist, which I propose is not a failure in the approach, but an indication that in these cases gene flow is not the dominant mechanism. Such exceptions should lead us to explore alternative hypotheses, such as selection and/or drift.

For some taxa, enough data have accumulated to move past evaluating simple dichotomous classifications — e.g. direct development versus planktonic development — and so to progress to quantitatively parameterize specific traits to develop a predictive model of dispersal potential (e.g. Treml et al. 2012). However, to build a complete picture we need more and better data for life-history and ecology (e.g. species abundances at the time of study [Burgess et al. 2014; Chapter 2]). We also need more long-term studies — both ecological and genetic — across various geographic scales (Chapter 3). To understand how modern patterns came to be, we need to understand variation over a suite of spatial and temporal scales in the past. To begin to understand how a species might respond to anthropogenically induced environmental change in the future, we need to better understand the modern eco-evolutionary landscape.

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5.2 Figures

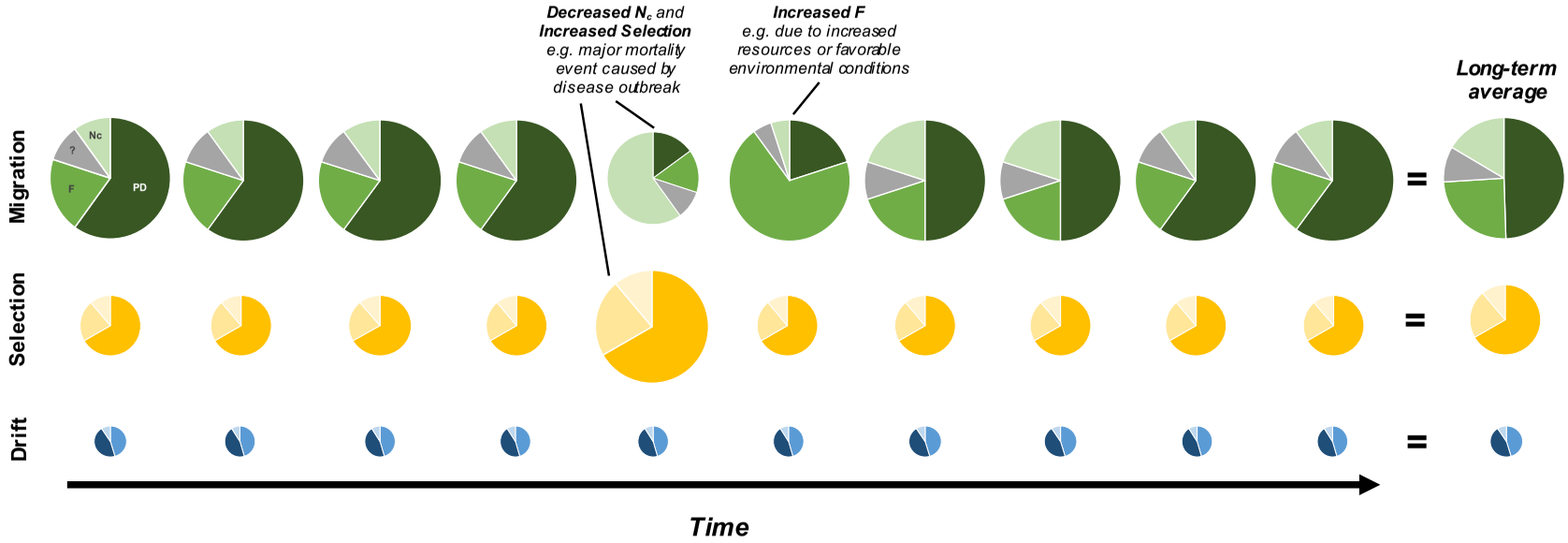

Figure 5.1 Illustration of hypothetical ecological meandering, in which the relative importance of a particular trait on genetic outcomes changes through time — e.g. by chance, due to environmental variation, ecological conditions, or trait evolution — and yet due to central tendencies of serial events potentially leads to evolutionary trend. Each pie slice represents a specific trait — e.g. pelagic duration (*PD*), fecundity (*F*), and census population size (N_c).