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REVIEW AND SYNTHESIS

Phenotype–environment mismatches reduce connectivity in the sea

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Abstract

The connectivity of marine populations is often surprisingly lower than predicted by the dispersal capabilities of propagules alone. Estimates of connectivity, moreover, do not always scale with distance and are sometimes counterintuitive. Population connectivity requires more than just the simple exchange of settlers among populations: it also requires the successful establishment and reproduction of exogenous colonizers. Marine organisms often disperse over large spatial scales, encountering very different environments and suffering extremely high levels of post-colonization mortality. Given the growing evidence that such selection pressures often vary over spatial scales that are much smaller than those of dispersal, we argue that selection will bias survival against exogenous colonizers. We call this selection against exogenous colonizers a phenotype–environment mismatch and argue that phenotype–environment mismatches represent an important barrier to connectivity in the sea. Crucially, these mismatches may operate independently of distance and thereby have the potential to explain the counterintuitive patterns of connectivity often seen in marine environments. We discuss how such mismatches might alter our understanding and management of marine populations.

Keywords

Connectivity, dispersal, larvae, local adaptation, phenotypic plasticity, recruitment.

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INTRODUCTION

In marine environments, a species' range is often characterized by a series of local populations (or demes) that are demographically connected to each other by the exchange of planktonic larvae (Grosberg & Cunningham 2001; Gaines *et al.* 2007). Demographic connections among populations are fundamental to their persistence, recovery from disturbance and demographic structure (Cowen & Sponaugle 2009). Hence, how well we understand and manage populations is fundamentally linked to how well we understand their connectivity (Palumbi 2004). Connectivity among populations can be affected by a range of factors, the most obvious of which are physical barriers to larval dispersal that limit the exchange of colonizers among demes (Pineda *et al.* 2007). However, barriers to dispersal need not be only physical: biological barriers to dispersal, while less studied, may also be common and may resolve counterintuitive patterns of connectivity (Grosberg & Cunningham 2001; Gaines *et al.* 2007). Here, we focus on one potential biological barrier to dispersal: phenotype–environment mismatches, whereby individuals that disperse to a new environment suffer heightened mortality before reproduction relative to locally derived individuals (sometimes termed immigrant inviability arising from local adaptation; Hendry 2004; Nosil *et al.* 2005). In other words, non-random mortality immediately after dispersal may reduce population connectivity, despite physical transport of larvae among populations. DeWitt *et al.* (1998) introduced the term 'phenotype–environment mismatch' to describe the reduction in fitness incurred when an organism that is specialized to one environment finds itself in an alternative environment. Here, we consider the ecological consequences of such mismatches for dispersal in marine environments, particularly for species whose population connectivity may poorly reflect their highly dispersive larval phase. We examine current theories of biological barriers to connectivity in relation to marine systems and argue that phenotype–environment mismatches, although underestimated, may be particularly important in taxa (including marine taxa such as marine invertebrates and coastal fishes, as well as terrestrial taxa such as plants) where dispersal

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occurs prior to reproduction. We then evaluate the evidence for phenotype–environment mismatches as biological barriers to connectivity in marine environments. Finally, we discuss how such mismatches might alter our understanding and management of marine populations.

How open are marine populations?

The life-history of many marine organisms (with the notable exception of pelagic species) includes a relatively sedentary adult phase and a dispersive propagule phase. During the latter, marine organisms are capable of dispersing remarkably far, along the lengths of entire coasts and even across oceans (Grosberg & Cunningham 2001). In contrast to many terrestrial organisms that have limited dispersal, the potential dispersal capabilities of marine organisms, coupled with the apparently continuous nature of open oceanic environments, has led to a view of marine populations as being replenished by recruits derived from other populations; a demographically 'open' population (Caley *et al.* 1996). In open populations, population persistence is determined by demographic processes operating at the metapopulation level, rather than by reproduction and survival within local populations alone.

The view that marine populations are demographically open has considerable intuitive appeal and for many years has persisted as a way of both understanding marine population dynamics and of managing exploited populations (Caley *et al.* 1996; Cowen *et al.* 2000; Palumbi 2004). However, there is ample evidence suggesting that species can exist anywhere on a connectivity continuum, with some being completely open while others are completely closed (Kinlan & Gaines 2003). To the extent that such variability reflects dispersal capability, it is perhaps unsurprising: ecologists have long expected populations to be largely closed for species with no planktonic stage, only locally connected for species with short larval periods and largely open for species that disperse widely (Kinlan & Gaines 2003). What is surprising, however, is the existence of species whose life-histories predispose them to relatively high connectivity, yet whose populations appear to be relatively closed (Grosberg & Cunningham 2001).

Recent genetic studies have revealed that populations are not necessarily as connected as one would expect, and that patterns of connectivity may be non-intuitive. There have been numerous reviews on the scales of dispersal by propagules in marine environments (e.g. Palumbi 1995; Kinlan & Gaines 2003; Cowen & Sponaugle 2009). We do not wish to retrace this ground here, but do wish to highlight some important points that are relevant to our discussion. First, while increases in pelagic larval durations tend to increase dispersal distances across a range of species, it appears that these species consistently fail to disperse as far as would be predicted, even after accounting for complex hydrography (Shanks 2009). Second, while genetic structure can appear homogenous over large spatial scales, it can be significantly heterogeneous at smaller scales (Taylor & Hellberg 2003). Third, genetic variation in neutral markers may reflect historical spatial structure, but not contemporary connectivity among populations (see Conover *et al.* 2009). Last, in a number of species, genetic structure does not always scale with physical distance among populations (Johnson & Black 2006; Hedgecock *et al.* 2007; Schmidt *et al.* 2008). Overall, marine populations are increasingly being viewed as less open than once thought and, in some cases, prone to higher-than-expected recruitment by locally produced larvae (Jones *et al.* 1999; Swearer *et al.* 1999; Almany *et al.* 2007; Becker *et al.* 2007). Yet, despite low estimates (based on both genetic and direct measurements) of connectivity, marine larvae are often capable of dispersing great distances (Grosberg & Cunningham 2001). We are therefore left with the paradox: why are some marine populations so poorly connected when their larvae can disperse so far? Why do some populations show fine scale genetic structure while others, with similar larval dispersal capabilities, do not? In other words, what are the barriers to connectivity in the marine environment?

BARRIERS TO CONNECTIVITY IN THE SEA

Pre-colonization barriers to connectivity

The ocean is less permeable to dispersal than one might think. There are numerous potential physical barriers to larval transport, including hydrographic fronts, isoclines and local retention zones that prevent or at least weaken the exchange of larvae among populations (Pineda *et al.* 2007). Physical barriers, however, are not the only hindrance to larval transport: biological barriers to dispersal may also act to limit larval exchange among populations.

For dispersing larvae, the plankton is a dangerous place. Larval mortality during dispersal is notoriously difficult to assess and estimates vary, but, for over 50 years, the prevailing view is that the bulk of mortality for species with long-lived larvae occurs at this stage (Thorson 1950; Morgan 1995). Larval mortality can occur because of predation and, in feeding larvae, starvation. Together, predation and starvation may account for > 90% of mortality while in the plankton (Morgan 1995). Ultimately, because larval mortality while in the plankton increases with the pelagic larval duration, the longer a pool of larvae spends in the plankton, the smaller the pool of larvae being transported. Thus, mortality during larval dispersal may reduce connectivity among populations, even in the absence of physical barriers.

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Post-colonization barriers to connectivity

Population connectivity requires more than just the simple exchange of settlers among populations: it also requires that exogeneous colonizers survive to reproduction (Hedgecock 1986; Pineda *et al.* 2007; Hamilton *et al.* 2008). Thus, even those populations with high proportions of larval exchange may still be poorly connected if exogeneous larvae die immediately after colonization. While post-dispersal mortality will weaken population connectivity overall, post-dispersal mortality may be relatively higher for larvae that leave the natal environment to disperse to a new population. Below, we discuss two post-colonization barriers to dispersal: (1) physiological costs of dispersal and (2), phenotype–environment mismatches.

Dispersing out of one's natal environment carries various costs. In addition to mortality during the dispersive larval phase, so-called deferred or indirect costs of dispersal that accrue during dispersal but manifest after colonization can also reduce connectivity. For species that produce non-feeding larvae, dispersal during the larval phase is energetically costly and any increase in larval duration can reduce post-colonization survival and performance (Pechenik 2006). As such, larvae that disperse long distances can have lower levels of energetic reserves – and hence, lower chance of recruiting successfully – than larvae that spend a short time in the plankton. These energetic costs of dispersal are only likely to apply to a subset of species (those with non-feeding larvae) and should act in a dispersal distance-dependent manner, similar to pre-colonization barriers to connectivity. In situations where food resources are more concentrated in coastal waters, populations of species with feeding larvae may also exhibit reduced connectivity, as dispersers are likely to settle in poorer condition than locally retained larvae. There is, however, an alternative post-colonization barrier to connectivity that could explain the unexpectedly high levels of self-recruitment in marine environments, as well as the decoupling of dispersal potential from actual connectivity, and will be the focus of the rest of this review: phenotype–environment mismatches.

PHENOTYPE–ENVIRONMENT MISMATCHES IN THE SEA

No two populations will ever experience identical conditions: physical gradients, biotic interactions and stochastic processes will inevitably result in variation among populations. Selection will generally generate a match between the local environment and the phenotype of individuals within that population (we elaborate on how such matches are generated below). Phenotype–environment matches should therefore increase self-recruitment by increasing the probability of survival of locally derived colonizers (Nosil *et al.* 2005). Bringing together these two elements (among population variability in environmental conditions and the generation of phenotype–environment matches) highlights several interesting, but largely unexplored, ecological implications. Below, we explore the processes that generate phenotype–environment matches and discuss the consequences of these matches for our view of connectivity in the marine environment.

What processes generate phenotype–environment matches?

In general, a good match between a population's mean phenotype and the environmental conditions that it experiences reflects the process of adaptation (the accumulation of heritable variation in response to selection). Given that environmental conditions supply the selection pressures that shape adaptive phenotypes, and the physical and biological properties of natural environments typically vary in time and space, selection may often vary among demes (Nosil *et al.* 2009). Evolutionary responses to spatially divergent selection – and, in particular, its interplay with gene flow – are the focus of an extensive body of literature and remain subject to debate (Kawecki & Ebert 2004; Nosil *et al.* 2009), much of which has centred on two supposed alternatives. On one hand, phenotypic plasticity (in behaviour, development, physiology, etc.) is predicted to evolve if gene flow among demes in which different phenotypes are selected slows or stops genetic differentiation as their phenotypes diverge (Via & Lande 1985). On the other hand, limited gene flow among such demes may favour the evolution of locally adapted phenotypes, whereby phenotypic divergence gives rise to genetic differentiation (and ultimately, perhaps, diversification at higher taxonomic levels). There is increasing awareness, however, that such responses may not be mutually exclusive, but together form part of an integrated strategy for adaptation in heterogeneous environments (DeWitt & Langerhans 2004).

Hence, phenotype–environment matches may result from both adaptive plasticity and local adaptation. In the latter case, individuals from locally adapted demes should have higher fitness in their native environment than individuals from foreign demes. This is the 'local vs. foreign' criterion for local adaptation, advocated by Kawecki & Ebert (2004) because it tests the efficacy of divergent selection. An alternative 'home vs. away' criterion (i.e. individuals perform better in their native environment than in other environments) also appears in the literature (indeed, both criteria are addressed by reciprocal transplant experiments), but may better test whether adaptation to one environment comes at a cost of adaptation to another (i.e. fitness trade-offs; Hereford 2009) or whether some demes consistently outperform others across environments (Kawecki & Ebert

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2004; their fig. 1), than local adaptation *per se*. Regardless, the consequences of local adaptation for our argument here are relatively straightforward: locally adapted propagules that disperse beyond their native environment may incur a phenotype–environment mismatch – that is, be at a selective disadvantage in the environment that they eventually colonize (Nosil *et al.* 2005).

In the case of adaptive plasticity, it is tempting to assume that it will buffer propagules against phenotype–environment mismatches as they disperse; however, the extent to which this occurs is unclear. Evidence of adaptive divergence in plasticity among demes, for example, suggests that plastic responses to environmental variation on one scale may be locally adapted on larger scales (Donohue *et al.* 2001). Even plasticity that is advantageous in native environments can only mitigate phenotype–environment mismatches to the extent that it allows dispersing propagules to produce a mean phenotype that closely matches the optimum where they settle (Ghalambor *et al.* 2007). This may rarely be the case: the fact that resident individuals tend to outperform immigrants (Hereford 2009) argues that plastic responses to environmental change are generally less than perfect (Ghalambor *et al.* 2007; see also DeWitt *et al.* 1998 for a detailed discussion of the costs and limits of phenotypic plasticity).

In the particular case of transgenerational plasticity, parental effects may match an individual's phenotype to a set of environmental conditions that it has not yet experienced (Marshall 2008). Such plasticity may be adaptive if offspring are retained within the parental environment (Galloway & Etterson 2007), but yield phenotype–environment mismatches comparable with those associated with the loss of local adaptation if offspring disperse to new environments. In the bryozoan *Bugula neritina*, for example, mothers exposed to a common pollutant (copper) produce copper-resistant offspring, but these perform much worse than offspring from copper-naïve mothers when the pollutant is absent (Marshall 2008).

Phenotype–environment mismatches – an old idea in a new ecological context

The idea that adaptive responses to differential selection among populations can ultimately decrease connectivity is not new (Nosil *et al.* 2005). In a range of systems (including marine ones; Koehn *et al.* 1980; Hedgecock 1986), it has been argued that the phenotypes of immigrants are likely to be less suited to the local environment than the phenotypes of locally derived individuals (Bilton *et al.* 2002; De Meester *et al.* 2002; Hendry 2004; Nosil *et al.* 2005). Typically, however, this effect has been considered in terms of evolutionary consequences. For example, phenotype–environment mismatches have been proposed to drive speciation (known as 'ecological speciation') and influence levels of local adaptation or maladaptation (Bilton *et al.* 2002; Nosil *et al.* 2005; Schluter 2009). Few studies, however, consider the ecological role that phenotype–environment mismatches play. While evolution and ecological processes are inextricably linked and can occur on similar timescales, they are often considered separately. Traditionally, the ecological consequences phenotype–environment mismatches have received far less attention.

Studies that do consider the ecological effects of phenotype–environment mismatches have mostly focused on terrestrial organisms with very different life-histories to those seen in marine environments. Because the former tend to disperse as adults, but the latter as larvae, phenotype–environment mismatches may have very different ecological effects in the sea than on land. In the case of adult dispersal, for example, immigrants to a new habitat can still mate with resident individuals, despite ultimately having poor survivorship (i.e. even genes that do not confer high fitness in the new habitat can pass to subsequent generations). Ronce & Kirkpatrick (2001) modelled this scenario for two populations of checker-spot butterfly that specialize on different plant hosts. They found that an influx of poorly adapted immigrants reduced the reproductive success of the subsequent generation (an effect known as 'migration load'), thereby reducing total population size and causing a higher proportion of immigrants to interbreed in the next round of mating. Such a process, as its effects iterate and intensify over multiple generations, may lead to extinction – a process termed 'migrational meltdown' (Ronce & Kirkpatrick 2001).

In marine environments, however, most post-dispersal mortality occurs immediately after colonization. Indeed, most new settlers die within a few days of settlement (Hunt & Sheibling 1997; Underwood & Keough 2001), a time when their small size may exacerbate their vulnerability to environmental stress or variation. Hence, unlike terrestrial systems where the consequences of phenotype–environment mismatches manifest *after* immigrants mate with local residents (resulting in migration loads), the consequences of phenotype–environment mismatches in marine systems are likely to manifest *before* immigrants mate with local residents. We argue that, this fundamental difference in the timing of when phenotype–environment mismatches manifest between terrestrial and marine environments will result in migration loads in the former, but reduced connectivity in the latter. The consequences and implications of the effect of this reduction in connectivity have been poorly explored.

Consequences of phenotype–environment mismatches in the sea

Phenotype–environment mismatches reduce realized connectivity, despite the effective transport of larvae among populations and may therefore be a barrier to connectivity

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Box 1 The effect of phenotype—environment mismatches on connectivity

We use a two-allele, one-locus metapopulation model to investigate the potential implications of phenotype–environment mismatches for interpatch connectivity. We model two different habitats set in an uninhabitable domain, which we treat as a two-patch metapopulation. The two patches are centred around $x = 0$ and $x = d$, each with radius R. Each patch is populated by a single, randomly mating, diploid species with genotypes AA, Aa and aa. For simplicity, the species is seasonal with non-overlapping generations, and with individuals reproducing only once before expiring. The species has a two-part life-cycle: during a dispersive phase, individuals leave their patch and disperse. If an individual survives this phase and is close to suitable habitat when it reaches competency, it will attempt to settle. Successfully recruiting individuals mature to become adults, which do not move from habitat patches. The limiting resource in both patches is space, with settling juvenile abundance considered saturating. The composition of the adult populations is decided by a post-settlement recruitment lottery.

The variables x_i, y_i and z_i denote the frequencies of adults from the three genotypes, AA, Aa and aa respectively, on patch i ($i = 1, 2$). The offspring resulting from random mating have genotypic frequencies:

$$Jx_i = x_i^2 + x_i y_i/2 + y_i^2/4,$$
$$Jy_i = (y_i^2 + x_i y_i + z_i y_i)/2 + x_i z_i,$$
$$Jz_i = z_i^2 + z_i y_i/2 + y_i^2/4,$$

where Jx_i, for example, is the number of juveniles with genotype AA on patch i.

Once released into the pelagic environment, juveniles disperse passively until they reach competency at time t. By this point, their distribution through space, $j(x, t)$, is defined by the diffusive dispersal kernel:

$$j(x,t) = \frac{L}{\sqrt{4K\pi t}} \exp\left[-\frac{x^2}{4Kt} - \theta t\right],$$

where K measures the diffusivity of the environment, L is the number of larvae initially released, and θ is the rate of mortality during dispersal. Of the juveniles born on patch i, a given proportion, $0 \le c_{ij} \le 1$, are transported to patch j and enter the recruitment lottery, and this proportion is symmetric between the two patches ($c_{ij} = c_{ji}$). A proportion $0 \le c_{ii} \le 1$ will return to their natal patch, while the remaining proportion $1 - c_{ii} - c_{ij}$ do not survive the dispersal process. These assumptions will be most valid for pelagic broadcast spawners with passive dispersal, and in locations where diffusive processes dominate dispersal (Siegel *et al.* 2008). Connectivity (both self-recruitment and dispersal between patches) is measured by the number of larvae that overlap each patch at the point of competency:

$$c_{ii} = 2\int_{x=0}^{R} j(x,t)\cdot dx, \text{and } c_{ij} = \int_{x=d-R}^{d+R} j(x,t)\cdot dx.$$

Juveniles enter a competitive post-settlement lottery for space in the new patch. Each of the three genotypes vary in fitness on each patch i, denoted w_{xi}, w_{yi} and w_{zi}, parameters that we assume without loss of generality to be < 1. These fitness parameters measure the relative recruitment ability at each patch, for each genotype. The genotypic frequencies of the new generation, x'_i, y'_i and z'_i, are thus:

$$\begin{aligned}
x'_1 &= w_{x1}\left(c_{ii}\,Jx_1 + c_{ij}\,Jx_2\right)/D_1,\\
y'_1 &= w_{y1}\left(c_{ii}\,Jy_1 + c_{ij}\,Jy_2\right)/D_1,\\
z'_1 &= w_{z1}\left(c_{ii}\,Jz_1 + c_{ij}\,Jz_2\right)/D_1,\\
x'_2 &= w_{x2}\left(c_{ii}\,Jx_1 + c_{ij}\,Jx_2\right)/D_2,\\
y'_2 &= w_{y2}\left(c_{ii}\,Jy_1 + c_{ij}\,Jy_2\right)/D_2,\\
z'_2 &= w_{z2}\left(c_{ii}\,Jz_1 + c_{ij}\,Jz_2\right)/D_2,\\
\text{where } D_1 &= \left(c_{ii}\,Jx_1 + c_{ij}\,Jx_2\right)w_{x1} + \left(c_{ii}\,Jy_1 + c_{ij}\,Jy_2\right)w_{y1}\\
&\quad + \left(c_{ii}\,Jz_1 + c_{ij}\,Jz_2\right)w_{z1},\\
\text{and } D_2 &= \left(c_{ij}\,Jx_1 + c_{ii}\,Jx_2\right)w_{x2} + \left(c_{ij}\,Jy_1 + c_{ii}\,Jy_2\right)w_{y2}\\
&\quad + \left(c_{ij}\,Jz_1 + c_{ii}\,Jz_2\right)w_{z2}.
\end{aligned}$$

We can determine the equilibrium community structure in the two patches using forward simulations, depending on the system parameters chosen. Because we are interested in the effect that phylogenetic–environment mismatches have on effective interpatch connectivity, we measure the equilibrium proportion ρ of reproducing adults on each patch that were exogenous recruits:

$$\rho = \frac{c_{ij}\left(w_{x1}Jx_2 + w_{y1}\,Jy_2 + w_{z1}\,Jz_2\right)}{c_{ii}\left(w_{x1}\,Jx_1 + w_{y1}\,Jy_1 + w_{z1}\,Jz_1\right) + c_{ij}\left(w_{x1}\,Jx_2 + w_{y1}\,Jy_2 + w_{z1}\,Jz_2\right)}.$$

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Box 1 *continued*

We parameterize the model as follows: first, we assume that $w_{x1} = w_{z2} = 1$, implying that AA individuals suffer no fitness disadvantage when settling in patch 1, while aa individuals suffer no fitness disadvantage in patch 2. Second, we let $w_{x2} = w_{z1} < 1$, conferring equal fitness disadvantages to AA settlers in patch 2, and aa individuals in patch 1. Finally, we assume that $w_{yi} = ½(1 + w_{x2})$, implying that heterozygotic Aa individuals are disadvantaged in both patches, by half the extent encountered by the homozygotic AA individuals in patch 2. The proportion of exogenous recruits is therefore symmetrical for both phenotypes and patches (Fig. a).

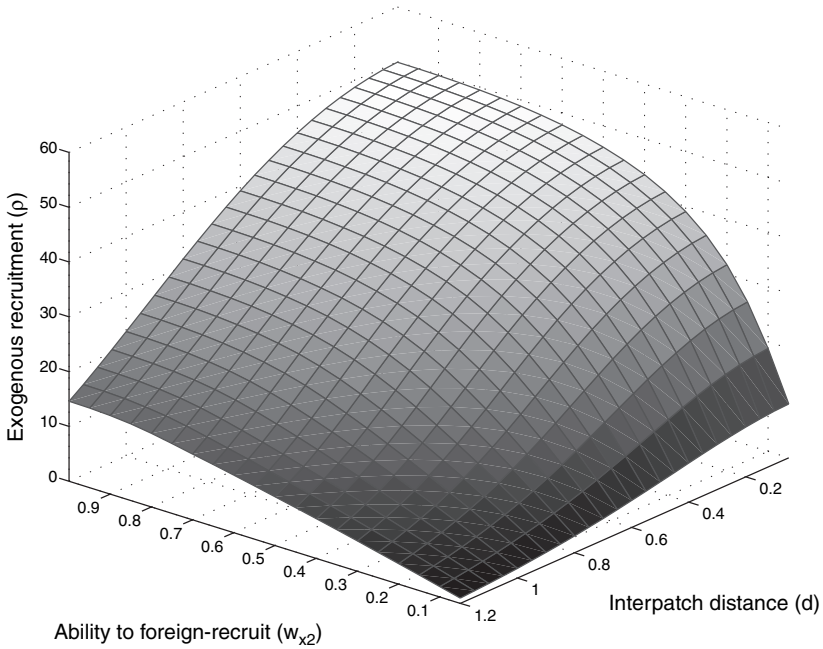

Figure a The proportion of exogenous recruits in a local patch (recruits in a given patch from both phenotypes that were spawned at the other patch). Connectivity between patches declines with increasing dispersal distance and increasing phenotype–environment mismatch. $K = 1$; $R = 0.15$.

that acts in a distance-independent manner (Box 1). Perhaps most importantly, phenotype–environment mismatches have the potential to explain why genetic relationships among populations do not always scale with distance (Johnson & Black 2006; Hedgecock *et al.* 2007; Schmidt *et al.* 2008). A view of connectivity that includes environmental matching between different populations has the potential to decouple connectivity from physical distance. For example, if biological barriers to dispersal are important to marine connectivity, then two distant populations that are adapted to similar environmental conditions may have greater connectivity than two close populations that are adapted to dissimilar environments (Fig. 1). This suggestion departs from the traditional view that the connectivity of marine metapopulations primarily scales with distance (Cowen & Sponaugle 2009).

Evidence for phenotype–environment mismatches in the sea

Our hypothesis that phenotype–environment mismatches reduce connectivity in marine environments relies on two crucial elements: (1) that the scale of environmental heterogeneity is smaller than the scale of larval transport and (2) that phenotype–environment mismatches induce mortality before reproduction. What evidence is there to support these suggestions?

The scales of environmental heterogeneity vary in the sea. While some environment gradients are likely to scale strongly with distance and exceed the scales of larval dispersal, others will not. For example, many coastal marine species vary more in abundance at small scales (m) than at large scales (10–100s of km). Consequently, there may be either selection for limited dispersal in the latter case, or an increased likelihood of phenotype–environment mismatches in the former. Regardless, microhabitat selection by larvae at settlement may be an important behavioural trait to minimize phenotype–environment mismatches at smaller scales. The selection pressures that shape dispersal and habitat selection are beyond the scope of this review, and we direct readers to Kisdi (2002) and Baskett *et al.* (2007) for detailed examinations of these issues. Here, we focus explicitly on the ecological consequences of phenotype–environment mismatches.

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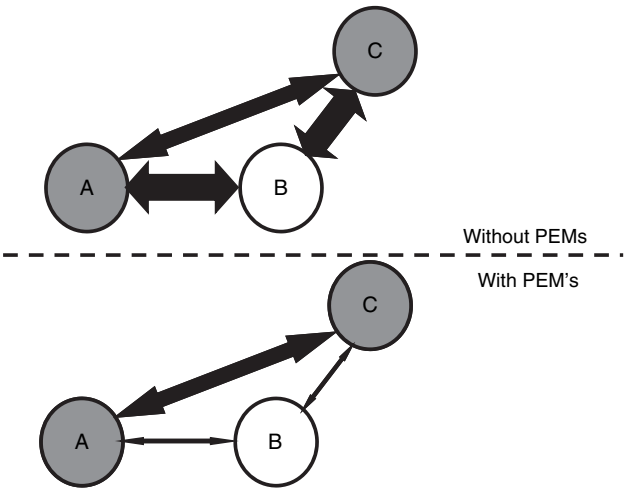

Figure 1 Schematic of the effect of phenotype–environment mismatches (PEMs) on the level of connectivity among populations. In the upper panel, in the absence of PEMs, connectivity scales with distance (as indicated by the thickness of the connecting arrows) despite the difference in the environment of population 'B' relative to populations 'A' and 'C' (as indicated by the differences in shading). In the lower panel, connectivity does not scale with distance such that there is relatively greater connectivity between populations 'A' and 'C' than either population with 'B' because of PEMs.

Empirical evidence of adaptive variation among marine populations has mounted in recent years. Box 2 summarizes those studies that have found foreign individuals to suffer increased mortality (relative to residents) when moved to a new population. The studies in Box 2 also provide some insight into the scale at which adaptive variation may occur. In some cases, where variation scales with geographic distance (e.g. Ayre 1995), phenotype–environment mismatches are unlikely to reduce connectivity. In other cases, however, local adaptation is apparent on very small spatial scales: for example, among microhabitats (rockpools vs. boulders) on rocky shores (Sherman & Ayre 2008), and along an intertidal gradient (Hays 2007). When local adaptation occurs over such small scales, phenotype–environment mismatches are likely to play an important role in reducing connectivity, regardless of propagule transport.

In addition to the suggestion of responses to divergent selection over small spatial scales in Box 2, there is further evidence that post-settlement mortality could be affected by whether a recruit is locally or exogenously derived. In the 1980s, Hedgecock proposed the 'sweepstakes hypothesis' for recruitment in marine invertebrate populations, under which only a small proportion of the population enjoy high reproductive success in a given time and place

Box 2 Responses to divergent selection in the sea

A survey of marine transplant experiments in which fitness components for local and foreign populations or closely related species were contrasted in the same selective environment. For each study, we report the number of contrasts, the approximate scale over which populations were transplanted, the frequency of local adaptation (i.e. the proportion of contrasts where local populations performed better in their native environment than foreign populations; the proportion where this advantage was significant is in brackets, if reported) and its mean magnitude.

Study	Species	No. contrasts	Scale of transplantation (km)	Frequency of local adaptation	Magnitude of local adaptation
Ayre (1985)	*Actinia tenebrosa*	12	≤ 4	0.58	−0.01
Ayre (1995)	*Actinia tenebrosa*	27	≤ 25, *c.* 800	0.74 (0.56)	0.34
Berger *et al.* (2006)	*Balanus glandula*	2	6	0.50 (0.00)	−0.11
Bertness & Gaines (1993)	*Semibalanus balanoides*	8	25–30	0.38	0.13
Blanchette (1997)	*Fucus gardneri*	2	0.1	0.00	−0.06
Blanchette *et al.* (2002)	*Egregia menziesii*	2	120–270	1.00 (1.00)	1.15
Boulding & Van Alstyne (1993)	*Littorina sitkana Littorina sp.*	6	≤ 0.5	0.67 (0.67)	0.53
Fawcett (1984)	*Tegula funebralis*	8	250–1500	0.75 (0.38)	0.12
Grosholz (2001)	*Botrylloides sp.*	1	≤ 60	1.00	0.56
Hays (2007)	*Silvetia compressa*	6	< 0.01	0.83 (0.50)	0.31
Janson (1983)	*Littorina saxatilis*	9	≤ 1	0.89 (0.89)	0.91
Piola & Johnston (2006)	*Bugula neritina*	2	*c.*40	1.00 (0.00)	0.12
Prada *et al.* (2008)	*Eunicea flexuosa*	2	≤ 0.03	1.00	0.26
Rolan-Alvarez *et al.* (1997)	*Littorina saxatilis*	6	≤ 0.05	0.83	0.55
Sherman & Ayre (2008)	*Actinia tenebrosa*	4	< 0.5	0.75	0.43
Yanick *et al.* (2003)	*Mytilus trossulus*	1	≤ 150	1.00 (1.00)	0.41

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Box 2 *continued*

Under the hypothesis of divergent selection, phenotype–environment matching arises from differences in the optimal phenotype across environments. Hence, measures of the relative fitness of phenotypes transplanted between environments can provide valuable insight into the selection pressures operating in each (Schluter 2000; Kawecki & Ebert 2004). We surveyed the literature for marine transplant experiments in which fitness components for local and foreign populations were measured in the same selective environment. We chose only studies conducted in natural environments, as these supply the actual selection pressures that drive phenotype–environment matching. Where studies incorporated further manipulations (beyond transplantation) that might obscure such matches, only unmanipulated control groups are included here. Survival was the only fitness component that we considered. We note that adaptive responses to divergent selection on other components of fitness (predator resistance, fecundity, mating success) also appear in the literature (e.g. Sanford *et al.* 2003), but were not included here because the effects of such components on connectivity are less clear. We recorded the fitness of local and foreign populations in each separate contrast (i.e. those conducted in different years or environments) per study, and the approximate scale of transplantation. Transplants involving multiple populations were reduced to two populations (local and foreign) per environment, after Schluter (2000, chapter 5). In such cases, the fitness of the local population was compared with the mean fitness of all foreign populations. We converted absolute fitness to relative fitness by dividing the fitness component of each population by the overall mean for that environment. We then quantified local adaptation, after Hereford (2009), as the relative fitness of the local population minus that of the foreign population. Thus, positive values indicate selection against hypothetical migrants into a given environment (i.e. local adaptation) and negative values indicate selection against local residents of that environment (Hereford 2009). For each study, we calculated the frequency of local adaptation (i.e. the proportion of contrasts in which local populations performed best) and its mean magnitude.

Our search yielded a total of 98 cases, spanning 16 studies on 14 marine taxa (all of which were sessile or sedentary organisms, presumably because these are most tractable to such work), in which the fitness of local and foreign populations was measured in the same selective environment. In a proportion of 0.75 (± 0.07 SE) cases, local residents enjoyed some degree of fitness advantage over migrants. Unfortunately, the statistical significance of the relevant contrast was reported in only 54 cases. Of these, significant local adaptation was detected in a proportion of 0.55 (± 0.13 SE) cases, increasing to 0.97 (± 0.02 SE) if populations were considered locally adapted when fitness in their native environment was equal to or greater than that of foreign populations (after Hereford 2009). A significant local disadvantage was detected in just 2 cases, reported by Fawcett (1984, his table 3) and Janson (1983), her table 6). The mean magnitude of local adaptation was 0.34 (± 0.06 SE), meaning that residents had, on average, 34% higher fitness than migrants. These results generally agree with Hereford's (2009) more comprehensive review of local adaptation (encompassing marine and terrestrial environments), in which local adaptation had a frequency of 0.65 (± 0.02 SE) when defined as a significant local advantage, or 0.71 (± 0.06 SE) when defined as a lack of local disadvantage, and a mean magnitude of 0.45 (± 0.04 SE). Overall, our survey suggests that local adaptation in marine environments may be relatively common, contrary to previous thought (e.g. Warner 1997), and that other adaptations to environmental heterogeneity, such as plasticity, may not fully counter the selective disadvantage that migrants may incur upon dispersal to a new environment.

A major caveat of our survey, however, concerns the degree to which local and foreign study populations may have survived differentially because of non-genetic effects arising from prior environmental experience (including that of maternal environment). Such effects, unless care is taken to minimize them – for example, by maintaining all individuals in standardized 'common garden' environments before transplantation – may bias results toward the detection of apparent local adaptation that is due more to acclimation than genetic differentiation. Kawecki & Ebert (2004) recommend that individuals be maintained in common garden environments for several generations before transplantation, but noted that this is rarely feasible for studies conducted in the field. Since this step was rarely described by the studies included in our survey, or was confined to a matter of days (but see Berger *et al.* 2006; and Piola & Johnston 2006), our conclusions must be interpreted cautiously and we direct interested readers to Kawecki & Ebert's (2004) more detailed treatment of this issue.

and are thus responsible for the majority of recruits in a cohort (Hedgecock 1986). This hypothesis led to two predictions: first, that genetic differentiation among cohorts should be high and second, that genetic variation among settlers within cohorts should be low relative to that of the adult population overall [in which multiple, genetically distinct cohorts of recruits have accumulated over time (Hedgecock 1986; Hedgecock *et al.* 2007)]. While many studies have supported the latter prediction, some have shown the reverse pattern – that levels of genetic diversity are high within single cohorts of recruits, but relatively low in the adult population (Pujolar *et al.* 2007; Selkoe *et al.* 2006; Hedgecock *et al.* 2007; Hepburn *et al.* 2009). Perhaps most interestingly, some studies show that genetic diversity within individual cohorts decreases over time and that post-colonization mortality is non-random with respect to colonizer genotype over time (Pedersen *et al.* 2000; Schmidt & Rand 2001; Penney *et al.* 2006; Selkoe *et al.* 2006; Andrade & Solferini 2007; Vigliola *et al.* 2007). Together, these lines of evidence suggest that single cohorts may be comprised of recruits from multiple source populations and that post-colonization mortality is higher in recruits derived from some populations compared with others. These studies are yet to conclusively show that genotypes that suffer higher mortality are those from exogenous populations, but it is intriguing that such differential survival occurs at all. Alternatively, these patterns of post-colonization mortality could be driven by the physiological costs of dispersal (e.g. Pechenik 2006). We note, however, that such a mechanism would still reduce connectivity by biasing recruitment in favour of locally derived colonizers.

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We have argued that marine populations may be poorly connected, but many population genetic studies suggest otherwise. In a series of papers, Conover *et al.* (2006, 2009) (see also Hedgecock *et al.* 2007) have argued that estimates based on neutral markers overestimate 'ecological' connectivity because only a few migrants per generation are sufficient to homogenize variation among populations. Spatial variation in quantitative traits (Q_{st}), moreover, may not correlate with variation in neutral markers (F_{st}). Thus, even populations with little variation in neutral markers may still experience highly divergent selection pressures (Conover *et al.* 2006). Comparing Q_{st} with F_{st} may therefore test whether divergent selection among populations increases the potential for phenotype–environment mismatches to reduce connectivity. Following Q_{st} and F_{st} of a cohort from settlement through to recruitment into the adult population would provide a powerful examination of the timing, strength and targets of divergent selection among populations.

Phenotype–environment mismatches in terrestrial systems

Thus far, we have concentrated on the consequences of phenotype–environment mismatches for the connectivity of marine populations, but what about terrestrial populations? Several attributes of many marine organisms make them especially prone to phenotype–environment mismatches: they produce highly dispersive offspring, suffer most of their mortality before reproduction and are sessile or sedentary after dispersal. Some terrestrial organisms, such as plants and wind-dispersed arthropods, share many of these same attributes, suggesting the potential for phenotype–environment mismatches to reduce connectivity in these systems also. We eagerly await tests of this prediction.

MANAGEMENT IMPLICATIONS OF PHENOTYPE—ENVIRONMENT MISMATCH IN THE SEA

The potential effects of phenotype–environment mismatches on connectivity in the sea may require a shift in the way we view and manage marine populations. We predict that changes in environmental conditions that occur in some populations but not others will affect the level of connectivity among them via the generation of phenotype–environment mismatches. Our predictions of how populations will respond to disturbance, the way that exploited populations are linked and the size and placement of marine refuges all depend on a good understanding of connectivity. This understanding, however, could be incomplete if we fail to consider the potential effects of phenotype–environment mismatches.

Marine protected areas (MPAs), spillover effects and phenotype–environment mismatches

One of the major predicted benefits of marine-protected areas is that they will act as source populations for surrounding, exploited populations. In some instances, such 'spill-over' effects do indeed occur (Palumbi 2004). Other studies, however, have failed to detect significant levels of connectivity between protected and exploited populations, even those separated by only small distances (Palumbi 2004). We suggest that phenotype–environment mismatches may play a role in reducing connectivity between protected and exploited areas, and that such mismatches could derive from the establishment of MPAs in two ways: first, by shifts in the phenotypes of exploited organisms within protected areas; and second, by changes to the local environment within protected areas.

Selection pressure from fishing has repeatedly been shown to induce rapid evolutionary changes in the phenotypes of exploited fish stocks: many exploited species of fish are evolving to mature sooner and reproduce at smaller sizes (Conover *et al.* 2006). Spillover from protected populations areas into exploited populations have been suggested to provide an evolutionary refuge from these shifts in the phenotypes of exploited stocks, thereby slowing the overall change in the phenotype of the exploited species (Baskett *et al.* 2005). Implicit to this suggestion is the notion that fish within marine-protected areas will retain or revert to the non-exploited phenotype. Thus, the evolutionary consequences of differences in phenotypes among exploited populations and those within MPAs have been considered in such studies; but what about more immediate ecological consequences? It has been suggested that individuals within MPA will quickly evolve an 'unfished' phenotype, whereby resources are used for growth rather than reproduction (Baskett *et al.* 2005). If an individual with an 'MPA phenotype' leaves an MPA as a juvenile, it may have lower fitness than individuals with a 'fished phenotype' outside the MPA because its risk of pre-reproduction mortality is relatively higher. Baskett *et al.* (2005) considered the evolutionary consequences of differential selection within and outside MPAs, but did not formally examine the consequences of this selection for connectivity. We suggest that the evolution of phenotypes that differ between MPAs and exploited areas could reduce connectivity (specifically, effective spillover from the MPA) in the presence of a phenotype–environment mismatch.

In addition to phenotype–environment mismatches derived from fishing impacts outside of MPAs, environmental changes within MPAs may also induce mismatches in the absence of fishing. Dramatic changes in community composition can follow the establishment of an MPA that are not reflected in areas outside (Micheli *et al.* 2004). Thus,

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the environments (and selection pressures) experienced by organisms could quickly diverge between protected and non-protected areas – particularly with respect to the abundances of large predators or their prey species, or to habitat availability (Micheli *et al.* 2004). If local adaptation in response to environmental differentials between protected and non-protected areas occurs, then a phenotype–environment mismatch could be generated and connectivity between the two areas could be reduced. Such a scenario remains speculative but, given that organisms do adapt to changes in community states, and to the abundance of predators (Boulding *et al.* 2007), we believe this scenario to be worth empirical examination. One prediction from our hypothesis is that connectivity among protected and non-protected areas could decrease over time as these environments diverge. Crucially, all our predictions depend on the relative scales of protected areas and the dispersal ability of the adult phase of the organisms of interest. Such effects are likely for species whose home ranges are exceeded by the size of MPAs, but less likely for those whose ranges are not.

We have cautioned that phenotype–environment mismatches could result in lower levels of connectivity among populations than would be predicted based on the transport of propagules alone. Although MPAs undoubtedly benefit the populations and communities within and outside their boundaries, and are crucial to future management strategies seeking to protect exploited resources (and biodiversity more generally), we suggest that connectivity among protected and non-protected areas is not be assured, particularly when environment conditions within each differ dramatically. This suggests that environmental quality outside of protected areas should not be neglected: rather, the converse may apply. Similarly, when considering a network of MPAs, most authors suggest that connectivity among them will maximize network resilience (Palumbi 2004). If phenotype–environment mismatches may indeed reduce connectivity, then park planners should focus not only on the physical distances between MPAs, but also the environmental differences between them.

Phenotype–environment mismatches and recovery from disturbance

Under the classic metapopulation view, populations whose abundance is greatly reduced by a disturbance, typically require replenishment from other populations within the metapopulation (Caley *et al.* 1996). If the disturbed environment returns quickly to its original state, then this view should hold: phenotype–environment mismatches, if they occur, will be only transient. However, if the disturbance induces a more lasting change in the local environment, then the disturbance could generate phenotype–environment mismatches, reducing the connectivity between the disturbed population and other potential source populations such that replenishment and recovery take far longer that would be anticipated. An example that many readers may already recognize, although perhaps not in a phenotype–environment mismatch framework, relates to the long-term effects of disturbance on 'ecosystem engineers' (i.e. species that create or modify habitat) (Stachowicz *et al.* 2002). If disturbance removes such species, others depending on them for habitat may no longer recruit back into the disturbed area, regardless of propagule flux among disturbed and undisturbed populations (Pandolfi *et al.* 2005).

Phenotype–environment mismatches may also hamper restoration efforts. Attempts are being made to restore degraded reefs via the transplanting of juvenile corals from other populations. If individuals from undisturbed environments express a phenotype that is not well matched to the disturbed environment, then such transplants may have poor success rate. Ironically, it may be that other degraded populations (whose mean phenotype better matches that of the disturbed habitat) provide the best source of recruits, even if the previously disturbed populations are smaller in size. Terrestrial restoration ecologists have known for some time that local adaptation plays an important role in determining the success species translocations and similar realizations are being made in marine systems (Baums 2008).

If the role of phenotype–environment mismatches is ignored, the potential exists to overestimate the capacity for exogenous recruitment to assist in the recovery of populations and communities from disturbance if the latter induce phenotype–environment al mismatches via lasting changes in local conditions. It has long been recognized that disturbance reduces population growth rates via reductions in population size. We suggest that disturbances may also reduce population growth rates may via reducing the rate at which disturbed populations are replenished by undisturbed populations because of the existence of a phenotype–environment mismatch.

CONCLUSIONS

Marine populations often show levels of connectivity that are surprisingly lower than would be predicted based on the dispersal capabilities of propagules alone. We suggest that population connectivity in the sea may be reduced by phenotype–environment mismatches, whereby exogenous colonizers have poorer survival, and thus a lower chance of contributing to the propagule pool in the next generation, than those that are locally derived. We argue that such mismatches can occur via the shaping of adaptive variation by selection pressures that can potentially diverge over surprisingly small spatial and scales in marine environments. Phenotype–environment mismatches are most likely to occur

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in species with sessile or sedentary adult stages (where the scale of dispersal exceeds the scale of environmental heterogeneity), so may be more common in marine invertebrates and coastal fish species than in pelagic species with highly dispersive adult stages. Whether such mismatches also reduce the connectivity of terrestrial populations remains unclear, but we predict them to be likely in organisms (e.g. angiosperms) that disperse before reproduction and have a sessile adult stage. Evidence of responses to divergent selection in the marine environment is becoming more common. While the idea of selection against immigrants is not new, the ecological and management implications of this phenomenon in marine environments have gone largely unconsidered, despite their potential importance. Our view of connectivity in the sea should be modified to consider not only physical barriers to the transport of propagules among populations, but also biological barriers such as phenotype–environment mismatches.

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