

# Local Adaptation in Marine Invertebrates

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## Keywords

connectivity, dispersal, gene flow, divergent natural selection, balanced polymorphism

## Abstract

Local adaptation in the sea was regarded historically as a rare phenomenon that was limited to a handful of species with exceptionally low dispersal potential. However, a growing body of experimental studies indicates that adaptive differentiation occurs in numerous marine invertebrates in response to selection imposed by strong gradients (and more complex mosaics) of abiotic and biotic conditions. Moreover, a surprisingly high proportion of the marine invertebrates known or suspected of exhibiting local adaptation are species with planktonic dispersal. Adaptive divergence among populations can occur over a range of spatial scales, including those that are fine-grained (i.e., meters to kilometers), reflecting a balance between scales of gene flow and selection. Addressing the causes and consequences of adaptive genetic differentiation among invertebrate populations promises to advance community ecology, climate change research, and the effective management of marine ecosystems.

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**Gene flow:** the movement of alleles from one population to another through dispersal or migration

**Direct development:** development without planktonic dispersal, often within brood pouches or benthic egg capsules

**Neutral molecular markers:** variable portions of the genome, not under selection, that can be used to make inferences about population processes or phylogeny

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## 1. INTRODUCTION: LOCAL ADAPTATION IN THE SEA

Local adaptation is the fine-tuning of populations to their local environment via natural selection. Natural environments are often heterogeneous, characterized by strong spatial variation in both abiotic and biotic factors. Persistent environmental gradients may impose divergent selection, such that populations evolve differences in morphology, physiology, behavior, or life history that provide a fitness advantage under those local conditions. Local adaptation thus results in resident genotypes that have a higher fitness in their native habitat than do foreign genotypes from more distant populations (Kawecki & Ebert 2004). Importantly, the diversifying effects of selection are opposed by the homogenizing effects of gene flow. Thus, if dispersal is high among populations, local adaptation will tend to be swamped out by the immigration of nonadapted genotypes from populations that lie outside of that selective environment.

There is a long history of study of local adaptation in terrestrial and freshwater habitats. Many species living in these systems are characterized by restricted dispersal and gene flow, increasing the potential for local adaptation (Leimu & Fischer 2008, Hereford 2009). Moreover, selective gradients in these habitats can be quite fine-grained, with strong and persistent differences in environmental conditions (e.g., light, temperature, nutrients) occurring over tens of meters. Not surprisingly, there is a large body of empirical evidence for local adaptation in terrestrial and freshwater species, including plants, insects, amphibians, and other taxa (Leimu & Fischer 2008, Hereford 2009).

In contrast, until recently, local adaptation has received comparatively little attention in marine systems (reviewed by Conover 1998, Sotka 2005, Conover et al. 2006). Most marine species have traditionally been viewed as a collection of demographically open populations that are interconnected by high gene flow. This expectation followed from the apparent lack of dispersal barriers in marine systems and the fact that most marine invertebrates and fishes have planktonic larvae that spend days to months in the water column (Grosberg & Cunningham 2001). However, this paradigm of well-mixed marine populations has changed considerably in recent decades as multiple lines of evidence now suggest that many marine populations are less connected than once thought (reviewed by Palumbi 2004, Levin 2006).

In particular, a large body of recent population genetic studies has documented considerable differentiation among populations of numerous marine species. Differentiation is typically stronger among species with direct development (reviewed in Bohonak 1999); however, differentiation may also occur in species with planktonic dispersal (e.g., Edmands et al. 1996, Sotka et al. 2004). Restricted connectivity among marine populations may arise from life history, larval behavior, and/or oceanographic features that lead to the retention of offspring near their natal habitats (Dawson 2001, Sherman et al. 2008, Morgan et al. 2009). More importantly, molecular subdivision is not a critical precondition for adaptive differentiation. The idea that a few successful migrants per generation may be sufficient to maintain genetic homogeneity between two populations is a useful guideline that has been repeated frequently in the literature (e.g., Díaz-Viloria et al. 2009, Goldstien et al. 2009, Hellberg 2009). Although this is likely true for neutral molecular markers (the focus of most population genetic studies), it is unlikely to be true for loci under selection (Hedgcock 1986, Slatkin 1987). Although this distinction is obvious to population geneticists, it is a caveat that has frequently been omitted from discussions regarding connectivity among marine populations (but see Hedgcock 1986, Conover et al. 2006, Marshall et al. 2010). This may contribute to the misconception that a few larvae traveling between sites during each generation may be sufficient to maintain homogeneity across the entire genome, thus precluding adaptive divergence. It is critical to realize that differentiation in loci under selection can occur in the face

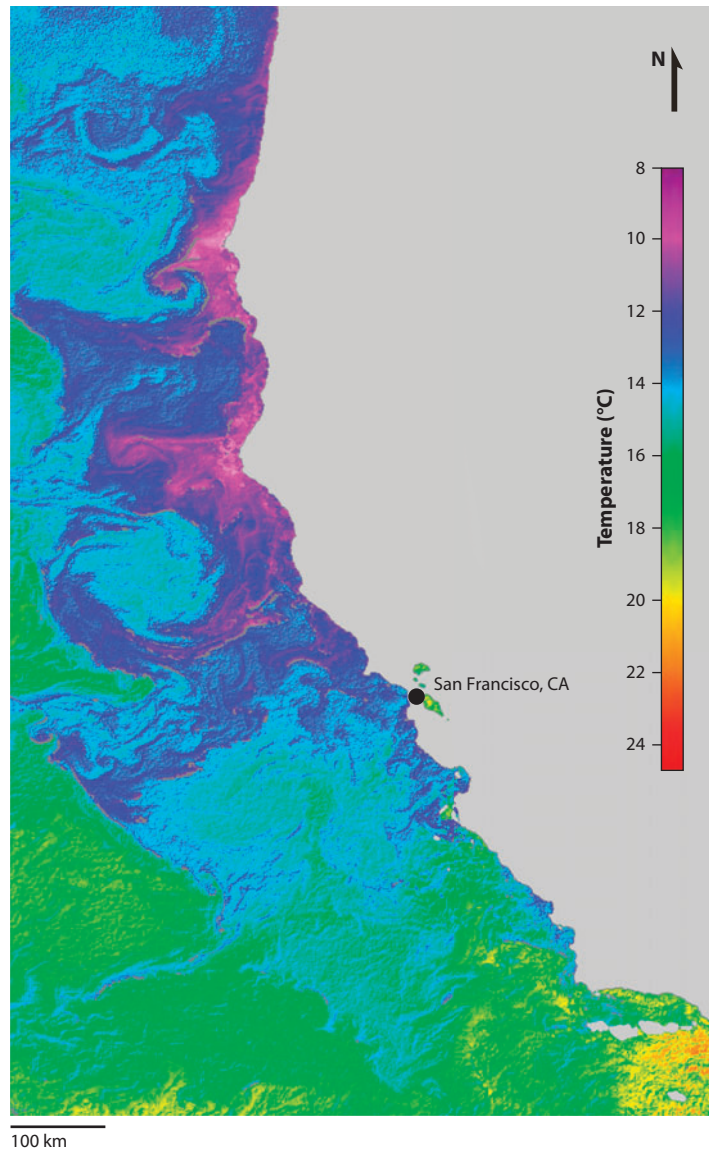
of considerable gene flow, so that populations that appear homogenous for neutral loci may still exhibit local adaptation (Conover et al. 2006).

A growing awareness of restricted connectivity among marine populations has been accompanied by a parallel realization that environmental gradients in the sea may be more fine-grained than has been traditionally appreciated. Historically, oceanographers tended to focus on large-scale variation in the open ocean, with less attention devoted to the nearshore environment, an area that is difficult to sample with large research vessels (Menge 1992). However, recent studies in coastal upwelling systems emphasize that persistent oceanographic features often generate strong alongshore variation in temperature, nutrients, pH, and other parameters over spatial scales of tens to hundreds of kilometers (Bustamante et al. 1995, Menge et al. 1997, Menge 2000, Navarrete et al. 2005, Feely et al. 2008) (**Figure 1**). These same oceanographic processes can play a major role in generating spatial variation in the delivery of phytoplankton and larvae to coastal sites with strong bottom-up influences on benthic communities (reviewed by Menge 2000). Importantly, these spatial patterns of oceanographic and biological variation are often persistent, as they are linked to stable features of the coastline such as coastal bathymetry and the location of rocky headlands (Menge et al. 1997; Navarrete et al. 2005, 2008; Broitman et al. 2008). Similarly, gradients of pollution, eutrophication, and hypoxia are increasingly common in coastal ecosystems, often concentrated near centers of urbanization, shipping, and agriculture (Breitburg et al. 2009). Thus, many coastlines are characterized by strong and persistent gradients (and more complex mosaics) of environmental conditions that have considerable potential to create spatially varying selection on marine species distributed over broad geographic ranges.

Although understudied, there is growing evidence that local adaptation to these conditions may be more common than has been recognized. Several excellent reviews have surveyed evidence for local adaptation in marine fishes (Conover 1998, Conover et al. 2006). Additional reviews have provided examples of local adaptation in marine invertebrates (Grosberg & Cunningham 2001, Sotka 2005, Conover et al. 2009, Marshall et al. 2010), but adaptive differentiation in these taxa has not been reviewed comprehensively.

Marine invertebrates encompass a taxonomically diverse suite of taxa, including many ecologically and economically important species. Marine invertebrates also have diverse life histories and dispersal potentials, making them particularly attractive study organisms for examining the interplay between gene flow and adaptive differentiation. Moreover, many of these animals are sessile or relatively sedentary, and thus are well suited to manipulative field experiments. Finally, many sessile invertebrates (e.g., some sea anemones, corals, ascidians, etc.) are clonal, which creates an opportunity to test the performance of genetically identical clones that have been transplanted among different environments (Ayre 1985, Grosholz 2001, Barshis et al. 2010), a design used commonly to study local adaptation in clonal plants (Leimu & Fischer 2008).

In this article, we review approaches to addressing local adaptation and survey experimental evidence for adaptive differentiation among populations of marine invertebrates. Our analysis emphasizes that (*a*) the scale over which adaptive differentiation occurs represents a balance between the scale over which gene flow occurs and the scale over which the selective gradient varies, and (*b*) genetic divergence can arise via local adaptation and/or purifying selection acting in each generation. As a result, adaptive differentiation among populations is expected to occur across a broad range of spatial scales and life histories in invertebrates and other marine organisms. We suggest that addressing spatial patterns of local adaptation is critical to advancing our understanding of community ecology, the impacts of climate change, and the spatial management of marine ecosystems.



**Figure 1**

Satellite image of sea surface temperatures along the west coast of the United States (October 22, 2008). Coastal upwelling plumes (*purple*) are associated with major headlands in northern California and create a mosaic of alongshore variation in water temperature, nutrients, pH, and other parameters over spatial scales of tens to hundreds of kilometers. Data courtesy of Natl. Ocean. Atmos. Admin. (NOAA)/Natl. Weather Serv., Monterey and NOAA Coastwatch.

## **2. EXPERIMENTAL APPROACHES TO STUDYING LOCAL ADAPTATION**

Experimental approaches can provide powerful tests of local adaptation. These approaches generally take two forms: (*a*) “common garden” experiments in the laboratory, and (*b*) reciprocal transplant experiments in the field. In a common garden experiment, individuals from different

populations are held under identical conditions in the laboratory. By minimizing the influence of environmental variation, this design seeks to identify the genotypic component of phenotypic variation. Several recent discussions have highlighted the pitfalls and challenges of common garden designs (Conover 1998, Kawecki & Ebert 2004, Conover et al. 2006). In particular, field-collected animals may retain the influence of environmental conditions experienced prior to collection. The occurrence of phenotypic plasticity (including inducible morphologies, developmental canalization, maternal effects, physiological acclimatization, etc.) is widespread in marine animals, with exposure to environmental variation inducing differences in morphology, physiology, behavior, and life history (Warner 1997, Hollander 2008). These plastic influences may often mimic local adaptation in the absence of genetic effects (Kawecki & Ebert 2004). Although acclimating field-collected animals under identical laboratory conditions for a period of several weeks before starting a common garden experiment may help reduce the effects of environmental history, these influences can be persistent, and in some cases, irreversible (Kinne 1962, Zamer & Mangum 1979).

To minimize the confounding effects of phenotypic plasticity, organisms may be raised under common conditions for their entire lifetimes before testing. However, even this approach may fail to erase the influence of environmental history if maternal effects are strong. Maternal effects have been understudied in marine systems, but a growing body of literature points to their importance (Marshall 2008, Marshall et al. 2008). Therefore, offspring of parents collected from different field sites may show variation due to persistent maternal effects, even if those offspring are reared under identical laboratory conditions. The solution to this problem is to breed and raise individuals from different populations through two or more generations in the laboratory (Conover 1998, Kawecki & Ebert 2004). However, raising marine animals (which often have a biphasic life history with planktonic larvae) through multiple generations in the laboratory can be labor intensive and logistically challenging and is likely a major reason why the study of local adaptation in the sea has lagged far behind analogous studies in terrestrial plants and insects.

An additional limitation of the common garden approach is that this design explicitly tests the role of a focal selective factor(s), and thus may neglect the response to other key factors present in nature but not manipulated in laboratory treatments. Reciprocal transplant experiments circumvent this limitation by transferring individuals between source habitats in the field and subsequently quantifying their fitness at each location. When the performance of local genotypes exceeds that of foreign genotypes, local adaptation is indicated (Kawecki & Ebert 2004). Although this is a powerful approach, reciprocal transplant experiments carry with them their own set of complications. First, this design should not be used when there is a risk of introducing nonlocal genotypes into study populations. Such introductions may occur either through the escape of transplanted individuals from experimental plots or through the release of offspring or gametes into local populations. Second, as with common garden studies, the presence of phenotypic plasticity may greatly confound interpretation of reciprocal transplant experiments. Reciprocal transplant studies generally use field-collected individuals, and nongenetic variation expressed in these individuals may persist long after organisms have been transplanted to a new environment. To minimize these confounding effects, individuals from each source population may be raised for two or more generations in the laboratory and then outplanted to all source habitats. Although this design has been used widely in the study of local adaptation in terrestrial plants (e.g., Hall & Willis 2006, Wright et al. 2006) and some insects (e.g., Karban 1989), it has rarely been used to explore local adaptation in marine organisms (but see Sanford & Worth 2010).

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**Maternal effects:**  
nongenetic influences  
of the maternal  
environment or  
phenotype on the  
phenotype of offspring

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### 3. SURVEY OF EXPERIMENTAL STUDIES

We surveyed the literature to identify empirical examples of adaptive genetic differentiation in marine invertebrates (**Table 1**). We included only studies that provided evidence of local adaptation from either common garden or reciprocal transplant experiments. Our survey thus omits many observational studies that have reported morphological or behavioral differences among field populations and invoked local adaptation as a potential explanation (e.g., Berry & Crothers 1974, Bingham & Young 1991). Similarly, our survey omits studies that examined adaptive differentiation by assessing allelic variation (see the section Nonexperimental Approaches, below), unless those studies also included an experimental component. Finally, we have attempted to identify and remove putative cases of local adaptation that were subsequently shown to be examples of divergence between cryptic species (e.g., McGovern & Hellberg 2003).

Our survey yielded 59 studies providing experimental evidence of adaptive differentiation in a taxonomically diverse group of marine invertebrates (**Table 1**). Our data set includes 39 species, with gastropods ( $n = 15$ ) and crustaceans ( $n = 11$ ) being the taxa most frequently represented. Fifty-three percent of the studies in our data set assessed local adaptation using a direct measure of fitness (i.e., survival or reproduction). The remainder used a proxy for fitness. Growth rate was the most common proxy used, whereas other studies assessed performance using physiological responses such as respiration rate, enzyme activity, or levels of stress proteins (Walsh & Somero 1981, Sokolova & Pörtner 2001, Barshis et al. 2010). In other cases, differentiation was documented in traits such as prey defenses or habitat selection that have plausible links to fitness.

Theory suggests that local adaptation should be particularly common in species with direct development (Struhsaker 1968, Behrens Yamada 1989; see also Hollander 2008). As expected, our survey yielded numerous examples of adaptive differentiation in species with direct development (**Table 1**). However, species that have planktonic dispersal comprise a surprisingly high percentage (66%) of the taxa listed (see the section Dispersal Potential and Adaptive Differentiation, below).

#### 3.1. Experimental Design

Of the 59 studies listed, 66% tested for local adaptation using a common garden design and the remaining studies were reciprocal transplant experiments (or occasionally transplants to a single common field site). Fifty-six percent of the studies used adult animals collected from the field rather than those raised in the laboratory. The evidence for local adaptation provided by studies of field-collected animals must be interpreted cautiously because trait variation among these populations could arise from phenotypic responses induced prior to collection (Kawecki & Ebert 2004). In the studies included in our data set, field-collected animals were acclimated to identical laboratory conditions for 1 to 6 weeks before the start of the experiment to minimize differences arising from variation in environmental history.

Approximately 25% of the surveyed studies tested F1 generation animals that were raised in the laboratory for their entire lifetimes. In some cases, field-collected adults were bred in the laboratory and the resulting F1 offspring were raised under common conditions for weeks to months before testing (e.g., Johannesson & Johannesson 1996). More commonly, F1 individuals were produced in the laboratory by spawning field-collected adults and were tested soon thereafter as larvae or juveniles (e.g., Ament 1979, Hoare et al. 1995). These approaches likely reduce influences due to environmental history, although maternal effects may still influence traits measured in laboratory-reared offspring. Our survey yielded only 11 studies that tested for local adaptation in populations that had been raised under common laboratory conditions for two or more generations to minimize the influence of phenotypic plasticity.

**Table 1** Survey of 59 studies providing experimental evidence of adaptive divergence among populations of marine invertebrates

Taxon <sup>a</sup>	Selective factor	Method <sup>b</sup>	Response variable(s)	Scale of divergence <sup>c</sup> (km)	Reference(s)
Anthozoa: <i>Actinia tenebrosa</i>	Unknown	RT(FC)	Reproduction	4	Ayre 1995
Anthozoa: <i>Actinia tenebrosa</i>	Unknown	RT(FC)	Growth, survival, reproduction	0.15	Sherman & Ayre 2008
Anthozoa: <i>Metridium senile</i>	Temperature	CG(FC)	Respiration, enzyme activities	500	Walsh & Somero 1981
Anthozoa: <i>Acropora millepora</i>	Temperature	CG(FC)	Coral bleaching	240	Smith-Keune & van Oppen 2006, Smith 2005
Anthozoa: <i>Pocillopora damicornis</i>	Temperature	CG(FC)	Coral bleaching	220	D'Croz & Maté 2004
Anthozoa: <i>Pocillopora damicornis</i>	Temperature	CG(FC)	Coral bleaching	650	Ulstrup et al. 2006
Anthozoa: <i>Porites lobata</i>	Temperature	RT(FC)	Growth, stress proteins	5	Barshis et al. 2010, Smith et al. 2007
Gastropoda: <i>Crepidula convexa</i> *	Pollution	CG(F1)	Copper tolerance, survival	150	Untersee & Pechenik 2007
Gastropoda: <i>Crepidula convexa</i> ,* <i>C. fornicata</i>	Temperature	CG(F1)	Growth	550	Ament 1979
Gastropoda: <i>Littorina saxatilis</i> *	Pollution	CG(FC)	Survival	10	Daka & Hawkins 2004
Gastropoda: <i>Littorina saxatilis</i> *	Predation, wave action	CG(F1), T(F1), RT(FC)	Growth	0.05	Janson 1982
Gastropoda: <i>Littorina saxatilis</i> *	Predation, disturbance	RT(FC)	Survival	<1	Janson 1983
Gastropoda: <i>Littorina saxatilis</i> *	Predation, wave action	CG(F1)	Morphology, habitat selection	<1	Johannesson & Johannesson 1996
Gastropoda: <i>Littorina saxatilis</i> *	Predation and environmental factors	RT(FC)	Growth, survival	<10	Johannesson et al. 1997, Rolán-Alvarez et al. 1997
Gastropoda: <i>Littorina saxatilis</i> *	Temperature, food, environmental factors	RT(FC)	Growth, reproduction	0.05	Pardo & Johnson 2005
Gastropoda: <i>Littorina saxatilis</i> ,* <i>L. obtusata</i> *	Temperature	CG(FC)	Enzyme activity	3,500	Sokolova & Portner 2001
Gastropoda: <i>Littorina scutulata</i>	Temperature, desiccation	T(FC)	Growth, survival, reproduction	550	Behrens Yamada 1989
Gastropoda: <i>Littorina sitkana</i> *	Temperature, desiccation	T(FC)	Growth, survival, reproduction	15	Behrens Yamada 1989
Gastropoda: <i>Littorina subrotundata</i> ,* <i>L. sitkana</i> *	Salinity, desiccation	CG(FC)	Salinity and desiccation tolerances, survival	5	Sokolova & Boulding 2004
Gastropoda: <i>Littorina obtusata</i> *	Crab predation, temperature	RT(FC)	Growth	400	Trussell 2000

(Continued)

Table 1 (Continued)

Taxon <sup>a</sup>	Selective factor	Method <sup>b</sup>	Response variable(s)	Scale of divergence <sup>c</sup> (km)	Reference(s)
Gastropoda: <i>Littorina obtusata</i> *	Wave action	CG(FC)	Growth	20	Trussell 2002
Gastropoda: <i>Nodilittorina hawaiiensis</i> (= <i>Littorina picta</i> )	Wave action, desiccation	RT(FC)	Survival	0.5	Struhsaker 1968
Gastropoda: <i>Melampus bidentatus</i>	Temperature	T(FC)	Cold tolerance, survival, reproduction	825	Hilbish 1981
Gastropoda: <i>Tegula funebris</i>	Predation	RT(FC)	Habitat selection, survival	410	Fawcett 1984
Gastropoda: <i>Nucella lapillus</i> *	Wave action, temperature, predation	CG(F1)	Growth, morphology	0.3	Kirby et al. 1994
Gastropoda: <i>Nucella lapillus</i> *	Predation, wave action	RT(FC)	Morphology, survival	1	Kitching et al. 1966
Gastropoda: <i>Nucella lapillus</i> *	Wave action	CG(FC)	Foraging activity	4	Hughes & Taylor 1997
Gastropoda: <i>Nucella canaliculata</i> *	Prey availability	CG(F2)	Feeding ability	130	Sanford & Worth 2009
Gastropoda: <i>Nucella canaliculata</i> *	Prey availability	RT(F2)	Growth, survival	565	Sanford & Worth 2010
Gastropoda: <i>Nucella canaliculata</i> *	Temperature	CG(F2)	Heat tolerance, survival	800	Kuo & Sanford 2009
Gastropoda: <i>Nucella ostrina</i> *	Temperature	CG(F2+)	Development rate	1,300	Palmer 1994
Gastropoda: <i>Bembicium vittatum</i> *	Temperature, wave action	T(F1)	Growth, morphology	450	Parsons 1997
Gastropoda: <i>Bembicium vittatum</i> *	Unknown	RT(FC)	Growth	0.5	Parsons 1998
Gastropoda: <i>Elysia viridis</i>	Variation between algal hosts	CG(F1)	Growth	14	Trowbridge & Todd 2001
Bivalvia: <i>Mytilus edulis</i>	Pollution	CG(F1)	Survival, reproduction	1,200	Hoare et al. 1995
Bivalve: <i>Mytilus edulis</i>	Predation	CG(FC), T(FC)	Shell thickness	450	Freeman & Byers 2006
Bivalvia: <i>Mytilus trossulus</i>	Temperature	T(FC)	Growth, survival	150	Yanick et al. 2003
Bivalvia: <i>Crassostrea virginica</i>	Temperature	CG(F7)	Growth, ciliary activity	500	Dittman 1997, Dittman et al. 1998
Polychaeta: <i>Nereis diversicolor</i>	Pollution	CG(FC)	Survival	75	Bryan & Hummerstone 1971
Polychaeta: <i>Nereis diversicolor</i>	Pollution	CG(F1)	Survival	2	Grant et al. 1989

(Continued)



**Table 1 (Continued)**

Taxon <sup>a</sup>	Selective factor	Method <sup>b</sup>	Response variable(s)	Scale of divergence <sup>c</sup> (km)	Reference(s)
Polychaeta: <i>Spirorbis borealis</i>	Variation between algal hosts	CG(F1)	Habitat selection	15	MacKay & Doyle 1978
Bryozoa: <i>Bugula neritina</i>	Pollution	CG(F1), RT(F1)	Growth, survival	65	Piola & Johnston 2006
Amphipoda: <i>Ampitboe longimana</i> *	Algal toxins, predation	CG(F2)	Growth, survival, reproduction	950	Sotka & Hay 2002
Amphipoda: <i>Ampitboe longimana</i> *	Algal toxins, predation	CG(F1)	Growth, survival, reproduction	450	Sotka et al. 2003
Amphipoda: <i>Eogammarus confervicolus</i> *	Unknown environmental factors	CG(F2)	Habitat selection	0.2	Stanhope et al. 1992
Amphipoda: <i>Paracalliope novizealandiae</i> *	Parasites	CG(FC)	Resistance to infection	35	Bryan-Walker et al. 2007
Isopoda: <i>Idotea balthica</i> *	Variation between algal hosts	CG(F1)	Growth, survival, reproduction	<100	Vesakoski et al. 2009
Isopoda: <i>Idotea balthica</i> *	Variation between algal hosts	CG(FC)	Growth, reproduction	60	Jormalainen et al. 2008
Copepoda: <i>Acartia hudsonica</i>	Dinoflagellate toxins	CG(F11)	Growth, survival, reproduction	650	Colin & Dam 2004
Copepoda: <i>Acartia tonsa</i>	Hypoxia	CG(FC, F1)	Habitat selection	2,300	Decker et al. 2003
Copepoda: <i>Scottolana canadensis</i>	Temperature	CG(F2+)	Body size, development rate, growth	750	Lonsdale & Levinton 1985
Copepoda: <i>Tigriopus californicus</i>	Salinity, temperature	CG(F2)	Reproduction, life history	4	Dybdahl 1989
Copepoda: <i>Tigriopus californicus</i>	Temperature	CG(F2)	Thermal tolerance, survival	200	M. W. Kelly, E. Sanford, R. K. Grosberg, unpublished data
Decapoda: <i>Libinia dubia</i>	Predation	CG(FC)	Camouflage selection	600	Stachowicz & Hay 2000
Decapoda: <i>Uca pugnax</i>	Temperature	CG(F1)	Development rate	150	Sanford et al. 2006
Cirripedia: <i>Semibalanus balanoides</i>	Temperature	RT(FC)	Survival	30	Bertness & Gaines 1993
Cirripedia: <i>Semibalanus balanoides</i>	Temperature	T(FC)	Allele frequencies, survival	0.0024	Schmidt et al. 2000, Schmidt & Rand 2001
Echinoidea: <i>Strongylocentrotus purpuratus</i>	Temperature	CG(FC)	Thermal tolerance	1,300	Osovitz & Hofmann 2005
Ascidacea: <i>Botrylloides</i> sp.	Temperature	T(FC)	Growth, survival	35	Grosholz 2001

<sup>a</sup>Taxa marked with an asterisk have direct development; all others have planktonic dispersal.

<sup>b</sup>Methods used are abbreviated as CG, common garden; RT, reciprocal field transplant; T, transplant to a single field site. Origin of animals used is indicated in parentheses as FC, field-collected; F1, first laboratory generation; F2, second laboratory generation, etc.

<sup>c</sup>Scale of divergence is the minimum distance (km) between two sites exhibiting significant differences in one or more response variables.

### 3.2. Selective Gradients

A wide variety of abiotic and biotic factors appear to drive adaptive differentiation among marine invertebrate populations (Table 1). Not surprisingly, there is considerable evidence that variation in temperature has led to adaptive divergence in physiological traits among populations distributed across a variety of scales (ranging from vertical gradients in the intertidal zone to latitudinal gradients). Other physical factors that likely impose spatially varying selection on marine populations include desiccation, salinity, and wave forces. There is also accumulating evidence that anthropogenic changes (including increased pollution and hypoxia) have led to adaptive divergence among populations.

Spatial variation in biotic forces may also shape adaptive differentiation among marine populations. Selection imposed by predation intensity frequently varies over a range of spatial scales, from short distances (tens of meters) along wave exposure gradients (Kitching et al. 1966, Janson 1982, Johannesson & Johannesson 1996) to latitudinal gradients that may select for behavioral and morphological variation among populations of potential prey (Fawcett 1984, Stachowicz & Hay 2000, Freeman & Byers 2006). It is also increasingly clear that some marine herbivores are locally adapted to differences in their algal hosts (Sotka et al. 2003, Vesakoski et al. 2009; reviewed by Sotka 2005). Exposure to natural toxins (Colin & Dam 2004), infection by parasites (Bryan-Walker et al. 2007), and variation in prey availability (Sanford et al. 2003; Sanford & Worth 2009, 2010) are other biological forces that appear to have selected for differentiation among invertebrate populations.

### 3.3. Geographic Pattern of Adaptive Differentiation

For species with broad geographic ranges, adaptive differentiation among populations can generate a variety of spatial patterns, ranging from countergradient variation across a latitudinal gradient (Conover et al. 2006, 2009) to more complex geographic mosaics of adaptation (Thompson 1999). Countergradient variation occurs when genetic influences on a trait oppose environmental influences, such that phenotypic differences across the gradient are minimized. For example, it has long been recognized that geographically separated populations of animals can exhibit similar rates of respiration or growth in their native environments, despite experiencing vastly different temperatures (Bullock 1955). However, when animals from distant portions of a geographic range are acclimated at a common temperature in the laboratory, populations from cooler environments often exhibit higher rates of respiration. Although such metabolic compensation may often reflect physiological acclimatization (i.e., phenotypic plasticity), in other cases, fixed genetic differences among populations appear to make a major contribution to this countergradient pattern (Somero 2005, 2010).

In our survey, 10 of the common garden studies reported countergradient patterns of local adaptation. As expected, the majority of these studies documented countergradient variation in rates of respiration, development, or growth across a latitudinal gradient of temperature (Ament 1979, Walsh & Somero 1981, Lonsdale & Levinton 1985, Palmer 1994, Dittman 1997, Sokolova & Pörtner 2001, Freeman & Byers 2006, Sanford et al. 2006). In all cases, physiological rates and/or growth were greater in populations from higher latitudes, a pattern also observed in several field transplant studies (Parsons 1997, Trussell 2000).

Other studies in our data set documented spatial patterns of adaptive differentiation consistent with geographic mosaics of selection. For example, along the northeastern Pacific coast, thermal stress experienced by intertidal organisms has been characterized as a geographic mosaic of hot spots and cool spots linked to the timing of extreme low tides during the summer months

(Helmuth et al. 2002). In central and southern California, the lowest tides during the summer often occur at night, reducing the exposure of intertidal organisms to stressful conditions. In contrast, at some higher-latitude sites, these extreme low tides can occur at midday during the summer. Recent evidence suggests that the resulting mosaic of thermal stress may impose selection on the thermal tolerance of intertidal snails. Second-generation, laboratory-reared snails from higher-latitude sites were found to be more tolerant of higher temperatures than were conspecifics from central California (Kuo & Sanford 2009). Similarly, biotic factors may vary in a nonlinear fashion with latitude, resulting in spatial mosaics of consumer populations that show varying degrees of local adaptation to their prey (Jormalainen et al. 2008; Sanford & Worth 2009, 2010).

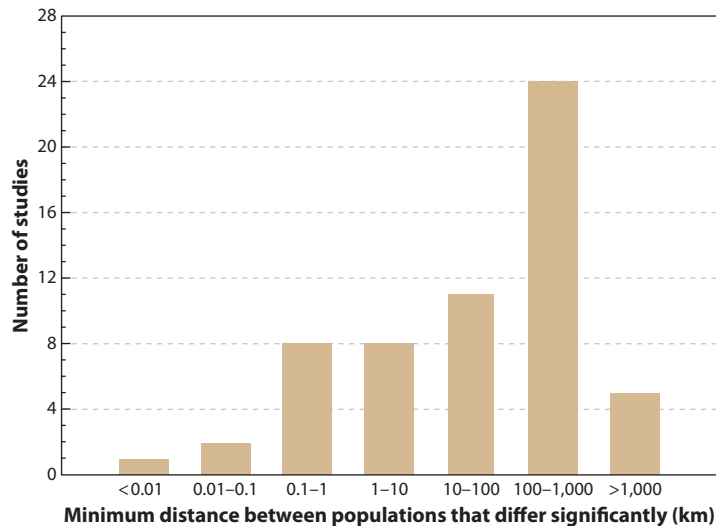
An additional spatial pattern of interest concerns the extent to which local adaptation is universal across all populations of a species versus being restricted to a subset of populations (Leimu & Fischer 2008, Hereford 2009). Reciprocal transplant experiments can address this pattern effectively, by testing whether each source population does better in its local environment than do genotypes from a foreign environment (Kawecki & Ebert 2004). In the 15 reciprocal transplant studies included in our survey, only 6 had results consistent with universal local adaptation. Interestingly, 4 of these were studies of intertidal snails that differed in shell morphology or size across intertidal gradients of temperature, desiccation, or wave exposure (Kitching et al. 1966, Struhsaker 1968, Janson 1983, Rolán-Alvarez et al. 1997). These studies indicate that there are fitness trade-offs that favor the evolution of contrasting morphologies in different environments (Hereford 2009).

In the other reciprocal transplant studies, local adaptation was evident in only a subset of the source habitats. In these cases, local adaptation was often documented under conditions where pollution, high temperatures, or low-quality food imposed selection on one or more populations (Piola & Johnston 2006, Sanford & Worth 2010, Barshis et al. 2010). Such selection favors stress-resistant genotypes that outperform genotypes from more benign environments when both are transplanted to stressful habitats. However, all genotypes may do similarly well when transplanted to benign habitats, suggesting that the trade-offs and costs of evolved stress resistance in these organisms may sometimes be difficult to detect (Piola & Johnston 2006, Sanford & Worth 2010). As discussed above, spatial variation in biotic and abiotic conditions may also create a mosaic of varying selection, such that local adaptation occurs at some sites but not others (Thompson 1999, Thompson & Cunningham 2002, Jormalainen et al. 2008).

For most species, the geography of adaptive differentiation among populations is poorly described. Characterizing these patterns requires sampling multiple populations to verify that the observed pattern is indeed correlated with the selection gradient of interest (Conover et al. 2009). There is a strong need for spatially intensive sampling of this type; 39% of the studies in our data set compared only two populations, and only 27% compared five or more populations.

### 3.4. Spatial Scale of Adaptive Differentiation

Our survey indicates that adaptive differentiation among populations of marine invertebrates occurs over a broad range of spatial scales (**Table 1**). Differentiation among populations distributed over regional scales (hundreds of kilometers) has been documented frequently (**Figure 2**). This scale of adaptation is consistent with the view that many selective gradients in marine systems are coarse-grained. For example, although water temperature may change abruptly over <100 km at major oceanographic boundaries (e.g., Point Conception, California), temperature changes along most coastlines are more gradual. Similarly, biological factors, such as predation intensity or the availability of algal hosts, are also likely to change over regional spatial scales that may incorporate geographic range boundaries of interacting species. For example, low-latitude populations of an



**Figure 2**

Scale over which adaptive differentiation has been observed in marine invertebrates. Bars represent the number of studies ( $n = 59$ ; see also **Table 1**) that documented significant differentiation between populations over various spatial scales. Although divergence was documented frequently at regional scales (hundreds of kilometers), it was also observed at finer scales ranging from meters to tens of kilometers.

herbivorous amphipod in the northwest Atlantic were found to be resistant to noxious chemicals produced by a co-occurring brown alga (Sotka & Hay 2002, Sotka et al. 2003). However, amphipod populations located in more northern regions beyond the range boundary of this algal species were less tolerant of these chemical defenses.

Differentiation among invertebrate populations has also been documented at a variety of finer spatial scales. At mesoscales (tens of kilometers), populations have evolved varying tolerances to alongshore gradients of environmental factors, including salinity and pollution (Sokolova & Boulding 2004, Untersee & Pechenik 2007). At scales of less than 1 km, differentiation can occur over short, vertical stress gradients within the intertidal zone (e.g., Schmidt et al. 2000, Janson 1982, Pardo & Johnson 2005) or along horizontal gradients of wave exposure covering a few hundred meters (e.g., Struhsaker 1968, Kirby et al. 1994). Collectively, these results suggest that adaptive differentiation in marine invertebrates may occur over smaller spatial scales than is known to occur in marine fishes. Conover et al. (2006) report that 60 km is the smallest spatial scale over which adaptive differentiation has been documented in a marine fish (see Imsland et al. 2001). However, the scale of adaptive divergence is poorly known in both marine fishes and invertebrates. Reducing this uncertainty will require spatially intensive sampling to determine the spatial scale over which differentiation among populations becomes nonsignificant (Conover et al. 2006).

#### 4. RESOLVING THE SCALE OF ADAPTIVE DIFFERENTIATION

Although local adaptation in the sea remains understudied, our literature survey yielded considerable experimental evidence that adaptive differentiation occurs in a diverse set of marine invertebrates. Key conclusions are that adaptive differentiation in marine invertebrates occurs (*a*) along a variety of selective gradients (both abiotic and biotic), generating patterns of countergradient variation and spatially complex mosaics of local adaptation, (*b*) across taxa with a

range of life histories, including planktonic dispersal, and (c) frequently over regional scales but also over much finer spatial scales, ranging from meters to tens of kilometers.

Evidence that adaptive differentiation can occur in species with planktonic dispersal and over relatively fine spatial scales runs counter to historical views about local adaptation in marine species (reviewed by Hedgecock 1986, Grosberg & Cunningham 2001). In this section, we attempt to reconcile these empirical trends with traditional expectations regarding local adaptation in marine systems.

#### 4.1. Dispersal Potential and Adaptive Differentiation

The connections among life history, dispersal, gene flow, and patterns of adaptive differentiation have long been recognized. The potential for local adaptation is increased in species characterized by restricted gene flow among populations (Endler 1977). Thus, species with direct development are expected to have far greater potential for local adaptation than those with planktonic larvae that may be dispersed large distances by ocean currents (Struhsaker 1968, Behrens Yamada 1989, Parsons 1998). Although accurately measuring dispersal distances in marine species remains a significant challenge, recent advances in the use of tagging studies, microchemistry, and population genetics have yielded improved estimates (Levin 2006). Analyses of these data suggest neighborhood sizes of planktonic larval dispersal ranging from 10 to 100 km for invertebrates and 50 to 200 km for fish (reviewed by Palumbi 2004). For species with direct development and/or limited movements as adults, neighborhood sizes for both marine invertebrates and fishes may be much smaller, on the scale of kilometers or less. Although there is overlap between the distributions of neighborhood sizes observed in marine invertebrates and fishes, these analyses suggest that many invertebrate species have neighborhood sizes smaller than those typical of fishes (Kinlan & Gaines 2003, Palumbi 2004). Therefore, a finer scale of adaptive differentiation within marine invertebrates versus fishes is consistent with expectations based on lower levels of dispersal and gene flow.

To what extent is the occurrence of local adaptation across different marine invertebrate species linked to their life history? Although our survey yielded numerous examples of adaptive differentiation in marine invertebrates with direct development (especially gastropods), a surprisingly high percentage of the cases identified (66%) were species that have planktonic dispersal. Some of these taxa, such as corals, sea anemones, and ascidians, have planktonic larvae that are non-feeding and thus often spend only a brief period in the water column (i.e., hours to a few days). However, other species listed (including many of the gastropods, bivalves, and crustaceans) have much longer planktonic durations lasting several weeks or longer. The occurrence of adaptive differentiation in these taxa is consistent with several possible explanations. First, as noted earlier, there is growing evidence that realized dispersal distances may be much shorter than expected in some species with planktonic larvae due to larval behavior or oceanographic features that retain larvae near their natal habitats (Levin 2006). Second, many marine invertebrates have very broad geographic ranges (thousands of kilometers), and populations separated by hundreds of kilometers may be only weakly connected to one another (Palumbi 2004). These populations might well show patterns of adaptive divergence related to coarse-grained selective gradients, such as water temperature. Finally, as discussed below, if selection is strong enough, differentiation may occur over relatively fine spatial scales, even in the face of considerable dispersal and gene flow.

#### 4.2. Local Adaptation Versus Balanced Polymorphism

In the strictest sense, local adaptation refers to populations that have differentiated genetically under conditions where low dispersal or active habitat choice have resulted in low gene flow

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**Neighborhood size:** an area large enough to include most of the offspring of a given set of parents following larval or juvenile dispersal

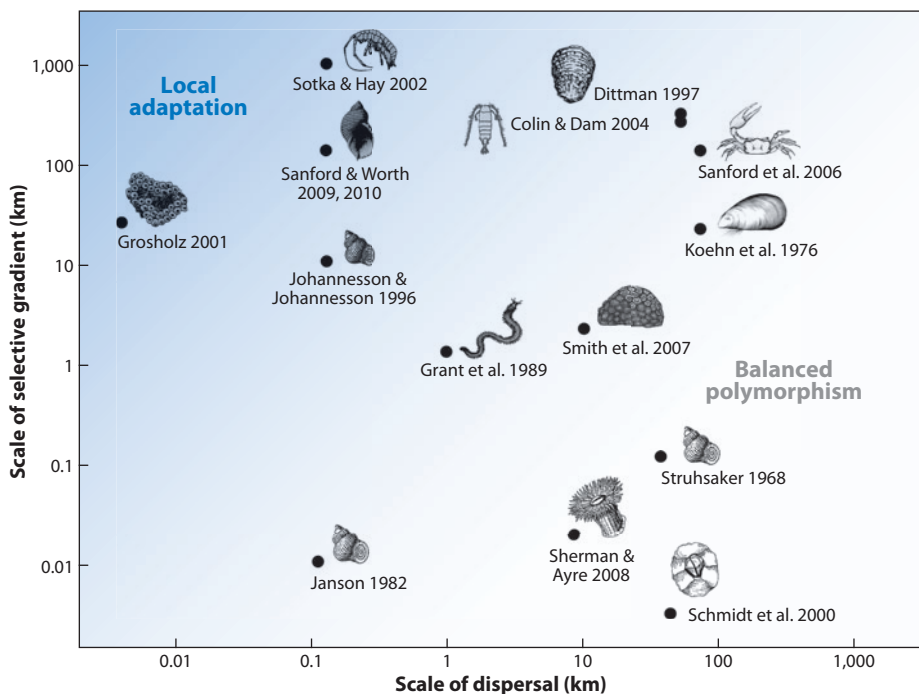
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**Balanced polymorphism:**

genetic variation that is maintained by balancing selection, such that no single allele always has the highest fitness

(Kawecki & Ebert 2004). Importantly, genetic differentiation may still arise among populations connected by high gene flow (Hedgercock 1986, Slatkin 1987). However, in this case, differentiation is maintained by strong selection following dispersal (i.e., by purifying selection acting in each generation). For example, Schmidt & Rand (2001) found that genotype frequencies in high and low intertidal populations of an acorn barnacle were generally homogenous if individuals were sampled soon after planktonic larvae had settled onshore. However, juvenile barnacles that had experienced a period of postsettlement mortality in the high and low intertidal zones showed strong allelic differences at the *Mpi* (mannose-6-phosphate isomerase) locus (associated with stress tolerance). This sorting out of genotypes via postdispersal mortality has recently been referred to as a “phenotype–environment mismatch” (Marshall et al. 2010). Although it is clear that such purifying selection can generate genetic differentiation (Conover et al. 2006, Marshall et al. 2010), several authors have emphasized that such a system is best characterized as a balanced polymorphism rather than strict local adaptation (Grosberg & Cunningham 2001, Schmidt & Rand 2001, Kawecki & Ebert 2004, Sotka 2005, Hays 2007, Somero 2010).

A key point is that local adaptation lies on a continuum with balanced polymorphism (Figure 3). Location along this continuum depends on the scale over which gene flow occurs and the scale over which the selective regime varies. When gene flow is restricted to a scale that is less than the scale over which a strong selective force varies, then the potential for local adaptation



**Figure 3**

Scale of dispersal versus scale of selective gradient in studies of marine invertebrate taxa. The distribution of points illustrates the continuum between local adaptation and balanced polymorphism. Systems with a scale of dispersal smaller than the scale of a strong selective gradient (*blue*) are expected to promote true local adaptation, whereas systems with a scale of dispersal greater than the scale of the selective gradient (*white*) are expected to promote balanced polymorphism. In the latter case, genetic differentiation among populations is maintained by recurring selection acting on each generation.

is increased. In contrast, when gene flow occurs over a spatial scale that is larger than the scale of the selective gradient, local adaptation is impeded and differentiation (if it occurs) must be maintained by purifying selection. Thus, barnacles whose larvae spend several weeks in the plankton might be locally adapted to a latitudinal temperature gradient but are unlikely to be locally adapted to the vertical gradient of temperature that occurs over several meters within the intertidal zone at a given site. Rather, if differentiation occurs between barnacle populations in the high and low intertidal zone, it must be maintained via purifying selection (Hedgecock 1986, Schmidt & Rand 1999).

Examples of purifying selection are common in many habitats (e.g., McNeilly 1968, Ehrlich & Raven 1969) and may generate important differentiation in marine systems at a variety of spatial scales (Marshall et al. 2010). Purifying selection is likely to be particularly important at very local spatial scales (e.g., across vertical and horizontal gradients in the intertidal zone) that are well within the dispersal range of the study organism (Struhsaker 1968, Schmidt et al. 2000, Hays 2007, Sherman & Ayre 2008). Postsettlement mortality may also generate selective mortality over regional scales of hundreds of kilometers, for example, along salinity gradients in estuaries (Koehn et al. 1976; Hilbish 1985, 1996). Mortality during planktonic larval dispersal across temperature gradients has also been hypothesized to generate regional sorting of genotypes (Sanford et al. 2006). In many empirical examples of genetic differentiation, it is difficult to discern where a particular study system lies on the continuum from local adaptation to purifying selection. This uncertainty often arises because of lack of information regarding the actual scale of gene flow among populations (e.g., Bertness & Gaines 1993, Brown et al. 2001). Nevertheless, distinguishing between local adaptation and purifying selection is important as the operation of these two phenomena may have different ecological and evolutionary consequences (see the section Broader Implications of Local Adaptation, below). Fortunately, advances in genomics and the analysis of specific candidate loci provide potentially powerful techniques for identifying the contribution of purifying selection to the maintenance of genetic differentiation, as we discuss in the next section.

## 5. NONEXPERIMENTAL APPROACHES

Most work on local adaptation has focused on experimental approaches to identifying differences among populations. However, several recent molecular techniques make it possible to identify adaptive differentiation among populations nonexperimentally. These methods have considerable potential to address the mechanistic basis for adaptation. In addition, by sampling early life stages versus adults, these methods may also help identify the contribution of purifying selection to the maintenance of genetic differentiation.

Early molecular approaches used  $F_{ST}$ - $Q_{ST}$  comparisons to identify traits under spatially varying selection. In this context,  $F_{ST}$  is a measure of population subdivision in neutral molecular variation, and  $Q_{ST}$  is a measure of subdivision in quantitative traits. Whenever traits vary among populations and can be shown to have a genetic basis (typically in a common garden), the possibility remains that these differences are due to genetic drift. However, if  $Q_{ST}$  can be shown to be significantly greater than  $F_{ST}$ , drift can be excluded as the sole source of variation, leaving spatially varying selection as the agent of differentiation among populations.  $F_{ST}$ - $Q_{ST}$  comparisons have demonstrated adaptive differentiation in broadcast-spawning invertebrates, with almost no differentiation at neutral loci (Luttikhuisen et al. 2003), but also stabilizing selection across broad latitudinal gradients in other taxa (e.g., Edmands & Harrison 2003).

A more recent extension of the  $F_{ST}$ - $Q_{ST}$  comparison is the advent of population genomics, where whole-genome scans are used to identify loci thought to be under spatially varying selection. Whereas previous methods compared quantitative traits to differentiation at a few (putatively

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**$F_{ST}$ :** a measure of differentiation among populations for neutral molecular markers

**$Q_{ST}$ :** a measure of differentiation among populations for continuous phenotypic traits

**Genetic drift:** changes in allele frequencies, often in small, isolated populations, due to chance rather than natural selection

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**Cline:** a gradual change in allele frequencies or other traits observed in populations distributed along a spatial gradient

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neutral loci, whole-genome scans identify outlier loci thought to be under selection because they stand out against background levels of differentiation among populations. Genome-scan techniques can provide new insights into the genetic basis for adaptation. For example, Galindo et al. (2009) identified loci underlying differences in the high- and low-shore ecotypes of the snail *Littorina saxatilis*. They found that differentiation among sites for these loci was actually greater than differentiation among sites for neutral loci. This suggests that although there is convergence on the same two ecotypes across sites, different alleles may be involved in this parallel adaptation.

A significant drawback to the genome-scan technique in nonmodel organisms (where the genome has not been sequenced) is that the identification of candidate loci tells us little about the identity or function of the genes involved in local adaptation. Bridging the gap between candidate loci and gene function is not a trivial process. Wood et al. (2008) were able to sequence four candidate loci underlying ecotypic differences in *L. saxatilis*. As expected, they found sequence differences between ecotypes, but the functional significance of these differences remains largely unknown. Identification of the genes linked to candidate loci is more straightforward in organisms with full genome sequences, and the new availability of the whole genome of the purple sea urchin (*Strongylocentrotus purpuratus*) has made this technique available for a widespread and ecologically important species (Pespeni et al. 2010).

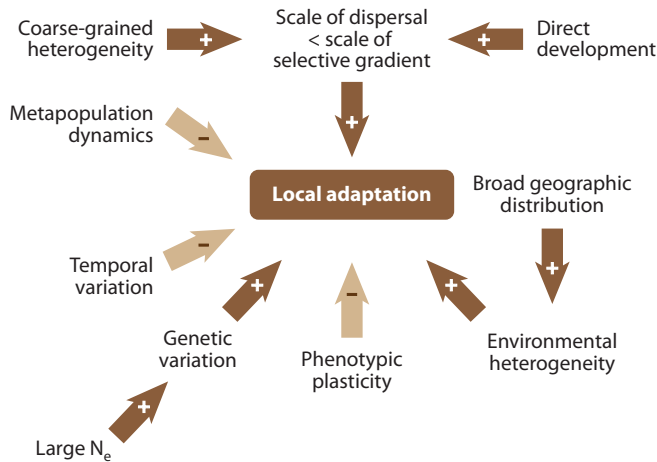
An alternative to the whole genome scan is to look for a relationship between environmental variables and allele frequencies in candidate genes with known or suspected function (e.g., Hilbish & Koehn 1985, Burton 1986; reviewed in Schmidt et al. 2008). For example, a strong connection between a cline in an enzyme and its function can be seen in the mussel *Mytilus edulis* and the *Lap* (Leucine amino peptidase) locus (Hilbish & Koehn 1985). The *Lap*<sup>94</sup> allele shows an alongshore cline in Long Island Sound, New York. The selective force creating the cline appears to be a gradient of salinity, and the enzyme is involved in osmoregulation, cleaving proteins to change the osmolarity of cells. The change in frequency of the *Lap*<sup>94</sup> allele appears to be the result of balanced polymorphism rather than true local adaptation. Allelic frequencies were generally homogenous along this estuarine gradient when populations were sampled soon after mussel larvae had settled onshore. However, a strong cline became apparent in juvenile mussels that had experienced a period of postsettlement mortality.

Both the candidate gene and whole genome scan techniques are still in their early phases of development. However, both approaches hold the potential to integrate disparate scales of ecology and evolution, from natural selection across broad latitudinal clines to the mechanistic basis of adaptation at the level of cells and genes. Moreover, sampling individuals at different life stages provides a powerful opportunity to compare planktonic larvae (or newly settled juveniles) with adults (e.g., Hilbish & Koehn 1985, Schmidt et al. 2000, Schmidt & Rand 2001). These analyses can lend insight into whether genetic differentiation is present at settlement, or is maintained via postsettlement mortality of inferior genotypes (i.e., balanced polymorphism).

## 6. FACTORS THAT PROMOTE OR CONSTRAIN LOCAL ADAPTATION

In addition to the homogenizing effects of gene flow, other factors may constrain local adaptation, most notably temporal variation and phenotypic plasticity (**Figure 4**). In species with high levels of gene flow, phenotypic plasticity will be favored over local adaptation, as long as there are no great costs to plasticity (Warner 1997, Kawecki & Ebert 2004). Indeed, in a meta-analysis, plasticity was greater in species of marine invertebrates with higher dispersal (Hollander 2008). Plasticity should constrain the evolution of local adaptation because it represents an alternate mechanism for achieving adaptive phenotypes in heterogeneous environments. For example, in the tidepool copepod *Tigriopus californicus*, acclimation to higher temperatures contributes much





**Figure 4**

Factors expected to promote (*dark arrows*) or constrain (*light arrows*) local adaptation.  $N_e$  = effective population size.

more to variation in thermal tolerance within populations than does additive genetic variation (M. W. Kelly, E. Sanford, R. K. Grosberg, unpublished data). This plasticity may constrain adaptation to higher temperatures if it tends to mask underlying genetic variance. The relative importance of phenotypic plasticity and local adaptation in setting niche breadths for marine invertebrates is not well understood, in part because of the difficulties in sorting out the roles of phenotypic plasticity and local adaptation in producing differences among populations.

Local adaptation will also be opposed by metapopulation dynamics because population extinction and recolonization will erase any adaptation that has occurred over the life span of the population (Sultan & Spencer 2002). To the extent that disturbance regularly creates localized extinctions (Kritzer & Sale 2006), marine populations will tend not to adapt to heterogeneity that occurs at the scale of a metapopulation. Finally, local adaptation may be constrained by temporal variation in environmental gradients (Kawecki & Ebert 2004). Some gradients in marine systems are produced by characteristics such as coastal bathymetry and the location of rocky headlands, which are likely to be stable over evolutionary time (Menge et al. 1997; Navarrete et al. 2005, 2008; Broitman et al. 2008). However, variation that occurs over shorter time scales, such as changes in sea surface temperatures produced by El Niño–Southern Oscillation events, may tend to prevent adaptation to a single environmental regime.

## 7. BROADER IMPLICATIONS OF LOCAL ADAPTATION

A better understanding of local adaptation promises to advance our understanding in several areas of research, including community ecology, the study of the biological effects of climate change, and marine conservation.

### 7.1. Community Ecology

In recent decades, an expanding area of ecological research has focused on understanding how and why natural communities vary across large spatial scales (Witman & Roy 2009). An important component of these studies has addressed the causes and consequences of regional and latitudinal

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**Metapopulation dynamics:** local extinction and colonization within a set of spatially separated subpopulations that are linked by dispersal

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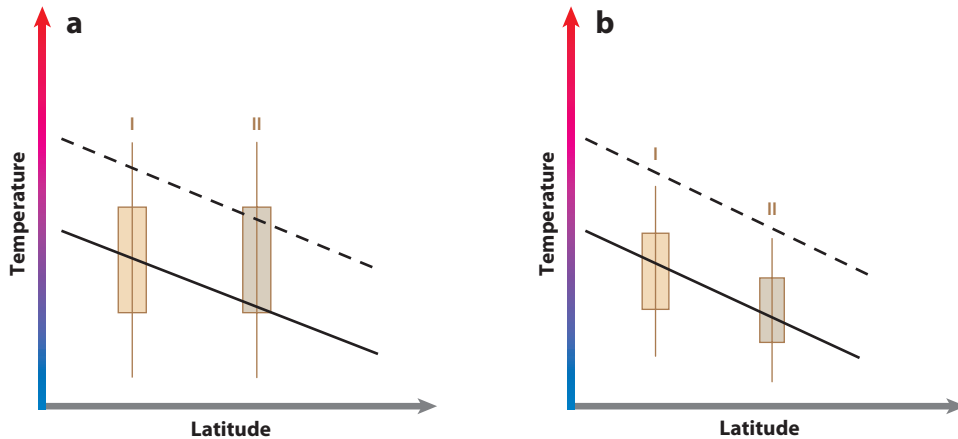
variation in the strength of species interactions (reviewed by Sanford & Bertness 2009). Pairs of species often co-occur and interact over broad geographic ranges, yet spatial variation in interaction strengths are rarely investigated at these large spatial scales. One tool for quantifying these patterns has been a comparative-experimental approach that establishes identical, replicated experiments at multiple sites along a geographic gradient. In marine systems, such studies have revealed considerable variation in the intensity or outcome of species interactions across scales of tens to hundreds of kilometers (reviewed by Sanford & Bertness 2009). This variation has been attributed to a wide range of underlying ecological factors, from gradients in abiotic stressors to changes in biotic context, including differences in the recruitment and abundance of key species. However, less attention has been devoted to the potential role that evolutionary processes may play in shaping regional and geographic variation in species interactions.

Theoretical and empirical work, primarily from terrestrial systems, suggests that spatial mosaics of abiotic or biotic conditions may create a landscape of varying selection intensity on interacting species (Thompson 1999, Thompson & Cunningham 2002). A growing body of research suggests that such geographic mosaics of selection may also be common in marine systems, resulting in populations of marine invertebrates that show varying degrees of local adaptation to algal hosts, prey assemblages, and predators (Stachowicz & Hay 2000; Trussell 2000; Sotka et al. 2003; Freeman & Byers 2006; Jormalainen et al. 2008; Sanford & Worth 2009, 2010). Increased attention to how these evolutionary processes may alter the community importance of the same species at different sites (e.g., Sanford et al. 2003, Sanford & Worth 2009) is likely to improve our ability to predict regional and geographic variation in community dynamics.

## 7.2. Macrophysiology and the Effects of Climate Change

A better understanding of local adaptation will also improve the accuracy of predictions about the impacts of climate change. Climate change has already resulted in poleward geographic range shifts for many species, and continued changes in species' distributions are anticipated (Parmesan & Yohe 2003). Predictions of range shifts are based increasingly on climate envelope models, which use a species' current distribution to describe its environmental niche and then map that niche on to space under future environmental conditions (Pearson & Dawson 2003). These models assume that every population of a species has the same environmental niche and may underestimate extinction risk in species with strong local adaptation, where individual populations have a narrower range of tolerances than the species as a whole (**Figure 5**). This problem may be especially important for corals and intertidal invertebrates, some of which appear to be living close to the edge of their upper thermal limits (Hughes et al. 2003; Somero 2005, 2010).

Recent work has described differences in the physiological tolerances of populations of marine organisms living across broad latitudinal gradients, but it is unclear whether most of these differences represent local adaptation or phenotypic plasticity (Osovitz & Hofmann 2005, Place et al. 2008, Somero 2010; but see Kuo & Sanford 2009). It is critical to distinguish between the effects of local adaptation and phenotypic plasticity in producing differences among populations because these two phenomena lead to different predictions regarding the vulnerability of populations to extinction. If differences among populations are due to phenotypic plasticity, each population has the potential to achieve the full range of tolerances found in the species as a whole. If differences are due to local adaptation, poleward populations may be unable to achieve higher thermal tolerance without gene flow from more tolerant populations. Recent work also suggests local adaptation to complex mosaics of thermal stress, suggesting that patterns of population-level extinction may be more complex than simple poleward range contractions (Kuo & Sanford 2009). Climate change may accentuate other abiotic mosaics along coastlines, including hot spots of decreased pH



**Figure 5**

Implications of local adaptation for predictions regarding the impacts of climate change. Box plots show the hypothetical distribution of temperature tolerance phenotypes in two populations lying along a latitudinal temperature gradient. Solid black lines show the current gradient of maximum temperature; dashed black lines show the future gradient. Populations can persist if they have some tolerance values lying above the new threshold. In (a), with a broad range of phenotypes within populations and no local adaptation, both populations persist. In (b), with a narrower range of phenotypes within populations and local adaptation, neither population persists, although population II could persist with gene flow from population I. Note that the persistence of each population depends not just on the range of tolerance phenotypes in the species as a whole but also on the distribution of those phenotypes among and within populations.

associated with centers of upwelling (Feely et al. 2008, Hauri et al. 2009). The degree to which calcifying marine invertebrates may be locally adapted to such alongshore mosaics of ocean acidification has not yet been explored.

Earlier in this review, we drew a distinction between true local adaptation and balanced polymorphism, where maladapted genotypes arrive in a population every generation and are removed by selection. This distinction is also important to making accurate predictions about the effects of climate change. If interpopulation differences in environmental tolerance are due to balanced polymorphism, then the full range of phenotypes found in the species are available to each population every generation, and so the narrower tolerances of individual populations should not lead to a greater extinction risk.

### 7.3. Marine Conservation and Spatial Management

Improved knowledge of local adaptation will also likely inform the conservation and spatial management of natural populations. Efforts to design effective networks of marine protected areas have emphasized the importance of demographic connectivity (reviewed by Palumbi 2004). However, there is growing interest in ensuring that reserve networks also protect genetic diversity to promote resilience to environmental change (Bell & Okamura 2005, Baums 2008, Miller & Ayre 2008). Although genetic diversity is generally assessed using neutral molecular markers, there is often a poor correlation between neutral genetic variation and quantitative genetic variation in functionally important traits (Hedgecock 1986, Conover et al. 2006). Thus, there is a need for

management planning that addresses spatial patterns of local adaptation. In particular, locally adapted populations might be a conservation priority if they act as sources of genotypes that replenish areas following disturbance. For example, McClanahan et al. (2007) suggest that coral reefs in areas of lower water turnover may include populations that are locally adapted to elevated temperatures. Although these same sites may experience the greatest rates of temperature increase in the future, resident corals might be of particular conservation value if these populations are highly adapted to stressful conditions (West & Salm 2003, McClanahan et al. 2007, Miller & Ayre 2008; but see Baskett et al. 2010). These considerations also highlight the need to characterize the mechanisms that maintain differentiation among populations. If genetic differences among coral populations are maintained by recurring selection imposed by periodic warm water events, then differences in thermal tolerance represent a balanced polymorphism. In this case, populations at stressful sites would likely hold a subset of genetic variation that is also present in the coral metapopulation as a whole. In contrast, populations that are truly locally adapted might indeed hold novel stress-resistant genotypes, and such populations might merit special consideration for conservation.

There has also been considerable interest in the implications of local adaptation for both fisheries management and restoration efforts. If local adaptation is common in marine species, then care must be taken to ensure that stock enhancement and aquaculture do not compromise the fitness of native gene pools by introducing maladapted genotypes (Conover 1998). For example, there have long been concerns that hatchery-raised salmon may have a negative influence on wild, local salmon populations if interbreeding occurs (Taylor 1991). Analogous concerns likely apply to invertebrate fisheries as well. For example, there is evidence that commercially harvested bivalves, including oysters and mussels, can be locally adapted to temperature regimes (Dittman et al. 1998, Yanick et al. 2003). Knowledge of adaptive genetic differentiation among potential source populations may thus be essential to the success of stock enhancement efforts. Similarly, improved information about local adaptation is needed to guide the selection of source populations for restoration projects that focus on corals, oysters, and other foundation species (Baums 2008, Marshall et al. 2010; see also McKay et al. 2005).

### SUMMARY POINTS

1. Local adaptation is the fine-tuning of populations to their local environment via natural selection and results in resident genotypes that have a higher fitness in their native habitat than genotypes from more distant populations. Experimental approaches (including common garden designs and reciprocal transplants) are effective tools for identifying local adaptation.
2. Although understudied, local adaptation has been documented in numerous marine invertebrates in response to selection imposed by strong gradients (and more complex mosaics) of abiotic and biotic conditions.
3. Our literature survey suggests two empirical trends that run counter to the historical view that local adaptation in the sea should be observed primarily in comparisons between distant populations of species with direct development. First, species with planktonic dispersal comprise a surprisingly high percentage (66%) of the marine invertebrates known or suspected of exhibiting local adaptation. Second, adaptive divergence occurs over regional spatial scales (hundreds of kilometers) but also over relatively fine scales (ranging from meters to tens of kilometers).

4. Local adaptation is promoted when the spatial scale of gene flow is small relative to the scale over which a strong selective gradient varies. Local adaptation is impeded when the scale of gene flow is much greater than that of the selective gradient. However, genetic differentiation can still occur in the face of high gene flow when selection is strong; in this case, divergence is maintained by selection acting on early life stages during each generation, and the system is characterized as a balanced polymorphism. As a result of these combined processes, differentiation among populations is expected to occur across a broad range of spatial scales and life histories in marine organisms.
5. Distinguishing between local adaptation and balanced polymorphism is important as these two phenomena often have different ecological and evolutionary consequences. Improved molecular approaches can help identify the contribution of purifying selection to observed patterns of genetic differentiation.
6. Addressing spatial patterns of local adaptation in the sea is central to advancing our understanding of community ecology, climate change impacts, and the spatial management of marine populations.

## FUTURE ISSUES

1. Most marine species occur over broad geographic ranges and exhibit considerable spatial variation in key traits. In most cases, little is known about relative contributions of phenotypic plasticity versus fixed genetic variation to these differences. Although the importance of this question has been recognized for decades (Bullock 1955, Segal 1961), progress has been limited. Studies that breed marine organisms through multiple generations under common laboratory conditions are often logistically demanding but will be a critical component of future efforts to address this issue.
2. A growing body of population genetic studies demonstrates genetic differentiation among marine populations in neutral molecular markers. These studies provide important information regarding scales of gene flow, yet information is needed regarding corresponding differentiation in functionally important traits related to life history, physiology, and ecology.
3. A small, but expanding, body of work uses whole-genome scans to identify candidate loci involved in local adaptation. This approach promises to connect disparate scales of ecology and evolution, linking divergent selection among populations to the functional basis of adaptation at the level of individual genes.
4. There is much left to be learned about the factors that promote or constrain local adaptation in marine species. One promising approach to address this issue is to compare evolutionary processes in congeners with different life history characteristics.
5. Finally, there is a critical need for studies that rigorously quantify the spatial scale over which adaptive differentiation occurs in marine systems. Prior studies of local adaptation have frequently used two or three populations, which provides little information to address this question. Resolving the spatial scale over which local adaptation occurs in marine species has broad implications ranging from improved prediction of the biological impacts of climate change to effective management planning.

## DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

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## Errata

An online log of corrections to *Annual Review of Marine Science* articles may be found at <http://marine.annualreviews.org/errata.shtml>