

Spatial and temporal scales of adaptive divergence in marine fishes and the implications for conservation

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Knowledge of geographic and temporal scales of adaptive genetic variation is crucial to species conservation, yet understanding of these phenomena, particularly in marine systems, is scant. Until recently, the belief has been that because most marine species have highly dispersive or mobile life stages, local adaptation could occur only on broad geographic scales. This view is supported by comparatively low levels of genetic variation among populations as detected by neutral markers. Similarly, the time scale of adaptive divergence has also been assumed to be very long, requiring thousands of generations. Recent studies of a variety of species have challenged these beliefs. First, there is strong evidence of geographically structured local adaptation in physiological and morphological traits. Second, the proportion of quantitative trait variation at the among-population level (Q_{ST}) is much higher than it is for neutral markers (F_{ST}) and these two metrics of genetic variation are poorly correlated. Third, evidence that selection is a potent evolutionary force capable of sustaining adaptive divergence on contemporary time scales is summarized. The differing spatial and temporal scales of adaptive v. neutral genetic divergence call for a new paradigm in thinking about the relationship between phenogeography (the geography of phenotypic variation) and phylogeography (the geography of lineages) in marine species. The idea that contemporary selective processes can cause fine-scale spatial and temporal divergence underscores the need for a new emphasis on Darwinian fishery science.

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INTRODUCTION

The spatial and temporal scales of phenotypic and genotypic variation in marine systems are fundamental to the understanding of the ecological and evolutionary processes that influence biodiversity and provide a spatially explicit framework for conservation of resource species. Generally in the past, phenotypic variation has primarily been the province of ecologists, while genetic variation has been the focus of population geneticists. Although the need to merge these fields has been acknowledged for many years, recent discoveries on many fronts have drawn new attention to this problem. There is

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increasing evidence that adaptive divergence is a dynamic process that is tuned to agents of selection on scales much finer than previously believed.

There are two principal forms of genetic variation that are used frequently in evolutionary studies, especially those pertinent to conservation biology. One is molecular genetic variation in DNA sequences, products or markers that are presumed neutral to selection because they do not code for or influence phenotypic expression at the organismal level and are therefore unlikely to affect fitness. The other is variation in genes that determine phenotypic trait differences among individuals and thereby influence fitness, leading to adaptive divergence. The geography of neutral *v.* selected genes or traits provide very different insights into the ecology and evolution of species.

Molecular genetic surveys using neutral DNA markers have been the principal tool for studying the geography of genetic variation. Use of neutral markers allows the geographic structure of populations or lineages within species to be revealed (referred to as phylogeography) without the confounding effects of selection or environmental influences. In the absence of gene flow, random changes in neutral genetic variation, caused by mutation or drift, accumulate over long periods of time (thousands of generations) and allow the number and location of isolated gene pools within a species to be identified. Such gene pools have been designated as 'evolutionarily significant units' (ESU), and they have become the focal point for resource management and conservation (Moritz, 1994). More recently, studies of molecular genetic variation are being employed to estimate dispersal distances (Kinlan & Gaines, 2003) and connectivity among sites or oceanic regions (Palumbi, 2003).

Studies of the geography of phenotypic variation (*i.e.* 'phenogeography') have also been used to identify population structure although the interpretation of such patterns is much more difficult (Swain & Foote, 1999). Phenotypes often vary spatially in association with environmental gradients in abiotic or biotic factors such as temperature, salinity, predators or competitors. They may also vary over short temporal scales both within and among generations in response to selection, *i.e.* non-random survival or reproductive success of different phenotypes. A major goal of ecologists is to understand the causes and consequences of phenotypic variation. In such cases, a key question is whether phenotypic variation is environmental, genetic or both (*e.g.* genotype \times environment interaction). The answer can be obtained through the use of 'common garden' experiments where environmental variables are controlled so that the environmental and genetic components of phenotypic variation are revealed (often referred to as the 'quantitative genetic approach' because many phenotypic traits likely have a polygenic basis). Phenotypic variation that has an underlying additive genetic basis may be optimized by natural selection such that phenotypes are locally adapted to agents of selection in a given locale, provided that gene flow from other areas is not overwhelming. Hence, 'phenogeography' can be far more difficult to interpret than 'phylogeography' because the former is potentially influenced by too many confounding factors, *i.e.* phenotypic plasticity, genetics, selection and gene flow. Moreover, it is often the covariance between environments and genotypes in nature that is critical to understanding phenotypic patterns in the wild (Conover & Schultz, 1995).

Because it is adaptive (not neutral) genetic variation that affects fitness, it could be argued that the geography of adaptive genetic variation is more pertinent to conservation than 'phylogeography'. But because adaptive genetic variation is so difficult to measure, 'phylogeography' is often used instead. In so doing, the assumption is that the spatial structure of adaptive and neutral genetic variation is closely allied. This will be true only if gene flow is the dominant force controlling both.

Marine species with highly vagile and dispersive life stages generally have very low values of F_{ST} (defined as the fraction of the total genetic variation attributable to differences among populations) leading to an impression of high connectivity among widely distributed populations (Palumbi, 1992, 2003). If gene flow is high, it may preclude local adaptation, leading in theory to a close association between 'phylogeography' and the spatial structure of locally adapted genes. This view, however, is changing as new evidence suggests that natal homing (Thorrold *et al.*, 2001) and self-replenishment of local populations may be far more common in marine systems than anticipated previously (Jones *et al.*, 1999; Swearer *et al.*, 1999; Cowen *et al.*, 2006; Ruzzante *et al.*, 2006). Moreover, low levels of F_{ST} in oceanic species may also be attributed to the large population sizes that limit differentiation due to drift rather than high numbers of migrants (Allendorf & Phelps, 1981). If local recruitment is common, then local adaptation could occur on much finer scales. Knowledge of the geography of local adaptation in highly dispersive marine species, however, is poor. Until recently, few studies of local adaptation in marine fishes existed and in none of these has the spatial scale of local adaptation been explicitly defined.

New evidence suggests that the temporal scale of adaptive divergence may also be finer than previously believed (Hendry *et al.*, 2000; Stockwell *et al.*, 2003; Hairston *et al.*, 2005). The traits that are capable of rapid evolution include life-history and physiological characteristics that directly influence the viability and productivity of populations (Reznick *et al.*, 1997; Conover & Munch, 2002; Koskinen *et al.*, 2002; Walsh *et al.*, 2006). Traits that evolve rapidly also have the potential to display fine-scale spatial variation because ongoing selection is more likely to overcome the homogenizing effects of gene flow.

In this paper, the temporal and spatial scales of adaptive divergence are discussed with emphasis on marine species with large, open populations that lack obvious barriers to gene flow, *i.e.* those with exceedingly low F_{ST} . The interplay between local adaptation and gene flow, the geography of neutral *v.* quantitative genetic variation and the evidence for rapid evolution on contemporary time scales are reviewed, and the implications for conservation are discussed. First, the processes involved in and the evidence for local adaptation in marine species are considered.

LOCAL ADAPTATION AND THE GEOGRAPHY OF ADAPTIVE VARIATION

Local adaptation occurs when genotypes in their native habitat have higher relative fitness than genotypes originating from other habitats (Kawecki & Ebert, 2004). In other words, local adaptation is genotype \times environment interaction for fitness. It arises from spatially and temporarily varying selection,

a process driven by those environmental differences among habitats or time periods that influence fitness.

If there were no constraints on adaptive divergence, a world where local groups of individuals were finely tuned to the specific agents of selection in their immediate surroundings, where the individuals closely tracked environmental change through time might be imagined. But there are at least five factors that work against local adaptation. First and foremost is gene flow, which homogenizes genetic variation across habitats. Second, local adaptation can be confounded by drift, which may cause non-adaptive genetic heterogeneity across habitats. Third is unpredictable, temporal environmental variability, which essentially makes the optimal phenotype a moving target. Fourth, is the lack of heritability for trait variation, an essential ingredient of evolution. Finally, negative genetic correlations or trade-offs among traits may constrain adaptive variation. Any of these factors, singly or in combination, may reduce the degree of adaptive divergence among habitats or populations of a species.

The potential for local adaptation is typically deduced from studies of 'phenogeography': the distribution of phenotypic variation in nature. Because phenotypes are also influenced by environmental factors, phenotypic patterns in nature may or may not have a genetic basis. Hence, a 'common garden experiment' is required to disentangle the environmental and genetic components of phenotypic variation (Conover & Schultz, 1995). Standardizing the environment allows the genetic component of phenotypic variation to be revealed. In designing these experiments, several potentially confounding factors must be accounted for. First, to avoid environmental effects prior to transfer, experimental subjects must be reared throughout their entire lifetimes under standardized conditions. Second, to avoid the possibility of maternal effects, the parents of the experimental individuals also require rearing under standardized conditions. Third, because of the likelihood of genotype \times environment interaction, the experiments should be done across multiple environmental conditions encompassing the range found in nature. Finally, to be certain that the genetic variation revealed is adaptive rather than due to chance, phenotypes originating from many different locations along a gradient, at least three, must be tested. The labour and risk involved in rearing marine fish for 'common garden experiments' may explain why studies of 'phylogeography', which require only field collections and analysis of DNA, far outnumber those investigating the genetic basis of local adaptation.

While 'common garden experiments' have frequently been employed to identify local adaptation in freshwater species, similar studies of marine fishes have only recently become prominent. Studies of marine species distributed across steep ecological gradients, such as the east coast of North America, have proven especially useful for revealing the geography of adaptive divergence.

A surprising discovery has been the prevalence of a highly cryptic form of genetic divergence known as countergradient variation (CnGV). CnGV occurs when the genetic influences on a plastic, phenotypic trait are distributed in nature such that they counteract environmental influences across an ecological gradient (Levins, 1968; Conover & Schultz, 1995). In nature, CnGV generates phenotypic similarity, in some cases so much so that specimens from the wild may appear identical. Hence, the underlying genetic variation is hidden. If plasticity

can be accounted for by measuring environmental differences among sites, then evidence of CnGV can be derived from field comparisons. Only from 'common garden' or reciprocal transplant experiments, however, can the genetic basis of CnGV be confirmed. Over the past decade, evidence of CnGV has been published for 26 fish species, about half of which are based on 'common garden experiments' (Table I). Most of these involve physiological traits that are compensatory in nature, such as genotypes with elevated growth rates being found in environments where the growing season is short (Conover & Present, 1990) or genotypes that are especially efficient at extracting carotenoid pigments, being found in environments that lack such substances (Craig & Foote, 2001). CnGV has also been identified with respect to body shape (Marcil *et al.*, 2006) and reproductive output (Klahre, 1998; Kokita, 2003). Beyond fishes, CnGV is common in numerous other poikilotherms including insects (Levins, 1968; Arnett & Gotelli, 1999), gastropods (Pardo & Johnson, 2005), amphibians (Berven, 1982), reptiles (Ferguson & Talent, 1993), a malacostracan (Vernberg & Costlow, 1966) and has been suggested in schyphozoans (Dawson & Martin, 2001). Although CnGV is not universal (Malloy & Targett, 1994; Lahti *et al.*, 2001; Lankford & Targett, 2001; Larsson *et al.*, 2005), its commonality attests to the broad significance of this form of adaptive divergence.

Cogradient variation (CoGV), where genetic and environmental influences work in harmony to accentuate phenotypic differences, has been identified less often than CnGV. Most examples involve skeletal morphology (Parsons, 1997; Trussell, 2000). In the Atlantic silverside *Menidia menidia* (L.), for example, genotypes with increased number of vertebrae are found in low temperature environments that induce more vertebrae (Billerbeck *et al.*, 1997).

Another common form of adaptive variation involves genotype \times environment interaction in which each genotype performs best under conditions common to its geographic origin. A classic example of such divergence in fishes occurs in the mummichog *Fundulus heteroclitus* (L.) (Powers & Schulte, 1998). At low temperatures, northern, cold-adapted genotypes of this species display higher swimming endurance than southern, warm-adapted forms, but not at high temperatures. Variation in swimming performance is tightly correlated with variation in allozymes of lactate dehydrogenase, thus confirming its genetic basis.

Several common misconceptions about the nature of local adaptation need to be clarified. First, is the notion that traits with high plasticity, such as physiological rates, are unlikely to display local adaptation. This derives from the expectation that high plasticity must be associated with low heritability and *vice versa*. Plasticity, the norm of reaction for a trait to an environmental factor, however, can be and often is heritable. Plasticity is not by itself a constraint on adaptive trait variation. Second, is the idea that local adaptation is necessarily a property of a population. This belief stems from the notion that population structure and adaptive genetic variation are both homogenized by gene flow, such that the spatial structure of the former should mirror the latter. Selection, however, can overcome moderate or even high levels of gene flow. This means genetic divergence can occur across environmental gradients even within populations. In silversides *Menidia* spp., for example, a genetic cline in vertebral number varies smoothly with latitude across the entire range of

TABLE I. Studies showing evidence of countergradient variation in fishes. Evidence resulting from 'common garden experiments' is indicated. All others are evidenced by field data only

Scientific name	Common name	Trait	Evidence from 'common garden experiments'
<i>Acanthurus bahianus</i> ¹	Ocean surgeonfish	Growth	
<i>Acipenser fulvescens</i> ²	Lake sturgeon	Growth	
<i>Alosa sapidissima</i> ³	American shad	Growth	
<i>Anchoa mitchilli</i> ⁴	Bay anchovy	Growth	
<i>Aplodinotus grunniens</i> ⁵	Freshwater drum	Growth	
<i>Carpiodes carpio</i> ⁵	River carpsucker	Growth	
<i>Catostomus commersoni</i> ⁶	White sucker	Embryonic development	
<i>Fundulus heteroclitus</i> ^{7,8}	Mummichog	Growth, embryo development	x
<i>Gadus morhua</i> ⁹⁻¹²	Atlantic cod	Growth, condition factor, energy allocation, feeding success	x
		Food conversion efficiency, body shape, maturation	x
<i>Gasterosteus aculeatus</i> ¹³	Three-spined stickleback	Growth	x
<i>Hippoglossus hippoglossus</i> ¹⁴	Atlantic halibut	Growth, food conversion efficiency, protein utilization	x
<i>Lepomis gibbosus</i> ¹⁵	Pumpkinseed	Growth	x
<i>Lepomis macrochirus</i> ¹⁶	Bluegill	Growth	
<i>Leuciscus leuciscus</i> ¹⁷	Dace	Growth	
<i>Macrhybopsis meeki</i> ⁵	Sicklefin chub	Growth	
<i>Menidia menidia</i> ¹⁸⁻²¹	Atlantic silverside	Growth, consumption, food conversion efficiency, lipid storage capacity, reproductive output	x
<i>Menidia peninsulae</i> ²²	Tidewater silverside	Growth	x
<i>Micropterus salmoides</i> ^{18,23}	Largemouth bass	Growth	x
<i>Morone saxatilis</i> ^{24,25}	Striped bass	Growth	x
<i>Notropis atherinoides</i> ^{5,26}	Emerald shiner	Growth	
<i>Oncorhynchus nerka</i> ^{27,28}	Sockeye salmon	Growth, sexual colouration	x
<i>Poecilia reticulata</i> ²⁹	Trinidad guppy	Sexual colouration	x

TABLE I. Continued

Scientific name	Common name	Trait	Evidence from 'common garden experiments'
<i>Pomacentrus coelestis</i> ³⁰	Damselfish	Egg size, clutch size, clutch mass	x
<i>Salmo salar</i> ^{31–33}	Atlantic salmon	Growth, digestion rate, energy intake, growth efficiency	x
<i>Scophthalmus maximus</i> ^{34–36}	Turbot	Growth, food conversion efficiency, food intake, RNA:DNA ratios	x
<i>Sphyrna tiburo</i> ³⁷	Bonnethead shark	Growth	

¹Robertson *et al.*, 2005; ²Power & McKinley, 1997; ³Conover, 1990; ⁴Lapolla, 2001; ⁵Braaten & Guy, 2002; ⁶Hamel *et al.*, 1997; ⁷Schultz *et al.*, 1996; ⁸DiMichele & Westerman, 1997; ⁹Salvanes *et al.*, 2004; ¹⁰Purchase & Brown, 2000; ¹¹Marcil *et al.*, 2006; ¹²Olsen *et al.*, 2005; ¹³Wright *et al.*, 2004; ¹⁴Jonassen *et al.*, 2000; ¹⁵Arendt & Wilson, 1999; ¹⁶Garvey *et al.*, 2003; ¹⁷LobonCervia *et al.*, 1996; ¹⁸Conover & Present, 1990; ¹⁹Billerbeck *et al.*, 2000; ²⁰Schultz & Conover, 1997; ²¹Klahre, 1998; ²²Yamahira & Conover, 2002; ²³Philipp & Whitt, 1991; ²⁴Conover *et al.*, 1997; ²⁵Brown *et al.*, 1998; ²⁶Pegg & Pierce, 2001; ²⁷Edmundson & Mazumder, 2001; ²⁸Craig & Foote, 2001; ²⁹Grether *et al.*, 2005; ³⁰Kokita, 2003; ³¹Nicieza *et al.*, 1994a; ³²Nicieza *et al.*, 1994b; ³³Finstad *et al.*, 2004; ³⁴Imslan *et al.*, 2000; ³⁵Imslan *et al.*, 2001b; ³⁶Imslan *et al.*, 2001c; ³⁷Lombardi-Carlson *et al.*, 2003.

two contiguous species (Yamahira *et al.*, in press). Hence, the interplay between gene flow and adaptive divergence is crucial to the question of whether or not the spatial scales of population structure and local adaptation are similar.

THE INTERPLAY BETWEEN LOCAL ADAPTATION AND GENE FLOW

Many marine species exist as large populations across variable environments that lack obvious physical barriers. In such species, genetic drift is not likely to confound adaptive divergence and, assuming that genetic variation is sufficient to allow evolution, the degree of local adaptation will be determined primarily by the interplay between gene flow and the selection differential among environments (Slatkin, 1973; Felsenstein, 1976; Endler, 1977). The level of gene flow necessary to constrain evolution in the wild has been the subject of debate for over five decades. Mayr (1963) argued that gene flow is a homogenizing force that can negate the effects of selection and, consequently, limit the extent of local adaptation. Numerous empirical studies including those on freshwater fishes have supported this viewpoint (Hendry *et al.*, 2002; Saint-Laurent *et al.*, 2003; Hendry & Taylor, 2004). Erhlich & Raven (1969), on the other hand, proposed that natural selection typically overwhelms gene flow in nature and local adaptation can, therefore, exist despite high gene flow. This view purports

that gene flow in nature is much less than would be predicted from the mere absence of physical isolation. Restricted gene flow can result from biotic factors that limit dispersal such as natal homing (Thorrold *et al.*, 2001), local retention (Swearer *et al.*, 1999) or differential survival or reproductive success of migrants (Koehn *et al.*, 1980; Hendry *et al.*, 2004; Nosil *et al.*, 2005).

Populations connected by high gene flow may nonetheless exhibit genetic differentiation if subject to strong divergent selection (Schneider *et al.*, 1999; Saint-Laurent *et al.*, 2003). This occurs if ongoing selection is strong enough to continually sort out inferior immigrant genotypes. Koehn *et al.* (1980) demonstrated that in the marine bivalve, *Mytilus edulis*, a geographic cline in the *Lap* locus exists across a salinity gradient over a distance of only 32 km. Despite broad-scale larval dispersal annually, the cline is maintained entirely by differential juvenile mortality in response to salinity. Hence, adaptive divergence persists despite high gene flow.

Studies of clinal variation across ecological gradients, like that of Koehn *et al.* (1980), are an especially useful method for examining the relationship between adaptation and gene flow (Slatkin, 1973; Lenormand, 2002). Consider marine species distributed along the east coast of North America, one of the world's steepest latitudinal gradients in temperature. Three plausible geographic patterns of adaptive genetic variation can be imagined. The first would be smooth clinal variation that could result either from gradual shifts in the environment that vary without discontinuity across the gradient (*e.g.* photoperiod) or from the homogenizing effect of gene flow among nearest neighbours as in a stepping stone pattern [Fig. 1(a)]. In *M. menidia*, for example, vertebral number is a genetically determined trait that varies gradually with latitude (Billerbeck *et al.*, 1997; Yamahira *et al.*, in press). A second possibility is a staircase pattern in which areas of little or no change in phenotype are separated by areas of rapid change that correspond with discontinuities in the environment such as at Cape Hatteras or Cape Cod [Fig. 1(b)]. Such discontinuities represent transition zones that may be associated with rapid changes in phenotype due to reduced gene flow, a steep gradient in selection, or both. *Fundulus heteroclitus* displays this sort of steep transition in the vicinity of New Jersey (Powers & Schulte, 1998). A third possible phenotypic pattern is the diminished phenotypic correlation with latitude at the tips of the distribution [Fig. 1(c)]. This pattern could result if peripheral populations frequently go extinct or experience bottlenecks and are re-established from the centre distribution. Such unidirectional gene flow could limit local adaptation at the extremes of a species' range (Kirkpatrick & Barton, 1997).

While there have been many recent studies demonstrating the existence of local adaptation in marine fishes, none of these have been conducted with sufficient detail to clearly identify either the spatial scale or the influence of gene flow upon local adaptation. As far as is known, the smallest spatial scale over which adaptive divergence has been confirmed is *c.* 60 km, involving variation in growth of juvenile turbot *Scophthalmus maximus* (L.) off Norway (Imsland *et al.*, 2001a). In work on the Atlantic silverside, Conover & Present (1990) and Billerbeck *et al.* (1997) compared trait variation along the east coast at intervals of *c.* 300–400 km, but the strong rank correlations with latitude at this scale suggested that the adaptive variation was finer than the sampling.

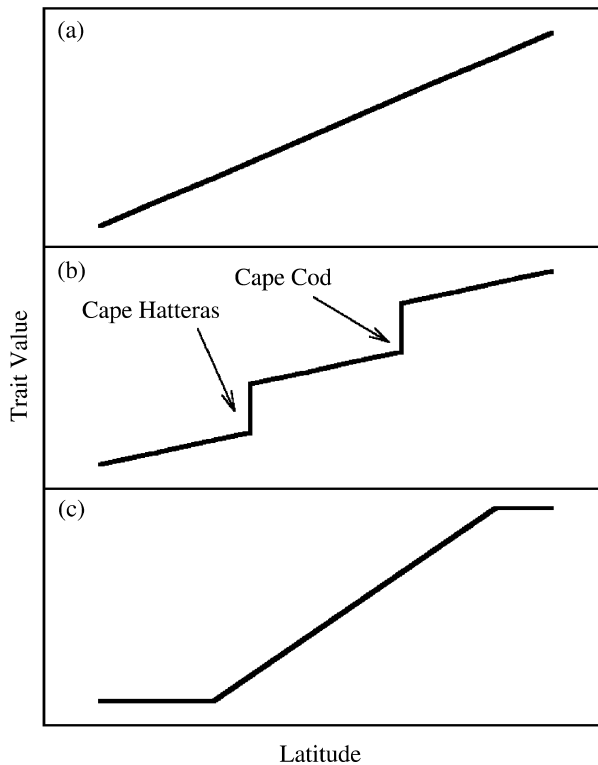


FIG. 1. Three plausible geographic patterns of adaptive genetic variation in trait value along the east coast of North America: (a) smooth clinal variation, (b) staircase pattern such as at Cape Hatteras and Cape Cod and (c) diminished phenotypic correlation with latitude at the tips of the distribution.

To define the spatial scale of adaptive variation, the sampling distance at which the correlation with environmental change becomes non-significant must be determined. Of course, the spatial scale of local adaptation probably varies throughout the range of a species (*e.g.* as in Fig. 1) so it may take a very large number of ‘common garden experiments’ to completely map the geography of adaptive genetic variation.

To reveal the interplay with local adaptation, direct measures of gene flow must be coupled with ‘common garden experiments’. Hendry *et al.* (2002) combined ‘common garden experiments’ with molecular genetic analyses to examine the interplay between gene flow and adaptive divergence in three populations of three-spined stickleback *Gasterosteus aculeatus* L. residing parapatrically in a lake, an inlet stream to the lake and an outlet stream from the lake. Stream fish had fewer gill rakers and greater body depth than lake fish and the differences were genetic. Performance trials suggested that each had higher fitness in its native habitat. There was, however, a negative correlation between gene flow and morphological divergence: outlet fish were less divergent from lake forms than were inlet fish because of a downstream bias in gene flow. Hence, while differential selection in stream *v.* lake habitats promoted adaptive divergence, the magnitude of divergence was constrained by gene flow. Moreover,

there was a gradual shift in morphological divergence from the lake to the outlet, but an abrupt shift from the lake to the inlet as would be expected from asymmetry in gene flow (Moore & Hendry, 2005). The three-spined stickleback populations in these studies were <1 km apart. Other lake-stream population pairs displayed similar patterns (Hendry & Taylor, 2004). Although the three-spined stickleback does not have a dispersive larval stage, the lesson is that the spatial scale of adaptive divergence can be very small even in the presence of gene flow. Similarly, Saint-Laurent *et al.* (2003) described evidence of adaptive divergence despite high gene flow in sympatric populations of rainbow smelt *Osmerus mordax* (Mitchill).

Few studies investigate the interplay between adaptive genetic variation and gene flow in marine environments. In the northern acorn barnacle *Semibalanus balanoides* populations occupying estuaries with lower flushing times, thus promoting less larval dispersal and less gene flow, were better adapted to local thermal stresses than their counterparts in estuaries with greater flushing times (Bertness & Gaines, 1993). In the tropical sea anemone, *Condylactis gigantean*, adaptive genetic differentiation exists among colour morphs inhabiting different reef habitats only 5 km apart despite the potential for high gene flow (Stoletzki & Schierwater, 2005).

COMPARING NEUTRAL (F_{ST}) AND QUANTITATIVE (Q_{ST}) GENETIC VARIATION

Molecular genetic surveys typically focus on markers presumed to be neutral to selection. Such studies determine the proportion of total genetic variation that occurs among populations (F_{ST}) and they provide estimates of genetic diversity. Only a small amount of gene flow is necessary to homogenize genetic variation that is neutral to selection (Vucetich & Waite, 2000; Palumbi, 2003), especially among large marine populations where differentiation due to drift is relatively low (Allendorf & Phelps, 1981). Hence, significant differences in F_{ST} among localities strongly indicate the existence of distinct populations. Comparisons of F_{ST} across numerous sites enable the geography of gene flow or 'connectivity' to be mapped for a given species. It is important, however, to understand the time scale for such differentiation. High values of F_{ST} are an unambiguous indication of the lack of gene flow over many generations up to the present. Very low or statistically non-significant values of F_{ST} , in contrast, may provide little about the recent history or present levels of gene flow. Low F_{ST} could mean: 1) ongoing panmixia among locations, 2) distinct lineages exist but have diverged too recently to be detected despite no current gene flow or 3) just enough gene flow exists to homogenize neutral markers despite extremely limited exchange of individuals on average among sites (*e.g.* an occasional long-distance dispersal event). Moreover, when F_{ST} is very small, the error on estimates of gene flow is very high and unreliable (Waples, 1998; Palumbi, 2003).

Q_{ST} is an analogous measurement for quantitative traits. It represents the proportion of quantitative genetic variation occurring among populations. Q_{ST} is calculated not from phenotypic variance directly (which includes environmental influences) but from the genetic components of phenotypic variance.

In practice, the among and within population components of phenotypic variance are measured in 'common garden experiments' where the environmental variance is standardized. Even in a constant environment, the within population phenotypic variance contains an environmental component that must be accounted for by comparing variance within and among families. Hence, a common experimental design would be a nested ANOVA with individuals, nested within families, nested within populations. The number of families that must be reared to reliably estimate the components of variance for just two populations makes this an extremely daunting task.

If a quantitative trait is neutral to selection, Q_{ST} will be equal to F_{ST} (McKay & Latta, 2002). Thus, a comparison of Q_{ST} to F_{ST} for a species with any given population structure is a test for selection on a given trait. When two populations display adaptive divergence for a given trait in response to directional selection, $Q_{ST} > F_{ST}$ is expected. Conversely, spatially uniform stabilizing selection on a given trait will result in $Q_{ST} < F_{ST}$.

Measuring F_{ST} among numerous locations so as to map the 'phylogeography' of a given species is relatively easy. It requires only that animals be collected at appropriate life stages and locations (e.g. spawning sites) and analysed for genetic markers by a variety of routine methods. To do the same for Q_{ST} is not only more laborious it is also fraught with potential failure due to the difficulty of rearing the egg and larval stages of most fish species. It would be a huge advantage, therefore, if F_{ST} and Q_{ST} were nearly equal in most species so that only the former needs to be measured. Equality would prevail if quantitative genetic variation is neutral to selection or if adaptive genetic variation is so weak that it is easily overwhelmed by gene flow. Unfortunately, not only are F_{ST} and Q_{ST} almost never equal, they are not even correlated. Recent meta-analyses show that Q_{ST} is almost always larger than F_{ST} and in some species the disparity is dramatic (Merilä & Crnokrak, 2001; McKay & Latta, 2002). Hence, it appears that quantitative genetic variation displays much more spatial variation than neutral genetic variation. This indicates that quantitative genetic variation is subject to divergent selection and that gene flow is generally insufficient to preclude local adaptation.

What about those cases where gene flow is very high? The primary concern in this paper is with marine species with highly vagile and dispersive life stages that generally have very low values of F_{ST} . Luttikhuisen *et al.* (2003) is the only study known that compares Q_{ST} to F_{ST} in a marine species with high dispersal. They found high Q_{ST} (0.4) for a bivalve, despite very low F_{ST} (0.02). Compared with non-marine species that have low F_{ST} , however, this result is not unusual. Of the 47 published Q_{ST} and F_{ST} comparisons reviewed, 14 involved $F_{ST} < 0.03$. Across those 14 studies, Q_{ST} was on average 10 times higher than F_{ST} (mean $Q_{ST} = 0.34$, range 0.01–0.8). Given the overall lack of correlation between Q_{ST} and F_{ST} (McKay & Latta, 2002), there is little reason to expect that local adaptation is any less likely to be found in marine species with high dispersal than in other species.

Only four studies compare Q_{ST} and F_{ST} in fishes. Among introduced populations of grayling *Thymallus thymallus* (L.), Koskinen *et al.* (2002) found that Q_{ST} for a variety of life-history traits was up to 4.5 times higher than F_{ST} (Table II). This study is particularly noteworthy in that divergence occurred

TABLE II. Comparative studies of divergence in neutral marker genes (F_{ST}) and quantitative traits (Q_{ST}) from published data for fish species

Scientific name	Common name	Mean Q_{ST}	Number of traits compared	Mean F_{ST}	Comparison
<i>Coregonus clupeaformis</i> ¹	Lake whitefish	0.58	5	0.24	Ecotype (dwarf/normal)
<i>Coregonus lavaretus</i> ²	European whitefish	0.02	20	<0.005	Morph (deep/deep)
		0.10	20	0.15	Morph (bay/bay)
		0.13	20	0.01	Morph (river/river)
		0.08	20	<0.005	Morph (shallow/shallow)
		0.11	20	0.02	Morph (shallow/deep)
		0.26	20	0.13	Morph (shallow/bay)
		0.32	20	0.13	Morph (deep/bay)
		0.25	20	0.13	Morph (deep/river)
		0.17	20	0.13	Morph (shallow/river)
		0.19	20	0.13	Morph (river/bay)
<i>Osmerus mordax</i> ³	Rainbow smelt	0.62	5	0.02	Ecotype (dwarf/normal)
		0.45	5	0.01	Ecotype (dwarf/dwarf)
		0.01	5	0.03	Ecotype (normal/normal)
<i>Thymallus thymallus</i> ⁴	Grayling	0.54	7	0.12	Lake population (lake 1/lake 2)
		0.23	7	0.10	Lake population (lake 1/lake 3)
		0.32	7	0.10	Lake population (lake 2/lake 3)

¹Rogers *et al.*, 2002; ²Østbye *et al.*, 2004; ³Saint-Laurent *et al.*, 2003; ⁴Koskinen *et al.*, 2002.

in only 80–120 years despite the potential constraints imposed by genetic drift due to small founding population sizes and evidence of severe bottlenecks. Saint-Laurent *et al.* (2003) compared population variation within and among pairs of dwarf and normal rainbow smelt ecotypes. Among ecotypes they found that Q_{ST} was 31 times higher than F_{ST} (Table II), despite synchronous use of the same spawning habitats. Two genetically distinct populations occurred within each ecotype, and Q_{ST} was 45 times higher than F_{ST} within the dwarf form but not the other (Table II). Østbye *et al.* (2004) studied four distinct sympatric morphs of the European whitefish *Coregonus lavaretus* (L.)

that spawned in different habitats (deep, shallow, river and bay). Populations within the four morphs were very similar, but among-morph variation differed depending on spawning location. Deep- and shallow-spawning fish showed strong adaptive divergence (Q_{ST} 2–13 times higher than F_{ST} ; Table II) in traits that influence foraging ability such as the size of gill rakers. For some traits, Q_{ST} was less than F_{ST} suggesting the existence of stabilizing selection. Among dwarf, normal and hybrid ecotypes of the lake whitefish *Coregonus clupeaformis* (Mitchill), Rogers *et al.* (2002) reported that Q_{ST} averaged 2.4 times higher than F_{ST} (Table II) with respect to burst swimming and other behaviours. Collectively, the above studies clearly show that even when gene flow is high, it is frequently insufficient to override the effects of selection on phenotypic divergence.

The reasons for the poor correspondence between F_{ST} and Q_{ST} are probably two-fold (McKay & Latta, 2002). First, the number of migrants required to homogenize neutral genetic variation is far less than that required to overcome selection. Hence, many situations likely arise where gene flow is high enough to prevent differentiation of neutral markers but not so high as to prevent local adaptation. Only if neutral loci are tightly linked to the locus under selection will neutral alleles display geographic differentiation that corresponds with local adaptation. Second, adaptive genetic variation may diverge at rates far greater than differentiation due to drift. Genetic variation caused by drift requires about N_e generations to become established, where N_e is the effective population size. Adaptive divergence, on the other hand, occurs at a rate proportional to the product of trait heritability and selection intensity and may, in theory, require only a few generations.

If neutral markers do not reflect divergence in quantitative traits, an alternative to the 'common garden' approach would be to target genes at the molecular level that are either known to be subject to selection or are linked to quantitative trait loci (QTL). While this can be a successful approach (Powers & Schulte, 1998; Canino *et al.*, 2005), two problems limit its usefulness. First, as with phenotypic traits, each locus probably responds differently to selection so many loci undergoing selection must be compared to obtain an overall index of genetic divergence. Second, differentiation at QTLs is likely to be much less than in the traits they affect (McKay & Latta, 2002). This occurs because most traits are polygenic and therefore selection on a trait is diluted over many loci. Moreover, covariances among allelic effects can cause polygenic traits to diverge greatly despite only minor differentiation in allele frequencies at the underlying QTL.

A promising integrative approach is to link molecular genetic variation to life-history and environmental differences based on precise sampling strategies that target specific life stages or locations (Bekkevold *et al.*, 2005; Case *et al.*, 2005; Ruzzante *et al.*, 2006). Such studies provide a basis for predicting and testing where adaptive genetic variation might be found.

THE RAPIDITY OF ADAPTIVE DIVERGENCE

In the past decade, there has been increased attention on rates of 'contemporary evolution', *i.e.* heritable trait evolution occurring on time scales of <100

generations. Contemporary evolution has been reviewed recently by numerous authors (Hendry & Kinnison, 1999, 2001; Reznick & Ghalambor, 2001; Ashley *et al.*, 2003). This topic is briefly summarized with an emphasis on aquatic organisms and includes a number of more recent examples that pertain to the evolution of harvested species.

A commonly used metric for quantifying the rate of evolution is the haldane (Hendry & Kinnison, 1999). The haldane (H) is defined as $(x_2 - x_1) (\sigma_p g)^{-1}$, where x_2 and x_1 are the trait means at two points in time, σ_p is the phenotypic s.d. and g is the time interval between samples, measured in generations. Theoretical studies of sustainable rates of evolution consider the balance between the erosion of genetic variation by selection and drift and the generation of variation by mutation (Lande & Shannon, 1996) and obtain estimates on the order of 0.01–0.1 H . Kinnison & Hendry (2001) compiled a database of 2649 rate estimates representing 30 animal species based on a review of 40 source articles. The median rate overall was 5.8×10^{-3} . They found, however, that the rate of evolution tended to be most rapid in the first few generations, generally slowing over longer time intervals. The average rate was found to decrease approximately inversely with generation time, $H = 0.7 g^{-0.96}$.

Numerous traits display contemporary evolution including those involving physiology, morphology, life history, phenology and behaviour (Reznick & Ghalambor, 2001). Traits expressed primarily in males tend to evolve more rapidly than traits expressed primarily in females or in both sexes equally (Zhang & Parsch, 2005). Life-history traits seem to evolve more rapidly than other characters (Kinnison & Hendry, 2001), though this result is enigmatic. Heritability of life-history characters is approximately one half that of morphological traits (Mousseau & Roff, 1987) and linear selection gradients on life-history characters are also about half of those for other characters (Kingsolver *et al.*, 2001). Together these imply that rates of evolution for life-history characters should be about one-fourth of those for other traits. Whatever the explanation, the fact that life histories display relatively high rates of evolution is extremely important in developing sustainable conservation strategies for harvested species.

Most examples of contemporary evolution come from introductions, invasions or habitat alterations. Particularly well studied is the evolution of tolerance to anthropogenic perturbations such as insecticide tolerance, resistance to antibiotics, herbicide resistance, heavy metal tolerance and pollution tolerance (Reznick & Ghalambor, 2001). The classic example is industrial melanism (Kettlewell, 1973). More recently the focus has been on the rates of evolution of invasive species (Lee, 2002) and on natives in response to invasion (Strauss *et al.*, 2006). The salt marsh copepod *Eurytemora affinis*, for example, has invaded freshwater habitats several times (Lee, 1999), resulting in dramatic physiological shifts in salt tolerance (Lee *et al.*, 2003) in under 200 years. The initial rate of evolution was almost certainly much higher as selection experiments generated substantial shifts in tolerance within one generation (Lee, 1999).

Some of the best examples of rapid adaptive divergence come from the fish literature. All of these involve divergence following introduction from a common ancestral stock. Classic studies on Trinidadian guppies *Poecilia reticulata*

(Peters) show that growth rates, fecundities, antipredator behaviour and life span all evolve in response to changes in the risk of predation (Magurran *et al.*, 1993; Reznick & Bryga, 1996; Reznick *et al.*, 1997; O'Steen *et al.*, 2002). These life-history differences evolved in <40 generations. Koskinen *et al.* (2002) found substantial evolutionary changes in life history among introduced grayling populations in <22 generations. Hendry (2001) described adaptive divergence in embryo and adult traits among introduced populations of sockeye salmon *Oncorhynchus nerka* (Walbaum) after only 13 generations.

In many harvested populations, fishing becomes the dominant force of mortality and it is highly selective with respect to size. Hence, fisheries-induced adaptive change is to be expected, and empirical studies confirm this prediction. The classic work of Ricker (1981) attributed declines in sizes of Pacific salmon *Oncorhynchus* sp. [especially pink salmon *Oncorhynchus gorbuscha* (Walbaum)] to genetic causes. Experimental studies confirm that such genetic changes in body size and yield in response to harvest can occur rapidly (Conover & Munch, 2002). In Atlantic cod *Gadus morhua* L., maturation reaction norms, defined as the probability of maturing as a function of age and size, shift consistently towards earlier maturation at smaller fish sizes across multiple, intensively fished Atlantic cod stocks (Olsen *et al.*, 2004). These shifts are almost certainly genetic because a plastic response alone would have caused early maturation at larger, not smaller, sizes. These changes are exceedingly rapid, *i.e.* on the order of 0.6–1.5 *H*. Intensively exploited Atlantic cod from the Gulf of St Lawrence display greatly reduced size at age that persisted after a moratorium on harvest (Sinclair *et al.*, 2002). Again, this change is probably genetic rather than environmental because lower densities and higher temperatures that prevailed during this period should have caused faster rather than slower growth.

There are now many studies indicating that evolution in response to environmental change or invasion is repeatable and predictable. Evidence for repeated evolution along similar lines comes from studies of the three-spined stickleback in which highly armoured marine populations have repeatedly invaded freshwater habitats and evolved genotypes with reduced armour and smaller sizes (Bell *et al.*, 2004). Recently isolated three-spined sticklebacks from Iceland evolved significantly shorter spines and fewer armour plates in <15 years; rates of spine evolution were $H = 0.47\text{--}0.8$ and for plate number were $H = 0.16\text{--}0.19$ (Kristjansson *et al.*, 2002).

Although not the main focus, it is of interest to connect microevolutionary change to patterns of macroevolution. For instance, how fast do traits involved in reproductive isolation evolve? The answer for three-spined sticklebacks from the White Sea basin is about eight generations (Ziuganov, 1995). In sockeye salmon, Hendry (2001) reported partial reproductive isolation arising in 13 generations. Incipient speciation in guppies has been observed in populations from Venezuela (Alexander & Breden, 2004). Significant differences in male colour traits and female preferences led to reproductive isolation among local populations despite little evidence of mitochondrial DNA differentiation.

Finally, it is worth considering when rapid evolution does not occur. A number of recent studies report negligible rates of evolution (or evolution in the opposite direction from that expected) despite strong selection and sufficient

trait heritability (Merilä *et al.*, 2001). There are a number of possible explanations for these results. First, it is possible the traits in question are being prevented from evolving by genetic correlations with other, unmeasured, characters (Lande & Arnold, 1983). Second, selection may vary spatially such that evolution is prevented from occurring by gene flow from regions with opposing selection gradients. Finally, it is possible that the trait is actually evolving but goes undetected because environmental influences on the phenotype oppose the direction of evolution (*i.e.* CnGV) resulting in little or no net change.

IMPLICATIONS FOR CONSERVATION

Emerging evidence of 1) the widespread existence of local adaptation in marine organisms, 2) the frequent occurrence of adaptive divergence despite gene flow, 3) the disconnect between the magnitudes and geography of neutral and adaptive genetic variation and 4) the emerging consensus that evolution in the wild can occur on contemporary time scales has been summarized. All of these observations stem from a common underlying source, *i.e.* selection is a dynamic, ongoing force that continually structures genetic variation in the wild. The influence of selection can be detected on both historic and contemporary time scales. These findings have numerous and profound implications for conservation, particularly with respect to conservation of harvested marine species.

Fish conservation genetics as applied to wild harvested stocks (excluding hatchery and restocking operations) has focused most of its attention on identifying and designating ESUs. There are two goals in doing so. One is to designate management units for stock assessment, the rationale being that each stock may display unique demographic and dynamic properties that must be incorporated into a management plan (Waples, 1995). If one stock is overharvested, for example, will it be replenished by migrants from elsewhere? The second goal is to protect genetic diversity. The gene pool of a population may harbour genetic diversity not found elsewhere in the species. Frequently, studies of 'phylogeography' are used to identify ESUs based on the F_{ST} criterion. Sometimes phenotypic characters and studies of dispersal and migration are included in such analyses. Rarely are 'common garden experiments' used to test whether apparent phenotypic differences or similarities represent genetic divergences such as CoGV or CnGV.

While the 'phylogeographic' approach has proven highly valuable in elucidating the geographical distributions of long-established lineages and patterns of gene flow within a species, there are at least three problems with its use in an ESU context. The first is interpreting the meaning of a non-significant F_{ST} . Because neutral markers are more easily homogenized by low levels of gene flow, F_{ST} is not very sensitive to the difference between relatively low gene flow and panmixia. Yet, the difference between restricted gene flow and panmixia may be very important in structuring adaptive genetic variation or in the identification of management units for fisheries. The second problem is that recently formed lineages that reflect contemporary gene flow may not be revealed by neutral markers unless they were established by a small number of

founders. Hence, contemporary but cryptic stocks may go unnoticed. Thirdly, the lack of correspondence between neutral and quantitative genetic variation means that 'phylogeography' cannot be used to map the geography of adaptive genetic variation, which is the form of genetic diversity most important to protect. This latter problem is one, which is only now beginning to be recognized.

Under the ESU paradigm, unique populations are the primary focus of conservation. The first step is to determine if a putative group is reproductively isolated (Waples, 1991). If so, then the potential for adaptive divergence based on phenotypic or habitat characteristics is assessed. This is an approach grounded in the belief that gene flow is the dominant force structuring both neutral and adaptive genetic variation in the wild. If selection rather than gene flow is the dominant force structuring adaptive genetic variation, as the discrepancy between Q_{ST} and F_{ST} would suggest, then the primacy of reproductive isolation in designating ESUs for protection of genetic diversity must be re-examined. For heritable traits that influence fitness, the distinctiveness of a gene pool is determined by the balance between gene flow and the selection gradient. It is not possible to determine which one is more important without measuring both and, unfortunately, selection is far more difficult to measure in the wild than is gene flow.

This is not to say that the ESU concept should be abandoned. After all, it is within gene pools where the instructions for survival and reproductive success in a given habitat are stored. But the discrepancy between Q_{ST} and F_{ST} should be heeded as warning that the process of defining an ESU for purposes of protecting adaptive genetic variation is far more complicated than simply measuring gene flow or mapping connectivity.

It is also necessary to recognize that the chief threat to genetic diversity may be the changes caused by human-induced selection that sort individual genotypes according to their fitness rather than the extirpation of populations. There is an emerging literature demonstrating that the ecology of individuals frequently departs significantly from the aggregate mean for a population (Bolnick *et al.*, 2003). With respect to foraging, for example, species that appear to be highly generalized are composed of individual specialists with a far more narrow food resource niche in a given habitat than for the population as a whole (Bolnick *et al.*, 2002). Studies show that repeatable differences in individual fish behaviour and physiological performance begin in the larval stage (Fuiman & Cowan, 2003). Many such individual differences are probably heritable (Koskinen *et al.*, 2002; Walsh *et al.*, 2006) and thus are subject to evolution. Knowing that life history, physiology and behaviour are capable of evolving rapidly on contemporary time scales (see above), conservation genetics must focus much more attention on the adaptive divergence within populations and how it responds to human-induced stresses. If one of the goals of conservation is to manage genetic change in wild populations, gene flow cannot be the sole focus while ignoring the effects of selection, especially given that the latter occur rapidly and influence directly the traits that confer fitness. Some examples of applying 'selection thinking' (Charnov, 1982) in a marine conservation context follow.

A great deal of attention is now focused on identifying patterns of connectivity in marine species with dispersive larvae. Three general approaches are

being pursued. One is to use 'phylogeography' to map patterns of gene flow through pair-wise comparisons of F_{ST} . This approach shows where very limited or no migrant exchange has occurred over long-term, historical time scales. The second is to couple hydrodynamic models of ocean circulation in a given area with knowledge of larval behaviour to estimate probabilities of dispersal (known as 'dispersal kernels'; Cowen *et al.*, 2006). This approach shows how much exchange of migrants among sites might be presently happening. The third, and probably the most difficult method, is to observe the movement of tagged individuals. The tag may be either natural (*e.g.* a genetic or chemical signature unique to specific parents or sites; Thorrold *et al.*, 2001) or artificial (larvae labelled with a rare chemical; Thorrold *et al.*, 2002). None of these methods identify the geography of adaptive genetic variation, which may be expected to differ from studies of gene flow or migration as follows.

Imagine the strength of selection likely to be exerted during the pelagic larval stage of a typical coral reef fish species. Studies that couple circulation models with larval survival probabilities suggest that in many cases the vast majority of successful recruits are those retained near source populations (Cowen *et al.*, 2006). This occurs because the likelihood of successful long-distance dispersal is a product of the probabilities of larval survival and of encountering a faraway reef habitat by chance. These probabilities are each so low that, when combined, the average rate of successful long-distance recruitment is exceedingly small. Local recruitment has higher average success because it minimizes the pelagic larval duration and increases the probability of encountering a reef at the appropriate stage of development. Hence, there must be enormous selection pressure acting on any attributes of larval performance (*e.g.* depth preferences and swimming orientation) or adult spawning behaviour (*e.g.* sites and periodicity) that increase local retention. Because circulation is strongly influenced by topography, the appropriate larval and adult behaviours are likely to be unique to specific locales. Hence, local adaptive divergence in larval and adult spawning behaviour should be expected. This divergence, however, will probably be invisible with neutral genetic markers because just a few successful, long-distance migrants are sufficient to create homogeneity. In the context of defining ESUs in the ocean, or designing marine protected areas as tools for marine conservation, it is the spatial scale of local adaptation that is most crucial. The studies of Koehn *et al.* (1980) and Stoletzki & Schierwater (2005) demonstrate that steep selection gradients and adaptive divergence can occur on spatial scales far less than the distance of larval dispersal. Field studies and 'common garden experiments' that test for intraspecific variation in larval traits of fishes should be employed more frequently to pursue such questions.

Another application of 'selection thinking' concerns the temporal scale of and adaptive response to fishing mortality. Many of the marine fishes that humans like to harvest have evolved bet-hedging life histories involving delayed maturity and a long reproductive life span (Winemiller & Rose, 1992). In the absence of fishing, such life histories evolve in response to exceedingly low and highly variable survival of early life-history stages, coupled with high and relatively constant adult survival. Such species build up massive quantities of biomass in the adult age classes that become the target of fisheries. In many

cases, fishing mortality rates greatly exceed the rate of natural mortality such that fishing becomes the dominant source of selection. Hence, fishing undermines the bet-hedging life-history strategy, selecting instead for traits associated with short life cycles such as early age and small size at maturity. Examples of such changes now exist (Olsen *et al.*, 2004).

Rapid evolution in response to environmental change is now so well documented in numerous organisms (Stockwell *et al.*, 2003) that the likelihood of adaptive divergence in response to harvest or other agents of selection should no longer be in question (Coltman *et al.*, 2003). The implications of contemporary evolution are just beginning to be explored in fisheries management. One of the critical issues, for example, is what traits will change and what effects these will have on the productivity and viability of populations. Most studies of fisheries-induced evolutionary change deal with only one trait such as growth rate or body size (Conover & Munch, 2002) or age or size at maturity (Olsen *et al.*, 2004). The evolutionary response to fishing mortality, however, is likely to involve numerous traits that have genetic or phenotypic correlations. Walsh *et al.* (2006) used selection experiments to demonstrate that removal of large fishes from harvested populations over five generations caused evolution not only of reduced size and growth rate but also lower food consumption, growth efficiency, fecundity, egg size, larval size, larval survival and number of vertebrae. Even behaviour, such as willingness to forage in the presence of predators, was altered. Nearly all of these changes reduce population growth rate and therefore the capacity to rebound following overexploitation. Such effects are evident in wild stocks that have failed to rebound such as the Gulf of St Lawrence and Newfoundland Atlantic cod stocks (Sinclair *et al.*, 2002; Shelton *et al.*, 2006). How long it will take to re-establish the original characteristics of a genetically modified stock is unknown but could be many generations.

Management regimes that minimize evolutionary change and protect population productivity are possible (Law & Grey, 1989). Because of their ecological benefits, no-take marine protected areas have been touted by many as a solution to the fisheries crisis but their potential role in protecting genetic variation has been underappreciated. No-take reserves represent refuges where only natural agents of selection prevail. Building on the earlier work of Trexler & Travis (2000), Baskett *et al.* (2005) used a quantitative genetic model to demonstrate that no-take reserves can protect against fisheries-based selection for early maturation and thereby increase yield and protect against population collapse. Interestingly, their work also showed that establishing maximum size limits (large fishes must be returned to the population) can accomplish the same results and with a higher biomass yield compared to marine protected areas.

A final example illustrates the pervasive influence of selection and links adaptive divergence of a marine harvested species to human health. Bricelj *et al.* (2005) demonstrated that softshell clams *Mya arenaria* from areas exposed to 'red tide' algal blooms evolve resistance to paralytic shellfish toxins (PST) compared to those from unexposed areas. Resistance was conferred by natural mutation of a single amino acid. PST resistance increases the tissue toxicity of *M. arenaria* in exposed areas, and consumption of PST-adapted clams causes severe illness in humans. In this case, adaptive divergence in a harvested species occurs in response to harmful algal blooms probably caused by a secondary

human influence, namely eutrophication. Unfortunately, what is good for the clams (PST resistance) is bad for people (paralytic shellfish poisoning). This is yet another example, where selection and adaptation play a major role in the ecology of a marine species with dispersive larvae, with huge implications for managing the fishery and human health.

Disparity in the geography and time scales of neutral and adaptive genetic differentiation has important implications for resource conservation. It forces the question what form of genetic variation, phylogeographic or phenogeographic, is most important to protect? It underscores the need to be extremely cautious about interpreting levels of genetic differentiation based only on estimates of gene flow, especially when F_{ST} is low. It provides the reminder that selection and adaptation are dynamic processes occurring on spatial and temporal scales that respond rapidly to contemporary management decisions. It calls for the development of a Darwinian approach to fishery science.

Conservation genetics of wild fish stocks has so far been concerned primarily with ‘phylogeography’, *i.e.* identifying populations and protecting them from extinction or introgression from alien gene pools. These are highly worthwhile endeavours. A more balanced approach, however, should be taken, one that recognizes that selection and adaptation are also principal causes of genetic change. Integrated studies of gene flow and adaptive divergence in marine species are required. Adaptive genetic divergence occurs rapidly, over small spatial scales, despite gene flow, and it codes for phenotypic traits that directly influence the viability of populations. Fishery management must begin to incorporate the Darwinian effects of human impacts on wild populations if marine species are to be harvested in a sustainable fashion over evolutionary time scales that may require little more than a few generations.

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