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2 **Going against the flow: Maintenance of alongshore**
3 **variation in allele frequency in a coastal ocean.**

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Running Head: PRINGLE AND WARES: MAINTENANCE OF COASTAL CLINES

16

1 **ABSTRACT**

2 Understanding the processes that develop and maintain diversity in coastal communities is an
3 important challenge, particularly given the conservation and management needs of these
4 ecosystems. Such diversity patterns include not only species distributions and interactions, but
5 also variation in genetic diversity. Alongshore variations in allele frequency along coastal oceans
6 are controlled by interactions between physical and biological forces. Here we model these
7 interactions in terms of Lagrangian descriptors of nearshore physical oceanography, the life
8 history dynamics of an individual species, and habitat quality. This model allows us to define
9 population boundaries within the species range as a function of the ocean circulation, spatial
10 habitat variability, and larval characteristics. From this, we can find quantitative criteria for the
11 persistence of regions of alongshore genetic variation. Our results show quantitatively that the
12 existence of phylogeographic patterns in species with high dispersal capacity along uniform
13 coasts with typical mean currents is surprising, and requires either strong selection gradients,
14 alongshore variation in the ocean currents and/or habitat quality, or a mixture of both. The
15 importance of this work for marine reserve design and understanding community-wide
16 evolutionary patterns are discussed.

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1 A classic problem in the study of marine biodiversity is how patterns of genetic
2 differentiation arise in an environment with few apparent barriers to dispersal, in species with
3 high capacity for dispersal due to larval/juvenile life history, and in regions where coastal
4 currents should promote population mixing (Palumbi 1994). Most phylogeographic studies of
5 coastal species emphasize the historical changes that could have initiated allopatry and the
6 process of genetic differentiation. Little attention is generally given to the processes that then
7 must maintain spatial genetic discontinuities in these populations, except in situations where
8 physiological or other barriers are apparent (*e.g.* the Florida peninsula preventing gene flow
9 between the Gulf and Atlantic lineages; Avise 1994, Lee and O’Foighil 2004). We will
10 quantitatively examine what processes allow spatial genetic discontinuities to persist in a coastal
11 ocean for species with a planktonic dispersal stage. Some – possibly most – of these patterns
12 (including gradual clines and phylogeographic ‘breaks’; see Avise 2000) may reflect the disparity
13 between migration and gene flow caused by selection (Palumbi 1994, Barton and Hewitt 1989,
14 Sotka et al. 2003, Sanford et al. 2003, Hare et al. 2005).

15 Many phylogeography studies involve an inherent assumption that the gene flow process
16 being described is selectively neutral – that is, that the pattern is evidence of dispersal limitation
17 alone, rather than incorporating factors that limit gene flow such as selection or ecological
18 interactions (as well as stochastic factors associated with historical vicariance and the
19 genealogical data themselves; Haydon et al. 1994, Irwin 2002). Here we present a model that
20 describes the interaction between selection (defined by the relative reproductive success of
21 individuals) and physical oceanography. We find that it is unlikely that a cline can persist in
22 species with high dispersive capacity in an advective environment for an ecologically significant
23 time without selection favoring the downstream allele, where downstream is defined with respect
24 to the mean direction of larval transport.

25 We find that there are two interrelated mechanisms by which a cline or other
26 phylogeographic pattern (hereafter, any population genetic discontinuity among different

1 geographic regions will simply be referred to as a cline) can persist in the coastal ocean in the
2 face of non-random dispersal of larvae. First, a spatial gradient in selection can be sufficient to
3 allow a cline to persist (Endler 1977, Hare et al. 2005). We extend prior results by quantifying
4 the strength of the selection gradient needed to allow a cline to persist as a function of larval
5 characteristics and local oceanographic conditions. Secondly, alongshore variability in habitat
6 quality or larval transport can create a region that is recruit-limited, leading to increased local
7 reproductive success and population retention. By explicitly including spatial variability in
8 population dynamics in our model, we find that these regions can allow a cline to persist at lower
9 selection levels than in the absence of alongshore variation.

10 Our model allows earlier results of Nagylaki (1978) and others who studied systems with
11 biased directional dispersal to be applied to a coastal ocean without the *a-priori* demarcation of
12 the spatial extent of populations. Through analysis of the effect of population dynamics on the
13 retention of alleles one can discover how to define populations (demes) in such a system, identify
14 “source” and “sink” populations, and show how these populations are related to the oceanic
15 circulation that drives dispersal and alongshore variation in habitat quality. Without such a
16 quantitative description of how abiotic forces interact to maintain geographic variation in genetic
17 markers, we are left with only a static view of how allelic diversity is regulated in natural
18 communities. This model shows how the observed spatial patterns of genetic differentiation arise
19 from the interaction of the circulation of the ocean, larval dispersal, and spatial variation in
20 habitat quality.

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23 **A Model of a Benthic Species with Planktonic Dispersal.**

24 The theoretical results derived below are obtained for an idealized model of a coastal
25 benthic organism with a planktonic larval stage. The retention of a population of this idealized
26 species in the presence of mean and variable alongshore flows has been described in Byers and

1 Pringle (2006; hereafter BP). In this section we describe this organism, and a simple numerical
2 model that describes its dispersal and population dynamics. Each adult produces N_{larvae} offspring
3 per lifetime that can recruit and grow to reproductively competent adulthood, if there is sufficient
4 empty habitat for the larvae to settle in (it is important to note that N_{larvae} does not include density
5 dependent mortality effects caused by habitat scarcity at settlement, but incorporates mortality in
6 the larval pool, and mortality after settlement but before reproductive competency). The organism
7 is assumed to live in a coastal habitat narrow enough that its larvae can spread across the cross-
8 shelf dimension of the habitat in a single generation, so that the habitat can be treated as one-
9 dimensional. The habitat has a carrying capacity of H_{dens} adults per meter. These and all other
10 parameters are defined in Table 1.

11 Each larva is dispersed a variable distance downstream from its parent. The mean
12 dispersal distance is L_{adv} , and the standard deviation of the dispersal distance is L_{diff} (see Figure
13 1). For simple circulation and behavioral regimes, L_{adv} is the distance the larvae are advected by
14 the mean currents and L_{diff} is the distance eddies and stochastic current fluctuations would diffuse
15 the larvae. BP quantifies these transport parameters as a function of larval behavior, inter- and
16 intra-seasonal current variability, and the interaction of current variability and multiple spawning
17 events. BP describes how these parameters may be estimated in regions of complex, spatial
18 varying coastal circulation. In order to draw order-of-magnitude conclusions for typical
19 organisms, we present from BP a simple estimate of L_{adv} and L_{diff} for an organism with simple
20 larval behavior in an ocean whose circulation statistics vary little over the dispersal distance of a
21 larva. Following Siegel *et al.* (2003), it can be shown that larvae that remain in the plankton for
22 a time T_m will move on average a distance

$$23 \qquad L_{adv} = UT_m, \qquad (1)$$

24 where U is the alongshore flow averaged over the time the larvae are in the plankton. Not all
25 plankton will move the same distance, however, due to the random fluctuations in the currents
26 associated with eddies, fluctuating wind driven currents, and other sources of temporal variability

1 in the ocean currents. These fluctuations lead to spread in larval settlement locations, and the
2 standard deviation of the larval settlement position will be, from Siegel *et al.* (2003),

$$3 \quad L_{diff} = (\sigma^2 \tau_L T_m)^{0.5}, \quad (2)$$

4 where σ is the standard deviation of the alongshore currents, and τ_L is the Lagrangian timescale
5 of the fluctuations of the mean alongshore currents, all defined at the depth or depths that the
6 larvae reside. U , σ , and τ_L are well-characterized properties of the coastal ocean, given an
7 understanding of the vertical distribution of the larvae. Siegel *et al.* find that these simple
8 estimates perform well in Central California. A comparison of dispersal distance of many species
9 by Shanks *et al.* (2003) has found that (1) overestimates dispersal distance for many species.
10 However, the linear relation between time in plankton and dispersal distance found in (1) remains
11 valid in this comparison. *All* of the parameters described above are a function of the location of
12 the parents. This perspective is analogous to a Lagrangian reference frame in fluid dynamics (see
13 Siegel *et al.* 2003), and must be kept firmly in mind when interpreting the results presented
14 below.

15 Some of the individuals in the population carry allele(s) that give the individual a fitness
16 advantage over other individuals. This is quantified with a selection coefficient s against all other
17 alleles in the population, as in Hartl and Clark (2000). The models below will be for alleles in
18 haploid organisms, or alleles at mitochondrial loci. They will also apply to alleles in the nuclear
19 (diploid) genome as well, if the selective advantage is additive, but the derivations below would
20 have to be altered in the case of overdominance or higher-order gene interactions. In the
21 comparison to observed clines presented below, it must be remembered that the required selection
22 is not necessarily imposed on the genetic markers that actually identify the cline; the individual,
23 not the gene, could be in this case the unit of selection (for a discussion of this, and its
24 implications for the retention of other novel diversity, see Barton and Hewitt 1989).

25 In order to illustrate and confirm some of the results below, it is useful to have an
26 individual-based numerical model of this idealized organism. The computer model is a

1 straightforward implementation of the organism described above. The habitat in the computer is a
2 one-dimensional array of settlement sites each of which can hold one adult, and each adult
3 produces N_{larvae} propagules that move away from the parent as described above. The larval
4 dispersal kernel used is Gaussian. However, the results below are not sensitive to this under
5 typical circumstances, as described in BP. If the larvae land on a site inhabited by an adult, they
6 die. If several larvae arrive at the same site at the same time, one is randomly chosen as a
7 survivor, with a weighting appropriate for selection, which results in a logistic density
8 dependence. Thus in the numerical model selection enters through competition, a form of soft
9 selection (*sensu* Wallace 1975), though the theory discussed below is developed for both soft and
10 hard selection mechanisms. The code for the model is in MATLAB and FORTRAN, and is
11 available from the authors.

12

13 **The Ephemeral Nature of a Cline between Neutral Alleles in a Uniform** 14 **Advective Environment.**

15 To understand how a gradient in allele frequency can be maintained against a mean
16 current in an organism such as described above, we will first examine the behavior of such a
17 gradient between two neutral alleles in a spatially uniform coastal ocean with a spatially uniform
18 habitat. To do so, a population of the idealized organism described above is separated into two
19 groups that differ only by a selectively neutral “marker” allele, with one allele (or allele class)
20 found in one portion of the habitat, and the other allele predominant in the remaining
21 “downstream” portion of habitat (Figure 2). The population density of the entire domain is at its
22 carrying capacity. The progeny of an offspring inherit the allele from their parent.

23 Individuals with either allele have the same dispersal characteristics, with their larvae
24 moving on average L_{adv} downstream with a standard deviation of L_{diff} . In figure 2, the temporal
25 evolution of this cline is shown. While both allelic populations move downstream, the upstream

1 allele (maintained under the same conditions that maintain the population along the coast, see BP)
2 rapidly displaces the downstream allele, and the downstream allele is lost from the population.

3 The cline moves downstream because, in this region with a saturated habitat, each adult
4 leaves on average only one offspring to replace an adult that has just died. This propagule is on
5 average L_{adv} downstream from the adult, and so the cline moves on average a distance L_{adv}
6 downstream over a single lifetime. For organisms with relatively long planktonic larval stages
7 (T_m on the order of many days or weeks), mean dispersal distances are often tens to hundreds of
8 kilometers per generation (Strathmann 1985, Kinlan and Gaines 2003, Shanks et al. 2003). For
9 such organisms, a cline between two neutral alleles in a spatially uniform domain would sweep
10 through a typical species' geographic range in a few tens to hundreds of generations. For most
11 species, this is a short time compared to either the time it takes to generate a cline through
12 isolation by distance and random genetic drift, or the time since Pleistocene glaciation – a
13 commonly proposed cause of historical allopatry.

14 However, the downstream alleles in figure 2 could persist in the domain if the adults
15 carrying these alleles produced, on average, enough surviving offspring. If this occurred, the
16 stochastic component of larval dispersal could return sufficient offspring to the location of their
17 parents to maintain the downstream allele in the domain. In the next sections, we discuss how the
18 individuals with the downstream allele might be able to produce more than one surviving
19 offspring, and define explicit criteria for the persistence of the downstream alleles in the domain.

20

21 **When Can an Allele be Retained in a Region?**

22 To understand the persistence of a cline in gene frequency along a coastal ocean, it is first
23 necessary to understand when an allele introduced into the center of a uniform coastal habitat
24 with a mean alongshore current will persist. This ocean has alongshore uniform hydrodynamics
25 and habitat, and thus L_{adv} , L_{diff} , H_{dens} , and N_{larvae} remain constant along the coast. Individuals

1 carrying the allele are introduced into the habitat at a density much less than the maximum
2 population density that could persist in the habitat, but in large enough numbers that the allele is
3 unlikely to be lost through stochastic fluctuations in gene frequency.

4 To understand the persistence of the introduced allele, we use a result from BP for the
5 persistence of a population. BP find that the descendants of an individual of a species introduced
6 into an empty habitat – regardless of allelic composition – will persist and be retained in that area,
7 and will grow to populate that area, if

$$8 \quad \ln(N_{larvae}) > L^2_{adv}/(2L^2_{diff}) \quad (3)$$

9 Eq. (3) is valid as long as the domain into which the species is introduced is much larger than L_{diff}
10 and L_{adv} , and if the dispersal kernel is neither leptokurtic (which would make it easier for the
11 introduced species to persist), nor of a finite extent not significantly greater than L_{adv} (BP).

12 When (3) and these criteria are met, enough larvae are returned to the location of the parents by
13 the stochastic component of larval dispersal (L_{diff}) to replace adult mortality, despite the
14 downstream transport of most larvae by the mean currents (L_{adv}).

15 The dynamics of the retention of a small number of alleles introduced into a population in
16 which they are initially scarce are identical but for one change, for the underlying question is
17 similar: when can the descendents of an allele introduced into a region persist in that region,
18 despite the tendency of the mean currents to transport most copies of the allele downstream?
19 The only change is that the relevant growth parameter is not the number of offspring an adult
20 would leave behind in a region in which the species is scarce (N_{larvae}), but is instead N_{allele} , the
21 number of copies of the allele carried by surviving – and successfully recruiting – offspring for
22 each copy present a lifetime earlier when the allele is scarce. Thus, the criterion for the retention
23 of the allele introduced into a population is

$$24 \quad \ln(N_{allele}) > L^2_{adv}/(2L^2_{diff}) \quad (4)$$

25 (this criterion will be explicitly tested in a numerical model below). When this criterion is met,
26 enough copies of an allele successfully recruit to the location of the introduction by the stochastic

1 component of larval transport that the population of the allele is maintained there, and indeed the
2 distribution of the allele would tend to extend upstream (BP), despite the transport of the average
3 larvae downstream. This can be seen in the bottom panel of figure 3, in which the introduced
4 allele grows in frequency at and upstream of the location of introduction. If the criterion is not
5 met, the total number of copies of the allele in the population would still tend to increase, but this
6 increase would be insufficient to maintain the allele frequency at the point of introduction. Thus
7 the density of the allele at the point of introduction would decay to zero, the mean location of the
8 introduced alleles would drift downstream, and eventually all copies of the allele would be lost
9 off the downstream edge of the domain. This is seen in the top panel of figure 3 and in figure 2.

10 The criterion above explains only how an allele introduced into the middle of a coastal
11 ocean could persist. It neither explains how the growth in the number of copies of allele, N_{allele} ,
12 could come about, nor does it explain how, if (4) is met, the downstream allele in a cline does not
13 spread upstream and homogenize gene frequency in the upstream direction. In the following
14 section, we focus on the dynamics of an allele in a population that is at the carrying capacity of
15 the environment everywhere. In this case, selection alone can increase N_{allele} and a spatial
16 gradient in selection is needed to allow a cline to persist but not spread upstream. In the
17 subsequent section, we examine the population dynamics of a region of alongshore variability in
18 habitat or circulation and find a different mechanism for the persistence of a cline.

19

20 **What Selection is Needed to Allow a Cline to Persist in a Uniform**

21 **Advective Environment?**

22 Gradients in selection have often been invoked to explain the persistence of clines in systems
23 with extensive gene flow (Endler 1977, Hare et al. 2005, and many others). However, we will
24 show below that in the presence of non-random components of larval dispersal and uniform
25 habitat, there is a minimum level of selection needed to allow a cline to persist. To do so, we

1 examine the model of a benthic organism given above in the limit that the habitat's carrying
 2 capacity is alongshore uniform, and the species has been present for long enough that its
 3 population has reached the carry capacity. In this limit, we quantify the minimum level of
 4 selection needed to allow an allele to persist, and find that it depends sensitively on the mean
 5 (L_{adv}) and stochastic (L_{diff}) components of larval dispersal distance. In order to do so, the increase
 6 in the number of copies of an allele that is rare in the population per existing copy of the allele per
 7 lifetime – the N_{allele} given above – will be calculated as a function of the selection coefficient s
 8 (see Hartl and Clark 2000) against all other alleles in a population in which the population is
 9 habitat limited everywhere. It will then be shown with a numerical model that when there is
 10 selection for an allele sufficient to satisfy the criterion (4) in and only in a downstream portion of
 11 a coastal ocean, a cline in allele frequency can persist in the coastal ocean.

12 In order to calculate N_{allele} from the selection s , we assume that the population in the
 13 habitat is limited by the scarcity of habitat, but the model could be easily extended to some other
 14 density dependent process. We also assume the allele of interest is scarce in the population, for
 15 as discussed above and in BP, this is the limit of interest for retention. N_{allele} can be written

$$16 \quad N_{allele} = (\text{Larvae per adult per lifetime}) * (\text{success in competition with other larvae}) * (\text{fraction} \\ 17 \quad \text{habitat free}) \quad (5)$$

18 “Larvae per adult per lifetime” is defined above as N_{larvae} , and is net of mortality in the larval pool
 19 and after settlement and before reproductive competency. N_{larvae} is defined for an adult that
 20 carries the allele with less selective advantage. The “fraction of habitat free” accounts for the
 21 fact that in this simple model, larvae that try to settle where there is an adult will die. The
 22 fraction of habitat free is represented by the parameter γ . If the larvae were to have sufficient
 23 behavior to avoid habitat occupied by adults and to seek out nearby available habitat, γ would be
 24 1.

25 The remaining term of (5) captures the relative reproductive success of adults with the
 26 allele of interest, and is where selection enters the equation. It can represent either soft or hard

1 selection mechanisms. The coefficient s is the selection coefficient against other alleles, and is
 2 defined so that if an adult that does not carry the allele of interest produces X larvae that would
 3 successfully recruit, an adult that does carry the allele of interest produces $X/(1-s)$ larvae that
 4 successfully recruit. This term can represent an ability to out compete other larvae for habitat, in
 5 which case it represents the likelihood that a single larva carrying the allele of interest arriving at
 6 an open piece of habitat can succeed in competition against N_{other} larvae without the allele. Or
 7 the term can represent a fractional increase in fecundity or survival in the larval or juvenile pool.
 8 Assuming that there are on average N_{other} other larvae competing for the same piece of open
 9 habitat, this term is

$$10 \quad \frac{1}{1 + (1-s)N_{others}} \quad (6)$$

11 The increase in the number of the selected allele can now be written

$$12 \quad N_{allele} = (\gamma N_{larvae}) / [1 + (1-s)N_{other}] \quad (7)$$

13 Because we assume the favored allele is scarce in the population, N_{other} in the above equation can
 14 be eliminated by noting that if there is no selection for the allele ($s=0$), it will not increase in the
 15 population and N_{allele} is one. N_{other} can then be found by setting $s=0$ and $N_{allele}=1$ in (7). This
 16 solution for N_{other} can then be substituted into (7) to give

$$17 \quad N_{allele} = \{ \gamma N_{larvae} \} / \{ (1-s) \gamma N_{larvae} + s \} \quad (8)$$

18 In the limit of $s \ll 1$ and $\gamma N_{larvae} \gg 1$, this can be written as

$$19 \quad N_{allele} = 1 + s \quad (9)$$

20 If (8) is substituted into the criterion for the persistence of an allele into the middle of a
 21 population, (4), it reduces to

$$22 \quad s > L^2_{adv} / (2L^2_{diff}) \quad \text{if } s \ll 1 \text{ and } \gamma N_{larvae} \gg 1 \quad (10a)$$

$$23 \quad \ln(\gamma N_{larvae}) > L^2_{adv} / (2L^2_{diff}) \quad \text{if } s \rightarrow 1 \quad (10b)$$

24 When (10) is true, an allele introduced into the middle of an alongshore-uniform domain will
 25 grow in number and fill the domain, because the increase in the number of copies of the allele due

1 to selection is sufficient to offset the tendency of advection to transport the allele downstream.
2 Note that if $L_{adv}^2/(2L_{diff}^2)$ is large enough and N_{larvae} small enough, an allele can be lost
3 downstream even if it is very strongly selectively favored ($s \approx 1$).

4 The derivations of these results in BP were only tested in a domain in which the
5 ecological and physical parameters did not vary in the alongshore direction. However, for a cline
6 in allele frequency to persist, (10) cannot be true everywhere, for if it were the downstream allele
7 would take over the entire domain. We hypothesize that if the selection for the allele only
8 satisfies (10) in a downstream portion of the domain, the cline will not move upstream, and will
9 occur immediately downstream of the location where selection becomes strong enough to satisfy
10 (10). When we test this conjecture in the numerical model of the population, it is found to be
11 correct (figures 4 and 5), as long as the downstream region is large compared to L_{adv} and L_{diff} .
12 This is the same criterion found for the validity of (3) in BP and references therein.

13 Thus for a cline to persist in a uniform environment in which the population is limited by
14 habitat scarcity, there must be a gradient in selection so that (10) is satisfied only in the
15 downstream portion of the domain. In this limit, the selection needed for a cline to persist
16 depends on the larval dispersal parameters L_{adv} and L_{diff} . This will be discussed further below.
17 However, it is first necessary to examine another limit, in which a cline is maintained by an
18 alongshore variation in either the ocean circulation or the habitat, and the subsequent reduction in
19 habitat scarcity.

20

21 **Persistence of a Cline Allowed by Alongshore Variation in Habitat and** 22 **Transport.**

23 In the last section, the number of successful offspring an individual could leave was
24 limited by the scarcity of habitat, and thus N_{allele} was driven by selection. The number of copies
25 of an allele left by an adult can also be increased if each adult is able to leave multiple offspring

1 because the environment is not, at least locally, habitat limited. These regions of enhanced
2 reproductive success can be areas in which N_{allele} satisfies (4), and thus can support a persistent
3 cline. In order to understand these dynamics, we examine the model in the limit where
4 alongshore variation in carrying capacity or larval transport produces regions of enhanced
5 reproductive success.

6 Of course, if a species' total population is in steady state, the average adult will only
7 leave a single offspring behind after its death. However, this need not be true everywhere in the
8 species range, for some regions can be source populations in which each adult has above average
9 reproductive success, while other regions can be sink regions (figure 6). This pattern of sources
10 and sinks can be seen most clearly in considering the entire range of a species in an environment
11 with unidirectional mean alongshore current. Adults in the center of the domain leave, on
12 average, one successful child per lifetime, for where the population growth is limited by density
13 dependence children can only survive to replace adults that have died. Adults near the
14 downstream edge of the species range largely fail to reproduce successfully as their progeny are,
15 on average, swept downstream and beyond suitable habitat. On the other hand, adults on the
16 upstream edge of the species range have a greater reproductive success rate because the larvae
17 produced at the upstream edge of the species range serve to repopulate both this region and the
18 area immediately downstream of it.

19 Similar regions of enhanced reproductive success can also form any place in the domain
20 where the supply of larvae from upstream is insufficient to fully supply the downstream region
21 with larvae, and so the population is below the local carrying capacity of the habitat. This can
22 occur either when larval transport from upstream is interrupted, or when available habitat
23 increases downstream. For example, the carrying capacity of the habitat triples downstream of
24 the 1300km point of figure 6. Reproductive success is high here and the population is recruit
25 limited, for the larvae produced in this region feel little competition from the small number of
26 larvae advected in from the poor habitat upstream. Another region of high reproductive success

1 and reduced population occurs downstream of a region of reduced larval transport between
2 kilometers 2500 and 3000, because few larvae are exported from there to settle downstream.

3 In these regions of enhanced reproductive success, eqs. (4) and (3) can be satisfied.
4 Thus, upon their deaths, adults in the regions will usually be replaced with recruits that originated
5 in the same region. These areas are thus retention areas (BP), and alleles in these regions,
6 including any novel alleles that may arise in these regions, will tend to persist in these regions.
7 Thus we can treat these retention regions as populations, in the classical population genetic sense.
8 This will allow us to apply classical population genetic results to these areas, and to analyze the
9 retention of a cline at these locations in terms of the migration between populations upstream and
10 downstream of the change in habitat or circulation.

11 At the upstream edge of the species domain, there is no immigration from further
12 upstream and the usual balance between mutation and drift will govern allelic diversity. In those
13 regions of high reproductive success in the interior of the species range, allelic diversity will be
14 governed not only by these processes, but also by the immigration of small numbers of
15 individuals from upstream. To understand the relative importance of these processes, it is
16 necessary to quantify the processes that create regions of high reproductive success and limit
17 immigration from upstream. The parameter $f_{migrate}$ is the ratio of the larval supply from upstream
18 to the supply that would occur if habitat and circulation in the retention zone extended infinitely
19 upstream, so that a smaller number indicates fewer larvae from upstream settle in the region (at
20 the upstream edge of the species range, $f_{migrate} = 0$). Where the reduced larval supply is formed
21 by an interruption in the alongshore transport of larvae, $f_{migrate}$ is the fraction of larvae which can
22 pass through the interruption. Where the reduced larval supply is caused by poor upstream
23 habitat, $f_{migrate}$ is the ratio between the carrying capacity upstream of and in the retention region.
24 When the population in the region of enhanced reproductive success is close to the carrying
25 capacity, then $f_{migrate}$ is also approximately the ratio of migrants to local recruits that settle in the
26 region of enhanced reproductive success (see appendix A).

1 If $f_{migrate}$ is much less than the mutation rate of a gene, classical population genetic results
2 suggest that the migration rate would be insufficient to homogenize the populations upstream and
3 downstream of the region of high reproductive success, and a cline could exist there solely due to
4 stochastic fluctuations in the frequency of neutral alleles (Nagylaki 1978, Hartl and Clark 2000).

5 However, if $f_{migrate}$ is greater than the mutation rate, some selection for a downstream
6 allele would be necessary to maintain it against immigration from upstream. The relative
7 importance of immigration and selection in a deme has been extensively studied in cases of
8 asymmetric dispersal (e.g. Kawecki & Holt 2002). In these studies, the frequency of the favored
9 allele in the population receiving migrants is $(1-s/m)$ for $s \ll 1$, where m is the ratio of migrants to
10 local recruits in the retention region. Since $m \approx f_{migrate}$, the frequency of the favored allele in the
11 retention region downstream of the variation in habitat or circulation is approximately

$$\text{Allele Frequency} = (1 - f_{migrate}/s) \quad (11)$$

12 for $f_{migrate} \ll 1$, $s \ll 1$, where s is the selection coefficient against all other alleles in the retention
13 zone. This is illustrated in figure 7, and derived more formally, along with a discussion of its
14 limitations, in appendix A. When $f_{migrate} > s$, the favored allele will be lost from the system and
15 the cline will disappear. When $f_{migrate} < s$, the allele and the cline will persist where there is the
16 change in alongshore larval transport or habitat.

17
18 At this point, it may seem that there is little difference between the classical problem of
19 two populations exchanging migrants and an advective coastal environment with alongshore
20 variation in larval transport or habitat. In both, reduction in larval transport between two regions
21 increases the ability of a cline to persist by reducing the migration between the two populations
22 [e.g. Slatkin 1985, Hare and Avise 1996, Rocha-Olivares and Vetter 1999, Lenormand 2002].
23 However, directional dispersal of the species changes the system in two fundamental ways. First,
24 in a system with directional dispersal, if the reproductive success in the downstream region is
25 reduced to the point that (4) is not satisfied, no non-zero $f_{migrate}$ will allow the favored allele to
26 persist only in the downstream region. Population dynamics, in particular the reproductive

1 success of adults in the downstream region, fundamentally govern the ability of an allele to be
2 retained in an advective environment, and the enhanced reproductive success is enabled by
3 alongshore variation in circulation or habitat. Secondly, directional dispersal prevents an allele
4 from flourishing everywhere it is selectively favored, as can be seen in figure 7. In this figure, an
5 allele is favored in the downstream nine-tenths of the domain, and there is a reduction of larval
6 transport in the midst of the region where the downstream allele is favored. Since the selection
7 for the allele is less than that required to satisfy (10), the cline is not able to spread upstream of
8 the location of the interruption of larval transport. The cline is instead pinned to the region of
9 alongshore variability in larval transport, even though the downstream allele is favored upstream
10 of that point. Thus clines will persist not where an allele begins to be favored, but where there is
11 a retention zone driven by alongshore changes in circulation or habitat, or where the selection
12 exceeds the minimum set by (10).

13
14

Discussion

15 **The maintenance of phylogeographic boundaries in a coastal ocean in a species with**
16 **a long planktonic duration:** To maintain population genetic boundaries in the coastal ocean
17 with alongshore *uniform* circulation and habitat, there must be a gradient in selection for the
18 downstream allele. There must be sufficient selection downstream of the cline to retain the
19 downstream allele against advection, and insufficient selection upstream of the cline to prevent
20 the cline from moving upstream. In such a relatively simple coastal ocean, and for species with
21 uncomplicated spawning and larval behavior, we can estimate the critical level of selection at the
22 cline. Substituting (2) and (1) into (10) produces an expression for this critical selection threshold
23 as a function of the circulation parameters and larval duration:

$$\begin{aligned}
 24 \quad s &> \frac{U^2 T_m}{2\sigma^2 \tau_L} && \text{if } (U^2 T_m)/(2\sigma^2 \tau_L) \ll 1 \\
 25 \quad s &\rightarrow 1 && \text{if } (U^2 T_m)/(2\sigma^2 \tau_L) \gg 1
 \end{aligned} \tag{12}$$

1 Increased mean currents (U) and reduced variability in the currents (σ) will tend to increase the
2 selection needed to retain an allele, while a decreased time in plankton (T_m) will reduce the
3 selection needed to retain an allele.

4 For most coastal oceans, the strength of the mean current U is comparable to strength of
5 the fluctuations of the current σ , so the term $U^2/(2\sigma^2)$ in (12) is of $O(1)$ (Winant *et al.* 1987 for
6 Central California, Lentz 2001 for the South Atlantic Bight, Beardsley *et al.* 1985 for the Mid-
7 Atlantic Bight, Hickey & Banas 2003 for the North West, Gangopadhyay *et al.* 2003 for the Gulf
8 of Maine, Boicourt *et al.* 1998 for the Gulf Coast). Thus the magnitude of the selection needed
9 to retain an allele will depend on the ratio T_m/τ_L . Where the larval planktonic duration T_m is much
10 greater than time scale of current fluctuations τ_L it will take strong selection to allow a cline to
11 persist in place. If the larval planktonic duration is much shorter than τ_L it will take moderate
12 levels of selection to allow an allele to spread upstream, and only moderate selection gradients to
13 preserve a cline in place. The time scale of current fluctuations in *most* coastal oceans is on the
14 order of a few days (Brink *et al.* 2000, Seigel *et al.* 2003, Davis 1985), and so moderate values of
15 s will suffice in species whose larvae disperse in the plankton for less than a few days. However,
16 if larvae with simple behavior are in the plankton for much more than several days, the selection
17 coefficient needed to allow a cline to persist increases dramatically. Kingsolver *et al.* (2001) find
18 that the median of observed levels of selection on quantitative traits in natural populations is
19 about $s=0.16$, though with a long tail of much higher selection levels. For single-locus patterns of
20 selection, a number of examples in marine populations are available for which s is apparently
21 much higher (reviewed in Eanes 1999, Rand *et al.* 2002). For most species with a larval
22 planktonic duration T_m longer than a few days, clines can only be retained along a coast with
23 relatively uniform current and habitat by high levels of selection.

24 A cline can also persist in a region where the mean current goes locally to zero or
25 becomes small, allowing L_{adv} to locally become much less than L_{diff} , and thus allowing weak

1 levels of selection to retain an allele (10). L_{adv} may also become small due to larval or spawning
2 strategies that enhance retention. BP describe several such strategies, such as the spawning of
3 larvae in multiple seasons with oppositely directed mean currents to reduce L_{adv} . Hare et al.
4 (2005) illustrate the importance of other mechanisms that may reduce transport across a region,
5 all of which can lead to significant genetically controlled clines.

6 Additionally, even for species with long planktonic durations, a cline can persist where
7 there is a reduction in larval pressure from upstream due to alongshore variation in circulation or
8 habitat. These regions of persistence will not be fully captured in analyses that neglect
9 alongshore variation in population dynamics. In these regions, the selection needed to retain the
10 downstream allele in a cline is a function only of the strength of the disruption of larvae supply
11 from upstream (11), and is not a function of larval duration. This allows clines to persist with
12 modest gradients of selection even for species with long planktonic durations. If $f_{migrate}$ is less
13 than the mutation rate for an allele, the cline can persist with no selection. Given the low median
14 levels of selection seen by Kingsolver *et al.* (2001), this model suggests that most clines observed
15 in species with long planktonic durations are associated with reduced larval supply from
16 upstream.

17 Of course, the magnitude of the limitation of upstream larval supply $f_{migrate}$ might be a
18 function of larval duration and dispersal distance. For example, $f_{migrate}$ could be small for larvae
19 in the surface waters where there is a region of mean offshore transport of the surface waters,
20 such as in an upwelling zone. In this case, a longer larval duration would increase the likelihood
21 of a larvae being lost offshore. This would decrease $f_{migrate}$ and allow the cline to persist with less
22 selection. The interruption of alongshore larval supply can also be driven by a region of poor
23 habitat, which supplies few larvae to a downstream region. For larval dispersal distances less
24 than the size of the region of poor habitat, no larvae could pass through this region from
25 upstream, and $f_{migrate}$ would not be a function of the dispersal distance and larval duration.
26 However, once the larval duration increased and dispersal distances L_{adv} or L_{diff} exceeded the size

1 of the region of poor habitat, $f_{migrate}$ would increase abruptly and the selection needed to preserve a
2 cline would increase. Thus our model suggests that, for species with long planktonic durations
3 and large ratios of L_{adv} to L_{diff} , clines will occur either in regions of elevated reproductive success
4 driven by reduced larval immigration from upstream, or the cline will be maintained by levels of
5 selection much larger than the median values found by Kingsolver et al. (2001), or both.

6
7 **The Central California cline in *B. glandula*; an Example of a cline in a species with a long**
8 **planktonic duration.** *Balanus glandula* is a well-studied barnacle present along much of the
9 Pacific coast of North America (Newman and Abbott 1980). Sotka *et al.* (2004) describe a cline
10 in both nuclear and mitochondrial allele families for *B. glandula* across a narrow region of the
11 Central Californian coast. This phylogeographic transition spans approximately 500km of
12 coastline between Pacific Grove, CA and Cape Mendocino, CA (Sotka *et al.* 2004). For this
13 analysis, we chose parameters appropriate for this species and for the oceanographic conditions in
14 this region. Using current meter data, we calculate in appendix B that L_{adv} is approximately 290
15 km and L_{diff} 240km.

16 In the absence of any alongshore variation in habitat or circulation the selection needed to
17 retain an allele here would be about $s=0.7$, if each adult barnacle could produce many surviving
18 offspring in a sparsely populated area. This selection is much larger than the median seen by
19 Kingsolver *et al.* (2001), though is within the range of selection coefficients observed. If the
20 selection for the downstream allele was greater than this in the cline, and less to the north, a
21 selection gradient alone could explain the cline.

22 However, it is likely that the circulation in this region would tend to greatly reduce the
23 selection needed to allow the cline to persist, and thus reducing the required selection to a more
24 typically observed value. Physical theory suggests that the change in the continental shelf width
25 between Pt. Reyes and Monterey Bay will cause a reduction of alongshore transport between
26 these two points, with the excess transport on the shelf moving offshore in the surface Ekman

1 layer (Pringle 2002). The reduction in the alongshore transport is expected to scale as the ratio of
2 the shelf width at the two locations, and thus there should be a five or tenfold reduction in
3 alongshore transport. Evidence from floats drogued to follow the surface waters (Sotka *et al.*
4 2004) supports this theory. Floats released to the south of the cline in late winter tend to move
5 along the coast and beach on the coast near Monterey Bay or to the south [e.g. the winter float
6 tracks in Winant *et al.* 2003], while floats released to the north of the cline tend to move offshore
7 between Pt. Reyes and Pt. Arena, and then stay offshore, never to return to the coast where a larva
8 could settle (Sotka *et al.* 2004, Brink *et al.* 2000, Davis 1985). Nearshore observations in
9 Monterey Bay support the idea that alongshore transport there is opposite to the prevailing mean,
10 and drives offshore transport (Storlazzi *et al.* 2003, Rosenfeld *et al.* 1994, and Graham and
11 Largier 1997). Thus the physical environment in the area of the cline provides the interruption of
12 the larval transport needed to allow a cline to persist. Studies of barnacle population dynamics in
13 the region of the cline support the idea that the population is limited by larval supply, and not by
14 habitat (Roughgarden *et al.* 1988 and references therein), suggesting that the interruption in larval
15 supply has set the stage for reproductive success, and thus the retention of alleles in this region.

16 Similar interactions between local adaptive processes and variation in nearshore physical
17 oceanography have been hypothesized to drive phenotypic and other macroevolutionary patterns
18 in other marine systems (Muss *et al.* 2001, Taylor and Hellberg 2003, Cowen *et al.* 2006).

19

20 **The present location and historical origin of a cline:** Evidence suggests that the age of a cline
21 at a particular location can be much less than the age of the genetic differences that form the cline
22 (Felsenstein 1975, Endler 1977). The differentiation of the allelic classes which form clines in
23 the *B. glandula* population appears to have formed > 100 kya (Wares and Cunningham, 2005).
24 However, the change in shelf width that Pringle (2002) posits as the cause of the interruption of
25 larval transport at the current cline location between Monterey and San Francisco Bay only exists
26 at current sea levels. When the sea level was ~ 100m lower in the last ice age (Graham *et al.*

1 2003), the shelf would have vanished, and the proximate physical cause of the cline would
2 disappear. Thus the current mechanism for fixing the cline in place may have only existed for the
3 last 10,000 years.

4 However, this model suggests a cline could persist even without refugia. If the current
5 interruption of larval transport in central California were to be removed, the cline would be
6 swept downstream until it re-established at the next location along the coast in which larval
7 transport were interrupted, or one of the other physical or biological mechanisms for cline
8 formation discussed above existed. If the mean currents experienced by larvae were always in
9 the same direction, and the retention zones are sufficiently separated as to prevent larval dispersal
10 from the downstream to upstream retention zone, then the cline would ratchet downstream from
11 one extent retention zone to the next as the retention zones came and went. For these reasons,
12 tracking phylogeographic boundaries in marine populations necessarily involves understanding
13 contemporary forces that limit the movement of individuals or their larvae. Many of these
14 transitions, along with biogeographic transitions, may have originated due to historical events; but
15 their current location may not be the site at which the transition originated.

16

17 **The relation of the above theory to existing phylogeographic theory:** It is well established that
18 the location and strength, or shape, of a cline can be modified by stochastic allele frequency drift
19 (Felsenstein 1975, Slatkin and Maruyama 1975), and a large literature looks at the effects of
20 selection and genetic drift in demes that undergo asymmetric migration (e.g. Nagylaki 1978,
21 Doebeli 1995, Lundy & Possingham 1998, Lebreton et al. 2000, Lenormand 2002, Kawecki &
22 Holt 2002). Some of the results derived above are foreshadowed in these papers, and the links
23 can now be made explicit. Nagylaki (1975) showed that an allele that was favored in a region
24 could be lost if there was a large amount of migration into that region from areas in which the
25 allele was not selected for. Nagylaki (1978) pointed out that it was easier to maintain an allele in
26 a deme which generated a net outflow of migrants than in one which was a sink for migrants, and

1 Kawecki & Holt (2002) argued that selection in sink regions would be relatively ineffective (c.f.
2 Doebeli 1995 and Lebreton et al. 2000). Lundy & Possingham (1998) argued that a deme would
3 only contribute to preventing the fixation of an allele if it were a source of migrants.

4 However, to place the results of these papers in the context of a coastal ocean, it is
5 necessary to identify the mechanisms that form populations or demes there. The tendency has
6 been to label regions of relatively uniform allele frequency as a population. This is not
7 appropriate, for in most of these regions any novel allelic diversity or stochastic fluctuation in
8 allele frequency that arises will be swept downstream by the mean currents, and will not
9 contribute to the evolution of allelic diversity at that point. We can only discover the boundaries
10 between populations by considering the spatial structure of habitat and circulation.

11 Regions downstream of a reduction in larval supply can retain stochastic fluctuations in
12 allele frequency and novel alleles that arise, and the region of enhanced reproductive success can
13 be considered a population. These regions also export larvae downstream, so they are source
14 regions for the downstream population. As Kawecki & Holt (2002) argue, selected alleles are
15 relatively easily retained in these regions, even if there is some migration into the population from
16 upstream. If immigration of larvae into this region is less than the mutation rate in the
17 population, a cline can exist even in the absence of selection. At the upstream edge of the species
18 range, where there can be no immigration of larvae from upstream, allele frequency will change
19 as one would expect for a population with symmetric dispersal (e.g. Kimura 1968).

20 The sink populations are those downstream of the regions of enhanced reproductive
21 success, in which density dependence limits the realized growth rate of the population. At each
22 of these regions, the population is maintained by immigrants from upstream, and the region
23 maintains the population downstream of it by exporting its larvae downstream. As predicted by
24 Nagylaki (1978), Kawecki & Holt (2002) and others, it takes a very large selection coefficient to
25 maintain an allele in the population in these sink regions (equation 10). Absent strong selection,

1 allele frequency at downstream regions is set by the gene frequency L_{adv} upstream, until in the end
2 it is set by the allele frequency at an upstream region of enhanced reproductive success.

3 In these downstream regions, the substitution rate will not equal the mutation rate.
4 Mutants will arise at a rate proportional to the population size, but will on average be distributed
5 further downstream each generation; given enough mutants over large distances with large
6 population sizes, a stochastic equilibrium defined by mutation and upstream diversity will hold.
7 This would predict increased levels of allelic diversity in downstream ‘sink’ habitats (Wares et al.
8 2001, Al-Rabab’ah and Williams 2004). However, as seen in figure 2 and in the associated text,
9 the distribution of any mutant allele would shift downstream by L_{adv} each lifetime. For species
10 with mean planktonic dispersal distances of tens to hundreds of kilometers, and species ranges of
11 thousands of kilometers in size, any mutant allele which arises outside of the downstream edge
12 will be lost off the downstream edge of the domain in a few tens to hundreds of generations, a
13 time perhaps insufficient to allow significant allelic diversity to develop (*e.g.* Hoskin 2000).

14
15 **Marine protected areas, fisheries, and the transport of clines:** The genetic homogeneity of a
16 population along the coast has been used to argue that the population should be treated as a single
17 population, a “stock,” for the purposes of fisheries management. The genetic homogeneity has
18 been assumed to indicate that the population is panmictic, and thus individuals in any part of the
19 population can replenish other parts of the population. But, as described above, this is not true in
20 downstream regions which are sink regions, and whose population is maintained by immigration
21 from upstream.

22 In such a population, harvesting could even encourage the formation of sub-populations,
23 if the harvesting in the interior of the domain created a region of small population in the midst of
24 a range, thus creating the interruption in larval transport needed to create locally high realized
25 reproductive success and thus the local retention of allelic diversity. Conversely, sufficient
26 harvesting could destroy a cline, and cause the upstream genome to invade downstream. Clines

1 can be maintained by weak selection in local regions where the realized growth rate is high
2 enough to satisfy (4), as discussed above. If a fisheries reduces the growth rate by harvesting
3 reproducing adults, the growth rate could well fall below (4), preventing retention, and allowing
4 the cline to be swept downstream. The local population would then be taken over by the
5 upstream population, which, while less adapted to local conditions, is anchored by some more
6 robust retention zone farther upstream.

7

8 **Directional dispersal in other environments:** Similar genetic dynamics to those described
9 above will exist in any system in which the dispersal of propagules is anisotropic with a preferred
10 direction of dispersal, for example in populations with wind-driven dispersal (e.g. Antonovics
11 1968, Kawecki and Holt 2002, Al-Rabab'ah and Williams 2004) or populations in the open
12 ocean. Qualitatively, the above results hold. However, the quantitative results for retention and
13 the maintenance of clines described above will only hold if the dimension of the population range
14 perpendicular to the direction of preferred dispersal is small enough that the population can
15 disperse across it in $O(1)$ generations. If it is not, the quantitative results described above must be
16 modified to include tendency of isotropic dispersal normal to the direction of preferred dispersal
17 to reduce the growth rate at a fixed point in space, a calculation similar to the classic calculations
18 of the relative importance of dispersal and growth made in Kierstead and Slobodkin (1953) and
19 Wroblewski et al. (1975).

20

21 **Summary:** The population genetics of the coastal ocean has long been understood as
22 resulting from the interplay of selection, random genetic drift, and migration (e.g. Palumbi 2003
23 and references therein). The interplay of these mechanisms in the coastal ocean for organisms
24 with planktonic larval stages is simultaneously governed by the ocean circulation and local
25 population dynamics. Thus it is only by taking the currents and population dynamics into
26 account that the population dynamics analysis of demes and sub-populations can be mapped onto

1 a continuous coastal ocean, with little in the way of natural boundaries. In doing so, it has
2 become clear that the maintenance of polymorphism in these systems is modified by advection
3 and local population dynamics. A cline will not usually be located where an allele becomes
4 favored. Instead, the cline will persist either where the selection for an allele begins to exceeds
5 (10) or where an alongshore variation in habitat or circulation produces a fractional reduction in
6 the upstream larval supply greater than the selection for an allele or the mutation rate. For species
7 with long planktonic durations, our model suggests the latter is more likely to set the location of a
8 cline.

9

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13

1 **Appendix A: Maintenance of a cline against migration from upstream.**

2 To quantify the relative importance of immigration and selection in the retention region
3 downstream of alongshore variation in the circulation or habitat, we examine the allele frequency
4 of an allele which is favored downstream of the change in circulation or habitat. The relative
5 frequency of this allele in the retention region downstream of the interruption is R_d , and the total
6 number of alleles in that region P_{reten} . We wish to find R_d as a function of the selection s against
7 all alleles but the favored downstream allele and the fractional reduction in the ratio of larvae
8 entering the retention region from upstream $f_{migrate}$. As part of the derivation, it is useful to define
9 N_m , the number of copies of the other alleles that enter the retention region to compete for habitat.
10 Parameters defined only in this appendix are not listed in table 1.

11 The number of copies of alleles which return to the retention region each lifetime will
12 scale as $N_{larvae}P_{reten}$. We assume that the immigration N_m is much smaller than $N_{larvae}P_{reten}$, and so
13 the number of copies of the favored downstream allele that compete for available habitat each
14 lifetime scales as $N_{larvae}P_{reten}R_d$, and the number of copies of the other alleles are N_m
15 $+N_{larvae}P_{reten}(1-R_d)$. From (6), we can then write the fraction of the larvae carrying downstream
16 allele which compete successfully for the available habitat as

$$17 \quad (N_{larvae}P_{reten}R_d)/[N_{larvae}P_{reten}R_d + (1-s)\{N_m + N_{larvae}P_{reten}(1-R_d)\}] \quad (\text{A1})$$

18 If the allele frequency is in steady state, the fraction of the larvae carrying the downstream allele
19 that recruit successfully must equal the fraction of the allele in the population, and so we can
20 solve for R_d by setting it equal to (A1) and solving for it. This results in

$$21 \quad R_d = 1 - \{N_m / (N_{larvae}P_{reten})\}(1-s)/s \approx 1 - \{N_m / (P_{reten}N_{larvae})\}/s \text{ if } s \ll 1 \quad (\text{A2})$$

22 This is the classic result that the balance of immigration and selection is governed by the ratio of
23 selection s to the fractional migration rate $m = N_m / (N_{larvae}P_{reten})$ when $s \ll 1$.

24 In order to get an estimate of how $N_m / (N_{larvae}P_{reten})$ varies with the strength of $f_{migrate}$, we
25 assume that P_{reten} is of the same order as the carrying capacity of the retention zone. This

1 assumption is valid when N_{larvae} is large, as in figure 6. Then, since without the interruption in
 2 larval transport, $N_{larvae}P_{reten}$ larvae from upstream would attempt to settle in the retention zone per
 3 lifetime, with the interruption there would be $N_m = f_{migrate}N_{larvae}P_{reten}$ larvae from upstream. The
 4 fraction of the downstream allele in the retention zone is then

$$5 \quad R_d = 1 - f_{migrate}/s \quad \text{if } s \ll 1 \quad (A3)$$

6 Equation (A3) becomes less than zero when the selection rate is not greater than $f_{migrate}$, which
 7 implies that the cline would not be maintained. Where it is greater, a cline can be maintained.
 8 The abundance of the downstream allele increases as one moves farther downstream from the
 9 retention zone, for selection will serve to increase the abundance of the allele as it is swept
 10 downstream from the retention zone.

11 The derivation for (A3) above makes three approximations that limit its accuracy. First,
 12 it assumes that there are none of the favored allele upstream of the variation in habitat or
 13 circulation, so that all migrants from upstream contain the un-favored alleles. Second, it assumes
 14 that P_{reten} is equal to the carrying capacity of the habitat in the retention zone, while it must
 15 actually be somewhat less to allow the enhanced reproductive success needed to preserve the
 16 cline. And third, it assumes that larvae spawned in the retention zone are as likely to return to the
 17 retention zone as those from immediately upstream. The first assumption would increase R_d ,
 18 while the second two decreases it. The exact impact of these assumptions depends on the exact
 19 nature of the alongshore variation of circulation and habitat, however in cases we have modeled it
 20 is relatively minor, changing the selection needed to allow retention by less than 30%. Equation
 21 (A3) is compared to model runs in which $f_{migrate}$ is set to 0.05 and 0.10 by removing $(1 - f_{migrate})$ of
 22 the larvae crossing a point 3/4 of the model domain from the upstream edge. The downstream
 23 allele is favored in the downstream 9/10 of the model domain. The models are then run for a
 24 large number of differing values of s , and the concentration of the downstream allele is shown in
 25 figure 7. Eq. (A3) is seen to capture the variability of R_d with s well.

26

1 **Appendix B: *Balanus glandula* dispersal and life history.**

2 *B. glandula*, like many other decapod crustaceans, has a planktonic larval form that feeds
3 and develops in the water column for 3-4 weeks before becoming competent to settle (Brown &
4 Roughgarden 1985). *B. glandula* broods larvae from Feb-Oct with the majority (about 90%)
5 being released early, and about 10% of the release from Aug-Sep (settlement is then Sep-Oct)
6 (Hines 1978). The brooding cycles for *B. glandula* are similar for populations in British
7 Columbia, central California, and southern California (Barnes and Barnes 1956), and late larval
8 stage individuals are found within the top 0.5m of seawater (Grosberg 1982).

9 L_{adv} and L_{diff} for *B. glandula* in the vicinity of the cline can be estimated from the mid-
10 shelf alongshore currents measured as part of the Coastal Ocean Dynamics Experiment in the
11 northern part of the cline, between Pt. Reyes and Pt. Arena. Lentz & Chapman (1989) estimate a
12 mean alongshore current U in the spring and early summer mid-shelf surface waters of 14 cm/s
13 southward with a standard deviation σ of 24 cm/s, and a fall mean current of 7 cm/s northward
14 with a standard deviation of 18 cm/s. Davis (1985) estimates that the Lagrangian timescale τ_L
15 was about 3 days. The net larval dispersal combining the early- and late-season larval releases
16 was calculated as in BP, in which the values of L_{adv} and L_{diff} for each spawning event is weighted
17 appropriately by the fraction of larvae released in each event, resulting in an estimate of $L_{adv}=287$
18 km and an $L_{diff}=240$ km. No attempt was made to compensate for different mortality rates in the
19 late spring versus late summer, for there is insufficient information to do so, though it is likely
20 that more larvae are lost offshore in the spring upwelling season as surface waters are transported
21 offshore by Ekman transport (Roughgarden *et al.* 1988). A relatively higher mortality in the
22 spring than in the fall due to offshore advection would increase L_{diff} and decrease L_{adv} .

23 Shanks *et al.* (2003) find for many species that behavior reduces the mean dispersal
24 distance, though it remains linearly related to the time in plankton. How this would affect the
25 results for *B. glandula* is unclear, for two reasons. First, there are not sufficient studies of the

1 behaviour of *B. glandula* larvae to determine the magnitude of any behavior related reduction in
2 larval transport. Secondly, the effects on retention and allele persistence depend on the ratio of
3 $L_{adv.}$ to $L_{diff.}$ and it is even less clear how this ratio might be affected by behavior. See (BP) for
4 more details on the interaction of behavior with retention.

5

1 **References**

- 2 Al-Rabab'ah, M. A. and C. G. Williams. 2004. An ancient bottleneck in the Lost Pines of central Texas.
3 Molecular Ecology 13: 1075-1084.
- 4 Antonovics, J. 1968. Evolution in closely adjacent plant populations. VI. Manifold effects of gene
5 flow. Heredity 23: 507-524.
- 6 Avise, J. C. 1994. Molecular markers, natural history, and evolution. New York, Chapman and
7 Hall.
- 8 Avise, J. C. 2000. Phylogeography. Cambridge, MA, Harvard University Press.
- 9 Barnes, H. and M. Barnes 1956. The general biology of *Balanus glandula* Darwin. Pacific Sciences 10:
10 415-421.
- 11 Barton, N. H. and G. M. Hewitt 1989. Adaptation, speciation and hybrid zones. Nature 341: 497-502.
- 12 Beardsley, R. C., D. C. Chapman, K. H. Brink, S. R. Ramp and R. Schlitz 1985. The Nantucket Shoals
13 Flux Experiment (Nsf79).1. A Basic Description of the Current and Temperature Variability.
14 Journal of Physical Oceanography 15(6): 713-748.
- 15 Boicourt, W. C., J. W.J. Wiseman, A. Valle-Levinson and L. P. Atkinson 1998. Continental Shelf of the
16 Southeastern United States and Gulf of Mexico: In the shadow of the Western Boundary Current.
17 The Sea. R. Allan R and K. H. Brink. New York, John Wiley & Sons. 11: 135-183.
- 18 Brink, K. H., R. C. Beardsley, J. Paduan, R. Limeburner, M. Caruso and J. G. Sires 2000. A view of the
19 1993-1994 California Current based on surface drifters, floats, and remotely sensed data. Journal
20 of Geophysical Research-Oceans 105(C4): 8575-8604.
- 21 Brown, S. K. and J. Roughgarden 1985. Growth, Morphology, and Laboratory Culture of Larvae of
22 *Balanus glandula* (Cirripedia, Thoracica). Journal of Crustacean Biology 5(4): 574-590.
- 23 Byers, J. E. and J. M. Pringle 2006. Going against the flow: Range limits and invasions in advective
24 environments. Mar. Ecol. Prog. Ser. 313: 27-41.
- 25 Cowen, R. K., C. B. Paris and A. Srinivasan 2006. Scaling of connectivity in marine populations. Science
26 5760: 522-527

- 1 Davis, R. E. 1985. Drifter Observations of Coastal Surface Currents During Code - the Statistical and
2 Dynamical Views. *Journal of Geophysical Research-Oceans* 90(NC3): 4756-4772.
- 3 Dawson, M. N. 2001. Phylogeography in coastal marine animals: a solution from California? *J.*
4 *Biogeography* 28: 723-736.
- 5 Doebeli, M. 1995. Dispersal and Dynamics. *Theoretical Population Biology* 47(1): 82-106.
- 6 Eanes, W. F. 1999. Analysis of selection on enzyme polymorphisms. *Ann. Rev. Ecol. Syst.* 30: 301-326.
- 7 Endler, J. A. 1977. Geographic variation, speciation, and clines.
- 8 Felsenstein, J. 1975. Genetic drift in clines which are maintained by migration and natural
9 selection. *Genetics* 81: 191-207.
- 10 Gangopadhyay, A., A. R. Robinson, P. J. Haley, W. G. Leslie, C. J. Lozano, J. J. Bisagni and Z.
11 T. Yu 2003. Feature-oriented regional modeling and simulations in the Gulf of Maine and
12 Georges Bank. *Continental Shelf Research* 23(3-4): 317-353.
- 13 Gaylord, B. and S. D. Gaines 2000. Temperature or transport? Range limits in marine species mediated
14 solely by flow. *The American Naturalist* 155: 769-789.
- 15 Graham, M. H., P. K. Dayton and J. M. Erlandson 2003. Ice ages and ecological transitions on temperate
16 coasts. *trends in Ecology and Evolution* 18: 33-40.
- 17 Graham, W. M. and J. L. Largier 1997. Upwelling shadows as nearshore retention sites: The example of
18 northern Monterey Bay. *Continental Shelf Research* 17(5): 509-532.
- 19 Grosberg, R. K. 1982. Intertidal zonation of barnacles: the influence of planktonic zonation of larvae on
20 vertical distribution of adults. *Ecology* 63: 894-899.
- 21 Hare, M. A. and J. C. Avise 1996. Molecular genetic analysis of a stepped multilocus cline in the
22 American Oyster (*Crassostrea virginica*). *Evolution* 50: 2305-2315.
- 23 Hare, M. P., C. Guenther and W. F. Fagan 2005. Nonrandom larval dispersal can steepen marine clines.
24 *Evolution* 59: 2509-2517.
- 25 Hartl, D. L. and A. G. Clark 2000. Principles of Population Genetics. Sunderland, MA, Sinauer.
- 26 Haydon, D. T., B. I. Crother and E. R. Pianka 1994. New directions in biogeography? *Trends in*

1 Ecology and Evolution 9: 403-406.

2 Hickey, B. M. and N. S. Banas 2003. Oceanography of the US Pacific Northwest Coastal Ocean and
3 estuaries with application to coastal ecology. *Estuaries* 26(4B): 1010-1031.

4 Hines, A. H. 1978. Reproduction in three species of intertidal barnacles from central California.
5 *Biological Bulletin* 154: 262-281.

6 Hoskin, M. G. 2000. Effects of the East Australian Current on the genetic structure of a direct developing
7 muricid snail (*Bedevea hanleyi*, Angas): variability within and among local populations. *Biol. J.*
8 *Linn. Soc.* 69: 245-262.

9 Irwin, D. E. 2002. Phylogeographic breaks without geographic barriers to gene flow. *Evolution*
10 56: 2383-2394.

11 Kawecki, T. J. and R. D. Holt 2002. Evolutionary consequences of asymmetric dispersal rates. *Am. Nat.*
12 160: 333-347.

13 Kierstead H, and L.B. Slobodkin 1953. The size of water masses containing plankton blooms. *J.*
14 *Mar. Res.*, 12(1). P. 141-147

15 Kimura, M. 1968. Genetic variability maintained in a finite population due to mutational
16 production of neutral and nearly neutral isoalleles. *Genet. Res.* 11: 247-269.

17 Kingsolver, J. G., H. E. Hoekstra, et al. 2001. The strength of phenotypic selection in natural populations.
18 *Amer. Nat.* 157: 245-261.

19 Kinlan, B. P. and S. D. Gaines 2003. Propagule dispersal in marine and terrestrial environments:
20 a community perspective. *Ecology* 84: 2007-2020.

21 Lebreton, J. D., M. Khaladi and V. Grosbois 2000. An explicit approach to evolutionarily stable dispersal
22 strategies: no cost of dispersal. *Mathematical Biosciences* 165(2): 163-176.

23 Lee, T. and D. O'Foighil 2004. Hidden Floridian biodiversity: mitochondrial and nuclear gene
24 trees reveal four cryptic species within the scorched mussel, *Brachidontes exustus*,
25 species complex. *Mol. Ecol.* 13: 3527-3542.

- 1 Lenormand, T. 2002. Gene flow and the limits to natural selection. *Trends in Ecology and Evolution* 17:
2 183-189.
- 3 Lentz, S. J. 2001. The influence of stratification on the wind-driven cross-shelf circulation over the North
4 Carolina shelf. *Journal of Physical Oceanography* 31(9): 2749-2760.
- 5 Lentz, S. J. and D. C. Chapman 1989. Seasonal Differences in the Current and Temperature Variability
6 over the Northern California Shelf During the Coastal Ocean Dynamics Experiment. *Journal of*
7 *Geophysical Research-Oceans* 94(C9): 12571-12592.
- 8 Lundy, I. J. and H. P. Possingham 1998. Fixation probability of an allele in a subdivided population with
9 asymmetric migration. *Genet. Res.* 71: 237-245.
- 10 Muss, A., D. R. Roberston, C. A. Stepien, P. Wirtz and B. W. Bowen 2001. Phylogeography of
11 *Ophioblennius*: the role of ocean currents and geography in reef fish evolution. *Evolution*
12 55: 561-572.
- 13 Nagylaki, T. 1975. Conditions for the existence of clines. *Genetics* 80(80): 595-615.
- 14 Nagylaki, T. 1978. Clines with asymmetric migration. *Genetics* 88: 813-827.
- 15 Newman, W. A. and D. P. Abbott 1980. *Cirripedia*. Stanford, CA, Stanford University Press. Intertidal
16 Invertebrates of the Central California Coast: 504-535.
- 17 Palumbi, S. R. 1994. Genetic divergence, reproductive isolation, and marine speciation. *Annu.*
18 *Rev. Ecol. Syst.* 25: 547-572.
- 19 Pringle, J. M. 2002. Enhancement of wind-driven upwelling and downwelling by alongshore bathymetric
20 variability. *Journal of Physical Oceanography* 32(11): 3101-3112.
- 21 Rand, D. M., P. S. Spaeth, T. B. Sackton, and P. S. Schmidt. 2002. Ecological genetics of *Mpi* and *Gpi*
22 polymorphisms in the acorn barnacle and the spatial scale of neutral and non-neutral variation.
23 *Integrative and Comparative Biology* 42: 825-836.
- 24 Rocha-Olivares, A. and R. D. Vetter 1999. Effects of oceanographic circulation on the gene flow, genetic
25 structure, and phylogeography of the rosethorn rockfish (*Sebastes helvomaculatus*). *Canadian*
26 *Journal of Fisheries and Aquatic Sciences* 56: 803-813.

- 1 Rosenfeld, L. K., F. B. Schwing, N. Garfield and D. E. Tracy 1994. Bifurcated Flow from an Upwelling
2 Center - a Cold-Water Source for Monterey Bay. *Continental Shelf Research* 14(9): 931-964.
- 3 Roughgarden, J., S. Gaines and H. Possingham 1988. Recruitment dynamics in complex life cycles.
4 *Science* 241: 1460-1466.
- 5 Sanford, E., M. S. Roth, G. C. Johns, J. P. Wares and G. N. Somero 2003. Local selection and
6 latitudinal variation in a marine predator-prey interaction. *Science* 300: 1135-1137
- 7 Shanks, A.L., B.A. Grantham and M.H. Carr 2003. Propagule dispersal distance and the size and
8 spacing of marine reserves. *Ecol. App.* 13(1): S108-S116.
- 9 Siegel, D. A., B. P. Kinlan, B. Gaylord and S. D. Gaines 2003. Lagrangian descriptions of marine larval
10 dispersion. *Mar. Ecol. Prog. Ser.* 260: 83-96.
- 11 Slatkin, M. 1985. Gene flow in natural populations. *Ann. Rev. Ecol. Syst.* 16: 393-430.
- 12 Slatkin, M. and T. Maruyama 1975. Genetic drift in a cline. *Genetics* 81: 209-222.
- 13 Sotka, E. E., J. P. Wares and M. E. Hay 2003. Geographic and genetic variation in feeding
14 preference for chemically defended seaweeds. *Evolution* 57: 2262-2276.
- 15 Sotka, E. E., J. P. Wares, J. A. Barth, R. K. Grosberg and S. R. Palumbi 2004. Strong genetic clines and
16 geographical variation in gene flow in the rocky intertidal barnacle *Balanus glandula*. *Mol. Ecol.*
17 13: 2143-2156.
- 18 Storlazzi, C. D., M. A. McManus and J. D. Figurski 2003. Long-term, high-frequency current and
19 temperature measurements along central California: insights into upwelling/relaxation and
20 internal waves on the inner shelf. *Continental Shelf Research* 23(9): 901-918.
- 21 Strathmann, R. R. 1985. Feeding and nonfeeding larval development and life-history evolution in marine
22 invertebrates. *Annual Review of Ecology and Systematics* 16: 339-361.
- 23 Taylor, M. S. and M. E. Hellberg 2003. Genetic evidence for local retention of pelagic larvae in a
24 Caribbean reef fish. *Science* 299: 107-109.
- 25 Wallace B. 1975. Hard and Soft Selection Revisited. *Evolution* 29:465-473.
- 26 Wares, J. P., S. D. Gaines and C. W. Cunningham 2001. A Comparative Study of Asymmetric Migration

1 Events across a Marine Biogeographic Boundary. *Evolution* 55(2): 295-306.

2 Wares, J. P. 2002. Community Genetics in the Northwestern Atlantic Intertidal. *Molecular Ecology* 11:

3 1131-1144.

4 Wares, J. P. and C. W. Cunningham 2005. Diversification before the most recent glaciation in *Balanus*

5 *glandula*. *Biol. Bull.* 208: 60-68.

6 Winant, C. D., R. C. Beardsley and R. E. Davis 1987. Moored Wind, Temperature, and Current

7 Observations Made During Coastal Ocean Dynamics Experiments-1 and Experiment-2 over the

8 Northern California Continental-Shelf and Upper Slope. *Journal of Geophysical Research-Oceans*

9 92(C2): 1569-1604.

10 Wroblewski, J.S., J.J. O'Brien and T Platt, 1975, On the physical and Biological scales of phytoplankton

11 patchiness in the ocean. *Memoires Societe Royale des Sciences de Liege*, 6^e serie, tome VII, pp.

12 43-57.

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1 Table 1: Parameters defined in the main section of the paper.

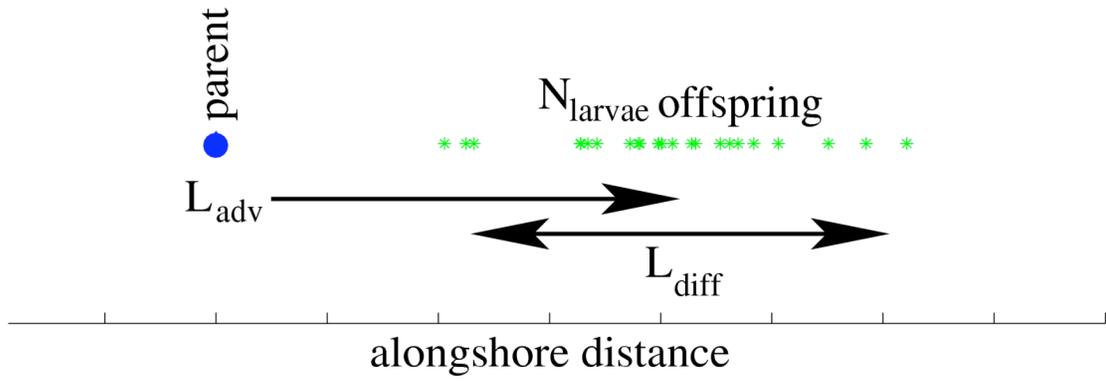
$f_{migrate}$	Fractional change in larval transport from upstream. An $f_{migrate}$ of 0.2 indicates that the transport of larvae from upstream of a point is one-fifth of what it is elsewhere.
γ	Fraction of the habitat that is not occupied by adults. If larvae have sufficient behavior to avoid settling on occupied habitat, $\gamma=1$.
H_{dens}	Maximum population per unit length of habitat.
L_{adv}	Mean distance larvae recruits downstream of its parents.
L_{diff}	Standard deviation of distance larvae recruits downstream of their parents.
m	Fraction of larvae in a retention zone entering from upstream of the retention zone.
N_{allele}	Number of additional copies of an allele in the population for each existing copy of the allele in the population a lifetime earlier.
N_{larvae}	Number of larvae an adult produces per lifetime that are capable of recruiting successfully and reaching reproductive age, if habitat is available. This number is net of all mortality in the larval pool and after settlement.
s	Selection against all alleles but the allele of interest, as defined in Hartl and Clark (2000).
σ	Standard deviation of Lagrangian alongshore currents experienced by planktonic larvae.
τ_L	Lagrangian timescale of alongshore currents experienced by planktonic larvae.
T_m	Time larvae spend in plankton.
U	Mean alongshore current speed experienced by larvae in plankton.

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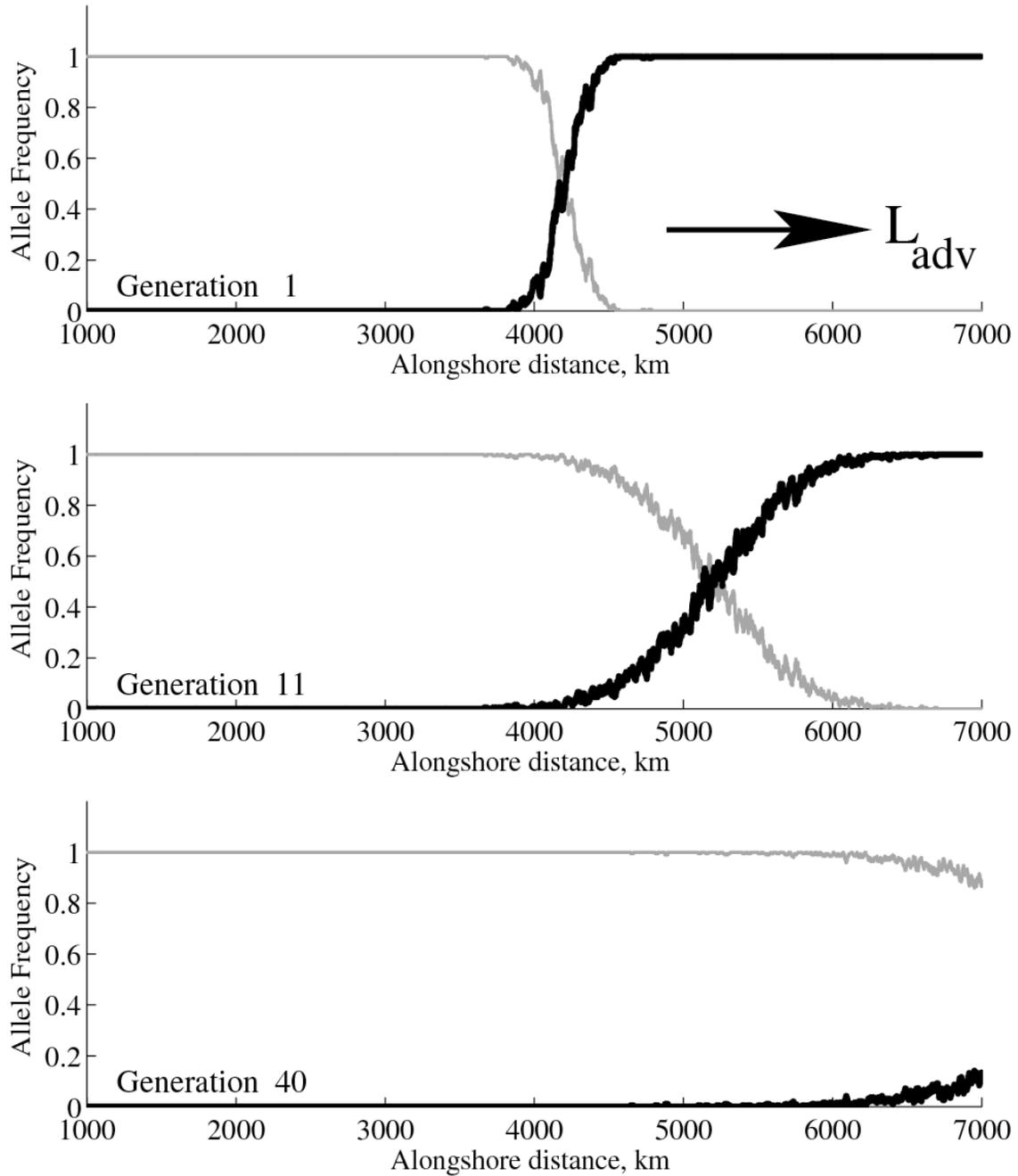


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4 Figure 1. A cartoon of the larval parameters L_{adv} , L_{diff} , and N_{larvae} showing the position of a single
5 parent and the offspring left by that parent after a lifetime.

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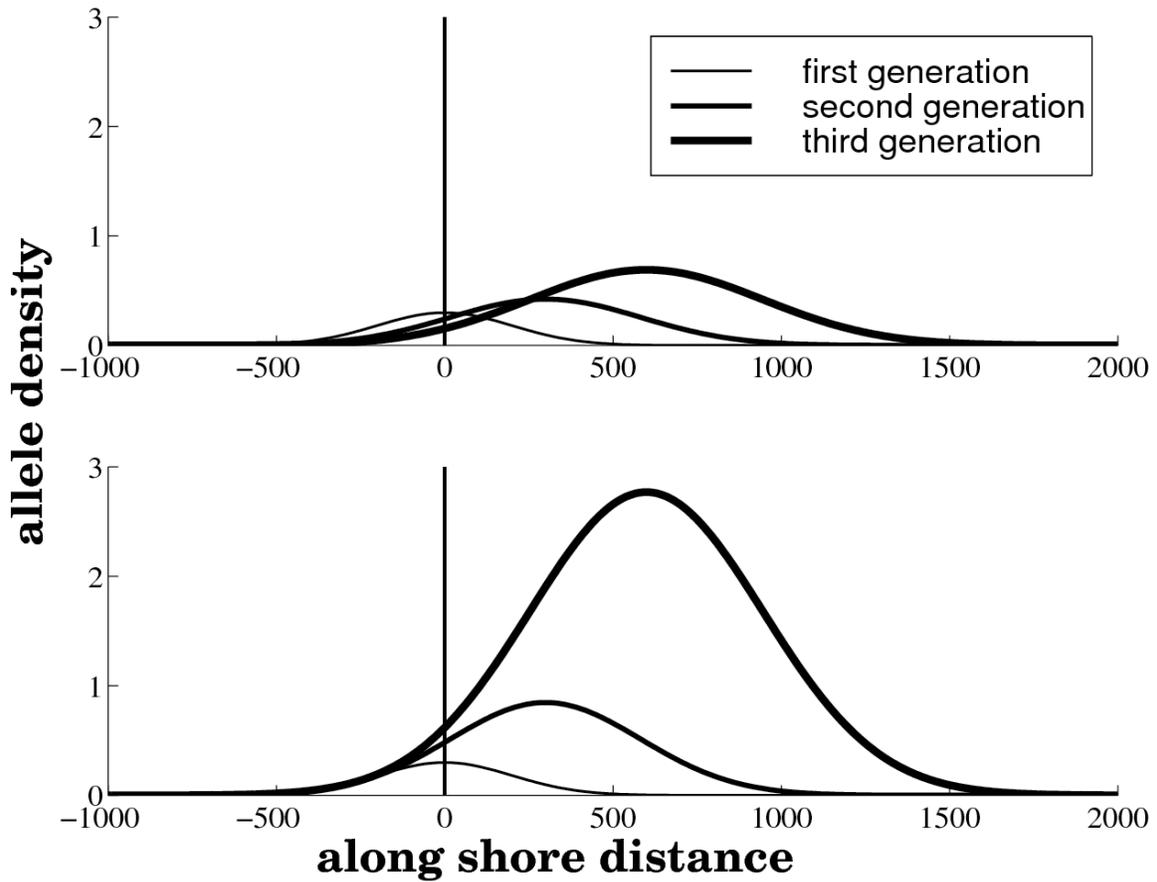
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3 Figure 2: The evolution of a cline between two selectively neutral alleles, here represented as
4 grey and black, in the numerical model. The larvae move on average $L_{adv}=100\text{km}$ downstream to
5 the right each generation, with a dispersion around that mean of $L_{diff}=150\text{km}$. The habitat is
6 saturated, so each adult leaves one surviving offspring at its death, on average.

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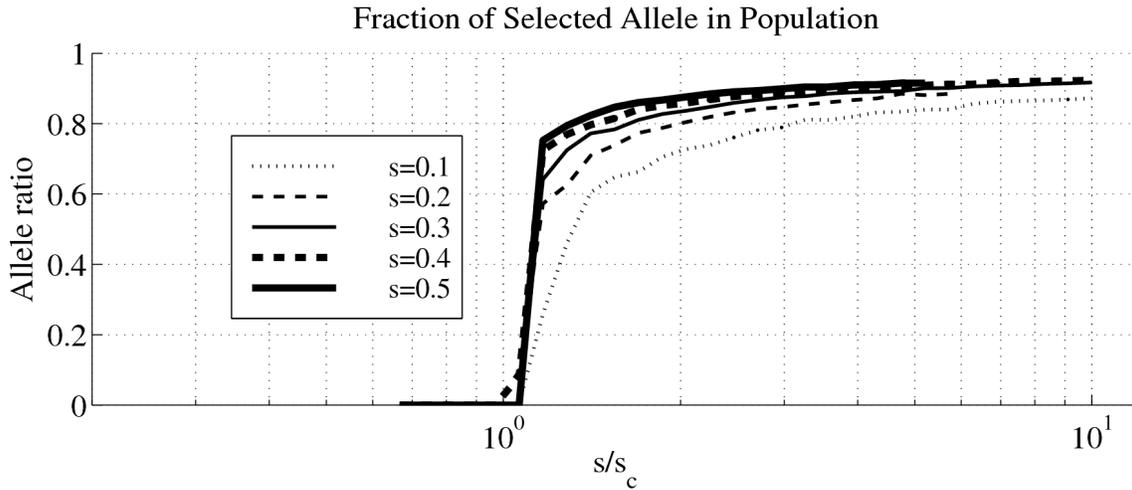


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3 Figure 3. The evolution of allele density in two populations in which an allele is introduced near
4 $y=0$. Allele density is the number of copies of a given allele per unit length. In both, $L_{adv}=300\text{km}$
5 and $L_{diff}=200\text{km}$. In the top panel, N_{allele} is 2, which was insufficient to allow the introduced allele
6 to persist at $y=0$. In the bottom panel, N_{allele} is 4, which is sufficient to allow retention. In both
7 panels the number of copies of the allele are increasing with time. However, note that at $y=0$, the
8 allele density is decreasing in the top panel, while allele density is increasing at $y=0$ in the bottom
9 panel, and the allele is also spreading upstream.

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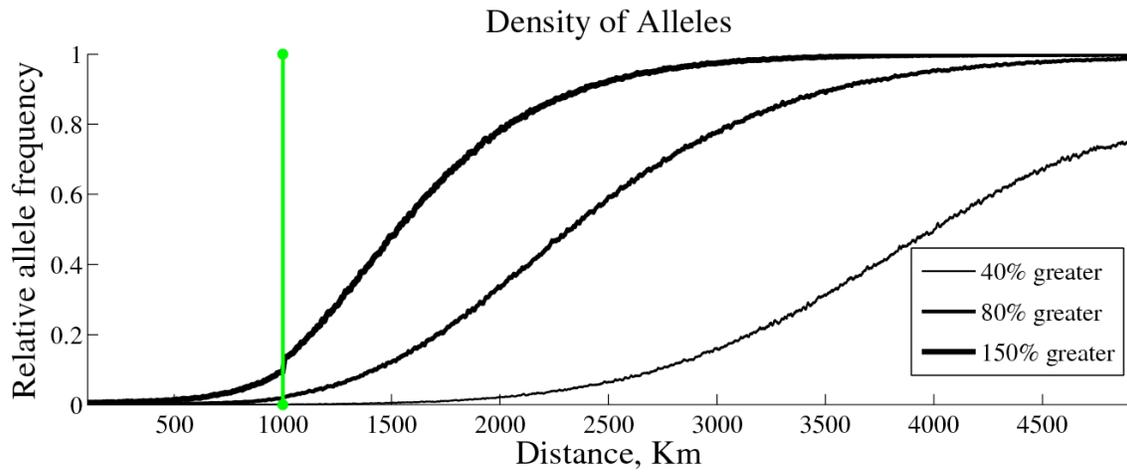
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3 Figure 4: The allele frequency of the favored allele in the downstream portion of the model
4 domain, as seen in figure 5. The allele is only favored in the downstream portion of the species
5 range. The allele frequency is shown as a function of the selection s normalized by the minimum
6 selection needed to satisfy (10), s_c . Where the frequency of the allele is zero, selection was
7 insufficient to retain the cline, and the downstream allele was flushed downstream and out of the
8 habitat. Where the density is finite, selection was sufficient to maintain the cline against the
9 mean current. The model was initialized with the favored allele in the downstream half of the
10 domain, and the model was run until the allele frequency had stabilized. The species modeled
11 had an L_{diff} of 200km, and L_{adv} is varied to change the critical selection needed to allow retention.
12 γ in these runs was ≈ 1.0 , for the modeled species is semelparous and spawns at the end of its
13 lifetime.

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Figure 5: The allele frequency of an allele which is selectively favored downstream (to the right)

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of the 1000km point of the domain, but not upstream of that point, in a numerical model. The

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selection is 40%, 80% and 150% greater than that needed to satisfy (10). The initial and

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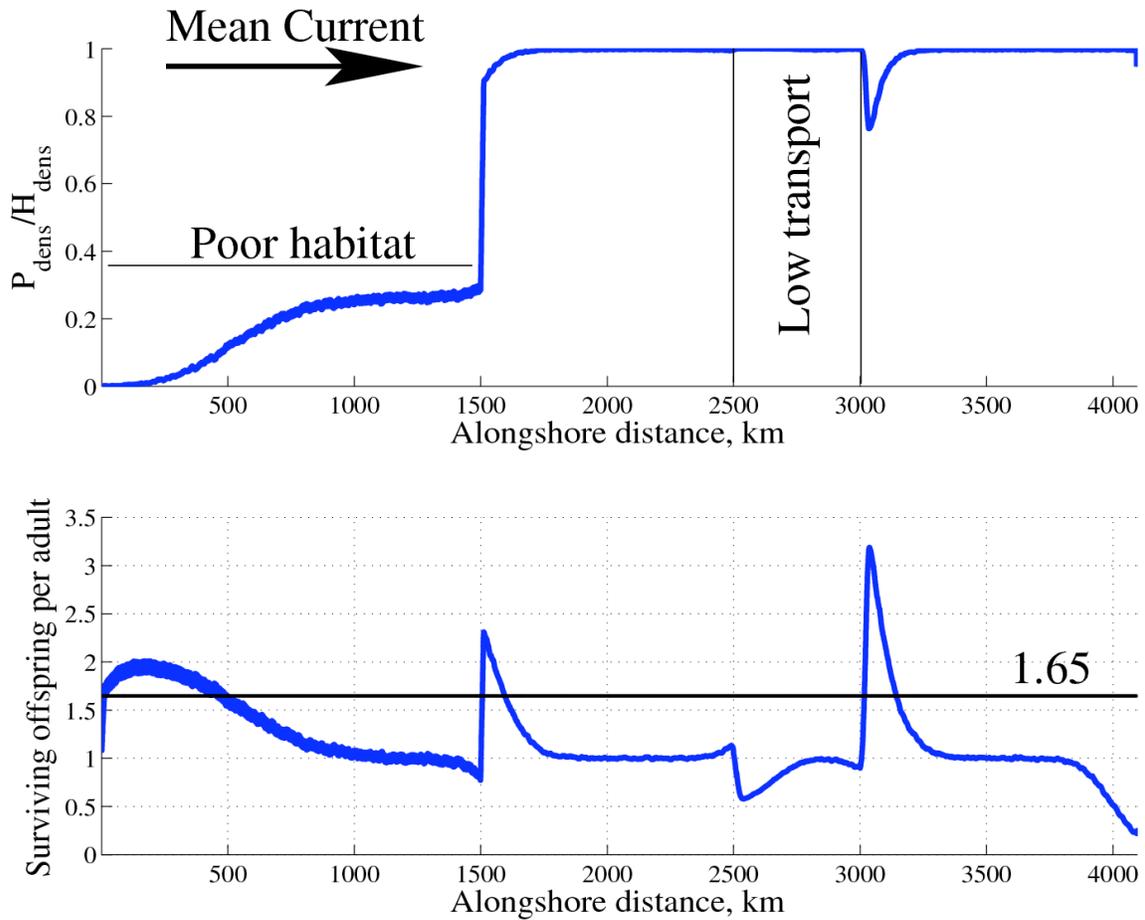
boundary conditions are as in figure 5. $L_{adv}=100\text{km}$, $L_{diff}=200\text{km}$, and the critical value of

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selection to allow the cline to persist is $s=0.1958$ for a semelparous species.

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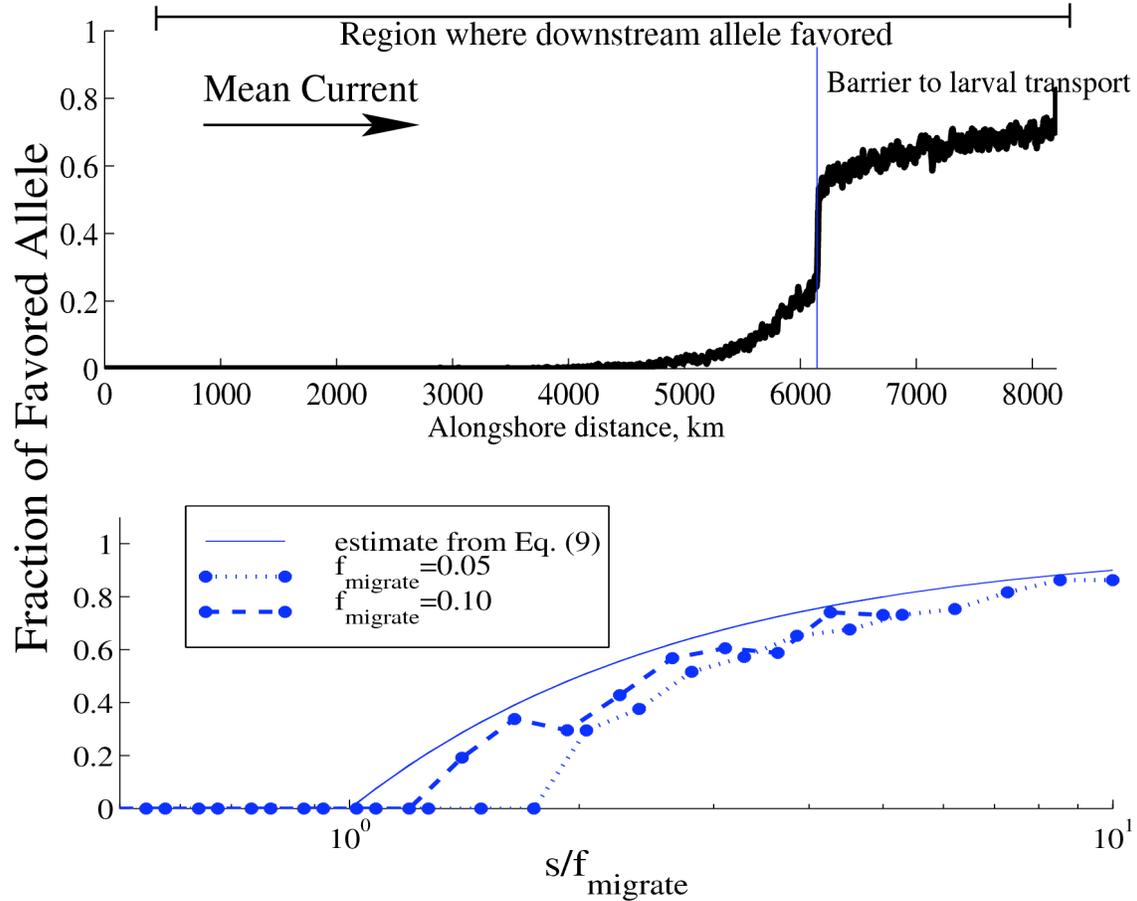


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2 Figure 6: A) The distribution of population density as calculated by the numerical model for a
 3 finite habitat with a region of poor habitat capable of carrying only 1/3 of the normal population
 4 between 0 and 1300km, and a region of weak alongshore flow and dispersion (1/10th normal)
 5 between 2500 and 3000km. The mean current is flowing to the right, and $L_{adv}=L_{diff}=400$ km
 6 outside the region of reduced alongshore flow and dispersion. B) The actual reproductive
 7 success in surviving offspring per adult, with the critical rate to satisfy (4), 1.65, marked with a
 8 horizontal line.

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2 Figure 7: (Top) The steady-state allele frequency of the favored allele in the numerical model.
3 The favored allele is favored downstream of 500km, and the barrier to larval transport is at
4 6100km. Organisms with the favored allele are released just downstream of the barrier at the
5 start of the numerical model run, and the model is run until the populations reach steady state.
6 The favored allele is selected by $s=0.16$, and 95% of all larvae are prevented from crossing the
7 indicated barrier to larval transport in either direction. (Bottom) to the allele frequency of the
8 favored allele in the population in the retention zone downstream of the barrier of larval transport
9 as a function of the selection for the downstream allele for both $f_{migrate}$ 0.05 and 0.1, and the
10 prediction of this ratio from (11). The selection is scaled by $f_{migrate}$, so that all curves will lie
11 upon each other. For both panels, $L_{adv}=200\text{km}$, $L_{diff}=300\text{km}$, and $N_{larvae}=6$. A discussion of the
12 validity of and errors in (11) is given in appendix A.