Limits to gene flow in marine animals with planktonic larvae: models of *Littorina* species around Point Conception, California

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Simulation models examined the process of gene flow in marine animals with planktonic larvae, and three factors that may influence it: ocean currents, planktonic period and spawning season. To focus on a realistic example, the models were based on measured ocean currents around Point Conception in southern California and the life histories of two intertidal gastropods, *Littorina scutulata* and *L. plena*. Results suggested that: (1) convergent ocean currents can create an effective barrier to gene flow that can be relaxed by temporal variation; (2) longer scales of temporal variation have a greater effect than shorter scales; (3) planktonic period has little effect above a minimum duration; and (4) an extended spawning season can eliminate gene flow barriers when currents vary seasonally. Failure of past studies to detect a phylogeographical boundary at Point Conception may be explained by extended spawning seasons and temporal variation at seasonal to millennial scales. These results fit a conceptual model of marine speciation in which short-lived, leaky barriers restrict gene flow, and divergence in a few genes may quickly produce reproductive isolation, resulting in cryptic sibling species. © 2004 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2004, **82**, 169–187.

ADDITIONAL KEYWORDS: computer simulation – dispersal – Littorinidae – ocean currents – spawning season – speciation.

INTRODUCTION

The life history of many benthic marine animals includes a planktonic larval stage that can last for weeks to months, perhaps even years (Thorson, 1950; Scheltema, 1986a; Levin & Bridges, 1995). With the help of currents, these larvae are capable of dispersing across ocean basins (Scheltema, 1986b; Palumbi, 1992; Brierley & Brandon, 1999). While theoretical work supports the hypothesis that dispersal can be adaptive (Hamilton & May, 1977; Motro, 1983; Rousset & Gandon, 2002), the scale of dispersal in many planktonic developers is much larger than expected as an adaptation for dispersal (Strathmann, Branscomb & Vedder, 1981; Strathmann, 1985). Thus, planktonic larvae do not appear to be an adaptation for dispersal, and the evolutionary consequences of the dispersal of planktonic larvae are different from the selective

forces, such as life history trade-offs or developmental constraints, that maintain those larvae. There are several predicted consequences of larval dispersal (Fig. 1). These include larger geographical ranges (Shuto, 1974; Hansen, 1978, 1980; Jablonski, 1986; Scheltema, 1989; Kohn & Perron, 1994) and higher levels of gene flow (Scheltema, 1971, 1986b; Shuto, 1974; Crisp, 1978; Féral, 2002). More gene flow should produce lower speciation rates (Bouchet, 1981; Hansen, 1982, 1983; Taylor, 1988; Pearse & Bosch, 1994). The combination of larger ranges and increased colonization ability should act as a buffer to reduce extinction rates (Scheltema, 1978; Hansen, 1980; Jablonski & Lutz, 1983). Lower speciation and extinction rates should produce longer-lived species (Hansen, 1978, 1980; Scheltema & Williams, 1983; Jablonski, Flessa & Valentine, 1985; Gili & Martinell, 1994).

While data have generally supported these predictions, the trends may be reversed in some cases. For instance, geographical ranges of non-planktonic devel-

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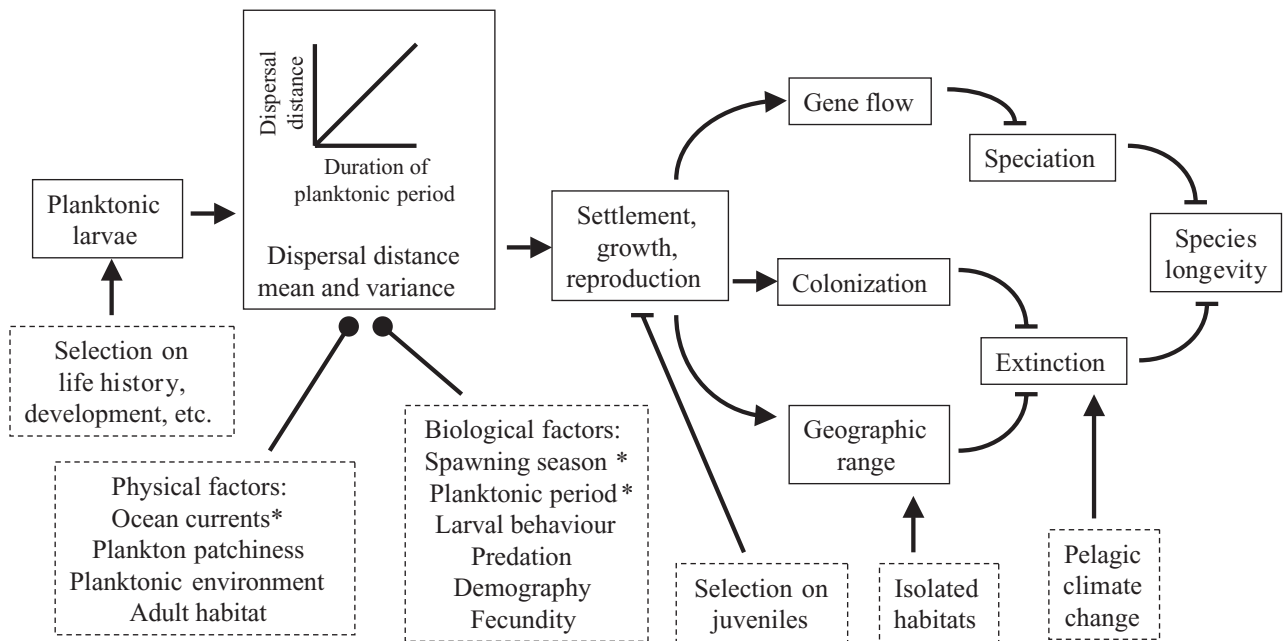*Current address: 1038 NW 32nd Street, Corvallis, OR 97330, USA. E-mail: hohenlohe@qwest.net

Figure 1. Conceptual view of the evolutionary consequences of planktonic larvae in marine animals. Arrows represent increases in rate, bars represent decreases, and circles represent the possibility of either an increase or a decrease. Some physical and biological factors that can limit or promote major processes are enclosed in dashed lines, and those specifically studied here are marked by an asterisk. See the text for further explanation.

opers may be larger than those of related planktonic developers when rare dispersal by rafting or drifting of adults (Ó Foighil, 1989; Helmuth, Veit & Holberton, 1994; Johannesson & Johannesson, 1995) establishes new populations in isolated habitats. These habitats then may have self-sustaining populations of non-planktonic species (Johannesson, 1988), while the off-spring of planktonic-developing colonists do not remain in the area to maintain a population (Efford, 1970; Johnson *et al.*, 2001). Extinction rates may be higher in lineages with planktonic larvae because of susceptibility to climate change affecting pelagic ecosystems (Valentine, 1986; Chatterton & Speyer, 1989; Poulin & Féral, 1996).

Here I focus on gene flow among populations, the restriction of which is necessary for speciation (Mayr, 1963). A relationship between dispersal potential and gene flow has been found in broad analyses of data from plants (Govindaraju, 1988) and animals (Bohonak, 1999; Dawson, 2001; Johnson *et al.*, 2001), as well as in several comparisons of closely related marine species that differ in mode of development: bivalves (Hoagland, 1986), fishes (Waples, 1987; Doherty, Planes & Mather, 1995), sea urchins (McMillan, Raff & Palumbi, 1992), sea stars (Stickle *et al.*, 1992; Hunt, 1993; Williams & Benzie, 1993), shrimp (Duffy, 1993), anemones (Russo, Sole-Cave & Thorpe, 1994), solitary corals (Hellberg, 1996), tuni-

cates (Ayre *et al.*, 1997), sea cucumbers (Arndt & Smith, 1998), gastropods (Todd, Lambert & Thorpe, 1998; Wilke & Davis, 2000), and bryozoans (Goldson, Hughes & Gliddon, 2001). Nonetheless, marine lineages with planktonic larvae exhibit high levels of species diversity (Kohn, 1983; Palumbi, 1992, 1994). Numerous factors may affect gene flow in planktonic developers, by limiting either the mean or the variance of larval dispersal distance (Fig. 1; Hedgecock, 1986; Palumbi, 1995), and their effects may be more widespread than previously thought (Benzie, 2000). These factors can be divided roughly into physical and biological categories, though the interactions between them may be most important (Jackson, 1986).

Point Conception in southern California (Fig. 2) provides a test case for examining limits to gene flow in planktonic developers. It has long been recognized as a biogeographical boundary based on species range endpoints (Valentine, 1966; Briggs, 1974; Burton, 1998). Summer surface currents are generally convergent (flowing toward each other from two directions and colliding, resulting in downwelling and/or offshore flow), and several other environmental factors show a marked shift at Point Conception (Dawson, 2001). The phylogeographical hypothesis thus predicts a genetic break within species that range across this landmark (Dawson, 2001). Nonetheless, several recent studies (Burton, 1998; Dawson, Staton & Jacobs, 2001; Miner,
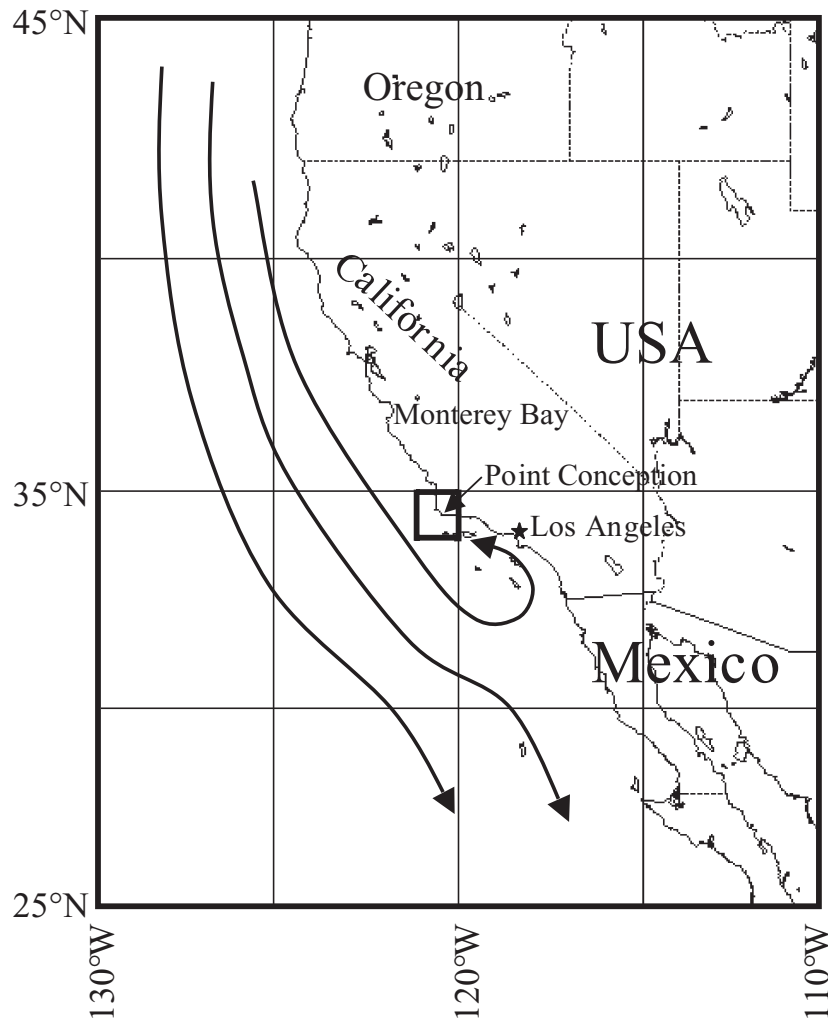
Figure 2. A portion of the west coast of North America, with the study area shown by the rectangle in the centre. Arrows represent the generalized summer current pattern (Hickey, 1998).

2002) have not found a phylogeographical boundary within species at Point Conception. Burton (1998) suggested that the faunas north and south of Point Conception are not closely related phylogenetically, so that the concentration of species range endpoints in this area does not reflect a barrier to gene flow producing *in situ* speciation. Dawson (2001), in contrast, suggested that Point Conception lies within a broader transition zone, in which Monterey Bay and Los Angeles (Fig. 2) actually represent more defined, concordant biogeographical and phylogeographical boundaries. The present-day ocean current patterns and environmental shifts, however, are still most pronounced at Point Conception and suggest the possibility of a barrier to gene flow.

Mathematical models of larval dispersal have generally fallen into a few major categories. Models of life history strategies (Vance, 1973; Jackson & Strath-

mann, 1981; Roughgarden, 1989) have identified trade-offs among egg size, number of offspring, precompetent and competent periods, and stage-specific mortality rates. These models have tested selective factors that maintain planktonic larvae. Demographic models (Roughgarden & Iwasa, 1986; Bence & Nisbet, 1989) have focused on population fluctuations among adult populations and a common larval pool, and have sometimes been built using actual life history data from a particular species (Hughes, 1990). Spatially explicit models have studied the effect of ocean currents on population dynamics and distributions either along a generic coastline (Alexander & Roughgarden, 1996; Gaylord & Gaines, 2000) or using oceanographic data from a specific geographical area (Craig & McLoughlin, 1994; Roberts, 1997). Gene flow can be added to these general model frameworks by incorporating neutral genetic variation as an additional vari-

able. Although some studies (e.g. Planes, Galzin & Bonhomme, 1996) have compared allozyme data to the predictions of generalized metapopulation models, none to date have predicted spatial gene flow patterns based on specific life history and oceanographic data.

Here I present a series of simulation models of gene flow resulting from planktonic larval dispersal, and I focus on the effects of variation in three factors: ocean current patterns, spawning season and planktonic period. The models combined several aspects of those discussed above: life history data from two intertidal gastropod species, ocean current data from the area around Point Conception, and explicit consideration of neutral genetic variation within species. They were designed to be more specific and realistic than many other modelling efforts, at some risk to generality. The models addressed two basic questions: (1) Could any of these three factors help explain the failure of empirical studies to find a genetic break at Point Conception?; and (2) What role could these three factors play, more generally, in limiting gene flow and facilitating speciation in marine animals with long-lived planktonic larvae?

METHODS

THE FOCAL SPECIES

The following simulation models used life history data from two similar, sister gastropod species, *Littorina scutulata* Gould, 1849, and *L. plena* Gould, 1849, which inhabit the high intertidal and splash zones of rocky shores along the Pacific coast of North America. The northern edge of both species' ranges is in southeast Alaska, beyond the northern boundary of the map shown in Figure 2; the southern limit of *L. scutulata* also stretches just beyond the southern boundary of Figure 2, while the southern limit of *L. plena* lies at approximately 30°N latitude. The temperate gastropod genus *Littorina* includes species with long-lived planktonic larvae (such as these two species) as well as species that develop in benthic egg masses or in a maternal brood chamber (Reid, 1996). The intertidal adults are ecologically similar and relatively sedentary, and the phylogeny of the genus is well established (Reid, 1996), so this genus is suitable for comparative studies. Genetic analyses of several *Littorina* species (reviewed by Ward, 1990) have generally followed the expected pattern of greater population genetic structure in non-planktonic developers. However, Ward's (1990) recalculation of allozyme data from Mastro, Chow & Hedgecock (1982) showed surprisingly high levels of genetic variation among populations of *L. scutulata* and especially *L. plena*. Kyle & Boulding (2000) examined haplotypes of the mitochondrial gene cytochrome b in four Pacific

species and found genetic population structure in *L. plena*, but not in *L. scutulata*. These species overlap broadly in their distribution, are remarkably similar in ecology and life history, and both release planktonic egg capsules from which planktotrophic veliger larvae hatch (Hohenlohe, 2002). Because of their similarity and their complex taxonomic history, these species have often been combined in ecological studies. Data from both species were used in constructing the models.

THE MODELS

Here I present and justify the important life history features and ocean current patterns used in these models; the mathematical and programming details are given in the Appendix. As with previous models focused on barnacles (e.g. Alexander & Roughgarden, 1996), using intertidal species allowed relatively simple mapping of potential adult habitat. An important difference from barnacle-based models, however, is that recruitment was not expected to be space-limited in *Littorina* species because adults are mobile, and because substrata do not typically approach complete coverage by these snails as they do for barnacles. Instead, adult mortality and fecundity were assumed to be density-dependent and recruitment to be density-independent. Recruitment dynamics are not well-studied in these species (Hohenlohe, 2002), but these assumptions are consistent with ecological studies (Chow, 1989).

I covered a rectangle measuring 90 by 110 km (1° longitude by 1° latitude), centred on Point Conception (Fig. 2), with a two-dimensional 1-km mesh. Adult populations were arrayed at meshpoints along the coast. To observe gene flow, two different genotypes originally populated separate sections of the coast in each run of the models (Fig. 3). These genotypes were inherited as mitochondrial haplotypes; that is, there was no recombination, and animals of one genotype produced only offspring of that genotype. In effect, the models ignored males. The genotypes were selectively neutral and had no effect on any life history parameters in any model.

At the beginning of each simulated year, each female released her annual output of offspring (with a few exceptions described below). In reality, these animals spawn broadly from spring to early autumn (Hohenlohe, 2002). However, collapsing spawning into a single event allows a precompetent period, during which larvae are developmentally unable to settle even if they encounter adult habitat, without requiring the computing power to keep track of age structure in the larval population (Gaylord & Gaines, 2000, used a similar technique). Below a total adult density (k), fecundity was density-independent, with an annual
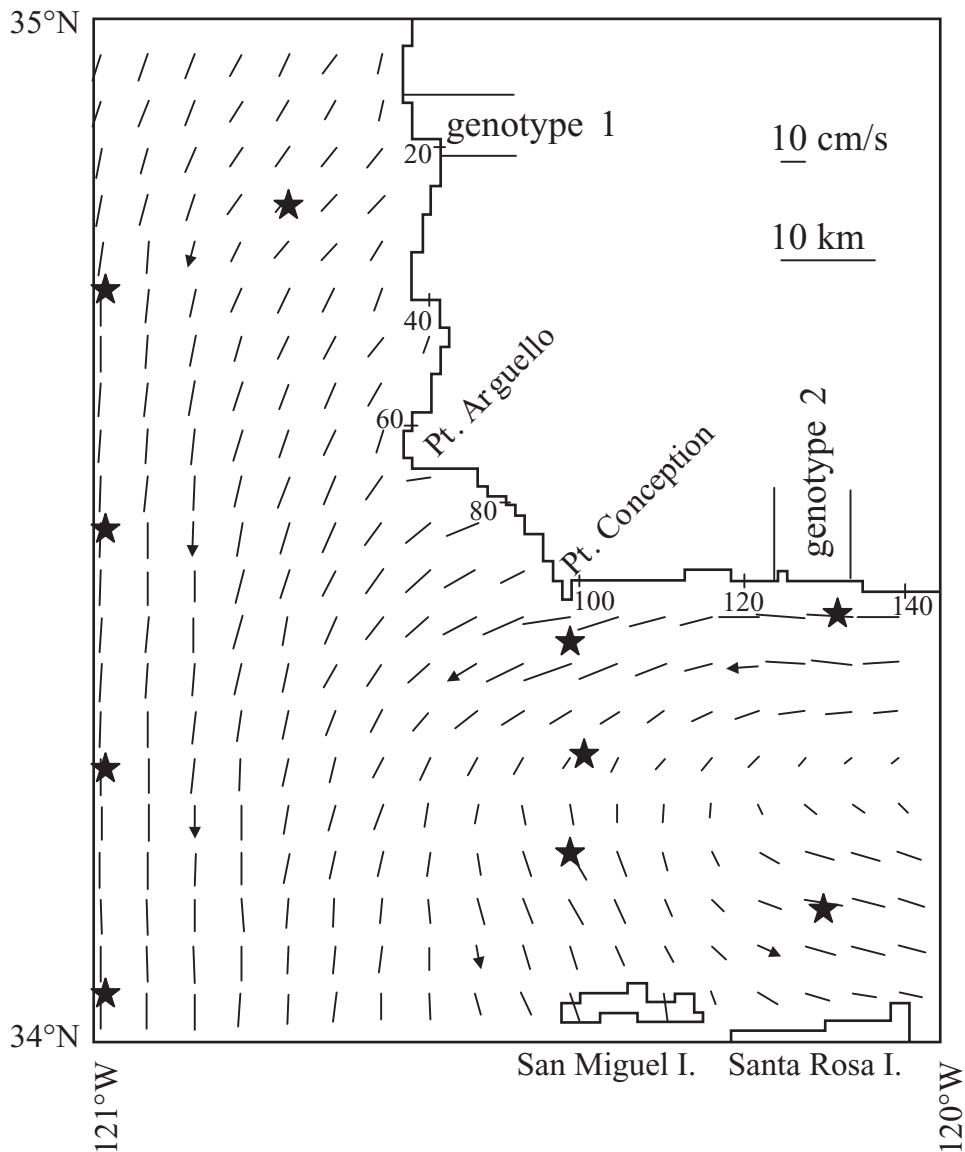
Figure 3. Map of the study area, digitized at a 1-km scale. Numbers along the coastline represent linear kilometres used in Figs 6–8, and locations of the original populations of the two genotypes are indicated. Current vectors represent the average, summer pattern in the top 10 m of the water column, showing speed and direction at their upstream end. Arrows are shown on only a few vectors for clarity. Stars represent current data points from buoys (Harms & Winant, 1998) and measured offshore flow (Hickey, 1998) used for interpolation of current patterns.

birth rate of 5000 females per female (Hohenlohe, 2002). Chow (1989) found that food becomes limiting and growth becomes density-dependent at high densities in *L. plena*, so at adult densities above k, fecundity decreased with increasing density. The first 20 days of larval life represented the precompetent period, including the week-long prehatching period during which egg capsules drift as passive, slightly negatively buoyant particles (Hohenlohe, 2002). After hatching, some growth appears necessary in these species before metamorphosis (Hohenlohe, 2002), and

this growth phase is also included in the precompetent period. After the precompetent period, larvae adjacent to suitable adult habitat settled at a rate that gradually increased, corresponding to the increase in sensitivity to settlement cues described in other animals (Doyle, 1975; Gibson, 1995). After the 40-day competent period, all larvae that had not settled were considered dead. During both the precompetent and competent periods, larval mortality occurred at a constant instantaneous rate of 0.2 day^{-1}, a rough estimate from the wide range (0.016–1.01 day^{-1}) given by Mor-

gan (1995a). This includes mortality from starvation, predation and UV damage, but not from offshore transport, which was modelled explicitly. Larvae were moved by currents, discussed below, and by diffusion. The diffusion constant of 10^4 cm^{2}s^{-1} is appropriate at the 1-km scale of the mesh (Okubo, 1971), so that currents, eddies and other water movement at scales smaller than the mesh were subsumed into this process of turbulent eddy diffusion. All boundaries in the models were absorbing; in other words, no larvae could enter from outside the boundaries, and larvae that left could not return. The larvae were treated in these models as passive particles. Gastropod veligers swim with cilia and are much less powerful swimmers than crustacean or fish larvae (Waples, 1987; Young, 1995). From a study of dispersal of bivalve veligers, McQuaid & Phillips (2000) concluded that veligers behave as passive particles and that their movement can be predicted from hydrographic data.

Larvae that settled entered the adult population and were able to reproduce the following year, as suggested by growth rates of the two species in nature (Hohenlohe, 2002). Chow (1989) found that adult mortality is greatest in winter and becomes density-dependent at high densities in *L. plena*, so in these models all adult mortality occurred outside the breeding season. Below k, adult mortality was set at 0.35 year^{-1}, at which rate 95% of adults died after the seven-year life span described by Behrens Yamada (1992); above k, mortality rates increased with total density.

All the simulations were run for 100 years, and the degree of overlap of the two genotypes after this period reflected the expected patterns of gene flow along the coast. It is important to note that the models were entirely deterministic; that is, they contained no stochastic processes. Although it is not possible to solve the models analytically, identical results were produced if the identical model was run twice, so no statistical analyses were used.

OCEAN CURRENTS

Because the focal species spawn broadly from spring to early autumn (Hohenlohe, 2002), summer current patterns were used. No data were available on the vertical position of *Littorina* larvae in nature, so for several reasons the simplifying assumption was made that they remain close to the surface. They are released from and must return to the high intertidal, and so they must therefore remain high in the water column once competent in order to encounter suitable settlement sites. Except for the prehatching period, they depend on phytoplankton for growth (Hohenlohe, 2002), so they presumably spend much of their planktonic life in the photic zone. For each current pattern,

a two-dimensional vector field was constructed to reflect average measured currents in the top 10 m.

Around Point Conception, the average summer current pattern includes the southward-flowing, alongshore California Current, which diverges from the coast near Point Conception. The Southern California Countercurrent, like a large eddy, flows north-west along the coast to meet the California Current (Figs 2 and 3; Brink & Muench, 1986; Hickey, 1998). Two scales of temporal variability have been documented. Intra-annual variability includes currents which cycle among four basic patterns (Fig. 4), spending roughly 4-day periods in each (statistically resolved by Harms & Winant, 1998). The first three of these patterns (Fig. 4A–C) are roughly similar to the average summer pattern in current directions, though not in velocity. The fourth pattern (Fig. 4D) is called the relaxation phase, because it is caused by a relaxation in wind forcing that maintains the southward-flowing California Current (Harms & Winant, 1998). During the relaxation phase, water sweeps from the southeast around Point Conception and northward along the coast. Inter-annual variability was observed in 1981 and 1984 by Chelton *et al.* (1988), when the relaxation pattern persisted throughout the summer.

In order to test the effects of ocean currents and different temporal scales of variability, the model was run under five sets of conditions, each of which included turbulent eddy diffusion:
1. Diffusion only: A control in which only turbulent eddy diffusion moved larvae in the absence of any currents;
2. Constant currents: In which average summer currents (Fig. 3) remained constant;
3. Intra-annual variation: Following the 16-day cycle described above (Fig. 4);
4. Inter-annual variation: In which one of every ten simulation years was spent in the relaxation phase (Fig. 4D), and the remaining years were spent in the constant summer pattern (Fig. 3); and
5. Combined variation: In which one of every ten years was spent in the relaxation phase (Fig. 4D), and the remaining years were spent in the 16-day cycle (Fig. 4).

PLANKTONIC PERIOD

The effect of total planktonic period was tested in additional runs of the model. As Jackson & Strathmann (1981) emphasized the importance of the ratio of precompetent to competent period in determining the likelihood of settlement, this ratio was kept constant. For these three runs, currents followed the 16-day cycle of the intra-annual variation run above, and all other conditions were identical to those described above.
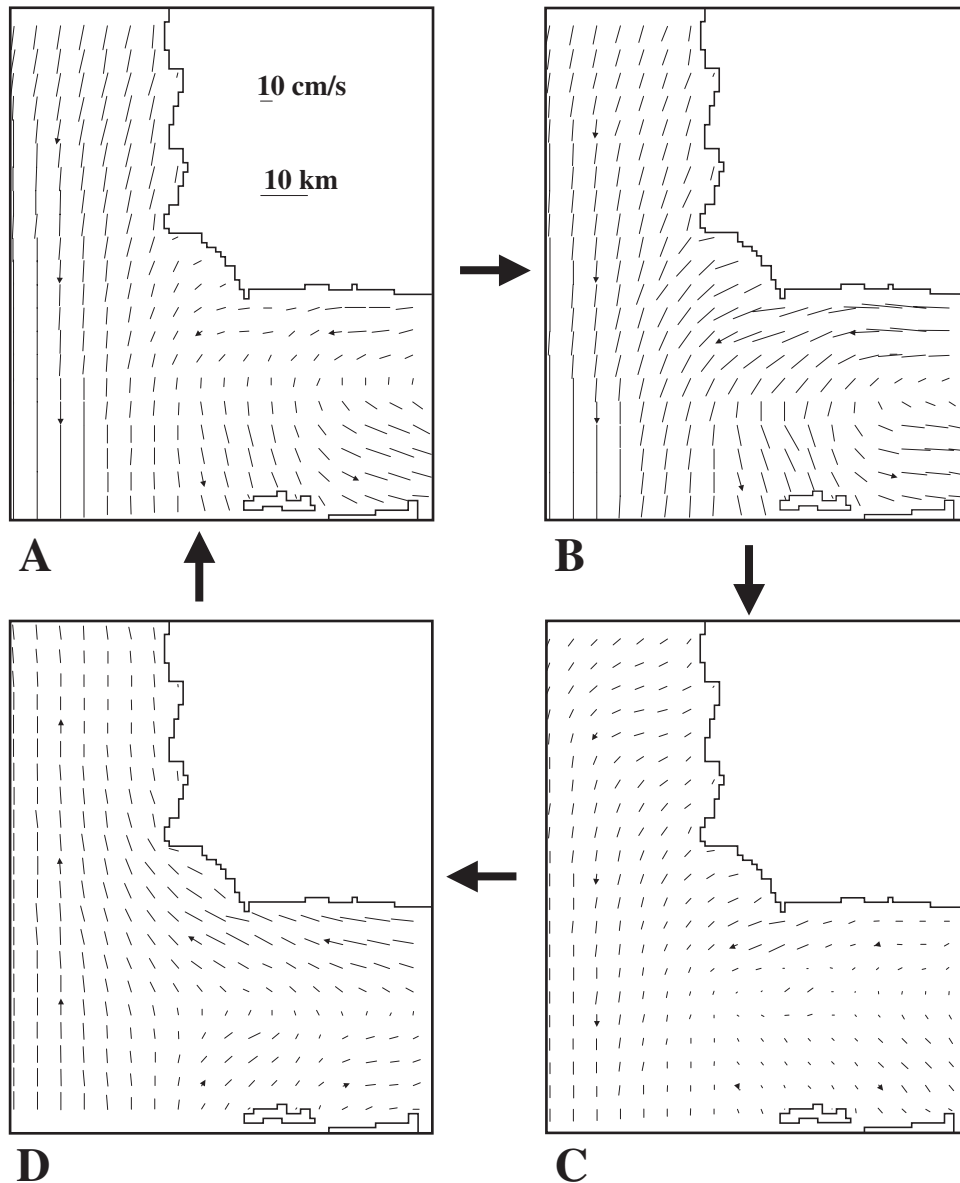
Figure 4. The 16-day intra-annual variation pattern in ocean currents described by Harms & Winant (1998). Models spent four days in each phase, moving clockwise as shown. The relaxation phase (*D*) was also used in the interannual variation models.

1. 30-day: With 10-day precompetent and 20-day competent periods;
2. 60-day: With 20-day precompetent and 40-day competent periods, identical to the intra-annual variation model; and
3. 90-day: With 30-day precompetent and 60-day competent periods.

SPAWNING SEASON

Chow (1987) observed spawning as early as February in California populations of *Littorina plena*. In order to test the effects of such early spring spawning, annual reproduction in two additional model runs was divided evenly between spring and summer seasons. In spring, the California Current typically continues around Point Conception and flows along shore to the south-east (Fig. 5; Hickey, 1979, 1998; Halliwell *et al.*, 1981). As in the other models, larvae that settled in the spring were not able to reproduce until the following year. All other features of the models described above were retained here. To ensure comparability, dividing the larvae of each reproductive season into two batches did not have any effect on the model
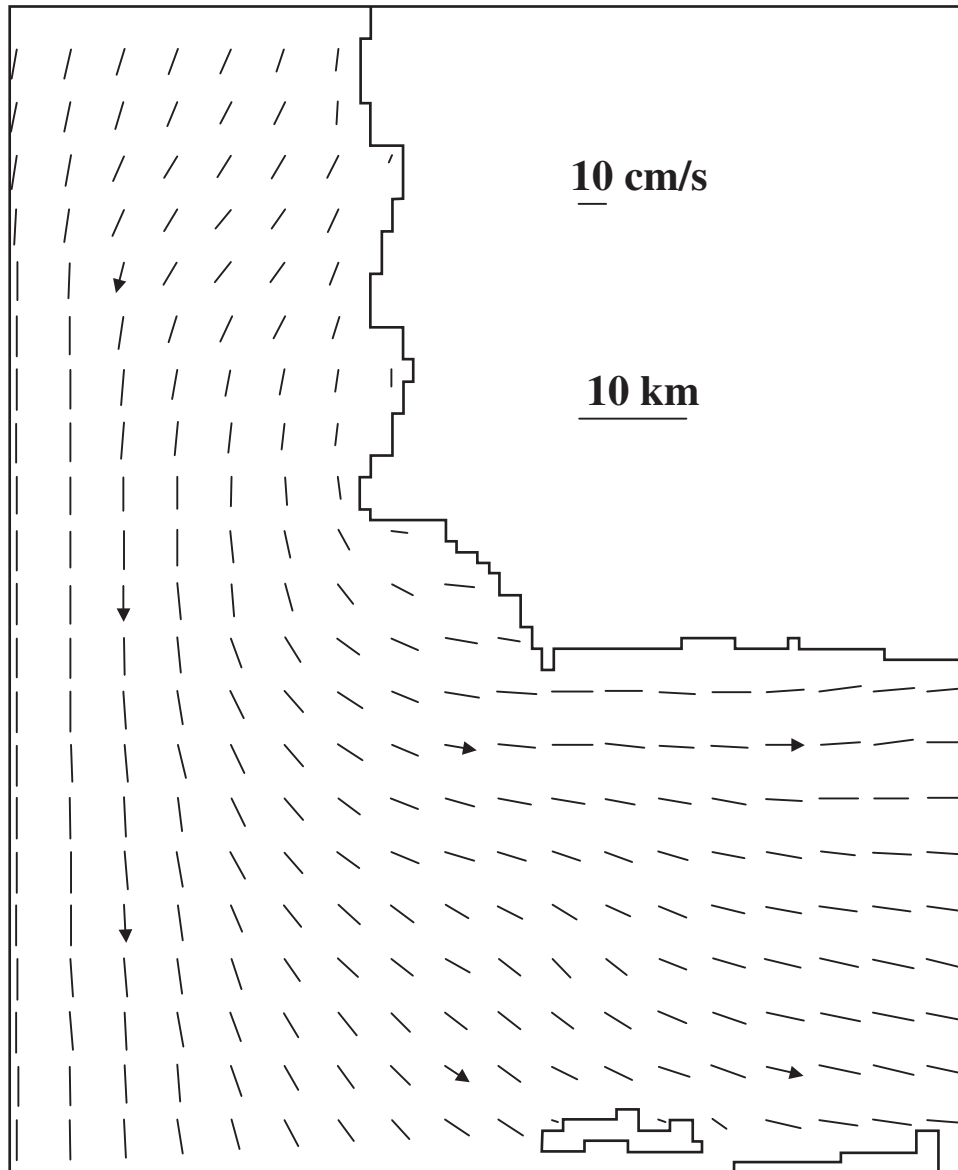
Figure 5. The spring current pattern (Hickey, 1979, 1998; Halliwell *et al.*, 1981), used in the spawning season models.

results; in a test run in which each batch of larvae encountered average summer currents, the results were identical to the constant currents model described above. Two versions of this spawning season model were run:

1. Constant summer: In which half the larvae encountered the spring current pattern (Fig. 5) and the other half encountered the constant summer current pattern (Fig. 3); and

2. Variable summer: In which half the larvae encountered the spring current pattern (Fig. 5) and the other half encountered the 16-day intra-annual cycle (Fig. 4).

RESULTS

In most of the models, the entire coastline was populated by adults within five years and populations stabilized within 50 years (Fig. 6 shows one example, the results of the constant currents model). After this point, adult densities and proportion of genotypes remained nearly stable, so that conditions at 100 years represent a long-term, more-or-less steady state. The patterns of gene flow along the coast can be seen in the proportion of genotypes. Proportions of genotype 1 in the adult population at each point along the coast after 100 simulated years for the ocean current variation
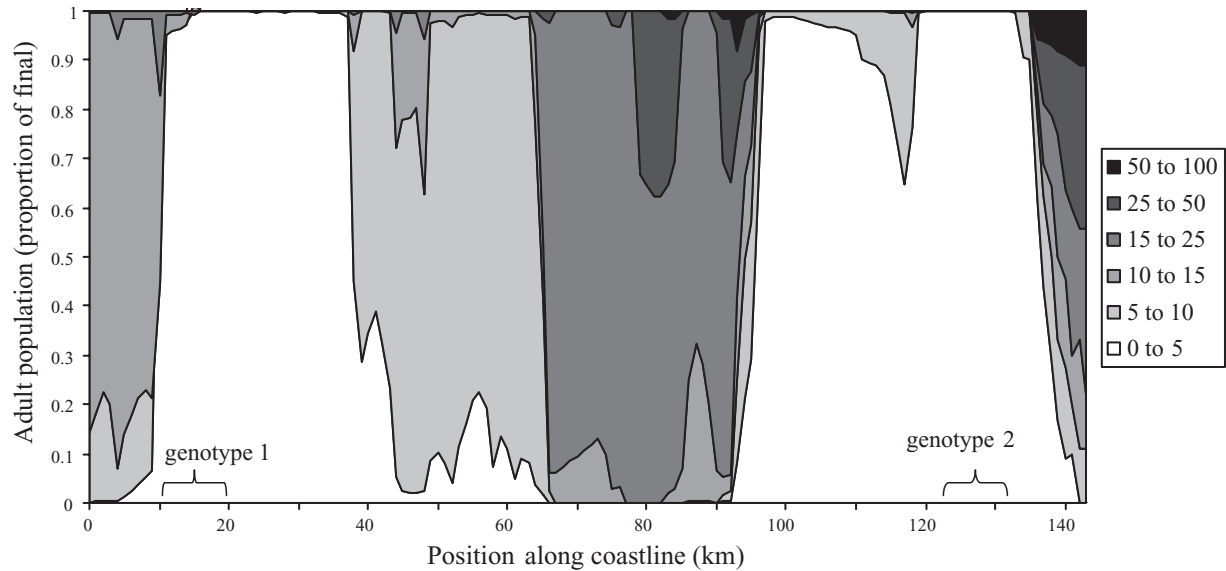
Figure 6. Gradual approach to a nearly steady state in the constant currents model. Shown in sequentially darker shades are the adult populations (combining both genotypes) along the coast, as a proportion of the final 100-year population, after 5 (white), 10, 15, 25, 50 and 100 years (black). With minor exceptions from kilometre 10–15, populations grew monotonically and never exceeded the final population size. Positions of the initial populations of both genotypes are shown, and a sharp break between the genotypes persisted at kilometre 80 (Fig. 7).
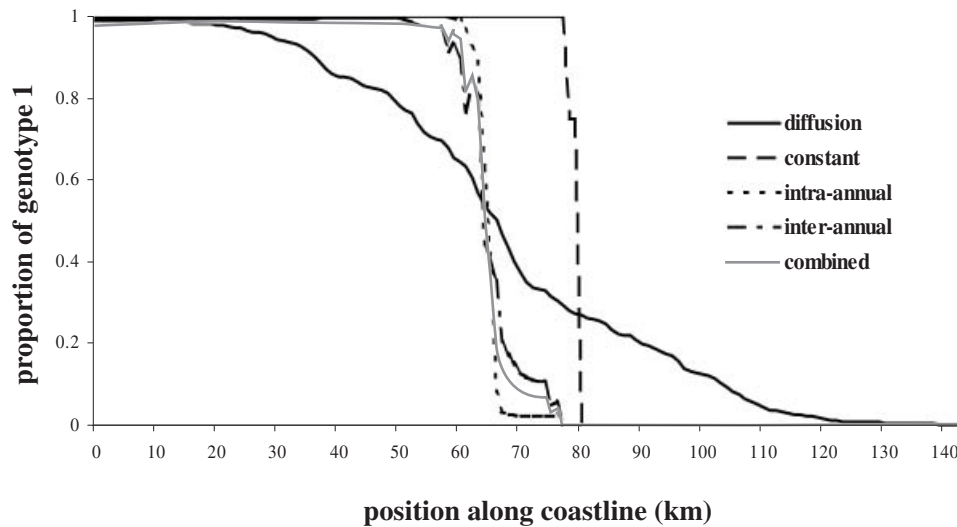

Figure 7. Proportion of genotype 1 in the total adult population at each point along the coast after 100 simulated years in the ocean current variation models. See the text for details of the five treatments.

models are shown in Figure 7. When diffusion was the only process moving larvae, a gradual cline of genotypes along the coast was produced. Constant currents in the summer pattern prevented either genotype from dispersing past a point on the coast between Points Arguello and Conception, producing a sharp genetic break. This break was pushed northward, but only slightly relaxed, by temporal variation in ocean current patterns. Inter-annual variation, which spent only 10 per cent of the time in the northward-flowing, relaxation phase (Fig. 4D), produced more mixing of the genotypes than intra-annual variation, which spent 25 per cent of the time in the relaxation phase. Combining both scales of temporal variation slightly reduced the mixing of the two genotypes compared to the interannual variation model.
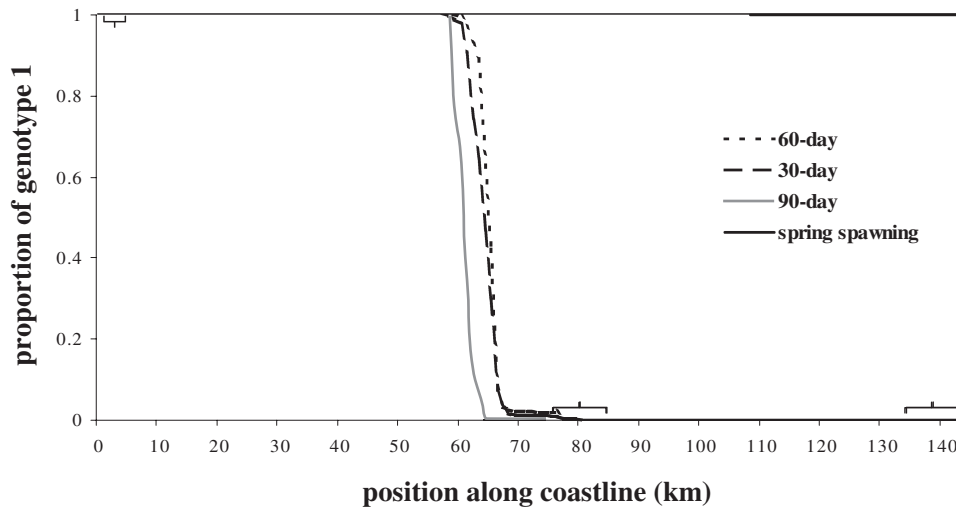
Figure 8. Proportion of genotype 1 after 100 simulated years in the planktonic period variation and spawning season models. Braces show stretches of unoccupied coast in the 90-day model. The results of the 60-day model, shown for comparison, are identical to the intra-annual model shown in Fig. 7. The results of the two spawning season models, constant summer and variable summer, were identical, so only one line is visible, showing genotype 1 along the entire coast. See the text for details of the models.

Total planktonic period did not substantially affect gene flow in these models (Fig. 8). The sharp genetic break produced by the intra-annual variation pattern with a 60-day period remained with both a 30-day and a 90-day planktonic period, although the longer period pushed the break approximately 4 km northward. The longer period model was the only one that produced large portions of unoccupied coastline, because higher total larval mortality over the longer 30-day precompetent period rendered some habitats not self-sustaining. These stretches of unoccupied habitat appeared within areas with only one genotype, so they were not associated with the break between the two genotypes.

Spawning season had a large effect on gene flow in the models (Fig. 8). In both of the models in which half of the spawning occurred during the southward-flowing spring current phase, genotype 2 was virtually eliminated from the study area after 100 simulated years, and genotype 1 occupied the entire coast of the study area. Spreading the spawning season over spring and summer current patterns produced the southward-biased gene flow pattern seen in empirical genetic work by Wares, Gaines & Cunningham (2001).

DISCUSSION

GENE FLOW

Several factors may limit gene flow in marine animals with long-lived planktonic larvae, and these factors may be roughly divided into physical and biological factors (Fig. 1). Physical factors include plankton patches that contain genetically distinct larval pools (Bucklin, 1991; Abraham, 1998; but see also Flowers, Schroeter & Burton, 2002). While it has not been documented as a barrier between established adult populations, temperature or other characteristics of the planktonic environment may exceed larval tolerances and limit dispersal (Behrens Yamada, 1977; Newman & McConnaughey, 1987; Richmond, 1990). A variety of ocean current patterns may prevent dispersal across an 'invisible barrier' (Palumbi, 1994) or limit the dispersal distance of long-lived larvae (Okubo, 1994). Larvae may be retained in nearshore circulation patterns, especially estuaries or bays (Levin, 1986; McShane, Black & Smith, 1988). A number of processes can result in periodic shoreward transport, including Ekman transport (a wind-driven circulation pattern that can result in flow perpendicular to the shore; McConnaughey *et al.*, 1992), tidal forces (Shanks, 1983; Pineda, 1991), El Niño events (Connolly & Roughgarden, 1999), and other patterns (Shanks, 1995). Sharp genetic breaks along a continuous habitat have been attributed to both convergent currents (flowing together from two directions) and divergent currents (flowing apart from a central area) (Kittiwattanawong, 1997; Rocha-Olivares & Vetter, 1999), as well as tidal fronts (Goldson *et al.*, 2001). DeWolf, Verhagen & Backeljau (2000) and Wares *et al.* (2001) have documented cases of directional gene flow as a result of consistent current patterns in the Atlantic and Pacific, respectively, creating higher genetic diversity downstream. Adult habitat, ranging from enclosed

estuaries to offshore areas exposed to larger flow patterns, affects the currents to which larvae are exposed immediately upon their release into the water column and has been correlated with levels of gene flow (Dawson, 2001).

For these *Littorina* species around Point Conception, the model results confirm that a consistent, convergent ocean current pattern can produce an effective barrier to gene flow. This barrier was shifted, but only slightly relaxed, by temporal variation in the current pattern. The scale of temporal variation plays an important role, and it appears that infrequent, longer periods of current reversal have a greater effect on gene flow than more frequent, shorter reversals. Thus, rare changes in currents, such as El Niño events that persist for a year or more (Glynn, 1988), should have a greater long-term effect than intraannual variation in current patterns. In particular, time scales of variation larger than those examined here may effectively remove barriers created by a generally convergent current pattern. Ocean current patterns vary not only on seasonal and annual scales, but also on evolutionary time scales (Moy *et al.*, 2002), so that present-day population genetic structure may not represent equilibrium under observed gene flow conditions. For example, Hellberg (1995) found that the forces of genetic drift and gene flow had reached equilibrium at small geographical scales in the solitary coral *Balanophyllia elegans*, but at a larger scale the signature of Pleistocene climatic fluctuations remained. This may make it more difficult in practice to relate gene flow patterns to ocean currents, unless long-term data on current variation are available.

Biological factors that may limit gene flow include predation (Burton & Feldman, 1981; Gaines & Roughgarden, 1987), selection on recently settled juveniles (Johnson & Black, 1984; Koehn *et al.*, 1984; Burton, 1986; Bertness & Gaines, 1993), demography (Benzie & Stoddart, 1992), and fecundity (Dawson, 2001). A variety of larval behaviours may also be important. Vertical migration is common in marine invertebrate larvae, for instance in decapod crustaceans (Young, 1995), and this behaviour may combine with vertical structure in direction and speed of ocean currents. Some estuarine species exhibit a heritable endogenous circatidal rhythm (Zeng & Naylor, 1996) or respond to exogenous tidal cues (Tankersley & Forward, 1994), and this can retain larvae near the parental habitat (Cronin & Forward, 1986) or even transport them farther into an estuary (Young, 1995). This movement would not be possible simply by horizontal swimming, because current speeds exceed horizontal swimming speeds of most larvae (Young, 1995). Larvae that remain close to the bottom may also avoid strong currents and spend most of their planktonic period close to the parental habitat (Knowlton & Keller, 1986; McShane *et al.*, 1988). These behaviours, however, are best studied in decapod crustaceans and may not play a role in other larvae, like the veligers of *Littorina* species, that swim with cilia (Levin, 1986; Young, 1995).

In general, planktonic period has been expected to correlate with dispersal distance and gene flow. For example, Waples (1987) and Doherty *et al.* (1995) found evidence for a correlation between planktonic period and gene flow in comparisons of fish species, and Dawson (2001) found the expected correlation across a wide range of taxa. However, Shulman & Bermingham (1995) found no relationship between planktonic period and gene flow in a similar study of fish species. The results of Scheltema (1989) and Emlet (1995), who examined larval dispersal and geographical range in molluscs and echinoids, respectively, provide indirect evidence against the correlation. While both authors found larger geographical ranges in species with planktonic larvae compared to those without, there seemed to be no effect of total planktonic period within planktonic developers.

The models presented here also predicted that variation in total planktonic period does not have a large effect on gene flow. Why the discrepancy? The results suggest that there is a minimum duration above which planktonic period has little effect. The relationship found by Doherty *et al.* (1995) predicted panmixis for species with planktonic periods greater than one month, and Dawson (2001) found no difference in degree of phylogeographical structure between taxa in intermediate (2–4-week) and long (≥8-week) planktonic period categories. The planktotrophic larvae of the *Littorina* species examined here require a week-long planktonic prehatching period plus significant larval feeding and growth before settlement and metamorphosis (Hohenlohe, 2002), so the 10-day precompetent period in the 30-day model is probably an underestimate. A precompetent period of several weeks is probably common among species with planktotrophic larvae (Levin & Bridges, 1995), and the models suggest that this minimum planktonic period is sufficient to produce the maximum levels of gene flow permitted by the ocean current regime at this scale. Also, Waples (1987) and Doherty *et al.* (1995) examined fish species whose larvae may use their swimming ability to retard, rather than enhance, dispersal and gene flow, compared to less powerful ciliated swimmers. The threshold planktonic period above which variation does not affect gene flow is likely to depend on life history and behaviour as well as geography and ocean currents in the species' range. It may be lower in species like gastropods whose larvae are less powerful swimmers than fish or crustaceans. It may also be lower when ocean currents are faster or

the species' range is smaller. This result bolsters previous predictions that extended planktonic development is not an adaptation for dispersal and gene flow (Strathmann, 1985), as extending the planktonic period would have little effect.

Extending the precompetent period does result in greater total larval mortality as expected (Jackson & Strathmann, 1981), which may keep some marginal habitats from being occupied because of insufficient larval supply, as in the 90-day model. However, here I assumed an equal reproductive output in all models. If there is a trade-off between precompetent period and parental provisioning, such that species with greater requirements for larval growth are able to produce more offspring with the same total energy allocation, higher numbers of offspring may balance increased total mortality and maintain similar numbers of recruits. This sort of trade-off is predicted (Vance, 1973; Christiansen & Fenchel, 1979; Strathmann, 1985), but has not been observed in these *Littorina* species. In addition, recent evidence suggests that larval mortality in nature may be much lower than previous estimates and lower than the rate of 0.2 day^{-1} used here (Johnson & Shanks, 2003).

Marine animals vary widely in the timing and length of their spawning seasons (Morgan, 1995b), and this influences the ocean currents that larvae encounter and the variability in the distance and direction of dispersal. The best examples are from estuarine systems. The tropical gastropod *Umbonium vestiarium* limits dispersal of larvae by spawning during minimum amplitude tides (Berry, 1986). Levin (1986) also showed that spawning cued to tidal rhythms in several estuarine species can produce dense patches of larvae that are retained close to the parental habitat. The model results suggest that spawning season may have a large effect on gene flow more generally. Shifting half of the reproductive output to the southward-flowing spring current eliminated the southern genotype after 100 years and removed any barrier to gene flow at Point Conception. Testing this result in nature would be straightforward with sympatric, related species that differ in length or timing of spawning season. Spawning season does not appear to play a role in the different population genetic patterns in *L. scutulata* and *L. plena* seen by Kyle & Boulding (2000), because these species do not differ substantially in their spawning seasons (Chow, 1987; Hohenlohe, 2002).

POINT CONCEPTION

These models suggested factors that may explain the failure of recent studies (Burton, 1998; Dawson *et al.*, 2001; Miner, 2002) to find a phylogeographical boundary at Point Conception. First, the spawning season results closely matched the southward-biased gene flow found in three species (two barnacles and a sea urchin) by Wares *et al.* (2001). All three of those species reproduce over several months, and two of them reproduce mostly during the spring during maximum southward flow around Point Conception (Hines, 1978; Strathmann, 1987). A similar pattern of spawning occurs in several other species along this coast (Strathmann, 1987). The best-studied Point Conception species, the copepod *Tigriopus californicus*, reproduces and is able to disperse all year long (Burton, Feldman & Curtsinger, 1979), so it experiences the full range of ocean currents around Point Conception. Second, the models suggested the importance of temporal variation in ocean currents, and actual variation in current patterns is much greater than modelled, particularly at larger time scales. The complex topography and forcing mechanisms in this area lead to abnormally high levels of variation at all temporal scales (Lynn & Simpson, 1987; Hickey, 1998), and these models incorporated only a subset of this variation. Even the observed interannual variation may not represent historic patterns (Moy *et al.*, 2002), so that phylogeographical patterns are unlikely to represent equilibrium under present conditions. Dawson (2001) also suggested other historical factors that may have produced more pronounced phylogeographical and biogeographical boundaries at Monterey Bay to the north and Los Angeles to the south.

Several other potentially important factors were not examined here, such as vertical variation in currents. As an approximation for the larvae of intertidal species, these models used currents from only the top 10 m of the water column. However, larvae that sink as little as 15 m over the inner shelf or 100 m over the outer shelf in summer may move from the southward-flowing California Current to the northward-flowing California Undercurrent (Hickey, 1998). Extending these models to three dimensions, as in the models of Smith & Stoner (1993), could test the effect of larval behaviour in these currents. In nature, other factors may also create barriers to dispersal. *Tigriopus californicus* shows limited dispersal among tidepool habitats because of high predation in the intertidal and strong selection, so that genetic structure is pronounced but the break at Point Conception is no deeper than several other breaks along the California coast (Burton, 1998). Finally, these models were limited geographically because of computing time. For example, it could be possible in nature for larvae from northern populations to ride the California Current offshore at Point Conception and back onshore farther south, beyond the boundaries of the models (Fig. 2). They or their offspring could then continue north or south along the coast.

MARINE SPECIATION

Most barriers to gene flow in the sea are 'leaky.' Biological factors, such as spawning season, larval behaviour and selection, do not erect absolute barriers to dispersal, but rather create general patterns and directions of gene flow. Ocean currents also follow predictable general patterns but vary seasonally and annually, which can allow some gene flow as at Point Conception. Cases like the Isthmus of Panama, an absolute barrier to dispersal of marine larvae, are probably the exception in the marine world (Palumbi, 1994; Lessios, 2001). In addition, ocean currents vary at millennial time scales along with climate (Sawada & Handa, 1998), so many of these leaky barriers to gene flow are transient. Nonetheless, they can leave lasting signatures on the genetic structure of populations (Hellberg, 1995; Benzie, 1999).

Incomplete barriers to gene flow may be important in the speciation process. These barriers appear to facilitate allopatric speciation in the sea, which may be obscured by subsequent overlap of species' ranges (Palumbi, 1996; McCartney, Keller & Lessios, 2000; Lessios, Kessing & Pearse, 2001). A congener to the species studied here, *Littorina saxatilis,* provides one example of sympatric divergence and speciation, where gene flow continues but is counteracted by divergent selection (Johannesson, 2001). Laboratory experiments on speciation have also emphasized the importance of diminished gene flow combined with divergent selection and the genetic mechanisms of pleiotropy or linkage (Rice & Hostert, 1993).

In many cases, reproductive isolation in marine animals can depend on very few genes that determine gamete incompatibility, so that genetic divergence sufficient to cause reproductive isolation may occur surprisingly quickly (Palumbi, 1994, 1998). More genes are likely involved in the differences in reproductive morphology that maintain reproductive isolation in animals with internal fertilization, such as *Littorina* species (Saur, 1990). Nonetheless, cryptic sibling species, which are reproductively isolated but very similar in morphology and habitat, appear widespread (Knowlton, 1993; Norris, Corfield & Cartlidge, 1996). Isolating mechanisms between sibling species include behavioural incompatibility, lack of synchroneity in reproductive activity, and fertilization barriers (Knowlton, 1993). Divergence in these characters may occur without accompanying divergence in other aspects of morphology or ecology, as seems to be the case in *L. scutulata* and *L. plena* (Hohenlohe, 2003), although divergent natural selection can also be a strong force for rapid divergence and reproductive isolation (Johannesson, 2001; Schluter, 2001). Allopatric divergence in mate-recognition systems may also be spurred by the presence of other related species (Schluter, 2001).

These observations support a conceptual model of marine speciation that includes a temporary and incomplete restriction of gene flow, caused by the interaction of physical and biological factors, combined with divergent selection and genetic factors like pleiotropy or linkage. Divergence occurs primarily in reproductive characters, perhaps only in a few key loci, and significant divergence may not occur in other characters, producing cryptic species. Because of the dispersal potential of species with planktonic larvae, ranges can quickly expand or shift when environmental conditions change. The new species, which diverged in allopatry, may become sympatric and obscure the geographical signature of their separation.

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APPENDIX

The models were written in the computer language C and run on Silicon Graphics Indy computers with a UNIX operating system. All equations in the models were rendered dimensionless by the following conversions:

1 unit of length = 100 m
1 unit of time = 10 000 s = about 1/9th of a day
1 unit of female adults = the maximum carrying capacity of one meshpoint (=1 linear km) of coastline.

Before the simulations began, the geography around Point Conception was digitized onto a 1-km mesh by defining each meshpoint as either dry land, open ocean, absorbing boundary (the open ocean edges of the map), or coastline. Meshpoints of coastline were either straight coast, inside corner or outside corner, each in one of four orientations (east-facing straight coast, north-facing straight coast, north-west-facing corner, etc.). Adult populations were tracked only at coastline meshpoints, and larval populations only at coastline or open ocean meshpoints. In the absence of detailed habitat information, the carrying capacity k was set to 1 unit of females at all points along the coastline. For the calculations below, west to east was considered the x-direction and south to north was considered the y-direction, with the origin in the southwest corner.

For each ocean current pattern, a map with a current vector at each open ocean meshpoint was constructed by interpolation using data from unevenly spaced buoys at which currents were measured (shown as stars in Fig. 2). For each meshpoint (i,j), the five closest data buoys were ranked from 1 (closest) to 5 (farthest), and the x-component of the current vector at (i,j) was calculated as:

$$x(_{i,j}) = x_1 \qquad \text{if buoy 1 is at } (i,j)$$

$$x_{(i,j)} = \frac{x_1 + x_2\left(\frac{d_1}{d_2}\right)^2 + x_3\left(\frac{d_1}{d_3}\right)^2 + x_4\left(\frac{d_1}{d_4}\right)^2 + x_5\left(\frac{d_1}{d_5}\right)^2}{1 + \left(\frac{d_1}{d_2}\right)^2 + \left(\frac{d_1}{d_3}\right)^2 + \left(\frac{d_1}{d_4}\right)^2 + \left(\frac{d_1}{d_5}\right)^2}$$

$$\text{if buoy 1 is not } (i,j),$$

where d_p is the distance of buoy p from the meshpoint, and x_p is the x-component at buoy p. The y-component of the current vector at each meshpoint was calculated similarly. Next, cross-shore (perpendicular to the shoreline) components of current vectors within 5 km of coastline were reduced by a factor of $0.2 * (5-d)$, where d is the distance of the meshpoint from the coast. While other methods of creating current maps from unevenly spaced buoy measurements, such as stream functions, were tested, this interpolation method appeared to produce the most smooth and realistic current patterns. Note that in this scheme there is no constraint of zero divergence of the two-dimensional velocity field, i.e. conservation of mass of the water, so that larvae can accumulate or be depleted at some meshpoints. While conservation of mass should be assumed in three dimensions, these models considered only the top 10 m of the water column. The substantial upwelling and downwelling in this area (Hickey, 1998) create sources and sinks of water in the surface layer, so that accumulation or depletion of larvae that behaviourally remain in the surface waters is expected.

Each year of the model included four phases (with important processes indicated for each phase): (1) release of larvae (birth rates); (2) precompetent period (diffusion, advection, larval mortality); (3) competent period (diffusion, advection, larval mortality, settlement); and (4) winter (larval mortality, adult mortality). The first and last of these phases were col-

lapsed into a single time step, while the second and third phases were solved iteratively as described below.

The number of offspring of genotype p produced at each meshpoint at the beginning of the year was:

$$b * a_p \qquad \text{if } A \leq k$$

$$\frac{b * a_p}{A + 1 - k} \qquad \text{if } A > k,$$

where a_p is the adult density of genotype p, A is the total adult density, k is the carrying capacity, and b is the low-density birth rate (5000).

During the precompetent and competent phases, the models were in the form of partial differential equations, which were converted to sets of many ordinary differential equations by the method of lines on the 1-km mesh. A time step of $\tau = 0.1$ units, or 1000 s, was used, and the ordinary differential equations were solved numerically using the second-order Euler method of the general form:

$$L(t + \tau) = L(t) + \frac{\tau}{2}(F(L(t)) + F(L(t) + \tau * F(L(t)))),$$

where $L(t)$ is the larval population of one genotype at a meshpoint, and $F(L(t))$ is the differential equation governing its change over time.

A diffusion constant of 10^4 cm^2/s was used, which is appropriate to the mesh size (Okubo, 1971) and equal to 1 in the dimensionless units used here. The diffusion term in the differential equation for larvae at meshpoint (i,j) was thus:

$$\frac{dL_{(i,j)}}{dt} = \frac{L_{(i+1,j)} - 2L_{(i,j)} + L_{(i-1,j)}}{m^2} + \frac{L_{(i,j+1)} - 2L_{(i,j)} + L_{(i,j-1)}}{m^2},$$

where m is the distance between meshpoints (1 km = 10 dimensionless units).

For advection of larvae by currents, upstream differencing was used. For example, if the current vector at meshpoint (i,j) flowed from north-west to south-east (with a positive x-component and a negative y-component), the advection term would be:

$$\frac{dL_{(i,j)}}{dt} = \frac{c_{x(i,j)}(L_{(i-1,j)} - L_{(i,j)})}{m} + \frac{c_{y(i,j)}(L_{(i,j+1)} - L_{(i,j)})}{m}$$
$$+ \frac{L_{(i,j)}(c_{x(i-1,j)} - c_{x(i,j)})}{m} + \frac{L_{(i,j)}(c_{y(i,j+1)} - c_{y(i,j)})}{m},$$

where $c_{x(i,j)}$ is the x-component of the current vector at (i,j). The last two terms in this equation derive from the chain-rule expansion of the original partial differential equation.

Larval mortality was modelled as exponential decay during the reproductive season:

$$\frac{dL_{(i,j)}}{dt} = -\mu L_{(i,j)}$$

where $\mu = 0.2$ day^{-1} (estimated from Morgan, 1995a). There was no adult mortality during the precompetent and competent phases.

Larvae adjacent to the coast settle and enter the adult population at the following rate per day:

0   during the precompetent period

$$\frac{C_t}{C_{\text{total}}} * 0.2 \qquad \text{during the competent period,}$$

where C_t is time from the start of the competent period, and C_{total} is the total length of the competent period.

During the winter phase, all larval populations were set to zero. Adult populations of each genotype at each meshpoint (i,j) were set to:

$$(1 - \lambda) * a_{(i,j)} \qquad \text{if } A \leq k$$

$$\frac{1 - \lambda}{\sqrt{A_{(i,j)}}} * a_{(i,j)} \qquad \text{if } A > k,$$

where $\lambda = 0.35$ year^{-1}, which results in 95% mortality after 7 year (Behrens Yamada, 1992). This completed one simulated year of the models.