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THE GEOGRAPHY OF MARINE LARVAL DISPERSAL: COUPLING GENETICS WITH FINE-SCALE PHYSICAL OCEANOGRAPHY

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Abstract. Efforts to understand the population dynamics of marine species with planktonic larvae have been stymied by the fact that the larvae recruiting to a location have little chance of originating from that site. Patterns of larval movement and the spatial scale of dispersal are expected to be major forces regulating the dynamics of marine populations and communities. Unfortunately, the scale and predictability of larval dispersal and its regulation by physical circulation remains unknown due largely to the impossibility of measuring dispersal in open marine environments. Here we exploit strong genetic differentiation among marine mussel populations in southwest England to measure larval dispersal among adjoining genetic patches. This approach allows estimates of larval dispersal over relatively great distances. We combine these measurements with results from a high-resolution model of coastal circulation to test the hypothesis that larval dispersal is regulated by physical circulation. We show that larval dispersal typically occurs over distances of ~30 km but in some cases was at least 64 km. The circulation model accurately predicted general patterns of larval transport between genetic regions, the scale of larval dispersal, and genetic isolation created by physical barriers to circulation. We demonstrate that physical circulation models and genetic measures of larval transport can be coupled to assess the geographic scale of larval dispersal in marine environments.

Key words: dispersal; hybrid; larval dispersal; marine larvae; marine mussels; Mytilus; *planktonic larvae; oceanography.*

INTRODUCTION

The life history of most marine species includes a larval stage that is transported in the plankton for the majority of its development, leading to the potential of dispersal over broad geographic areas (Thorson 1950, Strathmann 1985). Unfortunately, efforts to understand the population dynamics of such species have been stymied by the fact that the larvae recruiting to a location have little chance of originating from that site (Levin 1990, Nathan 2001). Therefore patterns of larval movement and the spatial scale of dispersal are expected to be major forces regulating the dynamics of marine populations and communities (Connell 1985, Gaines and Roughgarden 1985, Raimondi 1990, Gaines and Bertness 1993, Bertness et al. 1996, Eckman 1996, Wing et al. 1998, Morgan et al. 2000, Botsford 2001, Connolly et al. 2001). The scale and predictability of larval dispersal and its regulation by physical circulation in open marine environments, however, remain unknown due largely to the impossibility of measuring dispersal when larvae are minute (~200 μm) compared to the potential scale of dispersal (~km). Large dispersal capacity and larval dilution have proven insurmountable problems for direct approaches studying larval movement.

To measure larval dispersal directly it is necessary to mark massive numbers of larvae with respect to their geographic origin and to monitor their subsequent movement and recruitment. While this is generally extremely difficult, if not impossible, to do, a hybrid zone between two species of blue mussels in southwest England affords such a situation. Three genetically distinct populations abut, giving two ''genetic edges'' that can be used to detect the intrusion of foreign alleles from one population into another by larval dispersal. Relatively pure populations of *Mytilus galloprovincialis* inhabit much of the northern coast of Cornwall, while pure populations of *M. edulis* reside along the southern coast of England westward to Start Point (Hilbish et al. 2002: Fig. 1A). Between these populations is a hybrid zone, which contains mussels of mixed ancestry (Skibinski et al. 1983, Gardner 1994, Wilhelm and Hilbish 1998).

Allele frequency differences among these populations are abrupt and in known locations (Hilbish et al. 2002). Mussel populations to the east of Start Point have 100% frequencies of *M. edulis*-specific alleles; therefore, the presence of alleles specific to *M. galloprovincialis* among the spat would indicate they originated from the hybrid zone. On the other hand, *M. edulis* alleles occur at frequencies of about 5% in adult populations to the northeast of St. Ives (Hilbish et al. 2002, Skibinski et al. 1983). Significant elevation of

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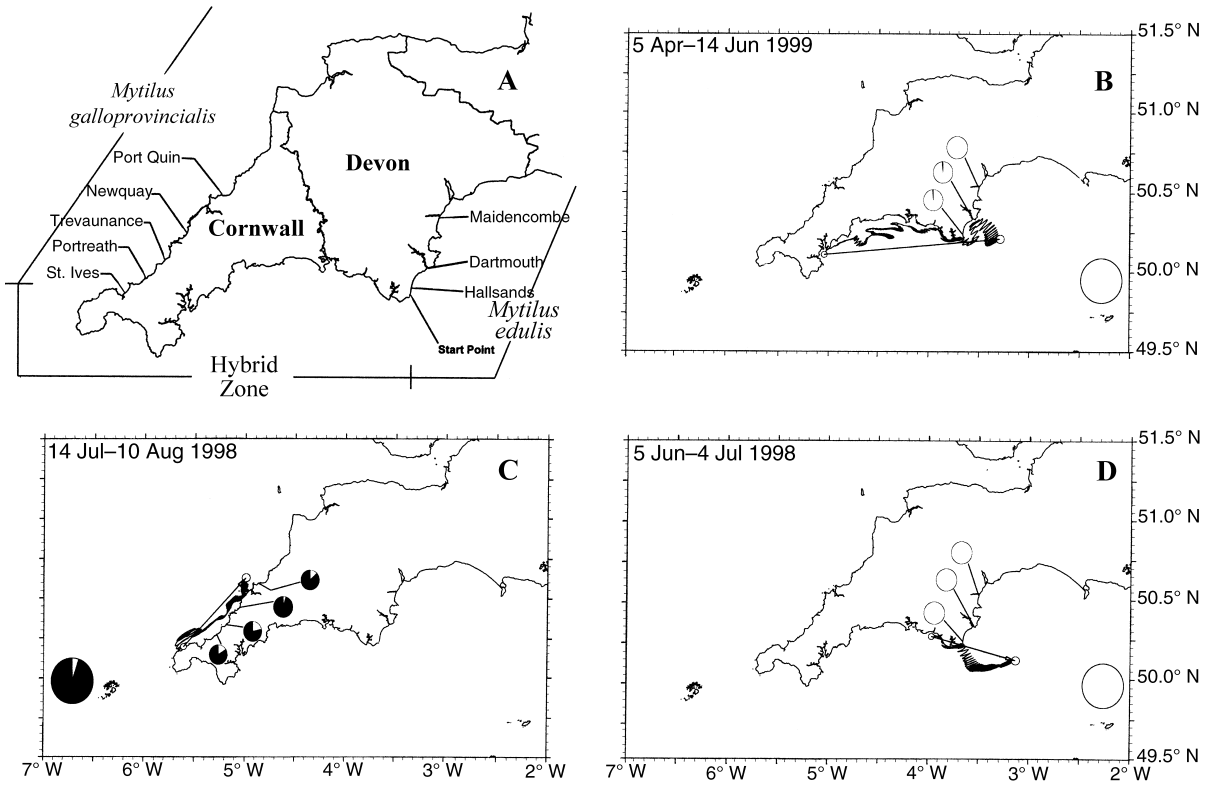

FIG. 1. (A) Map of southwest England showing the locations of sites where mussel spat were collected. Start Point and St. Ives represent the known genetic edges of the hybrid zone. Mussel populations along the coast north of St. Ives are predominantly *Mytilus galloprovincialis* while mussel populations to the east of Start Point are pure *Mytilus edulis*. (B–D) Examples of particle movement traces from a hydrographic model around southwest England. The small circle denotes the starting point of the particle while the large circle represents the ending point of the particle at the ''settlement date.'' Dates shown in the upper left corner of each plot represent the ''birth date'' and ''settlement date'' of particles shown. The large pie charts in the diagrams represent the frequency of species-specific alleles in the adult populations shown (black, *M. galloprovincialis*; white, *M. edulis*). Smaller pie charts within the maps show allele frequencies of newly settled spat collected at those sites on the ''settlement date.'' Plot B shows the rare movement of a particle from a hybrid-zone site to locations within the pure *Mytilus edulis* population. During this time period spat with *M. galloprovincialis* alleles were found at the two sites along the path of the particle, but not at the site beyond the path of the particle. Plot C shows the movement of a particle from within the hybrid-zone to several locations within the relatively pure *M. galloprovincialis* population. During this time period, three of four collection sites showed evidence of intrusion of hybrid-zone larvae into the *M. galloprovincialis* populations. Plot D gives a common result of a particle originating in the hybrid zone being advected away from shore at Start Point. There was no evidence of intrusion of hybrid larvae during this time period.

M. edulis specific alleles among the spat in north Cornwall would indicate they originated from the hybrid zone. Genetically ''marked'' larvae that cross the geographic positions demarcating the hybrid zone and either parental population provide a measure of the minimum distance the larvae traversed before settlement and subsequent recruitment.

We examined the dispersal of larvae from the hybrid zone into the *Mytilus edulis* genetic region east of Start Point and into the *M. galloprovincialis* region in north Cornwall (northeast of St. Ives) using genetic markers. We measured realized larval dispersal by examining recently settled juveniles (spat) that had settled within 10–14 days of the sample date. By measuring realized dispersal we avoid problems associated with whether larvae in the plankton are competent to metamorphose. We then compared these results with those derived from a model of the hydrography of southwest England to determine whether the dispersal of mussel larvae across the adjoining genetic regions can be predicted from patterns of surface circulation. Mussel larvae spend several weeks to several months in the plankton depending on water temperature and other environmental factors (Bayne 1976). Mussel larvae show strong negative geotaxis and positive phototaxis over most of their planktonic development (Bayne 1976) so it is reasonable to predict that they will be dispersed with residual surface currents. If larval movement is regulated predominantly by residual surface currents we expect the model to accurately predict the direction and scale

of larval movement. Alternatively, either vertical mixing of water masses or larval behavior may cause larvae to not be transported in surface currents in which case serious discrepancies between observed and predicted larval transport are expected.

Methods

Recently settled mussel larvae (spat) were collected at three sites containing pure *Mytilus edulis* adult mussel populations including Hallsands, Dartmouth, and Maidencombe, which range from 2 to 35 km east of Start Point. Collections were also made from Portreath, Trevaunance, Newquay, and Port Quin—four sites containing relatively pure *Mytilus galloprovincialis* populations. Portreath lies 14 km from the nearest known hybrid-zone site while Port Quin is 64 km away. Collections were made at all collection sites at low tide during spring tides (~2 wk interval) between June and August in 1996, and from May through October in 1998 and 1999. Spat were collected at the *M. edulis* sites in all three years but only in 1998 and 1999 at the *M. galloprovincialis* sites.

Spat were collected using both artificial (EKCO brand scouring pads (EKCO Housewares, Franklin Park, Illinois, USA) and pieces of burlap folded into thirds in each direction) and natural algal substrates (primarily *Ceramium ruburium*). Five artificial substrates were placed at mid-tidal height at each collection site by screwing them into plastic inserts. During each collection the artificial substrates were removed from the rocks, placed into labeled whirlpak plastic bags, and new substrates were deployed. Algae were collected from 10 or more microsites at each collection site, and placed in a labeled whirlpak plastic bag for transport.

Once collected the spat were removed from the substrates and preserved in 95% EtOH. Individual spat were genotyped by PCR of the *Glu*-5′ gene, which differs diagnostically between the two parental taxa (Inoue et al. 1995, Rawson et al. 1996). The PCR protocol was the same as described by Rawson et al. (1996) except using primers Me-15 and Me-16 developed by Inoue et al. (1995). The single-locus allele frequencies of the samples were then used to detect the intrusion of alleles from the hybrid zone into either of the parental taxa by comparing them to the background allele frequencies found in the adult populations. While use of a single locus inherently results in missing some second generation and beyond hybrid genotypes, it allowed us to assay more individuals and increase the power of this analysis.

We modified a two-dimensional surface circulation model, originally developed by Pingree and colleagues (Pingree and Griffiths 1980, Sinha and Pingree 1997), to project larval dispersal in southwest England. The model calculates depth-averaged currents by solving depth integrated hydrodynamics equations, which include tide generating forces and surface wind stress as a surface boundary condition to calculate a vector of water movement within each 5-km square plot of a numerical grid. The grid contains ~50 000 plots and encompasses much of the northeast Atlantic. The model has full nonlinear advection and has been thoroughly tested against data from coastal tidal gauges (Sinha and Pingree 1997). The model does not calculate three-dimensional currents or the effect of pressure gradients due to changes in the density structure of the water. We incorporated daily tidal and wind stress data to project a progressive vector over an expected period of larval development. The model was then run for three time periods for each observed larval settlement.

Larval settlement events were determined by using size/frequency distributions of collected spat. *Mytilus* spp. larvae typically settle when they reach a shell length of 250 μm (Bayne 1964). Using previously determined growth rates (Bayne 1965, Gilg and Hilbish 2000) we estimated that individuals of shell lengths between 250 and 500 μm had settled in the two weeks since the previous collection. For each observed larval settlement event, we back-calculated a larval ''birthdate'' using observed weekly nighttime mean sea-surface temperatures and the experimentally derived relationship between the rate of *Mytilus* larval development and temperature (Bayne 1965). Three estimated birthdates were used for these projections. A short projection assumed larvae settled as soon as they were developmentally competent. The long projection incorporated the maximum metamorphic delay prior to settlement, and the midrange projection assumed that larvae settled after a period equal to the average of the short and long projections. These estimates ranged from a maximum of 83 days in May to a minimum of 27 days by late summer.

A particle was released into the model from each of 20 locations on the birthdate and followed until the settlement date. The 20 locations span all three populations in southwest England (three in the *M. edulis* region, four in the *M. galloprovincialis* region, and 13 in the hybrid zone; Fig. 2A) and are approximately 15 km apart. Runs of the model were conducted for each developmental time period.

Results

Larval intrusion from the hybrid zone into pure *Mytilus edulis* populations located east of Start Point was rare. Out of a total of 39 collections containing recently settled spat (250–500 μm shell length), only seven contained any individuals with *M. galloprovincialis* alleles (Table 1). When spat of all size classes are considered, out of a total of 3507 individuals that were successfully assayed, only 15 contained an allele specific to *Mytilus galloprovincialis*. These individuals were typically heterozygous at the *Glu*-5′ locus, but one individual that settled at DM in 1999 was homozygous for the *M. galloprovincialis*-specific allele. Hybrid spat were found at each of the three collection sites and the pro-

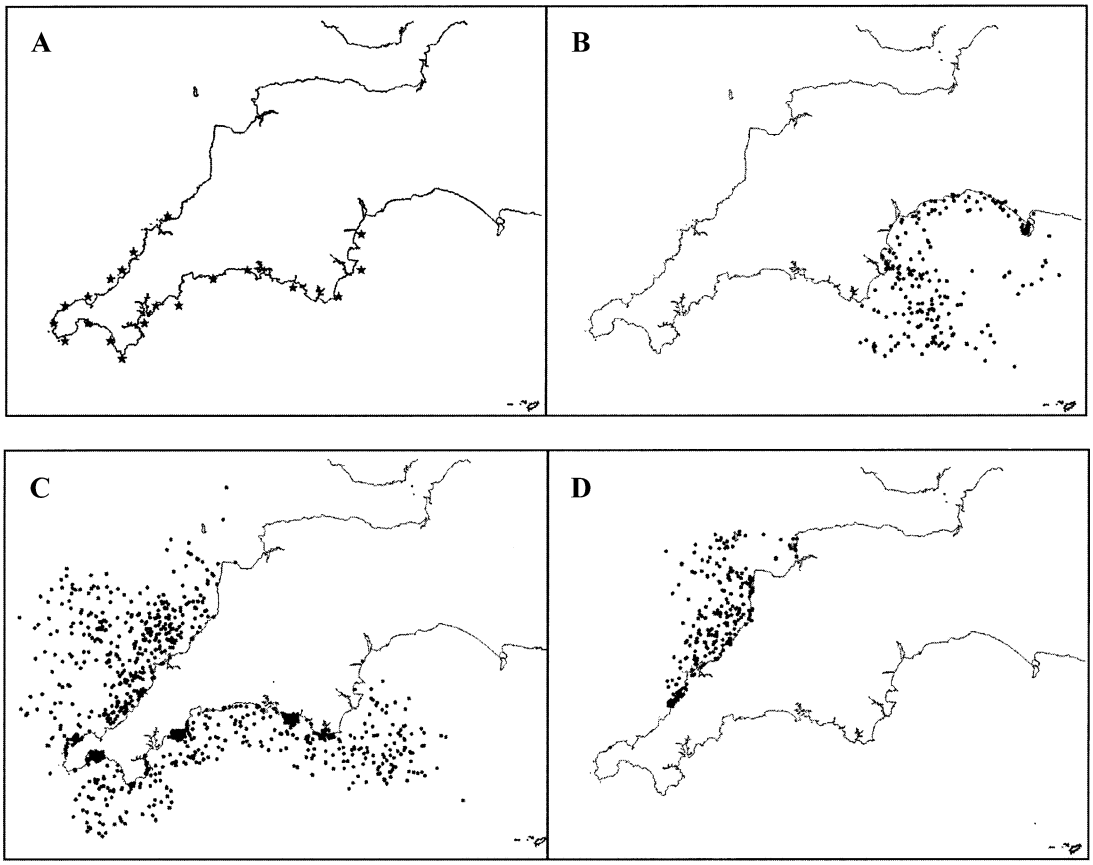

FIG. 2. (A) Release points and (B–D) endpoints of all projections of a high-resolution model of local physical oceanography. Panels B, C, and D show the endpoints of all projections that started at the sites east of Start Point, within the hybrid zone, and in north Cornwall, respectively. Particles originating within the hybrid zone are more likely to disperse, and disperse greater distances, into north Cornwall than to east of Start Point.

portions did not differ among sites in any given year (R × C G test: 1996, $G = 3.1$; 1998, $G = 0.6$; 1999, $G = 1.9$; df = 2), therefore, distance from Start Point did not strongly influence the probability that a location would receive larvae from the hybrid zone. Unfortunately, the overall lack of spat with *M. galloprovincialis*-specific alleles settling at sites east of Start Point does not provide enough statistical power to determine if there is a decrease in larval intrusion with distance into the *M. edulis* population. Consequently, hybrid larvae that settled at Hallsands dispersed a minimum of 2 km, while those that settled at Maidencombe dispersed a minimum of 34 km. It is quite likely that larvae actually dispersed much further since the above estimates only measure from the edge of the hybrid zone.

Larval intrusion from the hybrid zone into *Mytilus galloprovincialis* populations in north Cornwall is slightly more common than that observed into the *M. edulis* populations. Five samples of primary spat out of a total of 22 showed evidence of larval intrusion: four in 1998 and one in 1999 (Table 1). Each of these collections had significantly higher frequencies of *M. edulis* specific alleles than the adult populations in the region. Interestingly, three of the four collections in 1998 that showed significant elevation in the frequency of *M. edulis* alleles were on the same date (9 August) suggesting they were part of the same intrusion event. The genotype frequencies also support the intrusion hypothesis in each of the cases where significant deviations in allele frequency were observed (Table 2). Significant elevations in *M. edulis* allele frequencies were due primarily to an overabundance of *M. edulis*/*M. edulis* homozygotes—genotypes which are extremely rare in the adult mussel populations in north Cornwall.

Trevaunance was the only site in north Cornwall to receive two distinct spat settlements that had significantly elevated frequencies of *M. edulis* alleles in the same year (1998). When pooled across collection dates only the spat from Trevaunance in 1998 showed significant elevation of *M. edulis* allele frequencies over the year (Table 1). In fact, spat collected at Trevaunance in 1998 had more than three times the expected frequency of *M. edulis* specific alleles. One of the sites showing signs of significant immigration from the hybrid zone was Port Quin, which is the site furthest from

TABLE 1. Frequency of *Mytilus edulis*-specific alleles on different collection dates at locations in north Cornwall and east of Start Point.

A) East of Start Point

Collection date	Frequency, by location		
	Hallsands	Dartmouth	Maidencombe
1996			
5 June			0.993 (75)
16 June	1.00 (22)		0.989 (46)
5 July			1.00 (15)
18 July	1.00 (6)		1.00 (17)
1 August		1.00 (8)	
All spat	0.989 (87)	1.000 (30)	0.997 (523)
1998			
22 May		0.981 (27)	1.00 (191)
8 June	1.00 (17)	1.00 (32)	1.00 (94)
23 June		1.00 (54)	0.996 (121)
1 July	1.00 (12)	1.00 (7)	1.00 (48)
23 July		1.00 (1)	1.00 (9)
9 August			1.00 (2)
21 August			1.00 (11)
All spat	1.000 (157)	0.998 (259)	0.999 (1275)
1999			
19 May		1.00 (4)	1.00 (46)
28 May		1.00 (4)	1.00 (36)
13 June	0.990 (49)	0.986 (35)	1.00 (128)
29 June	1.00 (10)	1.00 (11)	1.00 (40)
11 July	1.00 (14)	1.00 (39)	0.981 (26)
29 July	1.00 (48)	1.00 (15)	1.00 (11)
10 August			1.00 (2)
All spat	0.996 (239)	0.995 (314)	0.998 (623)

B)North Cornwall

Collection date	Frequency, by location			
	Portreath	Treavaunance	Newquay	Port Quin
1998				
9 August	0.167 (9)†	0.217 (30)†	0.046 (11)	0.132 (19)†
21 August		0.143 (28)†	0.063 (8)	0.069 (51)
6 October	0.048 (63)	0.00 (31)	0.040 (100)	0.00 (6)
All spat	0.060 (133)	0.172 (163)†	0.078 (173)	0.077 (97)
1999				
29 August	0.00 (1)	0.167 (12)†	0.038 (105)	0.00 (1)
10 September		0.00 (9)	0.011 (47)	
25 September	0.043 (35)	0.00 (1)	0.00 (8)	
24 October	0.00 (2)		0.125 (8)	
All spat	0.071 (63)	0.071 (42)	0.054 (634)	0.115 (13)

Notes: The number of newly settled (<2 wk) spat assayed from each sample is given in parentheses. ''All spat'' includes both newly and previously settled (>2 wk) spat sampled over the entire season.

† Samples from north Cornwall that contained *M. edulis* alleles at significantly higher frequency than expected from background adult populations.

the hybrid zone, indicating that these larvae dispersed a minimum distance of 64 km.

The observed frequencies of *M. edulis* specific alleles in the spat, along with the frequencies characteristic of the adult populations for each region, can then be used to estimate the proportion of larvae each population contributed to the larval pool. Using the formula

$$F_S = X(F_A) + (1 - X)(F_B)$$

where F_S is the observed allele frequency of the spat, and F_A and F_B are the allele frequencies characteristic of each contributing adult population, the proportion of larvae each population contributed can be determined. While background allele frequencies are known for both the *M. edulis* and the *M. galloprovincialis* populations, the hybrid zone is more difficult to determine. Estimates based on the size/frequency distributions of adults at hybrid-zone locations, and the relationships between both fecundity and allele frequency with size give an estimate of *M. edulis* allele frequency of ~0.70. Spat collected from hybrid-zone locations, however, have much higher frequencies of *M. edulis* alleles, typically 0.90 (Gilg and Hilbish 2003). This discrepancy may be due to selection favoring individuals with *M. edulis*-like genotypes.

TABLE 2. Expected and observed single-locus genotype frequencies of primary mussel spat collected at sites in north Cornwall.

Site	Date	Genotype			*n*
		EE	EG	GG	
Expected		0.002	0.092	0.885	
Observed					
Portreath	9 Aug 1998†	0.111	0.111	0.778	9
	9 Oct 1998	0.000	0.095	0.905	63
	28 Sep 1999	0.029	0.029	0.943	35
Treavaunance	9 Aug 1998†	0.100	0.233	0.667	30
	25 Aug 1998†	0.071	0.143	0.786	28
	9 Oct 1998	0.000	0.000	1.000	31
	31 Aug 1999†	0.167	0.000	0.833	12
	13 Sep 1999	0.000	0.000	1.000	9
Newquay	9 Aug 1998	0.000	0.091	0.909	11
	25 Aug 1998	0.000	0.125	0.875	8
	9 Oct 1998	0.000	0.080	0.920	100
	31 Aug 1999	0.010	0.057	0.933	105
	13 Sep 1999	0.000	0.021	0.979	47
	24 Oct 1999	0.125	0.000	0.875	8
Port Quin	9 Aug 1998†	0.105	0.053	0.842	19
	25 Aug 1998	0.039	0.059	0.902	51
	9 Oct 1998	0.000	0.000	1.000	6

Notes: E represents the allele specific to *M. edulis* while G represents the allele specific to *M. galloprovincialis*.

† Samples that show evidence of larval intrusion from the hybrid zone based on allele frequency data.

While the presence of selection in the larval stage will influence our estimates of dispersal rates it will not affect our estimates of dispersal distance.

Using the estimate of 0.70 suggests that hybrid populations contributed approximately 1.3% of the larvae settling at locations east of Start Point in 1996, 0.4% in 1998 and 1.1% in 1999. The proportion of larvae immigrating from the hybrid zone into *M. galloprovincialis* populations in north Cornwall ranged from 7.8% in 1998 to 1.1% in 1999. Individual settlement periods, however, contained much higher proportions of immigrating larvae in both regions. For significant individual intrusion events the proportion of larvae originating from the hybrid zone and immigrating into populations east of Start Point ranged from 1.3% to 6.3%. In north Cornwall the proportion of immigrants from the hybrid zone during significant intrusion events ranged from 12.6% to 25.7%. If the allele frequency estimate of larvae produced by the hybrid zone is incorrectly low we have underestimated immigration rates into the *M. edulis* populations and overestimated immigration rates into the *M. galloprovincialis* populations.

One method of testing which of the allele frequency estimates is valid is to test the observed genotype frequencies during intrusion events for fit to a two population mixing model. Calculating the dispersal rate using the equation above, and assuming that both the north Cornwall and the hybrid-zone mussel populations are mating in Hardy-Weinberg equilibrium, we can estimate expected genotype frequencies using both allele frequency estimates of 0.7 and 0.9. The genotype frequencies differed from the mixing model in two cases: once with the 0.7 allele frequency estimate (Trevaunance, 31 August 1999, $G = 4.39$, df = 1, $P < 0.05$) and once with the 0.9 estimate (Trevaunance, 9 August 1998, $G = 3.97$, df = 1, $P < 0.05$). Thus, the outcome is robust no matter which allele frequency estimate is used.

In each collection period where intrusion was detected with genetic markers, intrusion was also predicted by the model projections. In several cases, the correspondence was striking. For example, for the settlement events observed in mid-June 1999, the model predicted larval transport from the hybrid zone to the region between Hallsands and Dartmouth (Fig. 1B). Spat obtained from these locations contained *M. galloprovincialis* alleles, indicative of larval intrusion, but Maidencombe, which was beyond the range of the projection, did not. Likewise, settlement events observed in north Cornwall in early August 1998 were predicted to contain larvae originating from the hybrid zone and genetic evidence of larval intrusion occurred at three of the four sample sites (Fig. 1C). It is important to note, however, that there is a large amount of variation in tracks produced in a given time period simply due to the geographical variation in release points. Therefore, it is possible to pick tracks that show many different results. In fact, the model predicted larval intrusions on several occasions, especially into north Cornwall, where there was no genetic corroboration. Detection of larval intrusion events are, however, dependent upon the presence of larvae in the plankton at the release point of the model and their subsequent

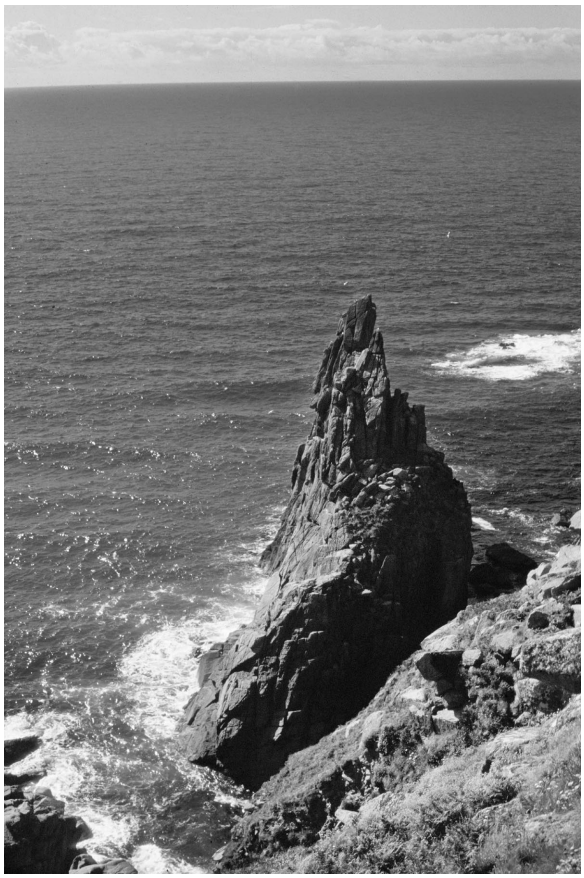

PLATE 1. Lands End, in the southwestern corner of Cornwall, greatly affects the circulation patterns and mussel distribution in the region. Prevailing winds from the south and west typically drive currents into Lands End whre they split paths with flow to the northeast along the northern coast of Cornwall and to the east along the southern shores of Cornwall and Devon. In the immediate area of Lands End and the Lizard, the currents are very dynamic, and mussel populations tend to be sparse. This is also a transitional area between the hybrid zone and the *M. galloprovincialis* population. Photo by T. J. Hilbish.

settlement at the sample sites. If the adults in a certain location did not spawn or the larvae died prior to settlement or settled at a location other than our collection sites, the model would predict larval intrusions that are never observed.

While specific predictions of larval intrusion events by the model were not completely reliable, the model accurately predicted the direction, relative rates, and distances of larval dispersal. The general directions of water movement predicted by the model were extremely consistent for each site, with little variation from March through October and no inter-annual variation (Gilg and Hilbish 2003). Particles released from sites within the *M. edulis* population remain east of Start Point in Lyme Bay (Fig. 2B) and particles released from sites along the northern coast of Cornwall typically travel to the northeast, away from the hybrid zone (Fig. 2D).

While most of the particles released from hybrid-zone sites remain within the hybrid zone, a large number penetrate the population boundaries of both parental species (Fig. 2C), but do not do so equally. The results of the model indicate that Start Point is a strong barrier to larval dispersal from the hybrid zone eastward. Most projections for this region predicted that larvae originating in the hybrid zone would be deflected offshore by Start Point and lost (Fig. 1D). Only 10% of the projections originating within the hybrid zone terminated east of Start Point and only 2% were within 10 km of shore where they may have resulted in significant settlement (Fig. 2C). The lack of movement of larvae from the hybrid zone across Start Point is, therefore, likely due to the presence of a circulation barrier (see Plate 1). On the other hand, the model predicts that dispersal from the hybrid zone into north Cornwall should be relatively common: 31% of the projections originating in the hybrid zone terminated in north Cornwall and 13% terminated within 10 km of the coast where settlement may be significant. Particularly striking is the prediction that larvae produced at Portreath and Trevaunance (the sites closest to the hybrid zone) will be dispersed to the northeast and that settlement at these locations is likely to contain larvae that originated from within the hybrid zone (Fig. 2). Portreath and Trevaunance received 80% of the documented genetic intrusions into north Cornwall and 57% of the larval settlement events at these sites contained larvae from the hybrid zone compared to only 11% of the events at Newquay and Port Quin. This suggests a decrease in larval intrusion with distance from the source.

Averaging the intrusion distance of all observed genetic intrusions, the genetic data show that larvae originating in the hybrid zone dispersed a mean distance of 24.3 km into populations east of Start Point and 30 km into north Cornwall. Maximum dispersal distances inferred from genetic intrusions into each region were 35 and 64 km, respectively. While these calculations are influenced greatly by the distance of our collection sites from the hybrid zone, the model predicted remarkably similar scales of dispersal in these regions. Using only those projections which crossed a population boundary, the model results predict mean dispersal distances from the edge of the hybrid zone to the populations east of Start Point of 23.1 km and of 53.9 km into north Cornwall. The projections of the model showing intrusion into the *M. edulis* populations east of Start Point do not usually disperse further than Maidencombe, the collection site furthest from the hybrid zone. Projections into north Cornwall, however, frequently went further than the sample site furthest from the hybrid zone (Port Quin). Therefore our sampling design may have underestimated the distance of genetic intrusions into north Cornwall.

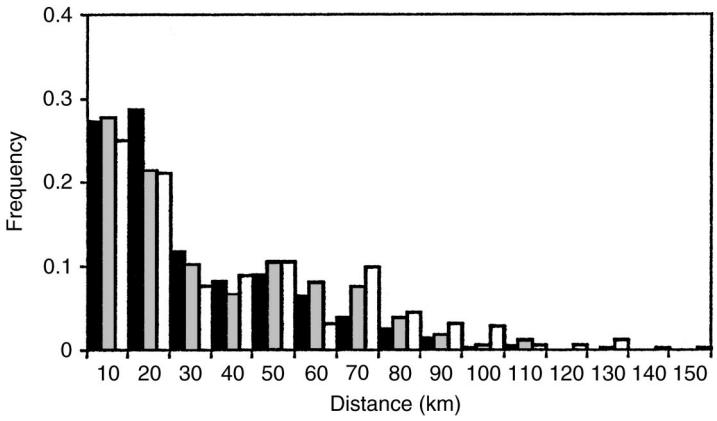

FIG. 3. The frequency of model projections that traveled a given distance for three estimates of developmental time (short, black; medium, gray; long, white). Only those model projections that terminated within 10 km of shore were included.

The close correspondence between the model predictions of larval transport across the genetic regions and the results based on genetic intrusions allow us to use the results of the model to estimate mean larval dispersal and its variance. This is important, since the use of larval intrusions across genetic boundaries to estimate dispersal is biased in two ways. First, larval dispersal may be underestimated since the distance of a genetic intrusion was measured in relation to the nearest edge of the hybrid zone; it is likely that larvae originated well within the hybrid zone and thus traveled farther than the genetic inference suggests. Second, dispersal may be overestimated since genetic intrusions can only be detected if larvae migrate a sufficient distance to cross a genetic boundary, meaning short dispersal distances may go undetected. The distribution of the length of all predicted larval trajectories that ended within 10 km of shore, including those that did not cross genetic boundaries, is given in Fig. 3. Development time significantly affected predicted larval dispersal, but not dramatically; the mean dispersal distance achieved by larvae with short, middle, and long development times were 26.0, 30.4, and 35.5 km, respectively. The longer the dispersal time, the more likely a projection would reverse its direction, thus limiting the distance traveled. Middle development times probably provide the most realistic estimates of larval dispersal since they neither require larvae to settle as soon as they are competent nor delay settlement for the maximum time possible. Over 70% of middle development time projections dispersed <50 km and only 2.1% dispersed over 100 km. Therefore, it seems reasonable to conclude that mussel larval dispersal in this region typically occurs on a scale of 60 km or less.

DISCUSSION

The use of a genetic marker allowed us to measure the dispersal of mussel larvae from a hybrid-zone population into neighboring parental populations. Hybrid larvae were found in small numbers at locations east of Start Point, whereas the adult populations in that area lack individuals with alleles specific to *M. galloprovincialis*. Genetic intrusion events were also detected in the *M. galloprovincialis* populations of north Cornwall, and significant elevation of *M. edulis* specific alleles was observed in several cohorts at three of the four collection sites and in both years. While individual settlement events in both regions could consist of 15% or more foreign larvae, the proportion of foreign larvae tended to be much smaller over the course of the year. The annual proportion of foreign larvae in collections, however, differed between regions. The maximum observed proportion of foreign larvae settling at sites in north Cornwall was nearly twice that observed east of Start Point. This indicates that Start Point is a relatively strong barrier to dispersal.

Though dispersal from the hybrid zone into each of the parental populations was relatively slight, its mere presence suggests that the hybrid zone should be expanding. This does not appear to be the case, as the present position of the hybrid zone in southwest England has been stable for at least 20 years (Skibinski et al. 1983, Gardner 1994, Hilbish et al. 2002). This suggests that the presence of selection against individuals with heterospecific alleles in both of the parental populations is limiting expansion of the hybrid zone.

The patterns shown in the hydrographic model corresponded well to the patterns in the genetic data, suggesting that the general patterns of mussel larval dispersal in this region can be accurately predicted using the local physical oceanography. Consistent with the genetic observations, the model predicts higher rates of dispersal from the hybrid zone into north Cornwall than east of Start Point. The dispersal distances into north Cornwall are also predicted to be greater than into the *M. edulis* population. In fact, based on the model results, it is surprising that there is not genetic evidence of even greater dispersal rates from the hybrid zone into north Cornwall. Detection of dispersal from the hybrid zone into the *M. galloprovincialis* populations along the northern coast of Cornwall, however, is more difficult than in *M. edulis* populations, since it is harder to detect the presence of foreign alleles against a consistently low, but nonzero, background allele fre-

quency. Consequently, settlements containing small numbers of intruding larvae will go undetected in north Cornwall. Thus, it seems likely that intrusion events from the hybrid zone into north Cornwall are more common than our genetic results suggest.

While the model appears to accurately predict the general patterns of larval movement throughout the region, its ability to predict specific events is limited. This limitation is due to both a lack of precision of our dispersal measurements and inadequacies of the model itself. Since we cannot track dispersal of larvae from fertilization to settlement the predictive power of the model will be in question. Only if we knew the precise birth and settlement dates and locations would we be able to determine if the model accurately predicts specific dispersal tracks. Since we are estimating dispersal time from laboratory observations and are determining the presence or absence of larval intrusions from sites >10 km apart, the best we can hope for is accurate predictions of the general patterns of larval dispersal rates, directions, and distances. This the model does very well. The model also lacks any estimate of mortality rate, so specific events predicted by the model may not occur due to death prior to settlement.

The timing of larval settlement also differed between the two parental populations. Spat were found in *M. edulis* populations from May through July, but were not present in the *M. galloprovincialis* populations until August. This difference, however, is not due to temporal differences in circulation patterns. Circulation patterns for each site were remarkably consistent throughout the seasons (Gilg and Hilbish 2003). The model shows that larvae dispersing from the hybrid zone across Start Point originated in the eastern part of the hybrid zone, while larvae dispersing into north Cornwall originated from the westernmost sites in the hybrid zone near the Lizard and Lands End (see Plate 1). The timing of reproduction of the hybrid-zone populations also appears to follow a geographic trend with eastern sites reproducing prior to western sites (Gilg and Hilbish 2003). Therefore, the differences in the timing of reproduction explain the differences in settlement time between the two regions.

The mean dispersal distances projected by the model correspond very well to estimates from the genetic data. The bulk of the projections traveled 30–60 km with a small number dispersing greater than 100 km. The mean intrusion distances based on genetic observations were 21.5 km east of Start Point and 30.0 km into north Cornwall; with a maximum observed intrusion distance of 64 km. While the genetic estimates are influenced by our choice of collecting sites, and may therefore be underestimates, the mean dispersal distances observed in this study are similar to those reported in two other systems (Koehn et al. 1980, Hilbish 1985, McQuaid and Phillips 2000). McQuaid and Phillips (2000) calculated dispersal distances of between 50 and 150 km from the rate of range expansion of the invading mussel *M. galloprovincialis* in South Africa. Hilbish (1985) and Koehn et al. (1980) estimated larval intrusion of $\sim$30 km from the comparison of juvenile and adult allele-frequency clines in the mussel *M. edulis*. Thus all three studies suggest dispersal of mussel larvae typically occurs on a scale of 30–50 km.

We have shown that local hydrodynamics accurately predicts both the scale and direction of larval dispersal. The hydrographic model predicts physical barriers to transport that coincide with boundaries between genetically differentiated populations. In some cases, the model accurately predicted episodes of larval transport between genetic patches. The correspondence between the results of the genetic analysis of mussel larval movement and of the physical circulation takes a large step toward solving a fundamental problem of marine population biology—Where do larvae come from? Our results indicate that the supply side of mussel population dynamics can be predicted from the local currents, the prevailing winds, and mussel populations within a range of $\sim$60 km. What is even more intriguing is the fact that this simple two-dimensional model, with no estimates of larval mortality or diffusion, was still able to accurately predict dispersal directions and distances. Therefore, similar models can potentially be used to explore larval dispersal in areas without significant genetic differentiation among populations. Since most marine species have a dispersing larval stage and lack the kind of genetic differentiation observed in this hybrid zone, the results of this study are far reaching. Other hydrographic models can likely be adjusted for similar uses and for other marine invertebrates with planktonic dispersal. The results of these models may also be used as a null hypothesis to determine whether larval behavior (i.e., vertical migration) can act to produce dispersal patterns inconsistent with neutral transport. These results are vital to resolving the scale of marine metapopulation dynamics and the design of reserves for marine conservation.

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