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The influence of coastal topography, circulation patterns, and rafting in structuring populations of an intertidal alga

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Abstract

Understanding the dispersal processes that influence genetic structure in marine species requires estimating gene flow in a dynamic, fluid environment that is often poorly characterized at scales relevant to multiple dispersive stages (e.g. spores, gametes, zygotes, larvae, adults). We examine genetic structure in the marine alga *Fucus vesiculosus* L., which inhabits moderately exposed shores in the northern Atlantic but releases gametes only under sunny, calm conditions. We predicted genetic structure would correlate with coastal topography because weather frequently varies across coastal promontories on the Maine shore when *F. vesiculosus* is reproductive, which causes one side to experience high levels of water motion (= no gamete release) while one side is calm (= gamete release). Furthermore, we expected that the effect of low dispersal capacities of gametes and zygotes would result in spatial genetic structure over short distances. Using surface drifters, we characterized near-shore circulation patterns around the study sites to investigate whether directionality of gene flow was correlated with directionality of currents. We found significant genetic differentiation among sites sampled at two different peninsulas, but patterns of differentiation were unrelated to coastal topography and there was no within-site spatial structuring. Our genetic and near-shore circulation data, combined with an examination of gamete longevity, support the dependency of gene flow on storm-detached, rafting, reproductive adults. This study highlights the significance of rafting as a mechanism for structuring established populations of macroalgae and associated biota and demonstrates the importance of coupling population genetics' research with relevant hydrodynamic studies.

Keywords: dispersal, *Fucus*, microsatellites, near-shore circulation, population genetics, rafting

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Introduction

Genetic connectivity in populations of sessile marine organisms is influenced by environmental factors that control the dispersal of gametes and larvae (e.g. Strathmann 1990; Yund 1995; Hilbish 1996; Palumbi *et al*. 1997; Bohonak 1999; Grosberg & Cunningham 2001). For example, hydrodynamic conditions affect the concentration and dispersal of gametes, zygotes, and larvae (reviewed by Levitan & Peterson 1995; Shanks *et al*. 2000; Yund 2000), and several studies demonstrate that duration of the planktonic larval stage is negatively correlated with spatial differentiation of population genetic structure (e.g. Waples 1987; Bohonak 1999; Riginos & Victor 2001). Despite the importance of the hydrodynamic regime, however, only a few population genetic studies of marine organisms consider the strength and direction of currents at adequate spatial scales (e.g. Palumbi *et al*. 1997; Billot *et al*. 2003; Gilg & Hilbish 2003; Viard *et al*. 2006), such as the large-scale currents that affect gene flow among distant locations in species with an open-ocean, larval stage (Palumbi *et al*. 1997; Gilg & Hilbish 2003; Sotka *et al*. 2004; Ketchington *et al*. 2006). Few studies have considered the effect of near-shore hydrodynamics on population genetics, although it is well recognized that the spatial and temporal heterogeneity of local circulation around coastal promontories and within embayments may facilitate or impede dispersal of propagules (Denny *et al*. 1992; Largier 2003; McCulloch

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& Shanks 2003). Offshore currents are particularly unlikely to predict dispersal capability and explain gene flow for intertidal species that lack planktonic developmental stages. Here, we consider population genetic structure of the intertidal alga *Fucus vesiculosus* L. in the context of coastal topography, near-shore circulation, and a critical re-examination of life-history stages that are likely to contribute to gene flow in this species, which is one of the most abundant species of moderately exposed shores of the north Atlantic.

Fucus vesiculosus is a dioecious (i.e. males produce sperm; females produce eggs) macrophyte that reproduces primarily from early September to late December on the coast of Maine, a period when weather is variable and storms are common. Environmental conditions should have strong effects on population structure in fucoids because high levels of water motion inhibit gamete release in fucoid algae (Serrão *et al*. 1996; Pearson *et al*. 1998); gamete release is therefore restricted to times when the local habitat is calm (Serrão *et al*. 1996; Berndt *et al*. 2002). This restriction is predicted to limit gene flow because fertilization success is close to 100% and occurs rapidly after release of gametes (Brawley 1992; Serrão *et al*. 1996; Pearson *et al*. 1998, 2004; Berndt *et al*. 2002). Furthermore, gene flow may also be limited, because zygotes are negatively buoyant, secrete sticky wall materials and adhere to substrata within 8–24 h post-fertilization, depending upon temperature (Kropf 1992), and planktonic developmental stages are absent.

Life-history and reproductive characteristics of *F. vesiculosus* might cause population genetic structure to reflect coastal topography at the geographical scale of a side of a coastal peninsula because prevailing zonal winds may create unfavourable conditions (i.e. high water motion) for gamete release on one side of a coastal peninsula while the opposite side of the peninsula is in a wind shadow where calm conditions allow gamete release (Berndt *et al*. 2002; J. F. Muhlin, M. A. Coleman, T. A. V. Rees, S. H. Brawley, in preparation). Consequently, spatial reproductive isolation may occur due to coastal topography. We hypothesized that population structure would be correlated with coastal topography if isolation of gamete release were the dominant process influencing genetic structure in *F. vesiculosus*. For example, we predicted that on the many north–south coastal peninsulas on the Maine coast, opposite sides of a coastal point would be significantly different from each other. That is, populations on the western side of a coastal peninsula would be significantly different from populations on the eastern side, in spite of the relatively low distances that would separate eastern or western populations; furthermore, because gametes could not disperse between two coastal peninsulas on calm days, high genetic structure among the same sides of coastal points could be predicted. Regardless of topographic correlation, and in consideration of data suggesting short-scale dispersal in fucoids (e.g. Kendrick & Walker 1991; Williams & Di Fiori 1996), we expected high levels of genetic structure that follow a pattern of isolation by distance, because this is common in marine species lacking high dispersal capacities at the gametic or larval stages (*sensu* Wright 1943; Johnson & Black 1998; Bohonak 1999; Bernardi 2000).

Using microsatellite markers, we analysed the genetic structure of *F. vesiculosus* among sites on the eastern and western sides of two coastal Maine peninsulas, while characterizing near-shore circulation patterns and geographical potential for fucoid dispersal with surface drifters. Large batches of marked oranges (fruit) were released to measure dispersal potential on a coarse scale, while inexpensive drifters equipped with GPS (Global Positioning System) were used to obtain finer resolution of dispersal potential and trajectories. Our goal was to test the degree to which directionality of surface currents and/or persistence of oceanic features (e.g. topographic eddies) explained the genetic structure revealed by microsatellite markers. In addition, we examined longevity of *F. vesiculosus* eggs and sperm and viability of zygotes produced from crosses with aged gametes in order to evaluate how these life-history stages contribute to gene flow. Our data suggest the importance of prezygotic factors (i.e. rafting reproductive adults) on genetic structure, a result that may be important for understanding genetic structure in a number of other marine species that are closely associated with fucoid communities.

Materials and methods

Sampling

A total of 320 *Fucus vesiculosus* individuals were harvested between October 2002 and May 2005 from two sites on the eastern and western sides of the Schoodic Peninsula (hereafter, Schoodic Point; 44°20′N, 68°03′W) and from two sites on the eastern and western sides of the Pemaquid Peninsula (hereafter, Pemaquid Point; 43°50′N, 69°30′W), Maine, USA (eight sites in all; Fig. 1). Both coastal peninsulas lie within the Gulf of Maine and were selected as replicate peninsulas to test whether genetic structure was correlated with coastal topography. Schoodic Point is separated from Pemaquid Point by about 500 km of convoluted coastline comprising bays, estuaries, and other coastal peninsulas and a point-to-point linear distance of about 140 km. Within a peninsula, sites were separated by 1–9 km (Fig. 1, identical sites to those of Coleman & Brawley 2005). Sites along each peninsula were located at similarly scaled distances from each other (Fig. 1). At each site, three transect lines (20 m each; total shore sampled = 60 m) were placed parallel to the shore through the middle of the *F. vesiculosus* zone. Mature, reproductive plants were sampled from each 20-m transect, which was

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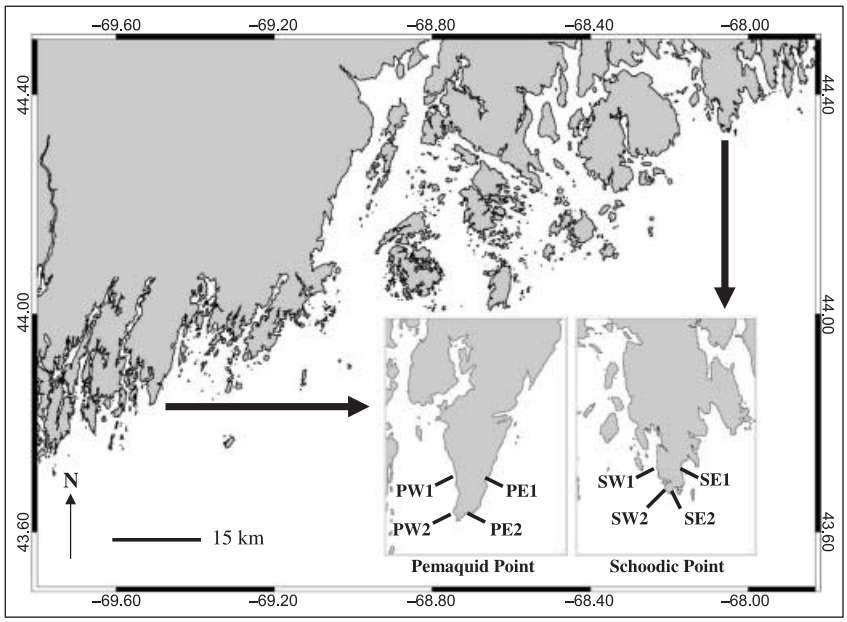

Fig. 1 Study sites at Pemaquid and Schoodic Points, Maine, USA. Sites are coded with P (Pemaquid) or S (Schoodic), and E (east) or W (west) with discrete numbers (1, 2) for sites on the same side of the points.

marked off in 0.5-m increments, using a random numbers' table to collect seven individuals from Transect 1, six individuals from Transect 2, and seven individuals from Transect 3 (i.e. $n = 20$ individuals). To avoid potential sampling of different individuals with coalescent holdfasts, we traced a single branch of each individual down to its holdfast. Twenty individuals per site were collected in 2002. An additional 20 individuals were collected for each site between 2003 and 2005 using the same methodology as in 2002 (i.e. total $n = 40$ individuals). All collected plants were placed in plastic bags and returned on ice to the laboratory.

DNA extraction and microsatellite genotyping

Deoxyribonucleic acid (DNA) was extracted from the meristematic tissue at the apical tips of each individual using a hexadecyltrimethyl ammonium bromide (CTAB)/Sephaglas (Amersham Pharmacia Biotech) procedure (Coyer *et al*. 2002). Individuals were genotyped using six microsatellite loci that are polymorphic in *F. vesiculosus* (Engel *et al*. 2003): L20, L38, L58, L78, L85, and L94. Polymerase chain reactions (PCR) were performed in 20 µL volumes containing 2 mM $MgCl_2$, 100 µM dNTPs (Invitrogen), 250 nM forward primer (2:3 labelled:unlabelled primer, Operon), 250 nM reverse primer (Operon), 0.5 U *Taq* (Promega), 1 × buffer (Promega), 5 µL of 0.5 ng DNA μL^{-1}, and water to adjust volume to 20 µL per reaction. Optimal thermocycler conditions were used as specified in Engel *et al*. (2003). PCR products were determined on an ABI 377 (for loci L38, L94, L78, L85, and L58) and ABI 3730 (L20) automated sequencer. Alleles were scored using GENESCAN, GENOTYPER, and GENEMAPPER 4.0 (Applied Biosystems).

Data analyses

Because populations were sampled at two different time periods (once in 2002 and again between 2003 and 2005), the homogeneity of temporal subsamples was checked at each site by comparing allele distributions of subsamples using an exact test (GENEPOP version 3.4, Raymond & Rousset 1995). None of the sites showed significant differences in allele distributions (after Bonferroni correction) between temporal subsamples (data not shown). Therefore, all genetic analyses and results given in the Results represent a pooling of individuals across the two collection times at each site.

Allele frequencies were estimated for each locus at all collection sites. Standard genetic diversity indices were calculated at each site and at all six loci; the number of alleles at each locus, gene diversity (H_E, *sensu* Nei 1978), observed heterozygosity (H_O) and fixation indices (F_{IS}) were computed using FSTAT 2.9.3.2 (Goudet 2002). In addition, heterozygote deficiencies and excesses were tested using 1000 randomizations of alleles among individuals. Genetic independence of loci at each site and over the entire data set was also checked using FSTAT software.

To investigate the organization of genetic diversity within and among sites, Weir & Cockerham's (1984) unbiased estimators of *F*-statistics were employed using FSTAT: the genetic variance among individuals in the total sample (F_{IT}) was broken down into the correlation of alleles within individuals within sites (F_{IS}), and the genetic differentiation among sites (F_{ST}). Pairwise (among sites) F_{ST} values were tested by permuting individuals among sites using FSTAT, and probabilities were corrected for multiple

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comparisons using Bonferroni corrections (Rice 1989). These pairwise comparisons were performed for each peninsula separately (four sites at a time).

To determine sources of significant genetic variation based on topography (eastern vs. western sides of each peninsula), an analysis of molecular variance (AMOVA) was performed using ARLEQUIN version 3.11 (Excoffier *et al*. 2005). We used this analysis to partition genetic differentiation, F_{ST}, into a between-sites (F_{CT}) and between-sites-within-(eastern or western) sides (F_{SC}) component. We computed 95% confidence intervals for *F*-statistics using GDA version 1.1 (Lewis & Zaykin 2001).

To test whether genetic distance increased with geographical distance within a site, spatial genetic structure analyses using SPAGEDI 1.2 (Hardy & Vekemans 2002) were employed. Relatedness coefficients between individuals were based on pairwise kinship coefficients (Ritland 1996). This software is designed to characterize associations between genetic relatedness and spatial distances, therefore permitting tests of isolation-by-distance processes (Hardy & Vekemans 2002). Specifically, the program computes pairwise statistics of genetic relatedness for all pairs of individuals and then regresses them on spatial distances (and/or their logarithm). The regression slopes can then be used to investigate dispersal distance parameters in the context of an isolation-by-distance process (Rousset 1997, 2000; Hardy & Vekemans 1999; Hardy & Vekemans 2002). To test for significant spatial genetic structure, permutation tests were performed. These permutation tests are equivalent to a Mantel test between matrices of pairwise genetic and spatial statistics. Because sites were sampled independently at two times, there was low positional accuracy for each plant location for a combined-time analysis. Therefore, spatial genetic structure analyses were not pooled. However, the statistical power of pairwise comparisons among 20 individuals was high, as each sampling time resulted in 190 pairwise comparisons. For each collection time (Time A and Time B, respectively), we performed 5000 permutations of individual locations among all individuals and tested the regression slopes. Because *F. vesiculosus* may occupy a vertical range in the intertidal zone greater than gamete or zygote dispersal distances, we evaluated the log-transformed geographical distances.

Characterizing circulation patterns and measuring dispersal potential

As a first-order approximation, we used labelled oranges (citrus fruit) to define the circulation patterns at our field sites in order to predict fucoid dispersal and to test whether the population structure revealed by microsatellites would be congruent with orange recovery. Oranges were ideal surface-current drifters; they are buoyant, biodegradable, easily detectable, and inexpensive, making many trials possible. During fall 2004 and 2005, 1700 labelled oranges were released over 17 deployments (100 oranges per deployment) near the study sites at Schoodic and Pemaquid Points. Throughout the reproductive season of *F. vesiculosus,* oranges were released as close to high tide as possible and deployed either from shore or from a lobster boat, 50–100 m away from the shore. Recovery of labelled oranges was a coordinated (and well-publicized) citizen-based effort. Each orange had a unique letter and number written on it and a message telling how to report the discovery of an orange.

To obtain finer resolution and to plot the continuous trajectory of surface drifters at shorter timescales, we developed and deployed two GPS-equipped surface drifters (further details available from J. Muhlin; J. F. Muhlin, R. A. Weatherbee, R. Stessel, in preparation). Both GPS drifters were deployed by boat 100 m from shore, left undisturbed, and later retrieved. Deployments occurred four times during August–October 2006, with each deployment and retrieval spanning 4–5 h. To evaluate whether the GPS drifters behaved similarly to oranges and rafts of floating fucoids that can form when adults are detached from the intertidal zone by storms, we released one dozen oranges with each drifter deployment, as well as five tagged *F. vesiculosus* individuals for three out of the four deployments. Upon drifter recovery, detection of oranges and tagged seaweed in the vicinity of the drifter was noted.

Surface circulation patterns are influenced by wind and tides. To control for tidal currents, GPS drifters were deployed as much as possible during the same phase of the tide. Wind data (wind speed and wind direction) from nearby Gulf of Maine Ocean Observing System (GoMOOS) buoys were obtained to understand the influence of wind conditions at the time of drifter deployments.

Gamete viability analysis

Effective longevity of gametes in *F. vesiculosus* was determined by releasing sperm from males and eggs from females into natural seawater and using these gametes in fertilization assays at different time points. Gametes were obtained by osmotic shock of *F. vesiculosus* receptacles (= reproductive tips of adults; Brawley 1991), and receptacles used to generate each batch of gametes were a subset of a pooled collection from 25 males and another pooled collection from 25 females, all from Schoodic Point. Fertilization assays were carried out at 15 °C in 10 mL seawater with a 5000:1 sperm-to-egg ratio (Brawley 1991). The first fertilization between freshly released gametes (t_o) was followed by subsequent fertilization of ageing sperm × fresh eggs, ageing eggs × fresh sperm, and fresh sperm × fresh eggs (controls), using batches of newly released gametes at each subsequent

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Table 1 Measures of genetic diversity and estimates of F_{IS} at the four polymorphic loci in *Fucus vesiculosus* at all eight sites. Significance levels are shown for F_{IS} values. **$P < 0.001$; N_A, number of alleles; H_E, Nei's gene diversity; H_O, observed heterozygosity (based on minimum sample size = 36). *P* value, probability associated with Fisher's exact test combined across loci on contingency tables of observed subsample allele distributions, none of the values was significant (Bonferroni-corrected threshold *P* value = 0.006 for $\alpha = 0.05$)

		Site							
		Schoodic Point				Pemaquid Point			
Locus		SW1	SW2	SE1	SE2	PW1	PW2	PE1	PE2
L20	*N*	40	38	39	40	39	39	36	39
	N_A	3	3	5	4	3	3	3	4
	H_E	0.397	0.444	0.353	0.289	0.555	0.471	0.585	0.213
	H_O	0.175	0.290	0.205	0.325	0.385	0.231	0.333	0.154
	F_{IS}	0.560**	0.348	0.419	–0.124	0.307	0.510**	0.431	0.276
L38	*N*	40	40	40	40	40	40	40	40
	N_A	3	2	3	3	2	3	3	3
	H_E	0.571	0.486	0.521	0.537	0.453	0.531	0.421	0.496
	H_O	0.550	0.500	0.625	0.450	0.475	0.650	0.475	0.750
	F_{IS}	0.037	–0.029	–0.199	0.162	–0.050	–0.224	–0.128	0.043
L78	*N*	40	40	40	40	40	40	40	40
	N_A	4	3	2	1	2	2	2	2
	H_E	0.347	0.244	0.182	0	0.354	0.049	0.119	0.025
	H_O	0.250	0.225	0.200	—	0.300	0.050	0.125	0.025
	F_{IS}	0.279	0.076	–0.099	—	0.152	–0.013	–0.054	0
L94	*N*	40	39	40	40	40	39	38	40
	N_A	5	3	3	3	4	3	3	3
	H_E	0.695	0.654	0.618	0.671	0.663	0.668	0.665	0.668
	H_O	0.625	0.667	0.675	0.500	0.775	0.718	0.763	0.675
	F_{IS}	0.101	–0.020	–0.092	0.255	–0.168	–0.074	–0.148	–0.010
P value		0.273	0.581	0.962	0.404	0.697	0.669	0.033	0.284
	Total *N*	40	40	40	40	40	40	40	40
	Total N_A	17	13	15	13	13	13	13	14
	Mean H_E	0.507	0.482	0.419	0.374	0.506	0.430	0.448	0.351
	Mean H_O	0.400	0.421	0.426	0.319	0.484	0.412	0.424	0.401
	Multilocus F_{IS}	0.204**	0.080	–0.018	0.148	0.045	0.041	0.052	0.052

time point (sperm = 6 time points, eggs = 16 time points; see Results) until fertilization success was lower than 10% for either sperm or eggs. The ageing gamete suspensions were kept in 500-mL beakers at 15 °C. Fertilization success (%) was evaluated by staining eggs with the fluorescent dye Calcofluor White (CFW, Sigma Aldrich) from a 0.01% stock to a final dilution of 0.0001%, approximately 2 h after gametes were mixed ($n = 3$ replicate dishes/treatment with 100 eggs counted per dish). Eggs/zygotes were determined with UV light excitation at a Zeiss IM-35 microscope; CFW stains zygotes but not eggs (Brawley 1991). Additionally, embryonic development and the lethal occurrence (%) of polyspermy (= an egg fertilized by multiple sperm) were compared in crosses of 50-h old eggs × fresh sperm with controls (fresh sperm × fresh eggs). After approximately 2 weeks post-fertilization, the health of the zygotes was evaluated and the percentage of polyspermic embryos was calculated. Polyspermy can be determined in fucoid embryos by a characteristic stunted morphology that develops before death (Brawley 1991).

Results

Population genetic structure in comparison to coastal topography

Twenty alleles were characterized across six microsatellite loci; two loci (L85, L58) were monomorphic in the populations surveyed in this study. The other four loci (L20, L38, L78, L94) had three to five alleles per locus (Table 1),

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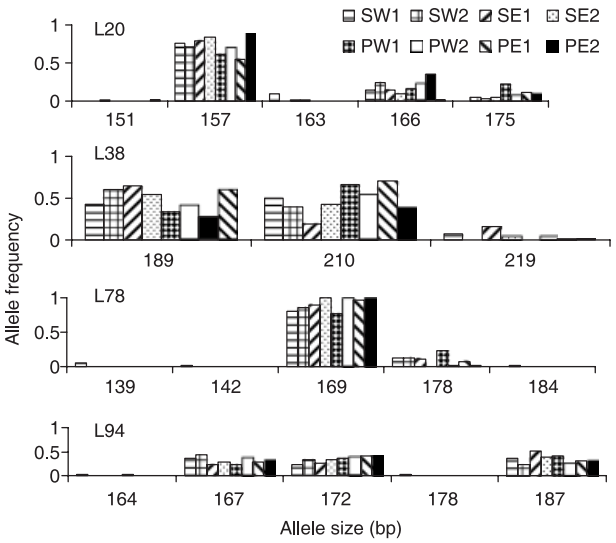

Fig. 2 Allele frequencies at the four polymorphic loci. L85 was monomorphic at 118 bp and L58 was monomorphic at 125 bp.

Table 2 Pairwise F_{ST} estimates among sites at Schoodic and Pemaquid Points are included in the lower left of the matrix. *P* values for each comparison are included in the top right of the matrix in italics. Significant *P* values after Bonferroni correction for multiple comparisons are $P < 0.0083$ and denoted with an asterisk

(a) Schoodic Point	SW1	SW2	SE1	SE2
SW1		*0.0033**	*0.0017**	*0.0033**
SW2	0.0151		*0.0017**	*0.0017**
SE1	0.0456	0.0502		*0.0017**
SE2	0.0185	0.0234	0.0292	

(b) Pemaquid Point	PW1	PW2	PE1	PE2
PW1		*0.0017**	*0.0100*	*0.0017**
PW2	0.0309		*0.2117*	*0.0017**
PE1	0.0187	0.0137		*0.0017**
PE2	0.0862	0.0344	0.1129	

and the most frequent alleles (eight out of 20; Fig. 2) were shared among all populations. Gene diversity per locus for the four polymorphic loci at individual collection sites ranged from zero to 0.695. Populations on the eastern sides of Schoodic and Pemaquid Points had significantly lower levels of gene diversity than populations on the western sides (Kruskal–Wallis test, $H = 4.08$, d.f. = 1, $P = 0.043$). None of the loci exhibited significant linkage disequilibrium ($P > 0.05$), suggesting that the loci segregate independently.

The low (0.077) overall F_{IS} value estimated (four polymorphic loci and eight study sites) was not significantly different from zero ($P = 0.322$); this result suggests that the populations were in Hardy–Weinberg equilibrium. Multilocus F_{IS} values were also low at the level of individual sites (Table 1). At Pemaquid Point, F_{IS} ranged from 0.041 to 0.052, but F_{IS} was more variable for the four study sites at Schoodic Point (–0.018–0.204; Table 1), where one site, SW1, showed a significantly positive multilocus F_{IS} value. The highest single-locus F_{IS} values were found in L20. Pairwise F_{ST} tests revealed patterns of genetic differentiation among sites (see below) but these were not correlated with their positions relative to the topography of the peninsulas. All pairwise tests among sites were significant after the Bonferroni correction at Schoodic Point (Table 2a). However, at Pemaquid Point, PE1 was not significantly different from either PW1 or PW2 (Table 2b).

Analysis of molecular variance (AMOVA) revealed that the overall differentiation was primarily due to differentiation between sites lying on the same side (east or west) of a coastal peninsula and not to differentiation between eastern and western sides (Schoodic, between-sites-within-a-coast, $F_{SC} = 0.0217$ (95% CI; 0.0210–0.0220), $P < 0.001$, between coasts, $F_{CT} = 0.0135$ (95% CI; 0.0130–0.0140), $P = 0.329$; Pemaquid $F_{SC} = 0.07255$ (95% CI; 0.0710–0.0750), $P < 0.001$, $F_{CT} = –0.0334$ (95% CI; – 0.0330–0.0350), $P = 0.834$). The degree of genetic differentiation was similar at each point (Schoodic $F_{ST} = 0.0368$ (95% CI; 0.0363–0.0373), $P < 0.001$; Pemaquid $F_{ST} = 0.0399$ (95% CI; 0.0387–0.0412), $P < 0.001$). These results led us to reject our hypothesis that sites on the same side of a coastal point would be more similar to each other than to sites on the opposite side of the coastal peninsula.

Furthermore, our data do not support the hypothesis that there would be strong spatial genetic structuring within a site due to limited dispersal of gametes and zygotes. Spatial genetic structure analyses within each site for both collection times did not reveal significant relationships between genetic kinship and separation distance among individuals along the 60-m transect line (15 out of the 16 tests, Table 3). One exception was observed: PE2 sampling time B had a significant positive relationship between kinship and separation distance (slope of the regression = 0.02, $P < 0.03$, Table 3).

Circulation patterns and dispersal potential for drifting, reproductive adults

Fucus vesiculosus adults often have small, paired air bladders at intervals along their stipes (Jordan & Vadas 1972). When adults are detached by waves or storms, they are buoyant enough to float for some period before senescence (they do not reattach). The likelihood of different dispersal trajectories from a single site on different days for wave-detached, drifting adults was demonstrated

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Table 3 Spatial genetic structure summary results. Permutation test *P* values of kinship coefficients (Ritland) and geographical distance are presented. The significant *P* value is in bold and denoted with an asterisk

Site/year	Observed value, slope of regression (ln(distance))	Permutation test *P* value H_1: obs < > exp.
SW1-A	0.00	0.72
SW1-B	0.01	0.55
SW2-A	0.01	0.35
SW2-B	0.00	0.91
SE1-A	– 0.01	0.48
SE1-B	0.00	0.85
SE2-A	0.01	0.31
SE2-B	– 0.01	0.42
PW1-A	0.01	0.52
PW1-B	– 0.03	0.15
PW2-A	– 0.02	0.15
PW2-B	**0.02**	**0.03***
PE1-A	– 0.01	0.55
PE1-B	– 0.01	0.63
PE2-A	0.00	0.70
PE2-B	0.00	0.85

by the orange recapture data and GPS drifter deployments. Orange recovery ranged from 0% return (deployments E, L, O, and P, see Fig. 3) to as high as 52% recovery (deployment K; Table 4). Oranges were sometimes recovered on the same side of a coastal peninsula as their deployment site, but on three of the seven deployments (16 November 2004, 5 October 2005, and 3 November 2005, see Table 4) recovery occurred on the opposite side of the coastal peninsula. Closer examination showed that recovery patterns differed according to the side (east vs. west) from which oranges were deployed. Most recovered oranges deployed from western sides of the Points were retained on the west side (197 of the 199 recovered oranges), whereas only 42% of the recovered oranges (11 of the 26 recovered) from deployments on the eastern sides of the Points were recovered along the eastern shores (Fig. 3). This difference in same- or opposite-side recovery according to side (east or west) of release was significant (Fisher's exact test on 2 × 2 contingency table, $P < 0.001$). The lower recovery of oranges on the eastern side (13 of the 225 oranges recovered) also suggests that retention of oranges may be higher on western shores while advection may be higher on eastern shores. Indeed, of the nine oranges recovered on the scale of kilometres away from the release site (Fig. 3), eight were released from eastern shores. Finally, recovery results were similar in 2004 and 2005 (e.g. compare recovery of deployments H and Q in 2005 with deployments C and D in 2004, Fig. 3, Table 4). This result suggests the existence of a near-shore circulation pattern that persists and directs dispersal in a southwesterly direction.

Potential for long- and short-distance dispersal of drifting adults over times shorter than one tidal cycle emerged from study of GPS-drifter tracks (Fig. 4). For example, with

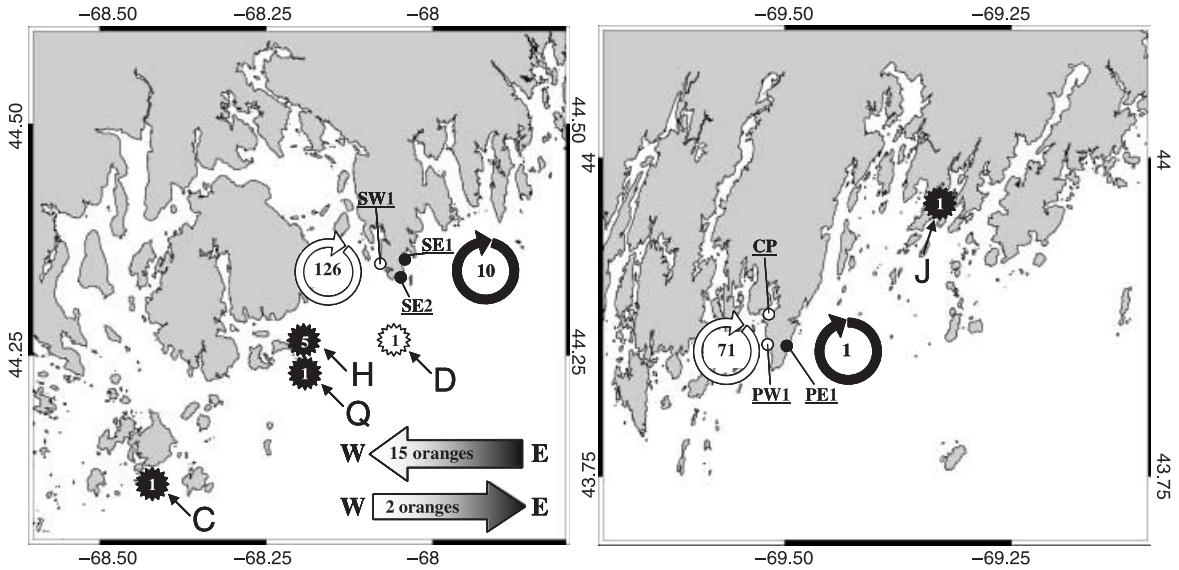

Fig. 3 Cartoon representation of orange release and recovery at Schoodic and Pemaquid Points. Deployment locations are underlined. Oranges deployed on eastern shores are denoted in black and oranges deployed on western shores are denoted in white. Numbers within each respective circle correspond to the total number of oranges that were recovered on the same side of a coastal point from where they were deployed. There were a number of long-distance dispersal events; the position where the oranges were recovered is denoted by a black or white circle (corresponding to whether deployments were on eastern or western shores), with a letter corresponding to the deployment period (Table 4). The number in the circle represents the number of oranges recovered at that location.

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Table 4 Orange recovery data from 17 deployments. Each deployment represents a release of 100 oranges. Deployment sites are shown in Fig. 3. CP, Colonial Pemaquid site was an orange deployment location north of PW1

Deployment letter	Coastal point	Site of deployment	Deployment date	% return	Recovered on same side (no.)	Recovered on opposite side (no.)	Long-distance recovery
A	Schoodic	SE1	29/10/04	6%	6	—	—
B	Schoodic	SW1	2/11/04	45%	45	—	—
C	Schoodic	SE1	16/11/04	1%	—	1	(1) c†
D	Schoodic	SW1	16/11/04	2%	—	2	(1) d†
E	Schoodic	SE2	16/11/04	0%	—	—	—
F*	Pemaquid	CP	20/9/05	12%	12	—	—
G*	Pemaquid	CP	20/9/05	15%	15	—	—
H	Schoodic	SE1	6/10/05	7%	1	6	(5) h†
I	Pemaquid	PW1	5/10/05	35%	35	—	–
J	Pemaquid	PE1	5/10/05	1%	1	—	(1) j†
K	Schoodic	SW1	5/10/05	52%	52	—	—
L	Schoodic	SE1	19/10/05	0%	—	—	—
M	Schoodic	SW1	19/10/05	29%	29	—	—
N	Pemaquid	PW1	19/10/05	9%	9	—	—
O	Pemaquid	PE1	19/10/05	0%	—	—	—
P	Schoodic	SW1	3/11/05	0%	—	—	—
Q	Schoodic	SE1	3/11/05	11%	3	8	(1) q†

Total number of oranges released: $N = 1700$. Mean recapture rate was 13%. *Three oranges were found within 2 days of deployment on the same side of the coastal point but tags were unreadable. †shown on Fig. 3.

a northern wind present on 8 August 2006, two drifters released simultaneously from PE1 and PW1 (Fig. 4a) moved southward in tracks that paralleled the coast (Fig. 4b). Upon reaching the tip of Pemaquid Point, the drifters synchronously travelled offshore to the southwest for several kilometres (Fig. 4a). Twelve oranges were also released with each drifter on 8 August, and 12 oranges were recovered within 10 m of the GPS-drifters at the end of the deployment. An example of dispersal over a shorter distance was found on 24 August 2006. On this date, both drifters moved northeasterly with a south–southwesterly wind (Fig. 4d). While the eastern-deployed drifter moved alongshore in a northeasterly direction, the western-deployed drifter encountered the coastline and was caught within an intertidal boulder field (Fig. 4c, inset). On 24 August, both oranges and tagged adult fucoids were released with the GPS drifters, and at least one orange and one tagged adult fucoid were observed within 10 m of each of the drifters when they were recovered. Thus, not only did the fucoid proxies (i.e. oranges, GPS drifters) migrate to a new intertidal site during this trial, but adult fucoids migrated into an intertidal boulder field where they could release gametes on the next calm day and potentially interbred with the attached fucoid adults growing there. We verified the fecundity of adults that rafted naturally to one of our study sites (SW1) after a strong storm in 2005; the receptacles of those individuals released large numbers of eggs and sperm (data not shown).

Evaluation of effective dispersal stages: Gamete viability and levels of polyspermy

Fucus vesiculosus eggs had greater longevity than sperm (Fig. 5). Sperm were competent (about 100% fertilization success) over 3 h, but only 40% of 7-h old sperm could fertilize an egg, and fertilization success of 13-h old sperm dropped to 2%. In contrast, the fertilization success of eggs remained high, = 80% over the first 24 h (Fig. 5). By 50 h, 40% of these eggs were still fertile, and even after 7 days, 6% could still be fertilized by fresh sperm. Some embryos formed in crosses of fresh sperm × aged eggs were normal, but as eggs aged, polyspermy increased (t-test, $P < 0.001$; Fig. 5, inset). At a 5000:1 sperm-to-egg ratio, fresh eggs fertilized by fresh sperm had expected (Brawley 1991) polyspermy levels of 27 ± 2% ($n = 3$ replicate dishes) but polyspermy was 78 ± 2% ($n = 3$ replicate dishes) for 50-h old eggs fertilized by fresh sperm (receptacles from same batch of individuals as controls).

Discussion

This study was undertaken with the goal of understanding the interactions between near-shore coastal oceanography and population genetics. Our results show significant population genetic structure in *Fucus vesiculosus*, but genetic differentiation did not correlate with coastal topography and did not exhibit spatial genetic

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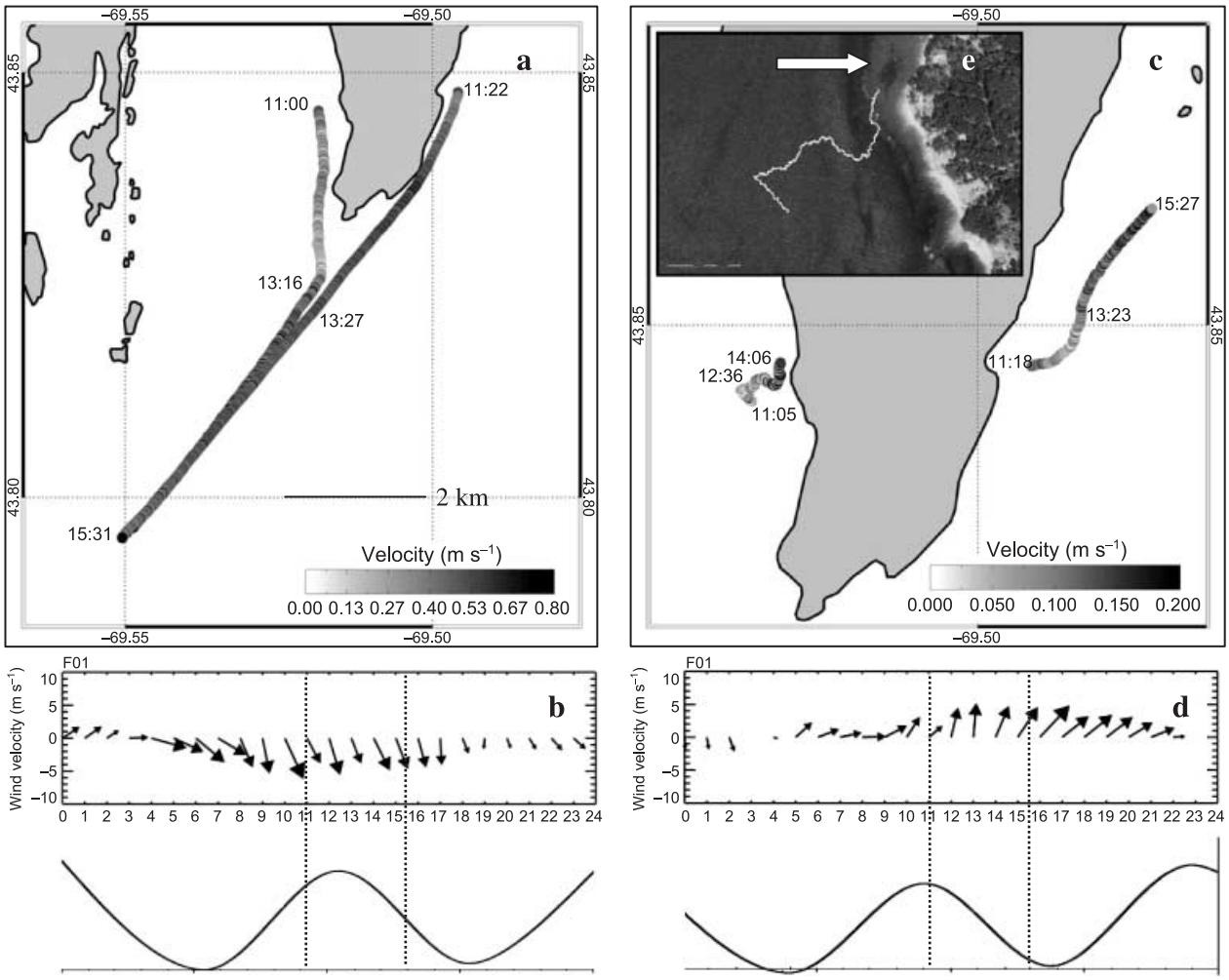

Fig. 4 Trajectories of GPS-equipped drifters (Fig. 4a, c; annotated with time). Below each drifter plot is the surface wind vector plot from the Gulf of Maine Ocean Observing System (GoMOOS) buoy F and the phase of the tidal cycle over the 24-h day of deployment (Fig. 4b, d). The period the drifter was deployed is denoted between dotted lines for each plot. Figure 4e shows the beaching event of a drifter on an intertidal boulder field (arrow).

structuring within a site. Instead, we propose that genetic structure is best explained by rafting of storm-detached adults, which release gametes when deposited at a new site by local circulation before they senesce (adults do not reattach). We demonstrate the potential for adults detached by storms to be rafted in multiple directions from their home site, and the beaching events we infer to be important to population genetic structure were simulated with coastal drifters (i.e. oranges, GPS-equipped drifters, tagged adult fucoids).

Life-history stages of fucoids and population genetic structure

Examination of the longevity of gametes and consideration of the dispersal ability of *F. vesiculosus* zygotes reinforce that effective dispersal via rafting adults is the primary influence on genetic structure at the scales examined here. Results from our gamete viability assays show that, sperm are too short-lived to be effective agents of dispersal, even though the natural sperm-to-egg ratio (Berndt *et al*. 2002) shows that some sperm remain available after eggs are fertilized. Although eggs are viable over many tidal cycles, they are fertilized quickly after release at levels close to 100% fertilization success, leaving few unfertilized eggs available for dispersal (Serrão *et al*. 1996; Berndt *et al*. 2002). Unfertilized eggs are negatively buoyant and relatively fragile. Even if eggs were able to disperse over long distances, we also find that older eggs are prone to lethal polyspermy, and thus the realized dispersal of eggs is predicted to be very low. Zygotes are an unlikely candidate for long-distance (kilometre-scale) dispersal,

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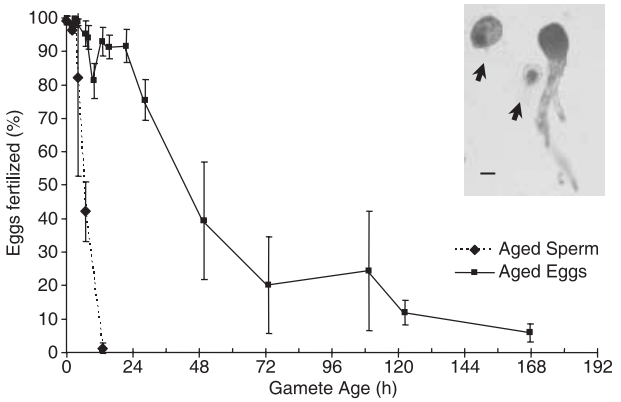

Fig. 5 Fertilization success (%) of aged gametes (mean ± standard deviation) based on crosses of aged eggs with fresh sperm and aged sperm with fresh eggs at each time (see Materials and methods). Photographic inset shows 11-day old embryos that were formed from a 50-h old egg × fresh sperm cross. One embryo is normal whereas two other embryos (arrows) died as a result of polyspermy; polyspermy was common in crosses with aged eggs (see Results). Scale bar = 100 μm.

because they are also negatively buoyant and secrete sticky wall materials a few hours after fertilization. Indeed, a number of researchers estimate the maximum range of zygote dispersal for fucoid algae as < 100 m, even in the context of initial dislodgement and reattachment of young, weakly attached zygotes (Chapman 1995; Dudgeon *et al*. 2001).

The lack of fine-scale genetic structure within nearly all sites could be interpreted in two ways. First, zygotes may disperse farther at local scales than previously thought. A possible scenario is an increase in water motion (i.e. following zygote formation under calm conditions) that carries zygotes along shore before they are firmly attached. Indeed, Dudgeon *et al*. (2001) with Calcofluor-labelled zygotes in a study of another fucoid alga, *Ascophyllum nodosum*, demonstrated that dispersal distances of zygotes were greater than predicted. Thus, the scale of zygote dispersal in *F. vesiculosus* deserves additional study. Second, gene flow via rafting, fertile material may create cohorts of recruits arising from different matings between local adults and rafting individuals from distant sites. This scenario would produce genetic differentiation without producing spatial patterns of genetic structure. Lack of spatial genetic structure at similar spatial scales to ours has been reported in other species of *Fucus* (Coyer *et al*. 2003, Coleman & Brawley 2005; Engel *et al*. 2005). PE2-B was the only location and time to exhibit a significant (positive) correlation between genetic relatedness and distance. Although significant, genetic relatedness increased with geographical distance, contrary to an isolation by distance-like process. We hypothesize that dispersal via zygotes may be responsible for this result. However, PE2-A did not demonstrate similar results. The resolution of our analyses (i.e. increased statistical power) could be improved with future studies to include increased samples sizes, additional loci and/or more polymorphic loci. However, the polymorphic loci included in our study, while having relatively low numbers of alleles per locus (three to five alleles per locus) point to migration, not mutation, as the governing process responsible for the distribution of alleles. Indeed, studies using large numbers of highly polymorphic loci, although increasing statistical power, can detect significant differences that may not be biologically meaningful (Waples 1998; Hedrick 1999).

Rafting and population genetic structure

Biologists have previously invoked rafting as the source for recolonization of rocky shores following large disturbance events (e.g. deglaciation; Ingólfsson 1995; Wares & Cunningham 2001). Our data highlight the likelihood that rafting is also important in structuring established coastal communities; the rafting trajectories demonstrated here are fully sufficient to account for a lack of isolation by distance, given effective interbreeding of rafted and attached fucoids. Significantly, not only will rafting affect population structure in *F. vesiculosus*, but the population genetics of many other algae and invertebrates that are transported within the rafts (i.e. epibionts) will be affected. For example, Ingólfsson (1995) identified 39 taxa associated with rafts of fucoid algae off Iceland while Thiel & Gutow (2005) tabulated over 50 macroalgal species known to raft and close to 700 taxa associated with rafting macroalgae. The kelp *Macrocystis pyrifera* had > 70 taxa associated with detached plants (Hobday 2000a). Radio-tracking of drifting *Macrocystis* (Harrold & Lisin 1989; Hobday 2000b; Hernández-Carmona *et al*. 2006) demonstrated transport over scales that would be expected to provide similar genetic connectivity to that found here in *F. vesiculosus*, but population genetics studies are required to determine whether it occurs.

Two benchmark studies that compare dispersal capabilities and life-history characteristics with population genetic structure in fucoid algae are those of Lu & Williams (1994) and Williams & Di Fiori (1996). First, Lu & Williams (1994) characterized genetic structure of *Halidrys dioica*, a dioecious macroalga that has dehiscent, buoyant, reproductive tips. The authors confirmed their prediction that a rafting reproductive strategy provided long-distance dispersal that results in high genetic diversity and little genetic structure. Second, Williams & Di Fiori (1996) examined the genetic diversity and structure of *Silvetia compressa* (as *Pelvetia fastigata*), a monecious species that is not buoyant, and they found low genetic diversity and high genetic structure. Although our initial hypotheses

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predicted genetic diversity and structure of *F. vesiculosus* to be similar to *S. compressa*, our results suggest that *F. vesiculosus* may have an adaptive reproductive strategy more comparable to *H. dioica.* Indeed, the presence of air bladders on the vegetative thalli of many *F. vesiculosus* individuals would allow storm-detached thalli to travel a great distance before sinking. Fuller interpretation of the *H. dioica* study is restricted, as the authors recognized, by the lack of supporting local and regional oceanography in their study (Lu & Williams 1994).

Coastal oceanography, gene flow, and patterns of genetic diversity

Near-shore surface currents are the likely oceanographic feature driving *F. vesiculosus* gene flow around and between coastal points via storm-detached rafts, and such currents provide a mechanism for long-distance dispersal. The release of oranges and GPS drifters to characterize circulation patterns around sampling sites in our study allows realistic estimates of dispersal potential because both oranges and GPS drifters are proxies for rafting, reproductive individuals. These data, while specific for Schoodic Point and Pemaquid Point, provide insight into the ecology of dispersal and the influence of dispersal and near-shore oceanography for creating genetic structure. The oceanography of the northwestern Atlantic is well studied (see Townsend *et al*. 2006 for review). If near-shore circulation patterns are an extension of the dominant ocean currents in the area, then within the Gulf of Maine, they will be driven by the prevailing Gulf of Maine Coastal Current (GMCC) system. The mean GMCC current flows to the southwest (Pettigrew *et al*. 1998, 2005). The combination of genetic and surface drifter data in our study provides evidence for a persistent, residual, near-shore southwesterly current upon which local wind- and topographically driven flows impose substantial variability. At both Schoodic and Pemaquid Points, the southeastern sites (i.e. SE2 and PE2) generally had the lowest gene diversity, increasing around a coastal point to peak at the northwestern sites (SW1, PW1). Interestingly, very few oranges were recovered on eastern shores, suggesting that immigration could be lower there compared to western shores. Additionally, long-distance recovery locations of oranges released at Schoodic Point as well as a GPS drifter trajectory with a north wind at Pemaquid Point support a southwestern directionality of dispersal. Some further work is required to confirm that a local southwestern current explains our genetic diversity and orange recovery results, because a coupling between the GMCC and near-shore circulation patterns at Schoodic and Pemaquid Points is untested. Largier (2003) highlights the discrepancies and differences in near-coastal systems as opposed to coastal shelf systems. For example, coastal headlands can create topographic eddies, and flow speeds near the shore typically slow down and can create coastal retention zones. Additionally, the speed and direction of near-shore flow is characterized by near-surface currents, which may have a different direction than that of currents at depth (Largier 2003).

Our data demonstrate that patterns of genetic differentiation and connectivity within and among populations at a regional geographical scale are complex and that the importance of rafting, fertile material may be underestimated. Although models of dispersal and gene flow in intertidal species are becoming more refined (e.g. Gaylord & Gaines 2000; Gaylord *et al*. 2002; Siegel *et al*. 2003; Kinlan *et al*. 2005; Sotka & Palumbi 2006), they do not yet account for behavioural aspects of larval propagules and/or do not account for local circulation patterns that influence gene flow and dispersal at the appropriate scale for the organism under examination. Understanding genetic connectivity among populations through additional analyses of population genetic structure and near-shore circulation will lead to better understanding of the opposing interplay of gene flow and the forces of genetic drift and local adaptation via natural selection (Slatkin 1987; Lenormand 2002).

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