Temporal and spatial variation in the early recruitment of fucoid algae: the role of microhabitats and temporal scales

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ABSTRACT: The recruitment of a multi-species assemblage of fucoid algae, *Ascophyllum nodosum* (L.) Le Jolis, *Fucus vesiculosus* L., and *F. distichus* L. ssp. *edentatus* (Pyl.) Powell, onto artificial substrata over different temporal and spatial scales was examined on a semi-exposed rocky shore in Québec, Canada. Measurements were taken at daily (1 d), fortnightly (15 d), and monthly (30 d) periods in 3 microhabitats (exposed rock surfaces, under adult fucoids, and in tide pools) from July through September in 3 consecutive years (1998 to 2000). Recruitment was spatially and temporally variable among months and years with much less recruitment in 1998. Recruitment was consistently lowest in September. The density of reproductive adults did not generally affect the rate of recruitment, but the rate of recruitment was negatively correlated with wind speed, a possible indicator of wave action. Among microhabitats, the recruitment was over 10 to 50 times greater under the canopy relative to exposed surfaces and tide pools. Mortality of outplanted embryos was only slightly higher outside the canopy, which suggests that it is limited dispersal and not differential survival that leads to high numbers of recruits under the canopy. There were, however, no differences in the numbers of recruits accumulating from 1 to 30 d, suggesting that overall post-settlement mortality rates are extremely high.

KEY WORDS: Algae · Intertidal zone · Population dynamics · Rocky shores · Seaweed · Wind

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INTRODUCTION

The dynamics of a population can depend critically on the rate at which new individuals are added, i.e. the process of recruitment. In benthic marine algae, recruitment includes the dispersal and settlement of propagules (i.e. spores or zygotes), and their subsequent survival, and thus the dynamics of recruitment will depend, in part, on the temporal and spatial variation in the availability of propagules (Roughgarden et al. 1988). Unfortunately, the small size of most algal propagules makes it difficult to assess this variation, and often, the entire process has been inferred from the distribution of juvenile stages (Reed et al. 1988, Archambault & Bourget 1999), which can lead to incorrect interpretation of the true patterns of settlement (Keough & Downes 1982). It is also now apparent that

the timescale over which observations are made can affect the interpretation of different ecological processes. While this concern has been raised in studies of invertebrates and fish (e.g. Caffey 1984, Choat et al. 1988, Wilson & Osenberg 2002), very few studies of marine algae have closely examined the early events surrounding settlement and early survival (e.g. Edelstein & McLachlan 1975, Reed & Foster 1984, Pearson & Brawley 1996, Johnson & Brawley 1998; reviewed by Vadas et al. 1992). During the period from the initial settlement of propagules to the first appearance in the population, algae are likely to experience substantial mortality (Brawley & Johnson 1991, Worm et al. 2001), which can vary greatly in time and space (Ang 1991). Given that survival and development of the early post-settlement stages are required for the eventual establishment of adults, it is critical to understand this pro-

cess if we are to understand the dynamics of adult populations (Vadas et al. 1992).

Recruitment must often operate in 2 very different modes, the first being the continual replacement of individuals lost from the population and the second being the massive re-establishment of disturbed areas (Dudgeon & Petraitis 2001). The dynamics of these 2 situations are likely to vary considerably for 2 reasons: (1) the availability of propagules may differ as dispersal in some species of algae has been shown to be very limited (Santelices 1990, Norton 1992), and (2) the microenvironments into which propagules settle are vastly different — moist but with limited light under the adult canopy and dry and bright on recently disturbed surfaces. Survival among such microhabitats can vary from 0 to 100 % over spatial scales as small as 10 cm (Brawley & Johnson 1991) with those under adult canopies being the most benign, at least in the short term.

The rocky intertidal communities of the Gaspé Peninsula, Québec, are severely affected by ice scour (Archambault & Bourget 1983), and sessile invertebrates and perennial algae, principally fucoids, are generally restricted to low-lying areas between topographical high points. Interannual variation in this disturbance regime can, however, create patches within established beds of fucoids. This situation thus provides an excellent opportunity to study these 2 modes of recruitment in a perennial intertidal algal community. In the present study we examined the temporal and spatial dynamics of early recruitment in a complex of fucoid algae over a 3 yr period. By examining this process over different periods and within different microhabitats, we aimed to determine the spatial and temporal scales at which variation was greatest and infer the processes (e.g. limited dispersal, high mortality) underlying this variation.

MATERIALS AND METHODS

The study was conducted in the intertidal zone at Pointe-Mitis (48° 41' N, 68° 2' W; near Mont Joli, Québec, Canada), a semi-sheltered shore consisting of a series of rocky ridges interspersed with consolidated boulder fields or tide pools (Bourget et al. 1985). These boulder fields and the lower portions of adjacent ridges were dominated by 3 species of fucoid algae, *Ascophyllum nodosum* (L.) Le Jolis, *Fucus vesiculosus* L., and *F. distichus* L. ssp. *edentatus* (Pyl.) Powell, that formed dense canopies covering up to 80 % of the substratum. These perennial algae are not able to colonize the more exposed rocky surfaces (e.g. the top portions of ridges) due to ice scour and thus only occur in areas protected from abrasion by ice (Archambault & Bour-

get 1983). Tides are semi-diurnal at this site with a tidal range of 4.0 m.

Five study areas were haphazardly selected along a 150 m stretch of the mid-intertidal zone (see Lamote 2003 for specific locations). Areas were separated by ≥20 m and were naturally isolated by the rocky ridges that dominate this shoreline. Fucoid cover at the time of selection ranged from 25 to 80 % cover. Although individuals of all 3 species were usually present, most areas were dominated by a single species at any given time.

Recruitment was estimated over 3 yr (1998 to 2000) by the use of artificial substrata. These substrata were identical to those used in earlier studies (Johnson 1994, Johnson & Brawley 1998) and consisted of small, white disks (4 mm thick, 20 mm diameter) fabricated from Sea Goin' Poxy Putty (Permalite Industries), a filled epoxy putty, by a molding and casting process in which the top surface was given the rough texture of sandpaper (Johnson 1994). Holes were drilled and tapped so that the disks could be attached with small stainless steel machine screws to small, polycarbonate base plates (3 mm thick, 85 mm diameter) that could each hold 6 disks. These plates were attached to the substratum using stainless steel screws driven into plastic wall anchors placed in holes drilled into the rock surface at each location (Johnson 1994).

Disks were set out for 3 distinct time scales: 1, 15, and 30 d periods. For each period, 2 disks were set out on a single plate installed at each location, and at any given location, all the disks for the 1, 15, and 30 d periods resided on the same base plate (i.e. 6 disks per base plate; 2 for each period). Manipulation of disks always began as areas were being uncovered by the ebbing tide, but due to the number of locations (see next paragraph) and the distance between areas, the collection and replacement of disks took 2.5 to 3.5 h and thus could not be done at a quasi-simultaneous moment as in earlier studies (Pearson & Brawley 1996, Johnson & Brawley 1998). Areas were, however, always visited in the same order although individual locations within a given area were treated as they were located. After collection, disks were transported to the laboratory where all attached fucoid zygotes were counted within hours using a stereomicroscope. For 1 d recruitment, this protocol was repeated for 5 consecutive days during each spring tide series (i.e. twice each lunar month) for the 3 mo period in which fucoid algae are reproductive at this site (July to September). Observations could not be made for additional days because the period of low tide was only long enough during spring tides for the time required to visit all areas. For measurements of 15 and 30 d recruitment, a similar procedure was followed but with the 2 disks recovered and replaced after 15 and 30 d periods, respectively. After being sampled, disks were

reused, but first scrubbed with a toothbrush in fresh water to remove any embryos.

Within each area recruitment of fucoids was examined in 3 distinct microhabitats: emergent rock surfaces covered by a canopy of adult fucoids, emergent rock surfaces not covered by a canopy (representing scoured areas), and submergent rock surfaces without a canopy; henceforth 'canopy', 'exposed', and 'tide pool' microhabitats, respectively. This latter microhabitat was selected to control for effects of desiccation that were expected to be higher outside the adult canopy (Brawley & Johnson 1993) but was not included in the design until 1999. Eight locations were haphazardly selected in the canopy microhabitat, 2 in the exposed and 2 in the tide pool microhabitats under the condition that they were separated from each other by ≥1 m. This experimental design was unbalanced but permitted a better estimate of temporal variation in recruitment that was expected to occur primarily under the canopy (Johnson & Brawley 1998).

To estimate mortality rates, we also outplanted embryos of *Fucus vesiculosus* on putty disks in all 3 years. Experiments were limited to this species as its reproductive period spanned all 3 mo, and we assumed that mortality in this species would generally reflect that of the other species, given the overall similarity of their response to emersion stressors (Lamote et al. 2007). To obtain embryos, receptacles (the reproductive structures of fucoid algae) were collected from the field and stored in the dark at 10°C. Care was taken to avoid algae with obvious epiphytes (e.g. diatoms), but before any use, the receptacles were scrubbed with a toothbrush and rinsed with seawater to remove epiphytes from the receptacle surface. To induce gamete release, receptacles were then osmotically shocked by air-drying for 20 min followed by rinsing in cold fresh water for 5 min. They were then placed into filtered (5 µm) seawater where gamete release and fertilization occurred. After the release of gametes, but before attachment began (which typically occurs 4 to 5 h after fertilization [Kropf et al. 1989]), the 'solution' of seawater and zygotes was gently poured over putty disks and then left overnight in the dark at 4°C to allow attachment. The following morning attached embryos (now 16 to 20 h old) were counted and then outplanted into the field at the beginning of the low tide period by attaching disks to base plates located in the 3 microhabitats described in the previous paragraph ('canopy', 'exposed', and 'tide pool'). Six disks were attached to each of 2 replicate base plates separated by 1 m in each microhabitat in all 5 study areas (i.e. 6 disks × 2 plates × 3 microhabitats × 5 areas = 180 disks for each experiment). Disks were recovered the following day at the same tidal time, and the number of embryos counted again. Data from the 12 disks in each microhabitat were averaged to give 10 replicates of each Microhabitat-Month combination (5 areas × 2 experiments mo^{-1}).

The abundance of reproductive fucoid algae was determined twice monthly during the periods when recruitment measurements were taken. The density of mature adults was estimated using three 625 cm^2 quadrats haphazardly located within each study area. The number of receptacles was also determined for each mature adult fucoid found within the quadrat. Hourly wind speed and air temperatures were obtained from the Mont Joli airport, located 15 km from the field site, and were considered an approximation of the weather conditions at the field site.

Because of the unbalanced design and violation of certain ANOVA assumptions due to the very low recruitment outside of adult stands, we limited our analysis of temporal and spatial variation to the recruitment that occurred in the canopy microhabitat. We used a mixed ANOVA model (SAS v. 8.2) to analyze log-transformed data (x + 1) on the rate of recruitment at different periods (fixed; 1, 15, and 30 d), months (fixed; July, August, and September) and years (fixed; 1998, 1999, and 2000) in different areas (random; 1 to 5). To further avoid an unbalanced design, data used for this analysis were the mean monthly values for each period (i.e. values used for each plate were the mean of the 2 disks used for each period averaged over 2 and 10 d for 15 and 1 d periods, respectively). Prior to analysis, homoscedacity and normality assumptions were verified by the Shapiro-Wilks test. An LSD (Least Significant Difference) multiple comparisons test (using the square means of the Type III) was used for separation of means. Separate mixed analyses of covariance (ANCOVAs) using temperature, wind speed, density of mature plants, and density of receptacles as covariates were conducted to assess the effect of these factors on recruitment because of unbalanced designs due to missing data (e.g. missing wind speed data). To assess the variation of the mortality in the 3 microhabitats, a 3-way ANOVA (Year, Month, Microhabitat) was performed. Homogeneity and normality assumptions were again determined by the Shapiro-Wilks test. Contrasts were performed using Scheffé tests with adjustments to the critical *F*-value appropriate for unplanned contrasts. Linear regressions were performed using Statistica version 6 (Stathoff).

RESULTS

The 1 d recruitment of fucoid propagules varied significantly with respect to years, months, and areas (Tables 1 & 2, Fig. 1). Recruitment was much greater in 1999 and 2000 relative to 1998, and among the 3 mo was consistently lowest in September. In 1998, recruit-

Table 1. ANOVA (Proc Mixed) showing the effects of Area, Month, Year, and Period on the recruitment of fucoid algae under the adult canopy. Data used for the analysis consisted of the mean values for each of 8 plates located under the fucoid canopy for a given Area-Month-Year combination, (i.e. the average of the 2 disks plate^{-1} over the 10, 2, and 1 samplings for 1, 15, and 30 d recruitment periods, respectively)

Source of variation	df	F	p
Area	4	44.3	<0.01
Year	2	6.8	0.01
Year × Area	8	16.4	<0.01
Month	2	54.6	<0.01
Month × Area	8	0.5	0.82
Year × Month	4	5.4	0.01
Year × Month × Area	16	0.7	0.80
Period	2	0.1	0.55
Area × Period	8	2.6	0.02
Year × Period	4	1.1	0.38
Year × Area × Period	16	1.9	0.06
Month × Period	4	1.2	0.34
Month × Area × Period	16	1.3	0.25
Year × Month × Period	8	1.1	0.41
Error	977		
Corrected total	1079		

Table 2. Conditional effect of Month for each year and conditional effect of Year for each month showing variation of recruitment given the significant interaction between these 2 factors

Source of variation	Month	Year	df	F	p
Year × Month		1998	2	10.28	<0.01
Year × Month		1999	2	14.37	<0.01
Year × Month		2000	2	13.99	<0.01
Year × Month	July		2	6.22	0.01
Year × Month	August		2	2.16	0.12
Year × Month	September		2	0.59	0.55

Fig. 1. Daily (1 d) recruitment of fucoid embryos onto epoxy disks under an adult canopy in 5 study areas in July (J), August (A), and September (S) over a 3 yr period. Bars represent the mean ± SE of the 8 plates located in each area. The values used for each plate were the average of the ten 1 d periods sampled within a given month

ment was highest in July, but in the subsequent years of higher recruitment, July and August levels were similar overall (Table 2). Within a given month, 1 d recruitment was generally similar among the different areas, except for extremely high values (2500 to 3500 zygotes per disk) for single areas during some months (i.e. Area 1 in July of both 1999 and 2000 and Area 5 in August 2000). Patterns of 15 and 30 d recruitment of fucoid propagules generally paralleled those of 1 d recruitment, but 15 and 30 d recruitment was higher in 1998 (especially in July) and lower in 2000 (especially in August and September) relative to 1 d recruitment patterns (Figs. 2 & 3).

The number of recruits that accumulated over the entire month period was generally equal to or less than the daily average (Fig. 4) except in August and September 2000 when 1 d recruitment far exceeded 30 d recruitment. There was a similar lack of accumulation over the 15 d period as well (data not shown). As
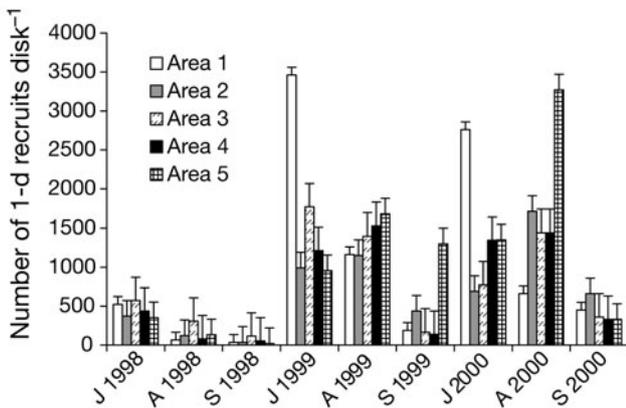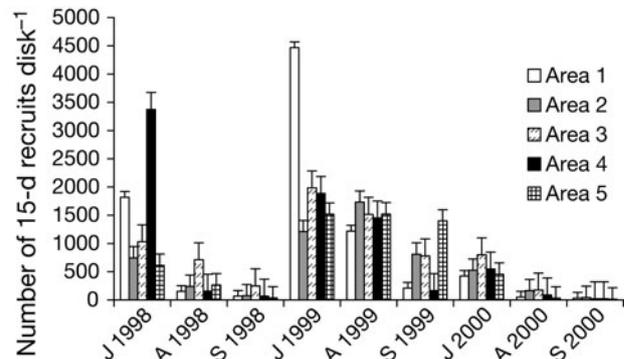

Fig. 2. Fortnightly (15 d) recruitment of fucoid embryos onto epoxy disks under an adult canopy in 5 study areas in July (J), August (A), and September (S) over a 3 yr period. Bars represent the mean ± SE of the 8 plates located in each area. The values used for each plate were the average of the two 15 d periods sampled within each month
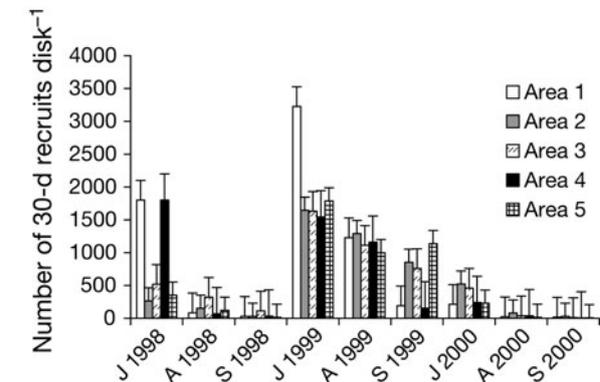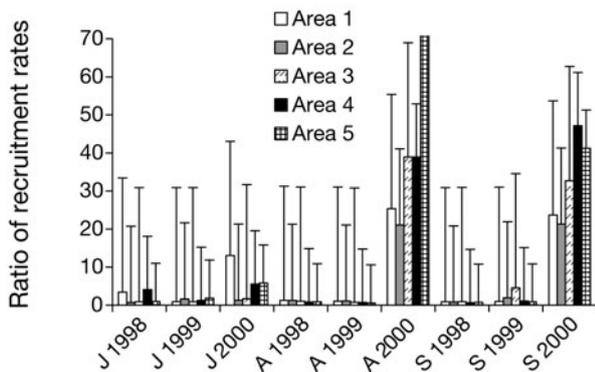

Fig. 3. Monthly (30 d) recruitment of fucoid embryos onto epoxy disks under an adult canopy in 5 study areas in July (J), August (A), and September (S) over a 3 yr period. Bars represent the mean ± SE of the 8 plates located in each area

Fig. 4. Ratio of 1 d to 30 d recruitment rates of fucoid propagules on epoxy disks in 5 study areas in July (J), August (A), and September (S) over a 3 yr period. Bars represent the mean ± SE of the recruitment on the 8 plates located in each area, which, in the case of 1 d recruitment, was calculated as the average of the ten 1 d periods sampled in each month. Note that the *y*-axis has been scaled to show the smaller values, and that the value for August 2000 was 250
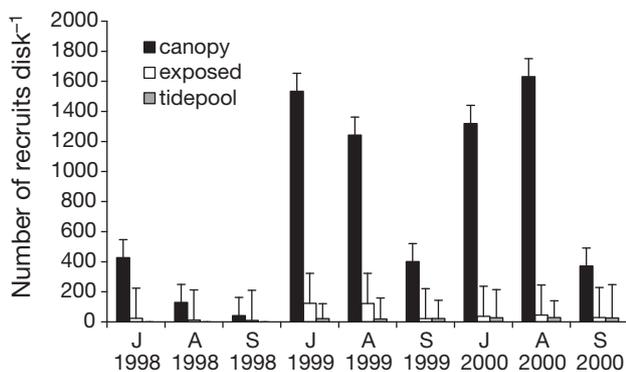

Fig. 5. Daily (1 d) recruitment of fucoids onto epoxy disks in 3 intertidal microhabitats in July (J), August (A), and September (S). Bars represent the mean ± SE of the plates located in each microhabitat pooled for all 5 study areas, using the average value for the ten 1 d periods sampled
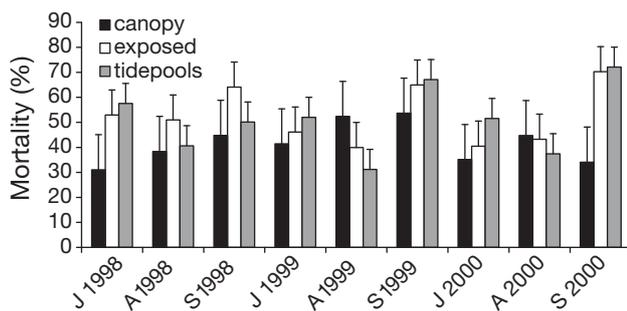

Fig. 6. Mortality of outplanted 16 to 20 h old fucoid zygotes in July (J), August, (A) and September (S) in 3 intertidal microhabitats. Bars represent mean ± SE (n = 10)

embryos were not distinguished from zygotes in these counts, we cannot assess if the algae on the 15 or 30 d disks had just settled (i.e. zygotes) or were established (i.e. embryos). Overall there was a significant correlation between 1 d recruitment and the 30 d recruitment (r = 0.43; p = 0.029; n = 45). This relationship was weakest in 2000 when daily rates remained high, but 30 d rates were even lower than in 1998 (Fig. 4). There was also a relationship between 15 and 30 d data (r = 0.85; p = 0.08; n = 45).

When examined by different microhabitats, the 1 d recruitment of fucoid zygotes was 10- to 50-fold higher under the adult canopy than in tide pools or exposed rock surfaces except during months of low recruitment, e.g. September (Fig. 5). Mortality of outplanted 16 to 20 h old embryos was remarkably stable and averaged 40 to 50% across all years and all months (Fig. 6). The 3-way statistical interaction was, however, significant (Table 3), but there was no clear pattern among the various contrasts except for mortality rates being lower under the canopy compared to the other 2 microhabitats (p < 0.005 for 10 of 18 contrasts) and higher mortality in September relative to July (p < 0.005 for 7 of 9 contrasts).

The density of mature algae varied consistently across the season (Fig. 7). *Ascophyllum nodosum* was most abundant in July with some mature plants found only in August. The abundance of *Fucus vesiculosus* was high in July and August but then declined during September. Finally, *F. distichus* ssp. *edentatus* had the reverse pattern: low abundance in July but then high abundance during August and September. Interannual variation did occur but mostly in the months of low fucoid abundance. An exception was the low abundance of *F. distichus* ssp. *edentatus* in August 2000,

Table 3. ANOVA (Proc Mixed) showing the effects of Year, Month, and Microhabitat on the mortality of fucoid zygotes outplanted for 1 d into 3 contrasting microhabitats: under the adult canopy, outside the adult canopy, and in tide pools. Data used for the analysis consisted of the mean values for 12 disks located on 2 plates in each microhabitat. Outplants were performed twice each month into 5 areas to provide 10 replicates of each Year-Month-Microhabitat combination

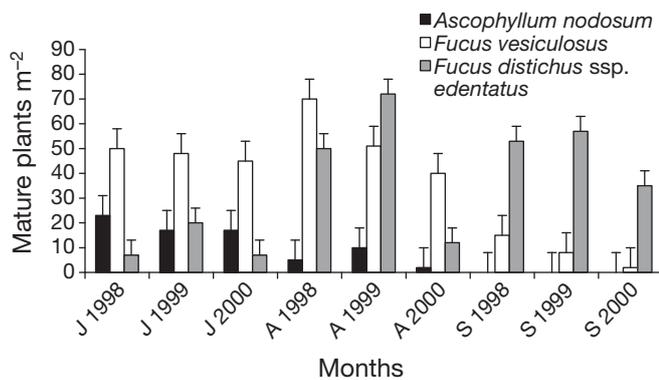| Source of variation	df	*F*	p
Year	2	1.34	0.2640
Month	2	86.86	<0.0001
Year × Month	4	5.34	0.0004
Microhabitat	2	37.93	<0.0001
Year × Microhabitat	4	8.38	<0.0001
Month × Microhabitat	4	25.83	<0.0001
Year × Month × Microhabitat	8	5.52	<0.0001
Error	243		
Corrected total	269		

Fig. 7. Adult densities of all 3 species combined in July (J), August (A) and September (S): *Ascophyllum nodosum*, *Fucus vesiculosus*, and *Fucus distichus* ssp. *edentatus*. Bars represent mean ± SE (n = 15)

which was 25% of the average abundance of the 2 previous years. The density of receptacles (pooled for all species) peaked in August for the first 2 years (data not shown; see Lamote 2003) when the 2 *Fucus* spp. were most abundant. August receptacle abundance was substantially lower in 2000, essentially at the same level of the other months. A correlation was not seen between the abundance of adults of all 3 species combined and daily recruitment (data not shown), but when examined at the species level, a positive correlation was found for 1 species, *F. distichus* ssp. *edentatus* ($R^2 = 0.76$; p = 0.06, n = 9, i.e. the average data from all sites for each of 3 mo over 3 yr). No effect of adult density or receptacle density on recruitment was observed, however, in the ANCOVA (Table 4). There was significant effect of wind speed on recruitment (Table 5) with decreasing daily recruitment with increasing wind speed ($R^2 = 0.76$, p < 0.05, n = 130, Fig. 8). There was no significant correlation with air temperature.

Table 4. ANCOVA (Proc Mixed) showing the effect of receptacles and density of mature adults on recruitment in canopy microhabitats. Adult and receptacle densities were used as covariates

Source of variation	df	F	p
Year	2	39.04	<0.01
Month	2	40.41	<0.01
Year × Month	4	21.73	0.01
Period	2	0.63	0.53
Year × Period	4	0.44	0.77
Month × Period	4	0.21	0.93
Year × Month × Period	8	0.18	0.99
Receptacles	1	0.17	0.68
Density of mature adults	1	0.72	0.39
Error	106		
Total	134		

Table 5. ANCOVA (Proc Mixed) showing the effect of the wind speed on recruitment during 3 years, 3 months, and on 3 periods of recruitment (1, 15, or 30 d old embryos). Wind speed was used as a covariate

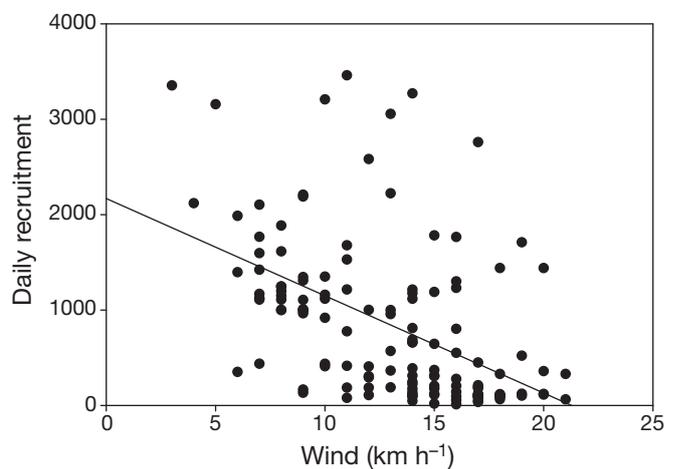| Source of variation	df	MS	F	p
Year	2	9.24	47.44	<0.001
Month	2	9.63	49.45	<0.001
Year × Month	4	0.34	1.76	0.142
Period	2	0.12	0.64	0.530
Year × Period	4	0.09	0.47	0.757
Month × Period	4	0.04	0.22	0.925
Year × Month × Period	8	0.04	0.19	0.992
Wind	1	0.92	4.74	0.032
Error	107	0.19		

Fig. 8 Number of 1 d fucoid recruits vs. wind speed during summer over a 3 yr period; $r^2 = 0.76$, p < 0.05, n = 130

DISCUSSION

Given the limited dispersal of fucoid algae, temporal variation in recruitment should depend ultimately on the abundance and fecundity of adults and early survival of propagules. Among different years and different months, we did not, however, find a strong relationship between the temporal abundance of receptacles or adults (little variation) and rates of recruitment (much variation), perhaps because we did not assess the abundance or maturity of gametes within receptacles, which can vary between months (Ang 1991, Wright et al. 2004). Moreover, we could not distinguish embryos at the species level; thus the specific contributions of individual species could not be discriminated. Temporal variation in the release of gametes (see Brawley et al. 1999 and Pearson & Serrão 2006 for reviews) occurs over much shorter time scales (1 to 14 d) than we addressed here and should have been averaged out by our sampling design (i.e. 10 d during each month).

Post-settlement mortality rates as measured by our outplanted zygotes also varied significantly among months and years but not nearly to the same degree that recruitment varied. Moreover, any trends were the opposite of what would be predicted, i.e. mortality rates were highest in 1999, the year with maximal recruitment. Our mortality estimates did not, however, include the critical period just after settlement. Attachment of the zygotes of these species generally occurs 4 to 6 h after fertilization when adhesive polymers are formed (Quatrano 1980). In the field zygotes were rarely out of water for more than 5 to 6 h whereas our outplanted zygotes had 16 to 20 h in the laboratory for attachment. Thus, variation in hydrodynamic forces immediately after settlement could explain the observed variation in recruitment. Hydrodynamic forces vary substantially at this site (Addy & Johnson 2001) both spatially and temporally, and the negative correlation between wind forces and recruitment could be the result of reduced settlement or increased dislodgment under conditions of increased wind-driven water movement as observed elsewhere (Vadas et al. 1990). Water motion can also inhibit gamete release (e.g. Pearson & Brawley 1996), but again such variation would have occurred at shorter time scales.

The lack of any accumulation of recruits on disks set out for 15 or 30 d periods shows that mortality rates were extremely high for these propagules. The numbers of zygotes on 15 or 30 d disks were surprising low; indeed, they were not different from or were even below average daily values, suggesting that there was no measurable recruitment occurring. (It should be kept in mind, however, that our study involved artificial substrata which may not precisely mimic the natural rock surface, especially in terms of attachment.) The inference of high mortality rates is consistent with our experiments that demonstrated that mortalities of 30 to 70% occurred over a single day for young stages (initially 18 h old). As discussed in the previous paragraph, mortality rates are probably even higher during the period immediately after settlement, but if this daily rate of mortality continued, only 1 recruit in 10 000 would survive 10 d ($0.5^{10} = 0.0001$) leading to trivial accumulation over time. Although mortality was slightly lower in the canopy microhabitat, large differences were not seen between the different microhabitats, which suggests that neither sweeping by adult fronds in the canopy microhabitat nor desiccation in the exposed microhabitat were important factors involved in the mortality of this stage. Thus another factor common to all 3 microhabitats must be responsible. Again dislodgment by water motion is the most likely candidate although certain grazers (littorinid snails and gammarid amphipods) are ubiquitous components of this community.

These results clearly demonstrate that shorter-term measurements are needed for estimating settlement rates of these algae as there was no accumulation of recruits over time relative to rates of daily recruitment. Estimates of settlement rates based on recruitment over longer periods of time would thus be quite misleading. Without direct observations of settlement, measures of 1 d recruitment are then our best estimates of settlement although they are conservative as there may be substantial loss during the 24 h period that disks were in place (see above). We observed continual settlement during the study period, typically varying from 10s to 100s of zygotes cm^{-2} d^{-1}, but at times reaching 1000s of zygotes cm^{-2} d^{-1}. From these data we can calculate annual rates of settlement assuming that the 3 mo period encompassed the entire reproductive season and that the days we sampled were representative (e.g. if our 5 d sampling periods coincided with lunar or semi-lunar peaks in gamete release [e.g. Andersson et al. 1994, Creed et al. 1996, Pearson & Brawley 1996, Serrão et al. 1996, Johnson & Brawley 1998; see review by Pearson & Serrão 2006], then we would have overestimated annual production; peaks in settlement do not, however, always fall during the time of new or full moon [e.g. Johnson & Brawley 1998]). We thus estimate that the total settlement during the reproductive season was from 0.9×10^7 to 2.6×10^7 zygotes m^{-2} yr^{-1} (= daily average $\times$ 30 d $\times$ 3 mo) depending on the year, which is consistent with earlier studies of fucoid algae (Ang 1991, Creed et al. 1996) and reinforces the idea that post-settlement mortality rates are extremely high in these algae (Vadas et al. 1990, Wright et al. 2004).

Spatial variation in recruitment was also observed in the present study at both spatial scales examined, among the 5 different study areas and among the 3 microhabitats. Variation among areas was mostly due to high recruitment in 2 of the 5 areas during certain months, but there was no consistent pattern over time. Patterns were much clearer among microhabitats where there was always 1 to 2 orders of magnitude higher recruitment under the adult canopy. These observations are consistent with previous studies showing the limited dispersal of fucoid zygotes (Johnson & Brawley 1998, Dudgeon et al. 2001, Arrontes 2002). The underlying mechanism is likely the release of gametes during low tide or periods of calm water conditions as observed generally in fucoid algae (e.g. Brawley 1992, Ladah et al. 2003; reviewed by Brawley et al. 1999, Pearson & Serrão 2006), which should increase settlement of zygotes near or under adults and would explain our observations of much higher 1 d recruitment within the canopy. We did not systematically examine recruitment patterns on natural surfaces, but recruitment on bare rock surfaces is rare at

this site and usually only occurred in lower zones on rock faces protected from direct sunlight (Lamote 2003). Higher recruitment of juvenile stages within adult stands of fucoid algae has also been observed elsewhere (Lubchenco 1983, McCook & Chapman 1991, Vadas et al. 1992, De Vogelaere & Foster 1994, Worm & Chapman 1996), and this pattern has often been ascribed to higher mortality in other microhabitats due to herbivory (Hawkins 1981, Lubchenco 1983, Cervin et al. 2004, 2005) or physical conditions (e.g. desiccation during low tide [Brawley & Johnson 1991, 1993], dislodgment during high tide [Vadas et al. 1992]). Our results suggest that dispersal and sources of mortality acting shortly after settlement may be fundamentally more important in determining this pattern unless areas without an algal canopy are limited in spatial extent (Cervin et al. 2005).

The high spatial and temporal variation in recruitment has been observed in previous studies of recruitment in algae (Ang 1991, Vadas et al. 1992, Wright & Steinberg 2001, Wright et al. 2004). Such variation can be an important determinant of local population abundance, but other factors such as density-independent mortality after settlement also play a role, and the relative importance of these processes can vary in time and space (Wright & Steinberg 2001, Steen & Scrosati 2004). Lazo et al. (1994) found that only 0.01 % of *Ascophyllum nodosum* survived annually and that the mortality was largely due to molluscan herbivores. Our results suggest also that the majority of mortality is occurring shortly after settlement and is likely due to wave dislodgment (Vadas et al. 1990, Serrão et al. 1996). Other causes such as desiccation (Schonbeck & Norton 1980, Santelices 1990, Brawley & Johnson 1991, Chapman 1995) or density-dependent competition (Ang & De Wreede 1992, Kendrick 1994, Steen & Scrosati 2004) are less likely possibilities, although the effect of grazing (e.g. Lubchenco 1983, Barker & Chapman 1990, Benedetti-Cecchi & Cinelli 1992, McCook & Chapman 1993) remains unexplored in this system.

Because we examined recruitment within a multi-species assemblage, it is difficult to distinguish the individual contributions of the different species. The reproduction of species of *Ascophyllum* and *Fucus* shows a seasonal periodicity (M. Lamote pers. obs.), and the asynchronous phenology of the 3 species did allow some temporal separation of their relative contributions. Temperature responses of germlings appear to reflect the temperature range in the species season of reproduction (Steen & Rueness 2004). *Ascophyllum nodosum* released gametes towards the end of June, followed by an abrupt loss of receptacles. This early reproduction combined with low abundance relative to the other species in these areas suggests that *A. nodosum* made a relatively small contribution to the recruits that we observed. Maturation

and gamete liberation of *Fucus vesiculosus* started towards the end of July and continued into early autumn. This phenology combined with its higher abundance supports the idea that *F. vesiculosus* was the primary contributor to the high recruitment observed in August. Finally, *F. distichus* ssp. *edentatus* became reproductive in August and was probably responsible for most of the recruitment observed in September as seen in Area 5 where *F. distichus* was dominant and a clear peak in recruitment was seen in August 2000 (Fig. 1), the time at which this species was in peak reproduction.

The results of the present study demonstrate the large variability in the processes of recruitment, the fundamental step in maintaining populations of fucoids. Spatial and temporal variation appear to be a consistent feature of marine populations, but this variation is often attributed to the decoupling of local population processes due to the open nature of many marine species. Due to the limited dispersal of propagules in this system, there should have been less decoupling of the reproductive effort of the adults, the settlement of zygotes and the recruitment of juveniles, yet high temporal and spatial variation were still persistent features of the system.

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