Dynamics of species interaction strength in space, time and with developmental stage

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Quantifying species interaction strengths enhances prediction of community dynamics, but variability in the strength of species interactions in space and time complicates accurate prediction. Interaction strengths can vary in response to density, indirect effects, priority effects or a changing environment, but the mechanism(s) causing direction and magnitudes of change are often unclear. We designed an experiment to characterize how environmental factors influence the direction and the strength of priority effects between sessile species. We estimated per capita non-trophic effects of barnacles (Semibalanus balanoides) on newly settled germlings of the fucoid, Ascophyllum nodosum, in the presence and absence of consumers in experiments on rocky shores throughout the Gulf of Maine, USA. Per capita effects on germlings varied among environments and barnacle life stages, and these interaction strengths were largely unaltered by changing consumer abundance. Whereas previous evidence shows adult barnacles facilitate fucoids, here, we show that recent settlers and established juveniles initially compete with germlings. As barnacles mature, they switch to become facilitators of fucoids. Consumers caused variable mortality of germlings through time comparable to that from competition. Temporally variable effects of interactors (e.g. S. balanoides), or spatial variation in their population structure, in different regions differentially affect target populations (e.g. A. nodosum). This may affect abundance of critical stages and the resilience of target species to environmental change in different geographical regions.

Keywords: per capita interaction strength; competition; facilitation; non-trophic; ontogeny; scale

1. INTRODUCTION

Interaction strengths estimate the magnitude of the effect of one species on another. Quantifying these magnitudes is considered essential for understanding and predicting the structure and dynamics of ecological communities [1–3]. However, accurately predicting these dynamics are difficult when species interaction strengths vary among environments in time and space.

Variability in the strengths of species interactions has been documented among competitor and predator-prey interactions from many ecosystems [4–6]. Interaction strengths often track environmental change by affecting organismal performance and, hence, the ability to interact with others. For instance, competition among sessile species varies along environmental gradients of productivity [7,8], and may switch to facilitative in stressful habitats [9,10]. Even subtle environmental changes may alter interaction strengths between key species with potentially cascading effects throughout a community [6].

Variable strengths among key links of a community interaction web caused by biotic factors (e.g. consumer control of the incidence of competition) can alter the structure of communities in the absence of environmental change [4,11–13]. Indirect effects underlie weak average, but highly variable, trophic interactions that magnify variation in community assemblages [4]. Likewise, contingent outcomes among competitors in a given environment may depend upon the order of arrival of the interactors, their initial densities or ontogenetic change in their competitive ability [1,14–17]. Priority effects (i.e. historical influences on the strength and outcomes of competitive interactions) like these are a principal mechanism underlying switches between alternative states [11–13].

Two types of priority effects have been identified [1]; those in which per capita effects are constant, but long-term dynamics depend on initial conditions (e.g. Lotka–Volterra models), or those in which the timing of arrival alters per capita interaction strength (PCIS). A pattern observed among both intra- and intercohort comparisons is increasing competitive advantage for the early colonist as arrival times of the interactors diverge [14,17,18]. This advantage stems from differences in size, aggression (in mobile species) or experience in a habitat [1]. However, among sessile species (e.g. barnacles and fucoid seaweeds on temperate shores) early colonists facilitate as frequently as they inhibit later arriving species [19–21] and it is unclear the conditions under which each prevails. In general, the mechanisms that cause interspecific interaction strengths to vary in space or time are less well characterized than are the patterns, or consequences, of that variability.

A recent analysis of key gaps in ecology identified the need to predict the strength and context dependence of species interactions across multiple scales associated with environmental gradients [22]. We have developed an experimental model for testing the variability of non-trophic interactions between the barnacle, Semibalanus balanoides (L.), and the fucoid alga, Ascophyllum nodosum (L.) LeJolis, by manipulating their order of settlement on

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Electronic supplementary material is available at http://dx.doi.org/10.1098/rspb.2010.2246 or via http://rspb.royalsocietypublishing.org.
rocky shores. These species co-occur abundantly on sheltered rocky shores throughout the North Atlantic Ocean and barnacle–fucoid interactions are often central to the dynamics of rocky shore communities in temperate coastal oceans [10,19,23,24]. Their widespread geographical distributions mean that S. balanoides and A. nodosum co-occur in a range of different environments. In the Gulf of Maine (GOM) USA, outflow from the Penobscot River establishes distinct thermal and current regimes to the south from that north of the river [25,26] to which co-occurring populations in these respective regions are exposed. Reproduction of both species is affected by temperature [27,28], and we postulated that this caused the per capita effect of barnacles on early life stages of A. nodosum to vary among regions of the GOM associated with changes in the timing of their interaction. This experimental system affords an opportunity to study both, the strength and context dependence of priority effects, and potential mechanism(s) associated with ontogenetic differences across regional spatial scales driven by thermal patterns in the GOM.

Ascophyllum nodosum reproduces annually in a narrow window spanning three to four weeks at a site, beginning when sea water temperatures reach 6°C [27]. Southern populations reproduce earlier (late March—April) than populations in the northern GOM (late May). Likewise, S. balanoides reproduces and settles earlier in spring in southern than in northern GOM populations (R. Kordas & S. Dudgeon 2004–2005, personal observation). However, the timing and the duration of settlement are more variable and broader than that for A. nodosum because transport during the long pelagic larval period [29] can uncouple settlement from local demographic schedules. Settlement tends to peak in March in the northeastern, GOM (R. Kordas & S. Dudgeon 2004–2005, personal observation). Taken together, barnacles settle before A. nodosum at sites in the southern GOM, they settle approximately contemporaneously in the central GOM and barnacles settle after A. nodosum in the northern GOM.

The change in the order of settlement of S. balanoides and A. nodosum in the warmer and more variable southern, versus the cooler and less variable northern, GOM (see [26]) may correspond with different observations of barnacle–fucoid interactions. Established barnacles facilitate recruitment of fucoids [20,21,24,30]. But we have observed that metamorphosis of a cyprid larva to a barnacle can smother previously settled germlings. Based on geographical variation in their respective settlement windows, we tested several hypotheses about the interactions between recruiting barnacles and germlings of A. nodosum. We hypothesized that PCIS varies with timings of barnacle and fucoid settlement, specifically that early settling established barnacles facilitate germlings, but later-settling barnacles (especially those that settle after A. nodosum) compete with germlings upon metamorphosis and early growth. Accordingly, we predicted that the strength of a positive association between barnacles and germlings is greater in the southern GOM where earlier settling barnacles are more likely to facilitate recruitment of A. nodosum.

We tested the hypothesis that interaction strengths track environmental change by comparing the size and the variability of per capita effects with established patterns of thermal variation in the GOM [25,26]. Finally, we tested the hypothesis that the strength of per capita effects of barnacles on A. nodosum germlings is sensitive to the presence of consumers. We focused on recruiting algal germlings for three reasons: (i) direct interactions of early life-history stages with facilitating or competing species are a matter of life or death, hence, estimates reflect effects on population growth rate; (ii) variability of priority effects that stem from tracking environmental change is more likely to be detected among early life stages; and (iii) germlings are a critical transitional life-history stage to the persistence of disturbed A. nodosum populations [31,32].

Interaction strengths can be characterized by a variety of concepts depending on the nature of empirical data (reviewed in [33–35]). The per capita effect of species i on an individual of species j is represented by elements of the interaction matrix (sensu [34]). Several authors have recommended empirical measures of per capita effects because it underlies all other interaction strength measures [34–37] and it is the metric used in this study. The potential for priority effects of non-trophic interactions (competition and facilitation) makes it necessary to measure per capita effects for identifying temporal variability in direction and magnitude. Estimates of per capita effects of non-trophic interactions are likewise necessary to complement studies of trophic interactions in order to predict their cumulative effects on community dynamics [3]. We provide evidence that priority effects can emerge because performance (growth and survivorship) of ontogenetic stages of interactors tracks abiotic features of the environment. Correspondence between environmental variability and variability of per capita effects provides evidence that interaction strength depends on environmental context and a basis for predicting net effects over broad scales of space and time.

2. MATERIAL AND METHODS

(a) Site description

Our study spanned four rocky coastal regions of the GOM (figure 1) with two on either side of the Penobscot River, which effectively divides the GOM into southern and northern regions; from warmest (and most variable) to coldest, Massachusetts ((Mass), Cape Cod Bay to Rye Ledge, NH); Southwestern Maine ((SW ME), Brunswick to the west bank of the Penobscot River); Central Maine ((C ME), east bank of the Penobscot River to Schoodic Point); Eastern Maine ((NE ME), Schoodic Point to Quoddy Head) [25,26,38]. The present thermal differences among these four regions capture the variability predicted by models to continue through time as regional climate changes and sites throughout the GOM become warmer and more variable [26]. All sites were moderately sheltered from hydrodynamic exposure and consisted of granitic benches with at least 1000 m² of a dense canopy of A. nodosum.

(b) Association between barnacles and A. nodosum germlings

Patterns of association between barnacles and fucoid germlings across regions were studied at 12 sites spread across the GOM (figure 1); six to the southwest of the Penobscot River in Maine (southern region) and six to the northeast...
At each site, we placed a 30 m transect parallel to the shoreline in the mid intertidal zone and counted the number of barnacles and fucoid germlings in 10–20 randomly placed 25 cm quadrats. We also classified each germling into one of three distance categories (0, 0 to 1, >1 cm) to the nearest barnacle.

Data characterizing the association between barnacles and fucoid germlings in quadrats were analysed using a three-way log linear model with the best-fit reduced model evaluated by the deviance of the $G$-statistic. This analysis tested if patterns of association between the frequency of germlings and barnacle abundance are the same among regions of the GOM. The frequency distributions of germlings across categories of distance to the nearest barnacle were compared among regions using a $G$-test (of homogeneity-Model II test of independence). Frequencies were used for both of these analyses, but percentages are presented in tables for clarity.

### (c) Experimental test of PCIS

At three sites in each of the four regions identified in the GOM (12 sites total, figure 1, electronic supplementary material, table S1), we estimated the *per capita* interaction strength (PCIS) in 2005. Shaded sites were used for both. Coloured areas indicate the gradient in temperature throughout the GOM; warmer colours indicate warmer temperatures (data representing spring from 13 May 2005, MODIS Aqua satellite). Bars along the coastline indicate the dates of *S. balanoides* and *A. nodosum* settlement relative to the regions. Mass, Massachusetts; SW ME, Southwest Maine; CME, Central Maine and NE ME, Northeast Maine. Nova Scotia excluded for clarity. See §1 for region boundaries and electronic supplementary materials for site names and global positioning system coordinates.

At each site, six 1 m diameter plots were cleared of organisms and in the centre of each plot, we installed two tiles seeded with germlings, one of which also had barnacles established, paired with one with barnacles removed (see seeding below). Of these six plots, two were caged (20 × 20 × 2.5 cm, 0.64 cm mesh), two had roof-only cages and two were unmanipulated. Tiles were installed flush with the substratum, censused at approximately three week intervals, and returned to the shore within 24 h of retrieval. At each census, we counted the numbers remaining of experimentally seeded stained germlings, initially settled barnacles and newly settled barnacles (post-field deployment).

Tiles were made of Poxy Quick marine epoxy putty (Permalite Plastics, Costa Mesa, CA, USA) moulded into 35 mm film canister caps and textured with no. 60 sandpaper pressed into the surface [39]. After drying, tiles were detoxified before deployment. Tiles were deployed in early March 2005 at Avery Point, Connecticut to allow natural barnacle settlement. Tiles were collected in April and maintained in running sea water until seeded with *A. nodosum* zygotes. Fertile male and female *A. nodosum* were collected from the Damariscotta River in late April and were induced to release gametes in the laboratory. Eggs and sperm were mixed together with Calcofluor white (Sigma, St. Louis, MO, USA), which stains the cell wall of developing zygotes (but not unfertilized eggs that lack walls) to distinguish...
exponentially seeded germlings from natural settlement following deployment at field sites [40]. Zygotes were seeded at a relatively uniform density onto tiles, half of which had live barnacles established, the other half from which barnacles were removed prior to seeding. Following zygote attachment, initial counts of germlings (using epifluorescence) and barnacles were made using a compound microscope (Olympus BX-60, Melville, NY, USA) at 20X, and tiles were deployed.

At each census, the number of germlings on each tile was estimated by converting counts from five subsamples comprising a known fraction of tile area to the whole tile and used as the datum. Mortality rate of germlings in a census interval was estimated as deaths$_t$ $(germlings_t - 0.5) / (germlings_{t-1})$ according to Keyfitz [41]. Survival in an interval was calculated as (1 - mortality rate) and converted to a weekly rate to standardize survivorships across census intervals that differed slightly in length using the following equation [42]:

$$l_s = e^{ln(l_{0s}/T)}$$,

where $l_{0s}$ raw survival data during an interval; $T$ time (in days) of a given census interval in either May, June or July.

We estimated PCIS (i.e. elements of the interaction matrix, sensu [34]) using a modified form of the dynamic index [35]. To test the effect of established barnacles, our PCIS measure used the difference in germling survivorship between tiles with and without barnacles from a given plot for each level of caging treatment:

$$PCIS_{barnacle, germling} = \frac{ln(k_B / l_B)}{D_B}$$,

where $l_{0B}$ germling survivorship on the tile with barnacles present; $l_{AB}$ germling survivorship on the tile with barnacles absent; and $D_B$, average number of barnacles for a given census interval.

Negative values indicate competition, zero implies no interaction and positive values indicate facilitation. In uncaged (control) treatments, estimates of PCIS represent the net strengths of facilitation or competition, respectively. In either case, PCIS values from caged plots can either not differ from, be lesser, or greater than those of controls. No differences between PCIS estimated in caged and uncaged plots would signify that neither consumers, nor indirect effects modify the strength of the competitive (less than 0) or facilitative (greater than 0) interaction between species. By contrast, lesser PCIS values in caged when compared with uncaged plots would indicate that germlings have relatively poorer survivorship in the presence of barnacles when consumers are absent, implying that the effect of consumers is to reduce the strength of competition below its maximum. More positive PCIS values in caged when compared with uncaged plots would indicate that germlings survive relatively better in the presence of barnacles. This pattern could emerge either from (i) coupling between facilitation and direct effects of grazing [20] or (ii) by cages eliminating negative indirect effects (e.g. consumption of barnacles by the dogwhelk, Nucella lapillus, which adversely affects germlings). Since our main interest was estimating $a_{ij}$ in this paper, consumer and indirect effects caused by numerical and food web structure responses are a pooled effect from the press perturbation imposed by our cages. This design also afforded analysis of consumer and indirect effects on mortality rates of $A. nodosum$ germlings by averaging the two tiles within a plot of a given caging treatment and comparing among levels of caging. From this analysis and per population estimates of competition, we partitioned total mortality of germlings into that from consumers/indirect effects, competition and other sources.

(d) Analysis of PCIS data
Analysis of the established barnacle effect used PCIS values as the response variable in a three-factor ANOVA with region, site (region) and caging treatment as independent variables. We established a priori contrasts to test specific hypotheses about regional patterns of PCIS and for testing cage effects. Highly non-significant sources of variation were post hoc pooled with the residual error term.

We estimated the PCIS of the putative competitive effect of later-setting barnacles on established germlings by regressing germling mortality (converted to weekly rates) on density of newly settled ‘arriving’ barnacles for each treatment (dynamic regression [35]). Regressions and treatments were compared using a three-factor ANCOVA to estimate the effect of arriving barnacles along with the other independent variables during each sampling interval: the independent variables were region, site (region) and treatment and the number of arriving barnacles in the interval was the covariate. The NE Maine region was excluded from ANCOVA from a lack of barnacle settlement by July, but was included in ANOVA. Highly non-significant sources of variation were post hoc pooled with the residual error term. Tests of homogeneity of slope proceeded from the highest to lowest order interaction and then to main effects. Values used for germling mortality and density of arriving barnacles were those of a single plot (i.e. they were pooled across the paired tiles (with and without established barnacles) of a plot). Densities of arriving barnacles were independent of densities of established barnacles on a tile throughout the experiment (Spearman’s $p < 0.07, p > 0.42$ for all months). Interval-specific mortality rates of germlings were calculated as above [43]. The number of arriving barnacles in a sampling interval was estimated from the difference between the observed number at the end of an interval, and the expected number at the end given the number at the start multiplied by spring and summer survivorships for juvenile barnacles in New England [42]. Final estimates of the slope to estimate PCIS were those of the reduced major axis. Germling mortality was arc-sine transformed and barnacle counts were log transformed prior to analysis.

(e) Analysis of effect sizes
Effect sizes for each source and census interval were summarized using MetaWin 2.0 [44] to evaluate the average and variability of effects by region throughout the experiment, and the cumulative distribution of effect sizes over the GOM. For estimating the contribution by competition to germling mortality at the population level, regional PCIS values were converted to regional estimates of germling mortality in the presence and absence of established barnacles.

3. RESULTS

(a) Association between barnacles and $A. nodosum$ germlings
Adult barnacles were present in moderate or great abundance in 94 per cent of quadrats sampled throughout the GOM in which $A. nodosum$ recruits occurred (table 1). Compared with sites in the southern GOM, $A. nodosum$ germlings were only half as likely to co-occur in quadrats...
when barnacles were abundant at sites in the north, where later-settling barnacles may compete for space with germlings and offset facilitation by prior years adults (table 1; a priori contrast $G_1 = 6.83, p < 0.001$). Similarly, nearly half of the germlings from northern populations were greater than 1 cm from the nearest barnacle, whereas in the southern GOM germlings were more frequently distributed close (less than 1 cm) to barnacles (table 1; $G_2 = 30.33, p < 0.001$). Our hypothesis that metamorphosis and growth of later-settling barnacles in the north eliminates germlings was not confounded by the alternative that the close association in the south results from greater barnacle or germling densities, because neither one varied significantly across regions (barnacles, $F_{1,8} = 0.37, p = 0.56$; germlings $F_{1,8} = 0.01, p = 0.93$).

### (b) PCIS
The strengths of non-trophic interactions varied among regions of the GOM. Previously established juvenile barnacles competed with germlings during May. The greatest competitive effect of barnacles on germlings occurred in May in the southern GOM with estimated $\alpha_{AB}$'s of $-0.0015$ and $-0.0025$ in Mass, and SW ME, respectively. By contrast, barnacles in the northern region had very weak competitive effects on germlings and estimates of $\alpha_{AB}$'s did not differ from 0 (figure 2a). The strengths of per capita effects of barnacles were region-specific ($F_{1,57} = 5.69, p = 0.024$); effects within a region were similar across sites (for both May and June, sites (region), $p > 0.20$). Seeding densities were the same across both sites and regions ($F_{region,3,8} = 1.48, p = 0.29, F_{site,region,8,132} = 1.67, p = 0.11$) and, thus, PCIS estimates were not an artefact of initial germling densities. Also, PCIS estimates were independent of established barnacle density in all months (May, $r = 0.23, p = 0.06$; June, $r = -0.00004, p = 0.12$; July, $r = 0.00006, p = 0.80$), therefore, large PCIS were not artefacts of low barnacle density.

Per capita effects of barnacles on germlings also varied within regions of the GOM between May and July. By June, juvenile barnacles in Massachusetts had a very weak average facilitative effect on germlings and no net effect was detected in SW ME. In the north, we estimated a per capita facilitative effect of juveniles on germlings of 0.0021 in C ME that enhanced weekly survivorship approximately 2.5 per cent. Barnacles had a weak competitive effect on germlings estimated to be $-0.0007$ in NE ME ($F_{region,3,47} = 3.20, p = 0.03$; figure 2b). By July, established juvenile barnacles had no effect on $A.~nodosum$ germlings in any region.

Overall, estimates of PCIS of juvenile barnacles were similar among caging treatments. This implies...
Figure 3. Weekly mortality rate of *A. nodosum* germlings during (a) May 2005 and (b) June 2005. For (a) columns represent mortality in each level of caging treatment across the four regions of the GOM. Shaded portions of each column indicate contributions by each source to germling mortality. Black bars, consumer and indirect effects; dark grey bars, competition; light grey bars, all other sources. Error bars represent standard errors of *n* = 18 in each region. Note the axis break in the ordinate. For, (b) columns represent mortality in each level of caging treatment at each site studied in the GOM. White bars, unmanipulated plots; black bars, caged plots; grey bars, control (root) plots. Values represent means ± s.e. of *n* = 2 for each combination of caging treatment (averaged across the tiles with and without barnacles in a single plot of a given level of caging treatment) and site in the four regions of the GOM.

Table 2. Summary statistics of regressions of *A. nodosum* germling mortality on estimated weekly settlement rate of *S. balanoides*.

<table>
<thead>
<tr>
<th>month</th>
<th>slope-β° (× 10^-3)</th>
<th>s.e. (× 10^-3)</th>
<th>PCIS° (× 10^-3)</th>
<th>n</th>
<th>F</th>
<th>d.f.</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>May</td>
<td>4.643</td>
<td>3.10</td>
<td>-4.643</td>
<td>51</td>
<td>3.32</td>
<td>1.41</td>
<td>0.076</td>
</tr>
<tr>
<td>June</td>
<td>2.222</td>
<td>0.94</td>
<td>-2.222</td>
<td>54</td>
<td>4.85</td>
<td>1.26</td>
<td>0.037</td>
</tr>
</tbody>
</table>

*Tests of homogeneity of slopes in both May and June showed that a single slope was the best estimate for all regions of the GOM. Only three regions were included in ANCOVA because no barnacles settled at sites in NE Maine by late July 2005. Other significant sources of variation from analyses are presented in the text.

Values of the slope of the regression of germling mortality on weekly settlement rate of barnacles represent PCIS values. For consistency with PCIS estimates of established juvenile barnacles using the log response ratio, the sign of the slope was changed to reflect a competitive per capita effect.

that consumers and indirect effects only weakly modify the per capita strength of non-trophic interactions between barnacles and germlings (*a priori* contrast of cage versus control treatments, May, *F*_1,57 = 0.08, *p* = 0.78; June, *F*_2,47 = 0.02, *p* = 0.98). We detected one instance of a cage artefact in Massachusetts during May, which suggested consumers (i.e. *Littorina* spp. and *N. lapillus*) negatively affected germlings more in ‘roof-only’ plots than in unmanipulated control plots (*a priori* contrast of roof versus control plots; *F*_1,57 = 5.21, *p* = 0.026, *F*_region:*cage,57,6,57 = 2.42, *p* = 0.04).

Mortality of germlings also increased with density of metamorphosed juveniles that settled during the experiment. The May estimate of PCIS was large, but variable, suggesting a weak average, but variably strong, effect (table 2), which became a consistent, strong effect in June. By July, survivorship was similar in all treatment combinations (i.e. all *p*-values > 0.05). Like non-trophic interactions, consumer and indirect effects caused variable mortality of *A. nodosum* germlings in space and time. During May, consumer and indirect effects significantly increased germling mortality by 12–13% in SW ME and C ME and slightly increased mortality (approx. 5%) in NE ME (*F*_treatment,2,58 = 7.14, *p* = 0.002; figure 3a). However, in June, their effects were diminished at all but three sites east of the Penobscot River (cf. figure 3a,b; *F*_region:*cage,57,6,57 = 1.92, *p* = 0.04), and by July were not detectable at any site. In Massachusetts, significant germling mortality caused by consumer/indirect effects was not detected during the experiment (May–July).

4. DISCUSSION

Our results demonstrate that per capita effects of barnacles on fucoid germlings vary in space and time and with developmental stage (i.e. the timing of the interaction relative to their settlement; figure 4). Barnacles that settled after and nearby fucoid germlings competed with them. We observed cyprid larvae overgrowing fucoid germlings upon metamorphosis to a juvenile barnacle. Establishment of a relatively large test (approx. 300 μm in diameter) can cover many developing germlings (approx. 70–100 μm in length) thereby outcompeting (killing) them. The strong effect may reflect their large size compared with developing germlings [3,45] and the consistency among regions reflects the ability of viable cyprids to metamorphose and grow in a variety of environments. The outcomes of interactions when barnacles settled before fucoids were complex and varied among regions and months. Thus, our hypothesis that
established barnacles facilitate fucoid germlings was only partially supported.

The hypothesis that barnacles established prior to settlement of fucoid algae facilitate their recruitment was motivated by previous studies of barnacles and fucoids [20,21,24,30,46] and by our observations of GOM populations. Data collected during winter (i.e., prior to current year settlements of barnacles and fucoids) demonstrated that germlings of A. nodosum rarely recruited to habitats lacking barnacles. Moreover, the earlier recruitment of barnacles relative to A. nodosum in the south corresponds with the stronger positive association between germling recruitment and barnacles in the southern compared with northern GOM locations. We also observed this same pattern in a second fucoid, Fucus vesiculosus (data not shown).

However, our experiments showed that established barnacles competed with A. nodosum germlings in the first month after outplanting (May) and competition was especially strong in the southern GOM. The established barnacles were juveniles that settled onto tiles ca two months prior to seeding with A. nodosum zygotes at the start of the experiment. At this stage of development, juvenile barnacles grow rapidly [47–49]. We readily observed juvenile barnacles outcompeting nearby germlings as they grew radially and dislodged or smothered them as they came into contact. The stronger competition during May in southern GOM populations implies that juvenile barnacles there grew radially more rapidly at this time than those in the northern GOM.

The strength of competition increased from May to June only in NE ME. In all other regions during June, the negative effect of juvenile barnacles on germlings weakened and shifted towards facilitation. Significant (strong) facilitation of germlings by juvenile barnacles was observed only in C ME. This region also had consistently greater germling mortality from consumers and indirect effects. We suggest that more slowly growing barnacles in colder waters north of the Penobscot River make a weaker competitive effect that is more than offset by their presence under strong consumer pressure, which affords germlings a refuge from grazing [20]. Shifts of interaction strengths towards weak facilitation, or no net effect, in the southern GOM and C ME may reflect either, or both, of two processes; slowed radial growth of barnacles (i) later in ontogeny and/or (ii) caused by thermal stress during emersion [10,50]. Competitive interaction strength may intensify in June in NE ME where later settlement in colder northern waters means barnacles are in earlier, rapidly growing ontogenetic stages relative to their southern counterparts. Additionally, thermal stress may be reduced in NE ME where cooler temperatures prevail during emersion, partly because of the earlier timing of low tides each day compared with sites to the south.

Throughout spring and summer, therefore, established barnacles had a weak average, but highly variable per capita effect on germlings. This pattern was consistent with our hypothesis that interspecific interaction strengths track environmental change (see also [6,7,9]). In Massachusetts, the southern-most region in the GOM, barnacles had a net weak facilitative effect on germlings, but effects were extremely variable between months (figure 4). SW ME and C ME lie on either side of the Penobscot River, the geographical boundary between the southern and northern GOM. In these areas, barnacles also transitioned between competing with, and facilitating, germlings in time, but with no net effect and less variability overall. In NE ME, the northern-most GOM region, per capita effects of barnacles on germlings were weakly competitive and varied little through spring and summer. Patterns of regional variability in PCISs are concordant with regional differences in the mean and variance of sea surface temperatures in the GOM [25,26]. Seasonal temperatures in the southern GOM (area 1 in [26]) are both warmer on average and more variable than those in the northern GOM (area 2 in [26]). Environmental variability is perhaps an important factor underlying weak average, but highly variable interaction strengths in natural communities at regional geographical scales (but see [45]).

(a) Consumer and indirect effects

Estimates of per capita effects of barnacles on A. nodosum germlings were very similar in the presence or absence of consumers and indirect effects. This was contrary to our prediction that gastropod consumers of barnacles (i.e., dogwhelks) and fucoids (i.e., littorines) would influence PCISs by altering abundances. If the fates of closely associated barnacles and germlings are non-independent, then resolving the effects that consumers have on non-trophic per capita effects may be difficult. Early life stages of barnacles and fucoids are commonly consumed inadvertently by the foraging activities of dogwhelks and littorines on their respective prey (P. Petraitis 1997, personal communication). With respect to indirect
effects, we infer that our census intervals (approx. three to four weeks) were sufficiently short to preclude their influencing estimates of direct effects inside and outside of cages.

Although consumers did not modify the strength of direct per capita effects of barnacles on germlings, they nevertheless contributed significantly to *A. nodosum* germling mortality. At the population level, consumers caused approximately 1–13% mortality of germlings per week. We scaled the effect of barnacles to per population interaction strengths to compare germling mortality caused by consumers with that owing to competition. At the population level, competition and consumer effects contributed similar magnitudes to the overall mortality of *A. nodosum* germlings. Competition accounted for 12–15% of germling mortality during May in Massachusetts where consumer effects were weak and in Maine plots that excluded these effects. However, in Maine plots with consumers, the contribution by competition to germling mortality was reduced to 1–2%. The inverse relationship between mortality from consumers and competition is consistent with prior evidence that consumers control the intensity of competition at the population level [24,51]. The contrast between caging treatments only weakly modifying barnacle effects on germlings on a per capita basis, but significantly reducing mortality from competition at the population level emphasizes that consumers in this system do not alter how competitors interact, but they do affect the frequency of the interaction.

(b) Ontogenetic variation in interaction strength

In contrast to previous studies [20,21,24,30], we found that barnacles compete as readily as they facilitate recruiting fucoid algae. The differences probably reflect the use of *Fucus* spp. and adult barnacles in previous studies and juvenile barnacles and *A. nodosum* in this study. We propose a model to accommodate the different outcomes whereby per capita effects of barnacles on recruiting fucoid changes during ontogeny. Our model proposes that competitive effects of barnacles on germlings are greatest upon, and immediately following, metamorphosis of cyprids to juveniles. The intensity of competition thereafter declines monotonically and eventually the nature of the interaction switches to facilitative. Our model of declining competition among sessile species differs from typical priority effects models of enhanced competition with increased lag times between settlements. The differences lie in the coincident roles that density and environmental factors play in space and time in affecting organismal performance, hence PCIS, during ontogeny.

We suggest that the rate of decline in the strength of competition depends on two parameters; the lag time between barnacle and fucoid settlements and the growth rate of juvenile barnacles relative to fucoid germlings. At one extreme, where barnacles settle either after, or just prior to, fucoids (i.e. lag time approaching 0) and grow relatively rapidly (e.g. barnacles in southern GOM versus *A. nodosum* germlings, which grow very slowly) barnacles compete strongly with fucoids and reduce their recruitment. At the other extreme, adult barnacles that settled in prior years (i.e. a lag of ≥1 year) and grow relatively slowly facilitate fucoids because they do not occupy increasingly more space and do provide refugia from grazers and desiccation [20,21,24,30]. Between these extremes, the duration and intensity of competition and the time at which barnacles become facilitators depend on the lag time of the following fucoid settlement, consumer pressure and environmental factors influencing relative growth rates of barnacles and fucoids. Potentially much greater lag times in the case of *F. vesiculosus* settlement in the GOM and much faster germling growth compared with *A. nodosum* may result in barnacles facilitating *F. vesiculosus* much more frequently than *A. nodosum*. Since our experimental design neither mimicked natural regional variation in lag times of fucoid settlement after barnacles nor used *Fucus* spp. as well as *A. nodosum*, support for this model requires additional experimental tests.

The factors hypothesized to underlie spatial and temporal variability of PCIS among barnacles and fucoids may be common to interactions involving priority effects. Priority effects often involve early, post-reproductive life-history stages. Fecundities and reproductive phenologies of species involved in ‘priority effect’ interactions are typically influenced by abiotic environmental factors (e.g. temperature, light, etc.). The strengths and/or nature of the ensuing interactions among species may vary with respect to timing or developmental stage of the interactors because organismal performance tracks environmental change and densities decline as juveniles perish.

The variability in the strengths of direct and indirect effects on *A. nodosum* germlings may contribute to the observed contingency in year-to-year recruitment of this community dominant. Moreover, the sensitivity of barnacle–fucoid interactions to environmental conditions ([10]; this study) suggests important consequences for these key species as regional climate changes. Observing this variability in interactions between these, and other, ecologically important species across regions may provide insight into their interactions through time and resultant community dynamics shaped by climate change.

Species interaction strengths track environmental change [6] and, in this case, predicted increases in environmental variability throughout the GOM should increase variability of interactions between foundation species of sheltered North Atlantic shores and others. Variability of interactions observed in C ME coincides with evidence for low resilience of *A. nodosum* stands to disturbance and switches between community states [52] compared with elsewhere in the GOM. Such coincidences suggest that climate change-induced variability of key species interactions may compromise the stability of natural ecosystems.

S.R.D. dedicates this paper to R. L. Vadas, Sr on the occasion of his retirement and thanks him for sharing his insight about the natural history of *A. nodosum* that underlies this research. R.L.K. thanks S. Arnold, S. Brawley, A. Johnson, L. Johnson, S. Johnson, R. R. Kordas, P. Petratis, A. Steen, J. Sullivan, G. Trussell, R. L. Vadas, Sr, R. Whittach, P. Yund and the staff at the University of Connecticut, Avery Point, University of Maine Darling Marine Center and Northeastern University Marine Science Center for help with logistics, providing supplies, laboratory space or fieldwork. We thank J. Bruno, C. Harley and laboratory, J. KUBLER, P. PETRAITIS, J. T. WOOTTON and two anonymous reviewers for reading the manuscript. This work was supported by grants to S.R.D.
from the National Institutes of Health (NIH), the CSUN Sponsored Programmes Office and the CSUN College of Science and Mathematics, and by grants to R.L.K. from the Ira C. Darling Marine Laboratory of the University of Maine, PADI Foundation and grants from the following programmes at CSUN: College of Science and Mathematics, Graduate Research and International Programmes and University Corporation and Associated Students. S.R.D. formulated the ideas of this study. S.R.D. and R.L.K. designed the experiments to test hypotheses contained herein. R.L.K. executed the study. R.L.K. and S.R.D. analysed the data and wrote the paper. The authors declare no competing financial interests. This is contribution number 168 of the Marine Biology Group at CSUN.

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