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Modeling variation in interaction strength between barnacles and fucoids

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Abstract

The strength by which species interact can vary throughout their ontogeny, as environments vary in space and time, and with the density of their populations. Characterizing strengths of interaction in situ for even a small number of species is logistically difficult and may apply only to those conditions under which the estimates were derived. We sought to combine data from field experiments estimating interaction strength of life stages of the barnacle, *Semibalanus balanoides*, on germlings of *Ascophyllum nodosum*, with a model that explored the consequences of variability at per capita and per population levels to the abundance of year-old algal recruits. We further simulated how this interaction affected fucoid germling abundance as the timing of their respective settlements varied relative to one another, as occurs regionally across the Gulf of Maine, USA. Juvenile *S. balanoides* have a weak estimated per capita effect on germlings. Germling populations are sensitive to variation in per capita effects of juvenile barnacles because of the typically large population sizes of the latter. However, high mortality of juvenile barnacles weakens the population interaction strength over time. Adult barnacles probably weakly facilitate fucoid germlings, but greater survival of adults sustains the strength of that interaction at the population level. Germling abundance is positively associated with densities of adult barnacles and negatively associated with that of juvenile barnacles. Metamorphosing cyprid larvae have the strongest per capita effect on germling abundance, but the interaction between the two stages is so short-lived that germling abundance is altered little. Variation in the timing of barnacle and *A. nodosum* settlement relative to one another had very little influence on the abundance of yearling germlings. Interactions between barnacles and germlings may influence the demographic structure of *A. nodosum* populations and the persistence of fucoid-dominated communities on sheltered rocky shores in New England.

Keywords

Per capita interaction strength; Population dynamics; *Semibalanus balanoides*; *Ascophyllum nodosum*; Gulf of Maine

Introduction

As the physiological performance of species changes with environmental variability in space and time, so too does the strength of their interactions with other species in a community. This variability in interaction strength in space and time may strongly affect community structure, hence, estimation of per capita effects among interacting species is expected to advance our understanding of, and capacity to predict, the dynamics of ecological communities. Previous studies quantifying per capita interaction strengths (PCIS) have distinguished strong interactors from weak ones and how each influences community structure (Paine 1992; Fagan and Hurd 1994; Wootton 1997; Berlow 1999; Sala and Graham 2002). To the extent that the relative strengths of these relationships among species remain the same in space and time, estimates obtained from experiments conducted over small spatial and temporal scales can characterize community dynamics in a given ecosystem relatively well (May 1973; McCann et al. 1998; Kokkoris et al. 1999).

Characterizing PCIS in field experiments for even a small number of species in a community is logistically difficult and may apply to limited natural situations, specifically those conditions under which the estimates were derived. The principal causes of such limitations stem from awareness that the strength, or even the nature, of interactions change with densities (Ruesink 1998), and in different environments (Bertness and Hacker 1994; Bertness and Yeh 1994; Hacker and Bertness 1995; Harley 2003). For instance, species that share broad geographic distributions can have interactions that switch between facilitative and competitive over the gradient (Leonard 2000). Sessile species, especially, may interact differently over a scale of meters as well (Dudgeon et al. 1999).

Species interactions change not only spatially, but temporally as well (Sanford 1999), a fact that complicates the use of static measures of interaction strengths, which are inherently rate functions, and are derived from experiments of variable duration. A corollary of temporal changes is that species do not always interact with one another the same way throughout their lives. Interactions may vary ontogenetically; the most obvious examples are those in which a species switches from prey to predator of another species as it develops from larval to adult life stages (Palomares and Caro 1999; Koster and Mollmann 2000). Temporal variation in species reproduction also governs interactions with other species and depends on the influx of offspring relative to environmental conditions and the reproductive timing of other species (Duffy and Hay 2000; Underwood and Keough 2001).

A combination of experimental data and modeling may provide better insight into the effect of one species on another than either approach alone. This pluralistic approach provides models with realistic estimates of parameter values derived from experiments under different conditions to enable projections of interspecific effects beyond typical small scales of space and time of field experiments. Moreover, these parameter estimates can be used to simulate experimental outcomes that address questions that may be logistically difficult or impossible to execute in situ.

The interactions between barnacles and fucoids on temperate rocky shores in the northern hemisphere provide a model system in which to explore the variability in PCIS in space and time, associated with variability in timing of propagule settlement, and between different ontogenetic stages across species. Both taxa are very common inhabitants of the mid intertidal zone, are easily amenable to experimentation and, consequently, much has been learned about the ecology of all of their respective life history stages (see reviews by Southward 1991; Chapman 1995; Schiel and Foster 2006). Fucoids, especially the canopy-forming species, *Ascophyllum nodosum* (L.) Le Jolis, act as ecosystem engineers by reducing thermal stress for under-story species, harboring consumers and modulating the flow of abiotic resources as well

as the arrival of propagules (Bertness and Leonard 1997; Petraitis and Dudgeon 1999; Leonard 2000). Barnacles may positively influence the abundance of canopy-forming fucoids by facilitating the recruitment of fucoid germlings (Lubchenco 1983; Chapman 1989; van Tamelen and Stekoll 1997) which otherwise appear to suffer high mortality (Johnson and Brawley 1998; Dudgeon and Petraitis 2005).

The fucoid, *A. nodosum*, and the acorn barnacle, *Semibalanus balanoides* (L.), coexist across much of their respective latitudinal ranges in the North Atlantic. Both *A. nodosum* and *S. balanoides* flourish in the mid and upper intertidal zones of granitic sheltered shores and can tolerate a wide range of environmental conditions (e.g., low salinity, extreme temperatures, desiccation). Whereas *A. nodosum* is much more abundant on sheltered shores, *S. balanoides* occurs abundantly across the spectrum of hydrodynamic exposures.

A. nodosum is a dioecious species that has great longevity (Åberg 1992a) if it survives its short dispersal (in the order of meters; Dudgeon et al. 2001) and protracted yearlong vulnerable germling state (Dudgeon and Petraitis 2005). Individuals become reproductive at a frond length of ~40 cm, which on sheltered shores of the Gulf of Maine (GOM) has been estimated to take about 9 years (Cousens 1985; Dudgeon and Petraitis 2005). Populations in the GOM reproduce annually in a narrow window spanning 3–5 weeks at any one site associated with seawater temperatures of 6–10° C (Bacon and Vadas 1991). It is remarkable that for the most abundant organism (in terms of biomass) on sheltered rocky shores of the Northwest Atlantic, with such a large annual investment in reproduction (Cousens 1985; Åberg and Pavia 1997), *A. nodosum* populations are typically lacking in yearling age recruits (Baardseth 1955, 1970; Vadas and Wright 1986; Vadas et al. 1990; Cervin et al. 2004; Dudgeon and Petraitis 2005). These characteristics of *A. nodosum* populations have prompted attention to the first year germling stage as a critical one influencing the demography of their populations (Dudgeon and Petraitis 2005).

S. balanoides, on the other hand, is hermaphroditic and relatively short-lived (~4 years), transitioning from a widely dispersing larva to benthic juvenile in 1.5 days (Pineda et al. 2002) and from juvenile to adult in 11 months (Connell 1985). The timing of settlement and density of barnacle cyprid larvae is highly variable year to year and spatially across the GOM (Wetthey 1985), but the trend is for barnacles to settle over a 4- to 6-week period in spring, and settling more densely in southern populations than those further to the north and east (R. Kordas, S. Dudgeon, personal observation). *S. balanoides* populations at sites in the GOM display a mix of age or stage structures that reflect the dynamics of recent settlement histories and mortality of established individuals as do barnacles elsewhere (Gaines and Roughgarden 1985).

Across their mutual geographic range, environments vary dramatically, especially in temperature, and reproductive functions of both species respond to thermal changes, such that more southerly populations reproduce earlier (Wetthey 1985; Bacon and Vadas 1991; Kordas 2006). Thermal sensitivity of reproduction coupled with their different longevity and capacities for dispersal results in newly recruited individuals of *A. nodosum* potentially encountering three separate ontogenetic stages of barnacles within a single season. The relative frequency and intensity of interactions in space and time between these different barnacle life history stages during the vulnerable yearling stage of *A. nodosum* may have implications for future mature *A. nodosum* populations at that site, as well as the associated community that *A. nodosum* populations strongly influence.

We sought to model the importance of an ontogenetically variable interactor, such as a barnacle, on *A. nodosum* populations. We developed a model in which cyprid and juvenile barnacles negatively affected the fucoid germling population and adult barnacles positively

affected it, in accord with earlier and more recent empirical results (Lubchenco 1983; van Tamelen and Stekoll 1997; Kordas 2006; Dudgeon unpublished data). The primary objectives were to: (1) determine which life history stage of barnacle has the greatest impact on a model population of the fucoid, *A. nodosum*; and (2) model how variability in the timing of propagule settlement of barnacles and fucoids relative to one another affected the abundance of year-old germlings. These objectives were met by modeling, using empirically derived parameter values, the sensitivity of germling survivorship to both, per capita, and per population, interaction strengths of cyprid, juvenile and adult barnacles, respectively, and by varying the timings of fucoid and barnacle settlement in model simulations. In addition to varying the timings of barnacle and documented *A. nodosum* settlements, we also tested the effect on germling abundance of broadening the settlement window of the latter to consist of a bimodal distribution with peaks in spring and fall; a pattern not documented in *A. nodosum*, but which characterizes another co-occurring fucoid, *Fucus vesiculosus* (L.). Our motivation was to evaluate two hypotheses of interest that are important, but that cannot be experimentally tested. First, we sought to test if the relative paucity of yearling recruits of *A. nodosum* (noted above) compared to the abundance of recruits of *F. vesiculosus* is associated with their respective phenologies. Second, we sought to evaluate how a shift in phenology, such as may occur as a result of climate change in the region, may affect the interactions between barnacles and *A. nodosum* and the demography of *A. nodosum* populations. These simulations were likewise tested with variable timings of barnacle settlement. Our aim in testing variability in reproductive phenology of barnacles relative to those of *A. nodosum* was to evaluate the differential effects that barnacles may have on fucoids spatially (e.g., across regions) or temporally as environmental change (e.g., warming) affects phenologies at a given site. Finally, we compare modeled and observed abundances of year-old *A. nodosum* germlings throughout the GOM and project how germling numbers may translate downstream to mature *A. nodosum* populations.

Materials and methods

Field collection of PCIS data

We defined four distinct coastal regions in the GOM that differ principally in thermal regime associated with regional circulation patterns; Massachusetts (Cape Cod Bay to Rye Ledge, New Hampshire), southern Maine (Brunswick to west bank of the Penobscot River), central Maine (east bank of the Penobscot River to Schoodic Point), eastern Maine (Schoodic Point into the Bay of Fundy). Colder waters in the Bay of Fundy move southwest along the Maine coast and are deflected offshore by Schoodic Point, and in this eastern region areas of upwelling can be found throughout the year (Apollonio 1979). To the west of Schoodic Point, the southwest flowing current is also deflected offshore by riverine output from the Penobscot River further south. The coastal current continues flowing southwest towards Brunswick and then into Massachusetts where water temperatures are much warmer than in the eastern region.

In each of the four regions of the GOM, we estimated the per capita effects of larval and juvenile barnacles on *A. nodosum* germlings at three sites. All 12 sites throughout the GOM were characterized by granitic benches having at least 1,000 m² of dense *A. nodosum* cover, an abundance of barnacles and low to moderate wave exposure [see Electronic supplementary material (ESM) S1 for site details].

Estimating PCIS of juvenile and larval barnacles on germlings required different experimental approaches. In the case of juvenile barnacles, we settled barnacles onto 6.3-cm² detoxified epoxy tiles (following Brawley and Johnson 1991) in early spring, allowed them to grow in running seawater for 2 months then scraped barnacles off half the tiles to create two treatments, tiles with and without juvenile barnacles. Onto all tiles, we seeded *A. nodosum* zygotes and installed one pair of barnacle/no barnacle treatments into each of six 1-m² cleared plots in the

mid intertidal zone. We estimated PCIS of juvenile barnacles on germlings using the natural log of the ratio of germling survivorship with barnacles present to that when barnacles were absent divided by the number of barnacles in the census interval (modified from Laska and Wootton 1998). PCIS estimates by region for each month are presented in ESM S2.

The per capita effect of barnacles on *A. nodosum* germlings was estimated at these same sites for 3 months when barnacle cyprid larvae also were settling. We used the dynamic regression approach of censusing *A. nodosum* germling mortality between sampling intervals as a function of the number of newly settled barnacles (see Pfister 1995; Laska and Wootton 1998). The slope (estimated as the reduced major axis model II) of germling mortality versus the estimated settlement density of cyprid larvae was used to estimate PCIS (ESM S2; see also Pfister 1995; Laska and Wootton 1998).

The model

The model simulates density (m^{-2}) of a fucoid germling population in response to barnacle population dynamics over a 15-month period (from 1 January to 1 April of the following year; Eq. 1 in Fig. 1). This corresponds to the period just prior to, and up to 1 year following settlement of a single annual cohort of *A. nodosum* in order to estimate the number of germlings that would survive the critical first year (after which mortality rate declines; Åberg 1992b; Dudgeon and Petraitis 2005). The model is deterministic and uses nonstationary parameters calibrated to weekly rates that were gathered from previous studies conducted in the GOM (ESM S2, Table 1) and elsewhere, and are expressed in density (m^{-2}). Data in ESM S2 were distilled to isolate the competitive values. Small positive values were perceived as noise and changed to zeroes to recalculate averages for Table 1. Our model is nonspatial, but simulations are conducted using parameters specific for regions of the GOM based on Kordas (2006). Model simulations were performed using Stella Research Software (version 7; Hanover, N.H.) using Euler's method of integration.

Separate parameters were established for fucoid zygotes (first week following settlement) and germlings (≥ 2 weeks after settlement) to distinguish the different survivorships of early life stages prior to, and following, generation of a rhizoid for attachment (Dudgeon and Petraitis 2005). Likewise, different life stages of barnacles (cyprids, juveniles, and adults) were treated as separate parameters in model equations, with unique PCIS to partition their effect on *A. nodosum* germlings. Age-specific survivorships of barnacles in model equations were taken from data in Petraitis et al. (2003). The survivorship of fucoid germlings was increased by facilitation (Lubchenco 1983; van Tamelen and Stekoll 1997) from adult barnacles (Eq. 2, Eq. 3) and decreased by competition (Kordas 2006) from juvenile and cyprid barnacles (Eq. 3, see Fig. 1).

Recruitment of *A. nodosum* germlings

Densities of *A. nodosum* zygote settlement were estimated from production values in Åberg and Pavia (1997) ($\sim 2.5 \times 10^9$ eggs m^{-2}), minus the number of those eggs that fail to become settled zygotes. We conservatively estimated a 70% fertilization rate of produced eggs, because eggs may be unreleased, aborted, or otherwise not viable (Serrao et al. 1996 estimates $>90\%$ fertilization of released eggs of *Fucus* spp. and we have observed many unreleased eggs in *A. nodosum* conceptacles). Additionally, most zygotes disperse beyond 6 m from their release point (Dudgeon et al. 2001) and many fail to settle and attach successfully on hard substrate. Thus, for most simulations, 6.5×10^6 zygotes m^{-2} were pulsed over a 5-week period in a step-wise and symmetric fashion to mimic natural settlement (i.e., fraction settling over weeks 1–5; 0.11, 0.22, 0.33, 0.22, and 0.11; Fig. 2a, black bars). However, we were also interested in how a different reproductive phenology for *A. nodosum* may impact the abundance of germlings from the cohort at the onset of the following spring. For a hypothetical broader

settlement window, we distributed the 6.5 million zygotes bimodally. Settlement began in April and extended through July and occurred again from the beginning of September to the end of December (this pattern characterizes that of a related fucoid, *Fucus vesiculosus* in Maine; S. Dudgeon, personal observation). Zygote settlement was pulsed over each period in a step-wise fashion; however, two-thirds of the total number of zygotes were pulsed over the first window (April–July), and one-third over the second window (September–December; Fig. 2a, grey bars). Zygote survivorship was held constant in all simulations.

Mortality of *A. nodosum* germlings

Total mortality of *A. nodosum* results from several factors, principally consumption by gastropods and abiotic stress during summer months (presumably temperature and desiccation; Dudgeon and Petraitis 2005), hence our mortality rate parameter values vary accordingly. Adult, juvenile, and cyprid *S. balanoides* have different per capita effects on germlings and all vary temporally and spatially across the GOM (Kordas 2006), although variability of adult PCIS is unknown, so the effect of each was factored into *A. nodosum* mortality separately.

Recruitment and mortality of *S. balanoides*

Cyprid survivorship values varied temporally but not spatially (see Petraitis et al. 2003). For simulations testing spatial variability, region-specific values for cyprid density were used (Table 1). For all simulations, the density of cyprids was pulsed over a 5-week period in a symmetric, step-wise fashion to idealize natural settlement distributions (fraction settling over weeks 1–5; 0.11, 0.22, 0.33, 0.22, and 0.11). *S. balanoides* mortality rate varied over time and with density of barnacles for all simulations based on published values (Table 1).

The timing of settlement and density of barnacle cyprid larvae is highly variable year to year and spatially across the GOM (Wetthey 1985). For simulations testing spatial variability, region-specific values for timing of settlement were used. Cyprid and adult barnacle density data were abundant in the literature, and represented our four regions in the GOM. The data for each region were highly variable so we calculated the geometric mean for cyprid and adult density for each region. Moreover, the geometric mean is useful to estimate average factors (Sokal and Rohlf 1995), in this case, how different barnacle abundance is between regions. However, the arithmetic mean is useful when several quantities (i.e., barnacle abundance in each region) are combined to estimate a quantity representing the mean for the whole geographic region. The arithmetic mean across all regions, therefore, was used as a baseline value for simulations when barnacle densities were held constant while other factors were tested (Table 1). Indeed, we found that the arithmetic, rather than geometric mean, was more representative of the densities of cyprids and adults when estimated for the GOM as a whole (R. Kordas, personal observation).

Barnacle survivorship changes early in life associated with temperature, desiccation, barnacle density (Bertness 1989), and consumption (Connell 1961; Petraitis 1990; Petraitis et al. 2003) and contributed to the juvenile mortality term. We varied juvenile survivorship in the model, ranging from 0.825 to 0.912 over 15 months. Survivorship was 0.912 during January to February, 0.825 from March to May, 0.875 from May to September, 0.912 from September to February, and 0.825 in March of the following year (Petraitis et al. 2003). Juvenile survivorship decreased by 0.002 with every increase of 2,000 barnacles to represent density-dependent mortality. Across shores in the North Atlantic there is very little variation in juvenile barnacle survivorship (discussed in Petraitis et al. 2003), so this variable was held constant for spatial simulations. There are very few data to describe spatial variation in cyprid survivorship in the GOM. Therefore, the values described above were used in all simulations, including those that tested spatial variation across the GOM (Table 1).

Densities of adult *S. balanoides* varied in spatial simulations corresponding to their regional abundances across the GOM. PCIS of adult *S. balanoides* on germlings was kept constant in all simulations, except those specifically testing the sensitivity of model output to this interaction. PCIS of adult barnacles on *A. nodosum* germlings has never been experimentally determined, so we tested a range of plausible values spanning 3 orders of magnitude to estimate the effect on germling abundance.

Mature *A. nodosum*

We projected the effects of barnacles on an *A. nodosum* germling cohort to the adult stand remaining 8 years later with a simple model. We estimated the age of sexual maturity from Cousens (1985), who suggests that in the GOM *A. nodosum* becomes sexually mature at about 40-cm frond length, and that it takes about 9 years for a frond there to reach 40 cm in length. We began with the germling density after a year (from above simulations) and assumed a constant annual mortality rate of 0.1536 (for individuals 1-year-old or older, in ice-free years; Åberg 1992a) to calculate the density of adult *A. nodosum* remaining in the cohort.

Model simulations and results

Variability in per capita effects of barnacles

Throughout the year, *A. nodosum* germlings interact with different life stages of barnacles. Once cyprids settle in the spring, *A. nodosum* germlings interact with cyprid, juvenile, and adult barnacles simultaneously. During autumn and winter, germlings are only exposed to the remaining maturing or adult barnacles. Adult barnacles facilitate other fucoid species (Lubchenco 1983; Farrell 1991), and so may also facilitate *A. nodosum* germlings, although it has not been experimentally measured. Juvenile barnacles compete with *A. nodosum* germlings as they grow radially, and may be an important factor in germling mortality. Previous experiments (Kordas 2006) found that the per capita competitive effect of juveniles on germlings ranges from 0 to -2.65×10^{-3} germlings/barnacle per week. Furthermore, the strength of the interaction varies temporally and spatially (ESM S2). In the northern regions of the GOM, barnacle cyprid larvae settle after *A. nodosum* zygotes, and have a short-lived, but strong per capita effect on germlings (Kordas 2006).

We modeled the response of a germling population to interactions with cyprid, juvenile and adult stages of barnacles. Moreover, we evaluated the sensitivity of this population to variability in PCIS of each of the three barnacle stages. We varied PCIS values across 3 orders of magnitude (absolute value range of 1×10^{-4} to 0.1) that bracketed empirically measured, or estimated, PCIS near the middle of that range. For these simulations testing sensitivity to PCIS, *A. nodosum* germlings settled contemporaneously with barnacle cyprid larvae (weeks 16–20 of a calendar year, corresponding approximately to the month of April, of a 65-week total simulation) and the arithmetic averages for the GOM of adult barnacle and cyprid larval abundances were held constant at 416 and 16,974 m^{-2} , respectively. All other parameter values were held constant across simulations testing sensitivity to PCIS using the time-averaged rates for each week of the simulation (Table 1).

Results

Control simulations estimated 84, 85 and 84 one-year-old recruits m^{-2} in the case of no interaction (PCIS = 0) between *A. nodosum* and cyprid, juvenile, and adult barnacles, respectively. These estimates are comparable to actual estimates of densities of year-old recruits of *A. nodosum* in natural populations ($\sim 40\text{--}60 \text{ m}^{-2}$) (Baardseth 1955, 1970; Vadas and Wright 1986; Vadas et al. 1990; Cervin et al. 2004). We present sensitivity data of germling populations to a given PCIS as the difference in germling number from the control simulation for easy visual interpretation (Fig. 3).

At measured, or estimated, PCIS (i.e., germlings/barnacle per week), cyprid larvae had no measurable effect and adult barnacles only weakly affected germling abundance. Germling abundance was insensitive to variation in cyprid PCIS, differing by less than a single recruit across 3 orders of magnitude change in PCIS (Fig. 3a). Variation in PCIS of adult barnacles across the same range caused greater changes in germling abundance. For large per capita facilitative effects (0.1 germlings/barnacle per week) by adult barnacles, *A. nodosum* germlings were 1.12 times more likely to survive, increasing density of the model population by 11% (Fig. 3c). Variation in PCIS of competition from juvenile barnacles had slightly weaker effects on germling abundance. Germlings in the presence of juvenile barnacles were 1.05 times more likely to die in their first year than in their absence using PCIS values ~ 0.0007 measured from field experiments (Kordas 2006). However, germling populations were sensitive to variation in juvenile barnacle PCIS; a large per capita effect of competition of 0.04 was sufficient to eliminate a cohort of germlings (Fig. 3b).

Variability in per population interaction strength

We estimated the sensitivity of model germling populations to variation in per population interaction strength (PPIS) of the different barnacle life history stages by systematic variations of population densities of adult barnacles and larvae. Six sets of simulations were performed that varied both adult and larval densities in opposite directions (i.e., one increased while the other decreased). Whereas one extreme consisted of the maximally observed larval recruit density observed in the GOM ($19,074 \text{ m}^{-2}$) and zero adults, the other extreme consisted of zero larvae and the maximal adult populations density ($5,300 \text{ m}^{-2}$) observed in the GOM. The five intermediate value simulations used proportions of 0.83, 0.67, 0.50, 0.33 and 0.17 times the maximum larval density and 0.17, 0.33, 0.50, 0.67 and 0.83 times the maximum adult density of barnacles, respectively. We partitioned the relative contributions of cyprid, juvenile and adult PPIS to changes in germling abundance by running three sets of these six simulations. The first tested the effect of juvenile barnacles by manipulating cyprid densities as described above, but setting adult and cyprid PCIS equal to zero. Thus, cyprid densities were filtered in to generate variable population numbers of juveniles, but cyprids themselves (and adults) had no effect. The second and third sets of simulations partitioned the relative contributions of adult and cyprid populations by either varying cyprid abundances in the absence of adult barnacles, or varying adult abundance in the absence of larval settlement. Non-zero PCIS parameters used in these simulations were those estimated from field experiments (ESM S2). For these simulations, we modeled contemporaneous settlement of fucoid zygotes and barnacle larvae from late April to late May (weeks 16–20 of a calendar year). All other parameter values were held constant across simulations testing sensitivity to PPIS using the time-averaged rates for each week of the simulation (Table 1).

Results

Germling density increased approximately 1 m^{-2} in simulations in which adult barnacle density increased, and juvenile barnacle density decreased, each by 0.17 of their respective maximal values (Fig. 4, grey bars). This pattern is driven largely by the facilitative effect of adult barnacles [cf. grey bars (representing change in germling density in response to simultaneous changes in cyprid and adult barnacle densities) with black bars (representing change in germling density in response only to change in adult barnacle density)]. Whereas facilitation by adult barnacles causes measurable increases in germling density at all barnacle population sizes tested, competition from juveniles causes measurable, but small, decreases in germling density only at the highest densities of cyprid larvae metamorphosing to juveniles. Cyprids themselves had no population-level effect on germling density at any size.

Variation in timing of settlement

Reproductive development and the timings of propagule release and settlement of *A. nodosum* and *S. balanoides* are associated with water temperature and ocean currents (Wetthey 1985; Bacon and Vadas 1991; Pineda et al. 2006). Each spring, sea surface temperatures begin to differ among regions across the GOM. Water in the southwest warms much more rapidly (up to 8–9°C warmer) than in the northeast where upwelling and current patterns cause 2–4°C water temperatures to persist late in spring (Apollonio 1979; Richert 2008). Consequently, reproduction of both barnacles and fucoids occurs predictably earlier in southern GOM populations than those further north and east. The settlement window of *A. nodosum* is confined to ~3–5 weeks at a given location (R. Kordas, S. Dudgeon, personal observation) associated with ~6–10°C seawater temperatures at high tide (Bacon and Vadas 1991). Timing of barnacle settlement also varies across latitude of the GOM, but the settlement window is more variable and tends to be broader, spanning 3–12 weeks (Pineda et al. 2006). This variability stems in part from their greater capacity for dispersal among regions, such that at sites along the central coast of Maine, cyprid larvae dispersing from southern populations may settle early, and those from more northerly populations may settle later, relative to barnacle cyprids from nearby populations that settle in mid spring. Therefore, barnacles can recruit before, contemporaneously with, or following settlement of *A. nodosum* depending on latitude (R. Kordas, personal observation). Timing of reproduction can have important consequences for the success of a cohort and persistence of a population. We modeled how variability in the timing of settlement of *S. balanoides* and *A. nodosum* relative to one another affected projected abundances of germlings at the onset of the following spring. We tested variability in the reproductive phenologies of barnacles with two different phenology for *A. nodosum* (one real, the other hypothetical) to separately address their consequences to demographic patterns of germling abundance the following spring. The two scenarios simulated the same number of settling zygotes, but they differed in their temporal distribution. The real window consisted of a 5-week settlement period in spring, whereas the hypothetical window (based on the phenology of *F. vesiculosus*) consisted of a bimodal distribution with peak settlements in mid May and late September (Fig. 2a, black and grey bars respectively). For both settlement patterns, the relative timing of the barnacle settlement window was varied across 17 different simulations ranging from windows spanning early February–March to late May–June. In this way, the effect of barnacles that settled before, contemporaneously with, or after the spring settlement of zygotes could be compared. For this analysis, two sets of simulations were run; one using the average density of barnacles, the other using the maximum density of barnacles observed across the GOM (Table 1). The per capita effects of barnacles were not varied for these simulations.

Results

The number of germlings over time largely reflects the settlement history for both real and hypothetical *A. nodosum* settlement windows (Fig. 2a; cf. grey lines and bars and black lines and bars). Contrary to our expectation, however, the variation in timing of the barnacle settlement window had little effect on the number of germlings the following spring for either settlement pattern (Fig. 2b). Comparisons of either absolute number or percentage change in germling numbers between the two settlement windows are confounded when the values differ so greatly in magnitude and likewise between the simulations of average and maximal barnacle densities, so we describe these changes in comparable terms of odds ratios of survival to the following spring in the context of the timing of barnacle settlement. The number of germlings in a hypothetical settlement window was completely insensitive to both the density of barnacles (average vs. maximum) and the timing of barnacle settlement; there were even odds of germling survival whether barnacles settled completely before or completely after fucoids. The number of germlings in a real settlement window was similarly insensitive to the timing of barnacle settlement. Germling number using the real *A. nodosum* settlement window was slightly more

sensitive to the density of barnacles. Germlings were 1.06 times more likely to survive under maximum barnacle densities than under average barnacle densities (Fig. 2b, cf. hatched vs. solid grey bars).

The most striking contrast was the difference between the “*Fucus*-type” settlement window that had ~23-fold the number of germlings than the “*Ascophyllum*-type” settlement window at the beginning of the following spring, despite the same number of settling zygotes.

Observed versus modeled abundances using region-specific parameters

Four model simulations were run in which parameters were varied specifically for each of the four regions of the GOM. We sought to determine whether patterns of germling abundance across these regions of the GOM estimated by a model driven principally by variation in timing, interaction strength and density parameters were comparable to patterns observed in situ. Thus, parameters for PCIS of each barnacle stage and densities of cyprid and adult barnacles (hence, PPIS), and the timings of both barnacle cyprid and *A. nodosum* zygote settlement were varied according to our data and observations throughout the GOM (Table 1, ESM S2; Kordas 2006), whereas all other parameters had the same value in all four region-specific simulations (Table 1). Settlement windows varied from March up to and including late April for simulations representing Massachusetts, from mid April to mid May for western Maine, from early May to early June for central Maine, and from mid June to mid July for eastern Maine.

Results

The pattern of year-old germling abundance across the GOM estimated by the model is similar to that observed across the GOM, and closely matches the actual abundances in natural populations of each region, with one possible exception in eastern Maine (Fig. 5; NE ME). Whereas the model predicts increased *A. nodosum* germling abundance from southwest to northeast GOM associated with declining densities of later-settling cyprids and fewer juveniles that negatively impact germlings, field data were too variable to resolve statistically significant differences in germling abundance among regions ($F_{3,9} = 0.98$, $P = 0.44$), though the data suggest that fewer germlings may occur at sites east of the Penobscot River in Maine (C ME and NE ME) than at sites to the south and west. However, we observed a precipitous decline in germling abundance between central and eastern Maine, such that *A. nodosum* germlings are conspicuously rare in eastern Maine from all but one site sampled. Including data from the suspected outlier site in eastern Maine (Destiny Cove) makes abundances estimated by the model match more closely actual patterns throughout the GOM.

Projection to mature *A. nodosum* densities

The results of above simulations estimating the abundance of year-old germlings from the cohort were projected to estimate the number that would reach maturity using the simple survivorship to maturity model (Fig. 1; Eq. 7). Since the densities of adults are directly proportional to the numbers of germlings surviving the first year, we can estimate the effect of barnacle life stages on future stand densities of *A. nodosum*. High densities of adult barnacles ($5,300 \text{ m}^{-2}$) by virtue of facilitation are expected to increase the number of individuals of *A. nodosum* surviving to maturity by 1.06 times. In contrast, the average density and approximate maximum PCIS of juvenile barnacles on germlings estimated from field experiments are expected to decrease the number of individuals of *A. nodosum* surviving to maturity by 1.28 times.

Discussion

Individuals of *A. nodosum* are large, often have great biomass and longevity, yet germlings during their first year of life are extremely vulnerable. The year-long germling stage may be

critical to persistence of *A. nodosum* populations (and the associated community) following a disturbance (e.g., ice scour) that necessitates colonization (Dudgeon and Petraitis 2005). Our model simulations reflect the poor survivorship that characterizes germlings of *A. nodosum*. Greater than 99.9% of germlings in model populations died in their first year as observed in natural populations. Dudgeon and Petraitis (2005) estimated that mortality of *A. nodosum* germlings exceeded 99% during their first year. Åberg and Pavia (1997) coupled reproductive effort data and abundance of recruits of *A. nodosum* to estimate a transition probability from egg to established individual of $\sim 10^{-8}$.

Outcomes of our simulations suggest that regional patterns of *A. nodosum* recruitment can be approximated by a model having region-specific parameters for the strength of interactions between germlings and barnacles, the size of the barnacle populations and the timing of barnacle settlement relative to *A. nodosum*. Moreover, our results suggest that barnacles have a modest, but significant impact on the early life stage demography of *A. nodosum* that later may influence the density of mature stands.

Interaction strength of barnacle life stages on germlings

Cyprid, juvenile and adult barnacle life stages each have impacts of different strength on model populations of *A. nodosum* germlings. Juvenile barnacles have a much greater negative impact on germlings than do metamorphosing cyprid larvae; germlings in the presence of juvenile barnacles were more than one-quarter more likely to die as germlings in the absence of juveniles, whereas germlings in the presence of metamorphosing cyprids were no more likely to die than germlings without cyprids present. In these simulations, population size of cyprids was slightly greater than that of juveniles, differing only because of the very early mortality of newly metamorphosed juvenile barnacles. However, the per capita effect typical of the interaction between juveniles and germlings was much less than that between metamorphosing larvae and germlings, in accord with the empirical results of Kordas (2006). Nevertheless, even when tested across the same 3 orders of magnitude range of PCIS with similar population sizes, germling populations were more sensitive to, and much more strongly affected by, juvenile barnacles. This is because the duration of interaction with germlings is very different for cyprid larvae and juveniles. Although cyprids are much larger (ca. 300 μm in length) than fucoid germlings (ca. 70 μm in diameter) and can smother clustered germlings upon metamorphosis to a barnacle (S. Dudgeon, personal observation), cyprids settle and metamorphose within 1–2 days (Pineda et al. 2002) making for a brief period of interaction. In contrast, juvenile *S. balanoides* potentially interact with germlings for much longer periods and they grow radially at the rate of 50 $\mu\text{m week}^{-1}$ (Crisp 1960) during which time they can dislodge many germlings as their basal area increases.

Comparison between adult and juvenile barnacles with respect to their relative strengths of interaction on *A. nodosum* germlings is complicated by the lack of direct estimates of PCIS, or PPIS, of adult barnacles on any fucoid germling. In contrast to juvenile barnacles, experimental evidence suggests that adults facilitate fucoid germlings (Lubchenco 1983; Farrell 1991; van Tamelen and Stekoll 1997). Adults increase the topographic complexity of the substrate creating microhabitats for other organisms. The small spaces between barnacles can trap moisture during low tides, reducing desiccation and thermal stress on germlings (Bertness 1989). Moreover, aggregated barnacles can deter consumers from foraging in the spaces between barnacles, reducing rates of germling consumption. However, facilitation of fucoids by adults is probably a weak interaction in New England because *S. balanoides* enhanced abundance of *F. vesiculosus* only when percent cover of adult barnacles exceeded 80% and the densities of grazers (principally *Littorina littorea*) were relatively low (Lubchenco 1983). Given these data, and the distribution of weak to strong interaction strengths from published studies, we hypothesize that the strength of facilitation is in the order of 4×10^{-3}

germlings/barnacle per week (corresponding to five furoid germlings per 100 adult barnacles per season). This absolute value of PCIS is comparable to that measured for juveniles, but is much weaker than the measured per capita effect of cyprid larvae on germlings (Kordas 2006).

Simulations testing different PPIS (by varying population sizes of larvae and adults at constant PCIS) showed that changes in germling abundance are driven primarily by changes in adult barnacle PPIS. This stems from the weaker competitive PCIS of juveniles than the facilitative PCIS of adults, despite (in most simulations) the greater initial population size of juvenile versus adult barnacles. This pattern is reinforced because, in accord with empirical data (Connell 1961; Bertness 1989; Petraitis 1990; Petraitis et al. 2003), the mortality rate parameter for juveniles is much greater than that for adults causing the population size of the former to decline much more rapidly than the latter. In other words, the persistence of adult barnacles sustains facilitative effects over time, whereas the strength of the competitive effect of juveniles declines throughout the remainder of the year as juveniles die and survivors transition to adults.

These simulations prompt hypotheses about the abundance of *A. nodosum* recruits at both site-specific and regional spatial scales. We expect that at sites with typically great numbers of recruiting barnacles, but a low density of adult barnacles, germlings of *A. nodosum* ≤ 1 year old will be rare. At such sites, facilitation of germlings by the few adult barnacles will be very weak and competition between germlings and juvenile barnacles will be strong until the latter population dwindles, shifting the balance to fewer germlings. This annual dynamic of barnacle populations is characteristic of sites with high larval flux due to moderately strong hydrodynamic transport (Caffey 1985; Gaines and Roughgarden 1985). Strong hydrodynamic conditions reinforce the trend towards fewer *A. nodosum* germlings because of their poor attachment strength in flowing water (Vadas et al. 1990). In addition to these direct effects of competition and dislodgement by hydrodynamic forces, germling abundance may also be reduced through inadvertent consumption, or bulldozing, by dogwhelks (*Nucella lapillus*) preying on juvenile barnacles.

On the other hand, we expect that sites at which survivorships of barnacles to adulthood are high, but the densities of cyprids settling year-to-year are variable, would be areas with higher than average densities of *A. nodosum* germlings. Such conditions would enhance facilitation by adults, especially in years with few newly recruiting barnacles. Sites at which barnacle recruitment is variable and tends towards low density settlement characterizes places with reduced water motion (Caffey 1985; Gaines and Roughgarden 1985). The well-known episodic recruitment by *A. nodosum* may coincide with locations with many adult barnacles during years with few barnacles recruiting (Vadas et al. 1990; S. Dudgeon personal observation). Water motion per se, as well as the associated patterns of interaction with different barnacle life stages, may act in concert to strongly affect the age structure of *A. nodosum* populations.

Likewise, we predict the abundance of germlings of *A. nodosum* to increase in populations not routinely scoured by ice as one moves further north and east in the western North Atlantic, across which the balance shifts towards a greater (and more variable) ratio of adult barnacles to settling cyprids (Wetthey 1984; Petraitis 1987; Minchinton and Scheilbling 1991; Leonard et al. 1998; Leonard et al. 1999; Hancock and Petraitis 2001; Bertness et al. 2002; Petraitis et al. 2003; Trussell et al. 2003; Kordas 2006; P. S. Petraitis, unpublished data). Data of germling abundance collected from sites throughout the GOM were too variable to corroborate this model prediction. The lowest density of year-old germlings was observed in the southern-most region, Massachusetts. However, germling abundance in natural populations was not consistently greater at sites east of the Penobscot River. In fact, sites in eastern Maine, except one (Destiny Cove), had negligible germling populations. Greater sampling of sites throughout the GOM, but especially in eastern Maine is necessary to determine if Destiny Cove is

representative, or an outlier, with respect to *A. nodosum* germling populations in this region. Destiny Cove is a very sheltered, long thin bay characterized by high *A. nodosum* cover and almost no grazers, and *A. nodosum* germlings were 3 times more abundant than at any other site in the GOM (Kordas 2006). The disparity between observed and expected outcomes for eastern Maine suggest that either the model greatly underestimates the negative effect of later-settling cyprids and juvenile barnacles on germlings, or processes not explicitly included in this model, like grazing or particular abiotic factors that may vary site-specifically, play an important role in *Ascophyllum* demography of this region. Nevertheless, the model effectively captures the magnitude of recruitment and early life stage mortality of *A. nodosum* germlings on sheltered rocky shores observed previously on both European and American shores (Åberg and Pavia 1997; Dudgeon and Petraitis 2005).

Reproductive phenology and germling abundance

Timing of reproduction, either the real phenology or hypothetical phenology, was the strongest determinant of germling population size the following spring. The hypothetical broad window phenology led to a 23-fold increase in germling survivors. This occurred for several obvious, but ecologically important reasons. First, the greater breadth of the hypothetical settlement window translates to later settlement of most of that population's zygotes compared to the real phenology, thus, these younger cohorts have not experienced the mortality associated with later ages prior to the arrival of the next cohort the following spring. However, in ecological terms, less temporally variable and greater population sizes of young juveniles upon arrival of the next cohort may change mortality rates for both cohorts and lead to greater overall abundance. Second, the later settling broad window germlings largely escape the negative impact of juvenile barnacles, many of which have died by the autumn settlement period, yet they benefit from facilitation by adult barnacles that survive better than juveniles throughout the year. Third, by having a portion of hypothetical zygotes settle in the autumn also provides an escape from high mortality rates of spring and summer, which real *A. nodosum* phenology zygotes cannot avoid. The hypothetical phenology allows for a continual supply of propagules throughout the year, and the greater population of hypothetical-phenology germlings indicated by the model is supported by observations of greater abundance of *F. vesiculosus* recruits compared to those of *A. nodosum* throughout the GOM (Kordas 2006).

The timing of the barnacle settlement appears to be less important to the abundance of recruits of *A. nodosum* populations. Like most marine organisms with a pelagic stage, patterns of barnacle settlement in the GOM vary annually in density, timing, and duration (Bertness et al. 1996; P. S. Petraitis, unpublished data). We hypothesized that these features of barnacle settlement might impact fucoid populations. Although the hypothetical *A. nodosum* phenology was insensitive to both the timing and density of barnacle settlement, the phenology characteristic of *A. nodosum* was slightly more sensitive to the density of settling barnacles. Germling abundance was greater either when germlings settled after barnacles, or when barnacle densities were simulated at maximum, rather than average values. More germlings survived 1 year under maximum, compared to average, barnacle densities because facilitation increases disproportionately due to the greater increase in number of adults compared to juveniles in the two cases. Germlings that settle after barnacles encounter fewer juveniles that negatively affect them, leading to greater survivorship after 1 year. Based on these outcomes, we suggest that interactions with barnacles may be more important to the population dynamics of *A. nodosum* than to the dynamics of *F. vesiculosus*, or other fucoids.

The potential sensitivity of interaction between early life stages of *A. nodosum* and larval, juvenile and adult stages of the barnacle, *Semibalanus balanoides* is particularly interesting in two respects: the foundation species role of *A. nodosum* on sheltered rocky shore ecosystems, and both species sensitivity of reproduction to temperature. Increased regional temperatures

during the past three decades have shifted the annual timing of reproduction by *A. nodosum* forward (earlier in the year) by several weeks (R. L. Vadas Sr., personal communication; S. R. Dudgeon, personal observation). A similar signature for *S. balanoides* may be obscured by its capacity for long-distance dispersal coupled with variability in thermal change from place to place. It is not known whether further global temperature rise will continue to shift phenologies, or alter the nature and/or strengths of interactions between life stages of these species. The observation that the interaction between these two common species is rather weak at the per capita level may contribute to the apparent stability of rockweed-dominated assemblages on New England rocky shores. If the interaction between barnacles and *A. nodosum* significantly influences and stabilizes their population dynamics, then alteration of this interaction as a result of environmental change may have implications for the structure of sheltered rocky shore communities in the North Atlantic.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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Fig. 1.

Flow diagram depicting the interaction of the barnacle, *Semibalanus balanoides* (S ; grey boxes) on the population model of *Asco-phyllum nodosum* (A ; white boxes). Solid lines connect equation parameters; dotted line indicates an ontogenic transition only. Equations indicated by numbers in parentheses: (1) $A_{(t+1)} = A_{(t)} + R_{A(t)} - Q_{A(t)}$, (2) $R_{A(t)} = A_{Z(t)} \times l_{A(t)} + (S_{a(t)} \times \alpha_{Sa,A})$, (3) $Q_{A(t)} = R_{A(t)} \times q_{A,O(t)} + (S_{j(t+1)} \times \alpha_{Sj,A}) + (R_{Sc(t)} \times \alpha_{Sc,A}) - (S_{a(t)} \times \alpha_{Sa,A})$, (4) $S_{j(t+1)} = S_{j(t)} + R_{Sc(t)} - Q_{Sj(t)}$, (5) $R_{Sc(t)} = S_{c(t)} \times l_{Sc(t)}$, (6) $Q_{Sj(t)} = S_{j(t+1)} \times q_{Sj(t)}$, (7) $A_{(t+8)} = A_{(t0)} \times l_A^7$. R refers to recruitment and Q to mortality; for full explanation of symbols, see Table 1

Fig. 2. Effect of fucoid phenology and timing of barnacle settlement on fucoid populations. **a** Real *A. nodosum*-type (black bars) and hypothetical *Fucus vesiculosus*-type (grey bars) settlement correspond to left-hand y-axis, fucoid germling density (unbroken lines), corresponds to right-hand y-axis over time, when cyprid and adult barnacle densities are highest and cyprids settle before zygotes. **b** Density of germlings of real and hypothetical settlement when barnacle densities are average (hatched bars) and high (solid bars) for different barnacle settlement periods (before, coincident, after) relative to fucoid settlement

Fig. 3.

Sensitivity of *A. nodosum* germling population to variability of per capita interaction strength (PCIS) of different life stages of *S. balanoides*. Bars indicate the change in the number of germlings from a PCIS equal to zero, **a** The competitive effect of cyprids on germlings (when cyprid PCIS = 0, there are 84 germlings m⁻², population of cyprids = 16,974). **b** The competitive effect of juvenile barnacles on germlings (when juvenile PCIS = 0, there are 85 germlings m⁻², population of cyprids = 16,974). **c** The facilitative effect of adult barnacles on germlings (when adult PCIS = 0, there are 84 germlings m⁻², population of adults = 416). Arrows in **a**, **b** indicate values typical of the interaction

Fig. 4.

Effect of barnacle per population interaction strength (PPIS) on the density of *A. nodosum* germlings m⁻², for each of three simulations changing densities of juvenile barnacles only (white bars), simultaneously changing juvenile and adult barnacle densities (grey bars), and changing densities of adult barnacles only (black bars). When only cyprids were interacting with germlings (juveniles and adults PCIS were zero), the change in germling density was zero for all cyprid densities. Heights of all bars represent the difference in germling density from 84 m⁻², when juvenile and adult barnacle PCIS both equal zero

Fig. 5.

Modeled and observed densities of germlings in the four regions of the Gulf of Maine (mean $\pm$ SE). *Black bars* indicate germling densities modeled in each region when the region-specific values for adult barnacle density, cyprid barnacle density, timing of settlement, and their respective PCIS were used (see Table 1 for values). *White bars* are the densities of germlings observed in each region. Methods and sites used in this data collection can be found in ESM SI. In NE ME, one site, Destiny Cove (DC), was considered an outlier and excluded *grey bar*. NE ME *white bar* shows the observed density of germlings when Destiny Cove is included. For abbreviations, see Table 1

Table 1

Semibalanous balanoides and *Ascophyllum nodosum* model parameters used in simulations. Data are relevant to the Gulf of Maine [except values derived from Connell (1961) and Aberg and Pavia (1997), in which data were collected from western Europe] and values were collected from the literature or prior experiments by the authors. All values are input weekly and are m^{-2} . *All* Nahant (Massachusetts) to Quoddy Head (Maine), *Mass* Nahant Massachusetts to New Hampshire border, *SW ME* Portland (Maine) to western shore of Penobscot Bay, *C ME* eastern shore of Penobscot Bay to Schoodic Pt (Maine), *NE ME* Schoodic Pt. to Quoddy Head (Maine), *AAR* average across regions, *AAT&R* average across time and regions, *PCIS* per capita interaction strength, *avg.* average, *max.* maximum

Symbol	Parameter (GOM avg. or max. values)	Value(s)	Region	Source
$I_{Sc(t)}$	<i>S. balanoides</i> cyprid survivorship	0.825 – 0.912 ^a	All	Connell (1961), Bertness (1989), Hancock and Petraitis (2001), Petraitis et al. (2003)
$S_{c(t)}$	<i>S. balanoides</i> cyprid settlement (avg. = 16,974) ^{b,d} (max. = 19,074) ^b	19,074 ^b	Mass	Wetthey (1984)
		16,142 ^b	SW ME	Bertness et al. (2002), Trussell et al. (2003), Kordas (unpublished data), Petraitis (unpublished data)
		6,995 ^b	C ME	Hancock and Petraitis (2001), Petraitis et al. (2003), Petraitis (unpublished data)
		6,995 ^b	NE ME	Kordas (unpublished data), Petraitis (unpublished data)
$q_{si(t)}$	<i>S. balanoides</i> juvenile mortality	Density-dependent	All	Estimated using data from Connell (1961), Bertness (1989), Petraitis et al. (2003)
$S_{z(t)}$	Adult <i>S. balanoides</i> density (avg. = 416) ^{c,d} (max. = 5300) 309 ^{c,e}	148 ^{c,e}	Mass	Wetthey (1984), Kordas (unpublished data)
		236 ^{c,e}	SW ME	Kordas (unpublished data)
			C ME	Petraitis et al. (2003), Kordas (unpublished data), Petraitis (unpublished data)
		19c,e	NE ME	Kordas (unpublished data), Petraitis (unpublished data)
$\alpha_{Sc, A(t)}$	PCIS: cyprid <i>S. balanoides</i> on <i>A. nodosum</i> zygotes (AAR = 0 to -1.01×10^{-2} ^a 0 to -4.44×10^{-2}) ^{a,d} (AAT&R = -2.16×10^{-2}) ^c	0 to -1.06×10^{-2} ^a	Mass	Kordas (2006), see Electronic Supplementary Material (ESM) Fig. 2
		0 to -2.83×10^{-2} ^a	SW ME	
		-7.01×10^{-2} ^a	C ME	
			NE ME	
$\alpha_{Sj, A(t)}$	PCIS: juvenile <i>S. balanoides</i> on <i>A. nodosum</i> germlings (AAR = -2.62×10^{-4} to -1.15×10^{-3}) ^a (AAT&R = -6.92×10^{-4}) ^c	0 to -1.61×10^{-3} ^a	Mass	Kordas (2006), see ESM Fig. 2
		0 to -2.65×10^{-3} ^a	SW ME	
		0 to -3.32×10^{-4} ^a	C ME	
		0 to -1.05×10^{-3} ^a	NE ME	
$\alpha_{Sa, A(t)}$	PCIS: adult <i>S. balanoides</i> on <i>A. nodosum</i> germlings	0 to 4×10^{-1} ^c	All	Tested in this study
$q_{A,O(t)}$	Other <i>A. nodosum</i> mortality	0.131 to 0.363 ^a	All	Dudgeon and Petraitis (2005)
$A_{Z(t)}$	<i>A. nodosum</i> zygote settlement	6.5×10^6 ^b	All	Åberg and Pavia (1997), Dudgeon et al. (2001)
$I_{A(t)}$	<i>A. nodosum</i> zygote survivorship	0.04 ^c	All	Dudgeon and Petraitis (2005)

^a Value varies with time over duration of model

^b Values are pulsed over a 5-week period

^c Values are constant over duration of model

^d Arithmetic mean

^e Geometric mean