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WHITE SEA ECOSYSTEMS

Synchronous annual recruitment variation in barnacles and ascidians in the White Sea shallow subtidal 1999–2010

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Abstract Multiple foundation species in a community may exhibit alternative ecological strategies. Barnacles *Balanus crenatus* Bruguiere and solitary ascidians *Styela* spp. often co-dominate on mixed sediments in the White Sea shallow subtidal, supporting numerous dependent organisms. Larvae of *B. crenatus* stay in plankton for several weeks, while ascidian tadpoles float for 1–2 days. Given this difference in spreading potential, we expected recruitment in barnacles and ascidians to be controlled by the factors operating at different spatial scales. In 1999–2010, we annually sampled the community dominated by barnacles and ascidians to relate their recruitment rates to the substrate space availability, abundance of adults, and climatic variables. Most barnacles recruited to the surfaces of shells, stones, and conspecific adults. Ascidian recruits were chiefly found on barnacles. Annual recruitment rates of barnacles and ascidians were strictly correlated and strongly depended on average temperatures of the preceding fall (positively), winter (negatively), and current summer (negatively). Variation of mean annual recruitment rates was 26-fold for barnacles and 30-fold for ascidians. We found no limitation of recruitment by hard substrate availability. Inconsistent with our original hypothesis, large-scale environmental factors similarly accounted for most annual recruitment variation in both foundation species studied.

Keywords Recruitment · Barnacles · Ascidians · The White Sea · Annual variation · Temperature

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Introduction

Marine benthic communities are widely dominated by organisms that are sessile or nearly so when adult, and thus depend much on propagule supply. A typical study of recruitment is focused on a single intertidal species with a planktonic dispersal period of several weeks like barnacles and bivalve mollusks (e.g.,

Roughgarden et al., 1988; Menge, 2000; Van der Meer et al., 2001; Beukema & Dekker, 2007). Natural assemblages, however, combine species with different life histories. Assessing the role supply-side ecological processes play in real multispecies assemblages is identified as a crucial challenge in marine ecology (Underwood & Keough, 2001).

Recent research on community functioning stressed the relative importance of facilitation, which had been generally neglected earlier in favor of competition and predation (Bertness & Callaway, 1994). Some strong facilitators like corals or kelp ("foundation species") positively affect many others (dependent species) and this imparts hierarchical composition of positive biotic interactions to terrestrial and marine communities, often with multiple foundation species acting as facilitation cascades (Angelini et al., 2011). Population ecology of foundation species and interactions between them are of critical importance to understand the structure of communities they shape.

In the White Sea shallow subtidal, mixed sediments frequently consist of small hard substrates like stones and empty mollusk shells, 1–10 cm in size, scattered over the bottom covered by muddy sand (hereafter "primary substrates"). Close to Solovetsky Island these substrates support the diverse assemblage dominated by barnacles *Balanus crenatus* (hereafter "barnacles") and solitary ascidians *Styela rustica* L., and sub-dominated by *Styela coriacea* (Alder and Hancock), *Molgula retortiformis* (Verrill), and several species of red algae. Most primary hard substrates underlying the epibenthic patches of aggregated barnacles and ascidians are empty valves of Greenland cockle *Serripes groenlandicus* (Bruguiere) which inhabits the surrounding muddy sand (Yakovis et al., 2008). Surface of the primary substrates is monopolized by clustered barnacles, which in turn offer space to ascidians (chiefly *Styela rustica*) and red algae. A number of dependent sessile organisms attach to the surfaces provided by all these foundation species, and also numerous mobile invertebrates inhabit the spaces formed by barnacles and clumped ascidians (Yakovis et al., 2005). Spatial patterns of abundance indicate that even the mobile fauna of the soft sediment around epibenthic patches is partially structured by barnacles and ascidians (Yakovis et al., 2004).

Although barnacles and ascidians both act as foundation species and ecosystem engineers (sensu Jones et al., 1994) in the same community, their life histories are rather different. Particularly, *Balanus crenatus* nauplii stay in plankton for 2–3 weeks (e.g., Herz, 1933) and *Styela rustica* tadpoles float for only 1–2 days (Khalaman et al., 2008). Within the community studied they also utilize different microhabitats: barnacles occupy the primary substrate and conspecific shells, whereas ascidians predominantly reside on adult (at least several years old) barnacles or their empty shells (Yakovis et al., 2005, 2008; Yakovis, 2007). We hypothesized that temporal patterns of annual recruitment variation in barnacles and ascidians would be controlled by different combinations of environmental drivers and parameters of the local habitat, like the primary substrate space and abundance of conspecifics. Given the apparent limitation of hard substrates on mixed sediments we assumed that recruitment rate of ascidians could be affected by abundance of resident barnacles, i.e., the surface area of their shells; surface areas of both the primary substrates and conspecifics were expected to influence the recruitment rate of barnacles. Because of the potential difference in dispersal range the larval supply of barnacles and ascidians presumably seemed independent, predicting no synchronicity in annual recruitment variation. In order to test these hypotheses we monitored the recruitment and adult population of barnacles and ascidians for 12 continuous years and related their recruitment rates to the local substrate space availability, abundance of adults, and climatic variables.

Methods

Study site

The Solovetsky Archipelago consists of six larger and numerous tiny islands located at the mouth of the Onega Bay of the White Sea. The surrounding bottom landscapes are diverse due to excessive variety of sediment types and flow regimes. Mixed sediments predominate at 5–15 m depths close to shores, where the current is relatively slow. Salinity is 24.4–27.6 ppt, summer bottom temperatures range from 5 to 8°C, and ice cover lasts from late November or early December–May.

The community dominated by barnacles *Balanus crenatus* and ascidians *Styela rustica* clustered on small stones and empty bivalve shells covers at least

several square kilometers of the bottom at depths of 12–15 m along the SW coast of the largest island (Yakovis et al., 2008). No definite signs of wave disturbance are observed in this habitat.

Sampling, laboratory analyses, and supplementary experiments

In July 1999–2010 SCUBA divers annually sampled 1.00 or 1.44 m^2 square frames, collecting every visible hard substrate with all the macrobenthic organisms attached. Frames were haphazardly placed at the depth of 12 m within a 100 m around the location 65°01.2′N, 35°39.7′E (Fig. 1), referred to as "Site 1" in our previous communications and hereafter (Yakovis et al., 2005, 2008). Every year we examined 2, 3, or 5 frames, in total 30 (Table 1). Each frame contained 15–85 (on average 35.8 ± 3.2) epibenthic patches: 60% on empty mollusk shells and 14% on small stones; 22% were fragments without an initial primary substrate based mostly on the remains of empty barnacle shells. We measured aperture length of each barnacle (hereafter "size"), both live and their empty shells (hereafter "dead barnacles") accurate to 1 mm, and individually wet weighed each ascidian collected within a frame accurate to 0.001 g. Since 2004 we also counted growth bands on the shell of each barnacle to determine its age with estimated accuracy of ±1 year (Varfolomeeva et al., 2008).

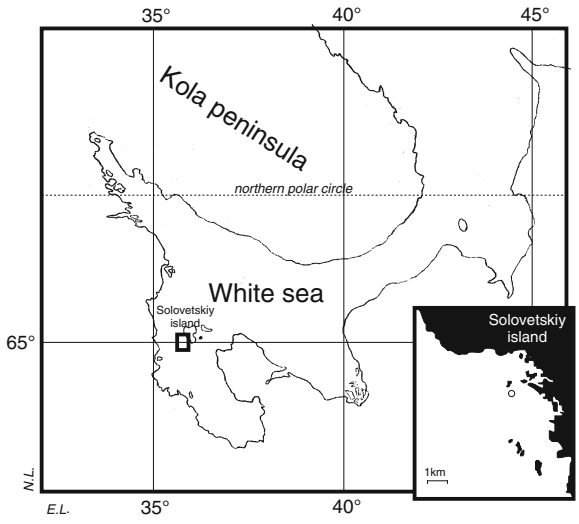

Fig. 1 Sampling site location (*encircled*, after Varfolomeeva et al., 2008)

Prior to weighing, we punctured ascidians through and squeezed them flat on a tissue paper to remove the extra water from inside. For every specimen examined we recorded the type of substrate, on which one was found (principal substrate types were live barnacles, empty barnacle shells, empty *Serripes groenlandicus* shells, ascidians, and red algae). Barnacles were weighed totally by frame accurate to 1 g.

We used previously established relationships to determine surface areas of live barnacles, their empty shells, and empty *Serripes groenlandicus* shells from linear dimensions (Yakovis et al., 2008, Appendix A). Surface areas of small stones were either measured using aluminum foil method (Marsh, 1970) or approximated using the overlaid square grid accurate to 0.25 cm^2. Only upper surfaces of the primary substrates that were located above the sediment surface were considered for area measurements. If a substrate contained neither live or dead barnacles nor ascidians beyond the size threshold of 0+ age, we assumed that this substrate had recently arrived to a habitat.

According to colonization experiments and growth bands analysis, in the White Sea *Balanus crenatus* life span is up to 10–11 years (Varfolomeeva et al., 2008). An ascidian *Styela rustica*, as shown by tracing tagged individuals, can live for 7 years (Khalaman, 2010). This longevity allows an annual sampling interval for a long-term recruitment rate study.

In order to determine the proper size or weight threshold to cut off most recruits from older residents we arranged 1 year long colonization experiments. In July 2000–2010 we placed empty *Serripes* shells convex side up on the bottom within 50 m from the Site 1. Shells were anchored to concrete bricks (2000–2008) or plastic mesh (2009–2010) so that they could be easily found a year after. After 1 year of exposure, the shells were removed and examined in the laboratory, each barnacle being measured. In total, 1,444 barnacles on 68 shells were examined. Modal size of barnacles was 1 mm and 99% of individuals were within 3 mm. The size threshold for barnacle recruits was thus set to 3 mm.

Ascidian recruitment to empty bivalve shells was almost negligible (see the "Results" section). Therefore, to assess the size of ascidian recruits in 2008–2010 we exposed 37 bivalve shells with 300 adult live barnacles on them, previously collected in close surroundings of the sampling site and cleared from any other macrobenthic organisms. Shells were

Table 1 Sampling design parameters

Years	Number of frames sampled	Area of a plot (m^2)	Average biomass of barnacles (g m^{-2})	Average biomass of ascidians (g m^{-2})	Total area of the primary hard substrates (cm^2 m^{-2})
1999	5	1.44	210 ± 41	105 ± 22	363 ± 53
2000	3	1.44	339 ± 43	96 ± 40	426 ± 62
2001	3	1.44	290 ± 35	92 ± 36	366 ± 35
2002	3	1.44	195 ± 55	35 ± 11	288 ± 67
2003	2	1.44	376 ± 89	98 ± 8	412 ± 14
2004	2	1.00	375 ± 44	63 ± 1	575 ± 4
2005	2	1.00	272 ± 9	60 ± 19	535 ± 85
2006	2	1.00	720 ± 95	145 ± 87	801 ± 89
2007	2	1.00	529 ± 111	145 ± 66	580 ± 72
2008	2	1.00	692 ± 63	98 ± 2	684 ± 36
2009	2	1.00	700 ± 42	133 ± 19	862 ± 142
2010	2	1.00	727 ± 189	134 ± 9	879 ± 39

also anchored on plastic mesh. After a year of exposure we examined barnacles' surface for ascidians and individually wet weighed the ones found (133 ind. in total).

Since most young *Styela rustica* and *S. coriacea* were morphologically indistinguishable, we analyzed the common pool of their recruits given that *S. rustica* was much more abundant, and substrate occupancy patterns in the two species were similar (see the "Results" section). Although only 76% of ascidian recruits weighed 0.001 g, and the two following weight classes (0.002 and 0.003 g) accounted for 8% of individuals each, we selected the 0.001 g weight threshold for further use. Ascidians may grow particularly slow for the first few years (Khalaman, 2010) and thus do not necessarily have distinct size-age cohorts. We assumed that the lowest possible threshold would allow less confusion of 0+ individuals with older residents.

Sea surface temperature measurements available for the Onega Bay of the White Sea are incomplete and irregular, especially from December to May, when the sea is covered with ice (International Comprehensive Ocean–Atmosphere Data Set, http://rda.ucar.edu/datasets/ds540.1). According to this limited data for 1998–2012, the correlation between monthly average air and sea surface temperatures is 0.77 ± 0.06 ($n = 110$). Air temperature, however, was recorded continuously throughout a year. Thus, we used seasonal and monthly averages based on the daily air temperature measurements at the meteorological station "Arkhangelsk" (64°30′N, 40°44′E; WMO index 22550) recorded in 1998–2010 (RIHMI–WDC weather archive; http://www.meteo.ru/english/climate/temp.php) as potential predictors of recruitment in barnacles and ascidians. This was the closest location for which a complete continuous weather data set was available, although it contained no sea surface temperature measurements.

Statistical analysis

The relationship between barnacle and ascidian recruitment and between their biomasses, the primary substrate area, and sampling year were estimated using Pearson correlation. Significance level was Bonferroni-adjusted to 0.01.

We used the following variables as potential predictors of annual recruitment rates in barnacles and ascidians: total area of the primary hard substrates (S_{PRI}, m^2 m^{-2}), total area of the primary hard substrates that had recently arrived to the habitat (lacking any sessile organisms larger than recruits) (S_{PRI+}, m^2 m^{-2}), total area of barnacle shells' surface (S_{BARN}, m^2 m^{-2}), total biomass of ascidians (B_{ASC}, g m^{-2}), as well as average temperatures of the preceding summer (T_{pSUM}), preceding fall (T_{pFALL}), winter (T_{WINT}), spring (T_{SPR}), and current June + July (T_{J+J}). We applied multiple regression analyses with these independent variables to explain the variation in total number of barnacle recruits, both living and dead ($R_{BARN,}$ ind. m^{-2}), ascidian recruits

(R_{ASC}, ind. m^{-2}), and the proportion of dead barnacle recruits in R_{BARN} (P_{+BARN}).

Means are given ±SE and significance level is 0.05 unless otherwise stated.

Results

In 1999–2010, average annual air temperatures ranged from +0.07°C in August 2002–July 2003 to +2.97°C in August 2007–July 2008 (Fig. 2). Since our sampling was carried out in July, we hereafter refer to a "year" as a corresponding July and the preceding 11 months. Thus, 1998–1999 and 2002–2003 were relatively cold, whereas 1999–2000, 2003–2004, and 2007–2008 were warm. Compared to the known historical range of average annual air temperatures in Arkhangelsk (from −1.89 to +3.27°C, based on the record since 1883) our whole observation period was rather warm.

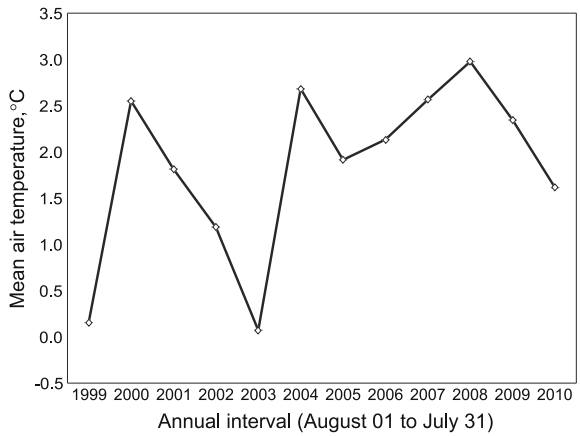

Fig. 2 Mean annual air temperatures in Arkhangel'sk (64°30′N, 40°44′E) in 1999–2010. Annual intervals shifted against a calendar year and last from previous August to July, e.g., 1999 means August 1, 1998 to July 7, 1999

Biomass of barnacles *Balanus crenatus* and the primary hard substrate surface area were highly correlated ($R = 0.87$; $P < 0.001$). Both parameters were generally increasing in 1999–2010 and correlated positively with sampling year ($R = 0.81$; $P < 0.001$ and $R = 0.74$; $P < 0.001$, correspondingly). Biomass of ascidians *Styela* spp. and surface area of newly arrived primary substrates did not show a clear long-term trend (Fig. 3). In terms of biomass, *Styela rustica* was about 14 times more abundant than *S. coriacea*. Both ascidian species achieved the highest biomass on barnacles and their empty shells, whereas 85% of *Balanus crenatus* biomass was associated with the primary substrates (Fig. 4).

Most barnacle recruits were found on the primary substrate and conspecifics, while small ascidians predominantly resided on barnacles (Fig. 5). We observed no growth rings on the shells of barnacles with aperture length of 3 mm and less. The fraction of dead barnacle recruits was higher on the primary substrate than on barnacles. Recruitment rates of barnacles and ascidians were strongly correlated ($R = 0.97$, $P < 0.001$ between R_{BARN} and R_{ASC}) with a high peak of 6,005 ± 1,817 and 449 ± 178 ind. m^{-2} in 2006 for barnacles and ascidians, correspondingly (Fig. 6). Max to min average recruitment

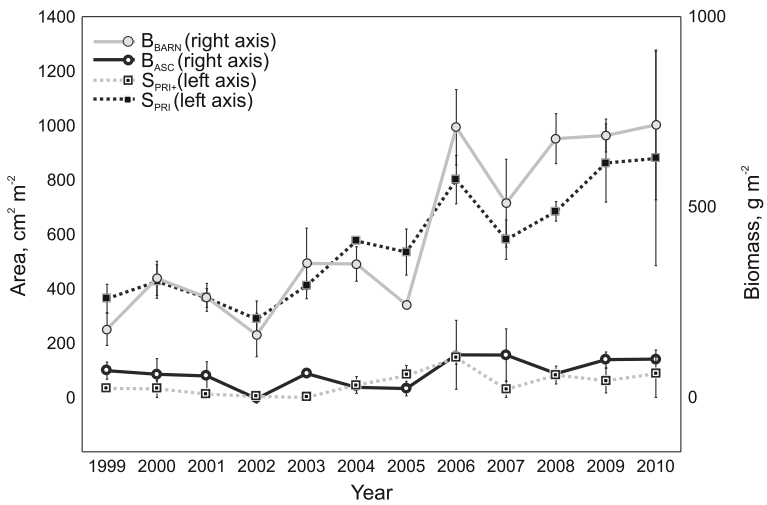

Fig. 3 Surface areas of the primary hard substrates (empty bivalve shells and small stones) and biomasses of foundation species, 1999–2010. S_{PRI}, total surface area of primary hard substrates; S_{PRI+}, surface area of recently arrived primary substrates (having no adult barnacles or ascidians on them); B_{ASC}, biomass of ascidians *Styela* spp.; B_{BARN}, biomass of barnacles *Balanus crenatus*. Means ± SE

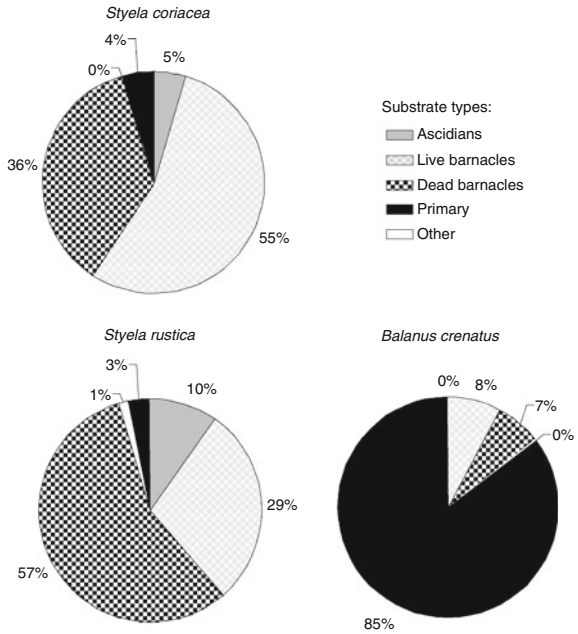

Fig. 4 Total biomass of barnacles and ascidians in July 1999–2010 by substrate type

rates ratio was about 26-fold for barnacles and 30-fold for ascidians. The fraction of dead barnacles in the total number of recruitsf ($P_{+\mathrm{BARN}}$) ranged from 6.2 ± 0.2% in 2006 to 75.8 ± 6.0% in 2010. Recruit numbers of barnacles and ascidians (R_{BARN} and R_{ASC}) were both significantly affected by mean temperatures of current summer (negatively), preceding winter (negatively), and preceding fall (positively), whereas substrate surface areas had no major effect on recruitment in either species (Tables 2, 3; Fig. 7). $P_{+\mathrm{BARN}}$ was significantly negatively affected by total recruitment rate of barnacles. In addition, the effect of current mean summer temperature was virtually significant ($P = 0.051$), positive, and rather strong (Table 4). Recruitment peak in 2006 had a disproportionately regular contribution to the age structure of barnacles in 2010; the following and preceding years with several times lower recruitment rates were almost equally represented in the population by the end of the observation period (Fig. 8).

Discussion

Regardless of the taxonomic distance and severe difference in life histories and larval planktonic period duration between barnacles and ascidians, their annual recruitment variation patterns were remarkably similar, which was inconsistent with our original

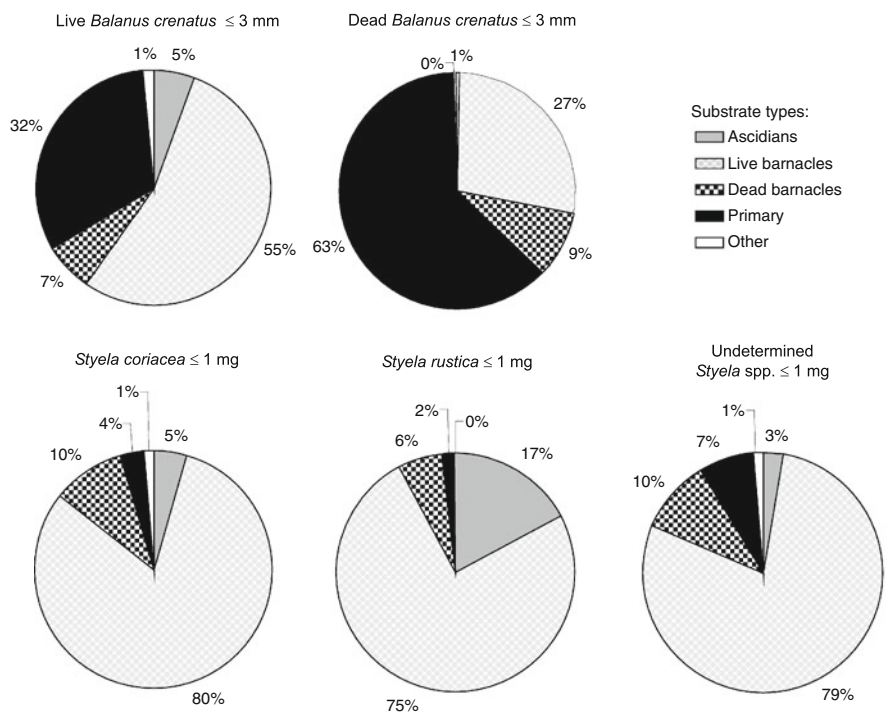

Fig. 5 Total number of recruits of barnacles and ascidians in July 1999–2010 by substrate type

Table 2 Effect of seasonal temperatures, substrate surface areas, and ascidian biomass on recruitment rate of barnacles *Balanus crenatus* (R_{BARN}), live barnacles and empty shells ≤3 mm pooled

Term	Beta	Standard error	*P*	Partial correlation	Tolerance
S_{PRI}	−0.51	0.39	0.213	−0.28	0.10
S_{PRI+}	0.50	0.28	0.086	0.37	0.21
S_{BARN}	0.18	0.34	0.602	0.12	0.14
B_{ASC}	0.12	0.17	0.488	0.16	0.56
T_{pSUM}	0.23	0.23	0.310	0.23	0.32
T_{pFALL}	**0.48**	**0.23**	**0.050***	**0.42**	**0.30**
T_{WINT}	**−0.42**	**0.15**	**0.011***	**−0.53**	**0.70**
T_{SPR}	0.14	0.15	0.342	0.21	0.73
T_{J+J}	**−0.39**	**0.17**	**0.032***	**−0.46**	**0.54**

Multiple regression results. Multiple $R^2 = 0.68$. Significant effects highlighted in bold

S_{PRI}, total surface area of the primary hard substrates; S_{PRI+}, surface area of recently arrived primary substrates (having no adult barnacles or ascidians on them); S_{BARN}, surface area of barnacles; B_{ASC}, biomass of ascidians *Styela* spp.; T_{pSUM}, T_{pFALL}, T_{pWINT}, T_{pSPR}, T_{pJ+J}, mean air temperatures of the preceding summer, fall, winter, spring, and current June and July, correspondingly

* $P \leq 0.05$

Table 3 Effect of seasonal temperatures, substrate surface areas, and ascidian biomass on recruitment rate of ascidians *Styela* spp. (R_{ASC})

Term	Beta	Standard error	*P*	Partial correlation	Tolerance
S_{PRI}	−0.28	0.40	0.493	−0.15	0.10
S_{PRI+}	0.37	0.28	0.197	0.29	0.21
S_{BARN}	0.06	0.34	0.861	0.04	0.14
B_{ASC}	0.17	0.17	0.334	0.22	0.56
T_{pSUM}	0.23	0.23	0.318	0.22	0.32
T_{pFALL}	**0.52**	**0.23**	**0.035***	**0.45**	**0.30**
T_{WINT}	**−0.35**	**0.15**	**0.030***	**−0.46**	**0.70**
T_{SPR}	0.05	0.15	0.720	0.08	0.73
T_{J+J}	**−0.38**	**0.17**	**0.041***	**−0.44**	**0.54**

Individuals weighing ≤0.001 g considered recruits. Multiple regression results. Multiple $R^2 = 0.68$. Significant effects highlighted in bold

S_{PRI}, total surface area of the primary hard substrates; S_{PRI+}, surface area of recently arrived primary substrates (having no adult barnacles or ascidians on them); S_{BARN}, surface area of barnacles; B_{ASC}, biomass of ascidians *Styela* spp.; T_{pSUM}, T_{pFALL}, T_{pWINT}, T_{pSPR}, T_{pJ+J}, mean air temperatures of the preceding summer, fall, winter, spring, and current June and July, correspondingly

* $P \leq 0.05$

hypothesis. According to multiple regression results, recruitment rates in both barnacles and ascidians were best predicted by mean seasonal air temperatures, and neither the abundance of resident adults nor the availability of substrate space had a significant effect on it. Spatial limitation and/or gregariousness might have affected recruitment patterns at the scale of individual hard substrates, i.e., centimeters (see Yakovis et al., 2008) but at the scale of meters climatic drivers were of principal importance. The highest rates were observed in 2006 preceded by a cold winter and a warm fall.

Long-living benthic invertebrates generally show high interannual variability of recruitment though the causes of such a variation often remain obscure. Kendall et al. (1985) traced annual recruitment of an intertidal barnacle *Semibalanus balanoides* along the coast of England for 12 years. They recorded severe interannual variation, which they attributed to climatic or hydrographic factors because the temporal pattern

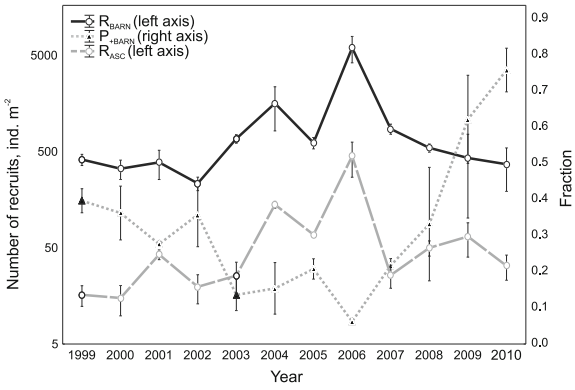

Fig. 6 Annual recruitment rates in barnacles and ascidians in 1999–2010. R_{BARN}, number of *Balanus crenatus* individuals, aperture length up to 3 mm, live barnacles and their empty shells pooled; R_{ASC}, number of *Styela* spp. individuals weighing up to 1mg, *S. rustica* and *S. coriacea* pooled; $P_{+\mathrm{BARN}}$, the proportion of empty shells (dead barnacles) in R_{BARN}

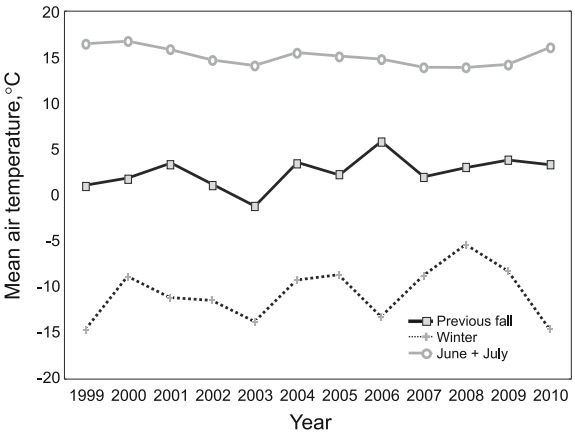

Fig. 7 Mean seasonal temperatures in 1998–2010 that had significant effects on recruitment rates of barnacles and ascidians

was similar at the sites 100 km apart. Noda and Nakao (1996) examined population dynamics of a subtidal snail in temperate waters for the continuous 7 years and found sporadic peaks of recruitment once every few years which they made no attempt to link with any environmental variables. In the Kandalaksha Bay of the White Sea a softshell clam *Mya arenaria* had the only (but heavy) recruitment event in 20 years of continuous observations at two intertidal sites, so that the whole population represented a single same-age cohort (Maximovich & Guerassimova, 2003). Gerasimova & Maximovich (2009) also monitored the

Table 4 Effect of seasonal temperatures, substrate surface areas, ascidian biomass, and barnacle recruitment rate on the fraction of dead barnacle recruits of their total recruits number ($P_{+\mathrm{BARN}}$)

Term	Beta	Standard error	P	Partial correlation	Tolerance
S_{PRI}	0.49	0.41	0.241	0.27	0.09
$S_{\mathrm{PRI+}}$	−0.37	0.30	0.225	−0.28	0.18
S_{BARN}	0.54	0.34	0.131	0.34	0.14
B_{ASC}	−0.17	0.17	0.334	−0.22	0.54
$\boldsymbol{R_{\mathrm{BARN}}}$	**−0.59**	**0.22**	**0.016***	**−0.52**	**0.32**
T_{pSUM}	−0.15	0.23	0.518	−0.15	0.30
T_{pFALL}	0.13	0.25	0.623	0.11	0.25
T_{WINT}	−0.26	0.18	0.164	−0.32	0.50
T_{SPR}	−0.14	0.15	0.360	−0.21	0.69
$T_{\mathrm{J+J}}$	0.40	0.19	0.051	0.43	0.43

Individuals with aperture length ≤3 mm considered as recruits. Multiple regression results. Multiple $R^2 = 0.70$. Significant effects highlighted in bold

S_{PRI}, total surface area of the primary hard substrates; $S_{\mathrm{PRI+}}$, surface area of recently arrived primary substrates (having no adult barnacles or ascidians on them); S_{BARN}, surface area of barnacles; B_{ASC}, biomass of ascidians *Styela* spp.; R_{BARN}, abundance of barnacle recruits, live and dead (empty shells) pooled; T_{pSUM}, T_{pFALL}, T_{pWINT}, T_{pSPR}, $T_{\mathrm{pJ+J}}$, mean air temperatures of the preceding summer, fall, winter, spring, and current June and July, correspondingly

* $P \leq 0.05$

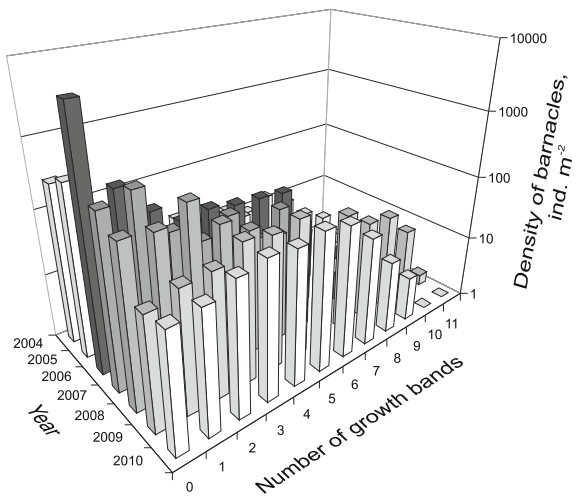

Fig. 8 Age structure of live *Balanus crenatus* in 2004–2010 based on growth band counts. Density increased by 1 prior to log-transformation

neighboring populations of several other subtidal and intertidal bivalves for 4–17 years and recorded high recruitment events at 2–5 year intervals depending on the species. Based on the constant presence of the larvae of *Mya arenaria*, *Macoma balthica*, and *Mytilus edulis* in plankton they speculate that the main source of interannual recruitment variation is the survival of juveniles in winter. Svane and Lundälv (1982a, b) followed population dynamics in two subtidal ascidian species for 10 years in boreal waters and found no correlations of recruitment with known environmental variables.

The number of recruits as counted in July is a result of several processes: reproduction, larval dispersal, settlement, and early post-settlement survival. According to our non-quantitative observations most 0+ barnacles that we have recorded were new-settlers but not survivals from the preceding year. For the Kandalaksha Bay of the White Sea Mileikovsky (1970) reports two summer abundance peaks of *Balanus* spp. larvae in plankton, in mid-July and early August. At the time we took our samples in mid-July; however, *B. crenatus* was always already settling, which indicates that in the Onega Bay settlement happens earlier than in the Kandalaksha Bay located about 200 km to the North–West. This is expectable given that in boreal waters *B. crenatus* spawns from March to October with a highest density in plankton achieved in April (Korn & Kulikova, 1995). In contrast, *Styela rustica* spawns and settles in mid-September (Khalaman, 2001); although nothing specifically is known about the breeding season of *Styela coriacea*, we have seen the smallest styelids (0.3 mm in diameter) solely in the samples obtained in September and October (personal unpublished data). Consequently, most of the smallest ascidians found in July are likely survivals from the preceding fall. Thus, warmer falls and colder winters seem to boost reproduction in barnacles, but early survival—in ascidians. Negative effect of current summer temperatures apparently implies reduced survival in both taxa.

In addition to direct developmental sensitivity to temperature, warmer fall can positively affect both reproductive success and survival via food availability. It leads to longer solar irradiation season caused by later ice cover formation contributing to feeding success of suspension-feeders. The observed negative effects of winter and summer temperatures are more difficult to interpret but still not unique. Möller (1986) sampled shallow boreal subtidal for 8 years and detected the 8- and 10-fold increase in abundance of recruits of *Mya arenaria* and *Nereis diversicolor*, consequently, following the extremely cold winter of 1978–1979. A number of other bivalve species also demonstrate an outbreak of recruits after unusually cold winters (see Beukema et al., 1998, and references therein). In case of an intertidal clam *Macoma balthica*, the population structure of which was monitored in the Wadden Sea for 26 years, there are two principal processes underlying this relationship. First, food deficiency in winter causes the more weight loss the milder the winter is and thus affects the breeding potential. Second, cold winters cut up the recruitment of predatory shrimps, which in turn results in lower early post-settlement mortality of clams (Beukema et al., 1998). Both processes are potentially applicable to barnacles and ascidians. The biology of these species in the White Sea is, however, fairly understudied: almost nothing is known about their most important predators and breeding physiology. Yet we may speculate that the "weight loss" mechanism can only be responsible for the negative effect of winter temperatures, whereas "reduced predation" can equally explain the effect of summer temperatures as well.

The average annual air temperature in the Arctic increases by about a degree in 50 years and the commonly accepted climatic model predicts further rising (AICA, 2004). This might, inter alia, affect benthic communities altering the temperature-dependent recruitment rates. Our results suggest, however, that for the community studied no major effect should be expected in the coming decades at least. Despite the strong variation in mean annual temperatures in 1999–2010, neither barnacles nor ascidians have shown a total recruitment failure in any of the years. Recruitment is considered an important driver of adults abundance when low or absent, but not when high (Menge, 2000). The changes we observed in the age structure of barnacles following the heavy recruitment of 2006 (Fig. 8) are consistent with this "recruit-adult" hypothesis. Severe increase in recruitment was evidently balanced by reduced survival.

Our present study is limited to the only location. According to the model, developed by Roughgarden

et al. (1988) for population dynamics of benthic species with a complex life cycle, the dependence of recruitment either on local factors, particularly space limitation, or on larval supply is site-specific. Myers (1998) who retested a large set of previously published environment–recruitment correlations with new data concludes that the proportion of correlations that can stand such a verification is low. He strongly advises to use the data from multiple populations to test general hypotheses about the relationship of recruitment and climate. Thus, to link dispersal ranges, climatic drivers, biotic interactions, and recruitment rates we need further long-term observations on multiple benthic species with alternative ecological strategies from different locations. The high consistency we have observed between recruitment rates in barnacles and ascidians, however, evidences that the relationships we found may be site-specific but hardly just a coincidence.

Limited hard substrate supply, complex multi-tier spatial structure, and high substrate occupancy suggested the strong space limitation in the community, dominated by barnacles and ascidians on mixed sediments in the White Sea shallow subtidal (Yakovis et al., 2008). Although competition for substrate space may still be considered important among adults or within certain microhabitats, our results clearly indicate that within a square meter of the bottom there is enough space to cope with an outbreak of recruits. Multiple coexisting foundation species may exhibit similar temporal patterns of recruitment despite the difference in life histories, unexpectedly shaped by large-scale environmental factors rather than small-scale biotic interactions.

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