



## Growth and survival of barnacles in presence of co-dominating solitary ascidians: growth ring analysis

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### ARTICLE INFO

#### Article history:

Received 30 March 2008

Received in revised form 30 May 2008

Accepted 10 June 2008

#### Keywords:

Ascidians

Barnacles

Dead:live ratios

Foundation species

Growth

Growth rings

Negative interactions

Survival

### ABSTRACT

Marine and terrestrial communities are often hierarchically structured by one or more foundation species, which provide habitats for many other taxa. Interactions between coexisting habitat modifiers may have strong effects on patterns and processes in the dependent assemblage. Yet they are rarely studied, especially at a small scale. Small epibenthic patches co-dominated by barnacles *Balanus crenatus* Brugiere and several species of solitary ascidians in the White Sea soft bottoms support many dependent species. Barnacles occupy bivalve shells, small stones and conspecifics. Ascidian clumps develop on barnacles and their empty shells. Previous observations suggest that at the patch scale ascidians may replace barnacles over several years likely because of the negative interactions between them. Barnacles have distinct annual growth rings on their shells, which we used to trace their growth and survival in the field. No difference between the patches with different dominants would evidence no pronounced negative effect of ascidians.

In the patches dominated by ascidians (A) or barnacles (B) collected at the same subtidal site in 2004 and 2005 we compared lengths of recent annual vertical growth increments and dead:live ratios of barnacles of the same age class according to the growth rings. Barnacles grew slower in A than in B, regardless of the biomass of conspecific neighbors. Dead:live ratios were higher in A for age classes 1+...2+ and 4+...9+. Estimated mortality risk between A and B increased with age of barnacles, from around 1:1 to 5.6 times greater in the 9+ age group. Because of the observed difference in growth and survival, the negative effect of adult ascidians on barnacles could not be excluded; alternatively, ascidians may prefer the patches with declining barnacles, or there could be an unknown external process that negatively affects barnacles and favors ascidians.

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### 1. Introduction

The distribution of species in marine and terrestrial communities often forms a mosaic of patches at different stages of succession (Watt, 1947; Menge et al., 2005). Patch dynamics may be driven by recruitment and competition between several functionally similar taxa [e.g. grasslands (Tilman, 1997), marine hard bottoms (Keough, 1984)]. However, patches may also be created or modified by foundation species [sensu Dayton (1972), hereafter FS] that create habitats for many other taxa. Population structure and dynamics of FS can influence the spatial structure and dynamics of the whole assemblage, as has been found in mussel beds (Tsuchiya and Nishihira, 1986), seagrass meadows (Bruno and Kennedy, 2000), and aggregations of tube-building worms (Zühlke, 2001). The structure of these assemblages is hierarchical, with the FS on the top and with numerous dependent species (Bruno et al., 2003).

Intraspecific competition affects the performance of sessile benthic FS and the structure of their small-scale aggregations [see Dayton (1985), Pullen and LaBarbera (1991), Rose and Dawes (1999), Stewart et al. (2007) for examples from kelp forests, barnacle clusters, seagrass beds and macroalgal clumps, respectively]. Multiple FS often coexist, as in mixed forest stands (Veblen et al., 1979) and mixed kelp forests (Dayton, 1985). However, interactions between multiple FS have been examined mostly in transition zones between the areas in which they are dominant (Witman, 1987; Bertness et al., 2006). FS dynamics in small-scale patches have been ignored, despite the potential for strong effects on dependent assemblages at these spatial scales.

Small epibenthic patches dominated by barnacles *Balanus crenatus* Brugiere and several species of solitary ascidians [*Styela* spp., *Molgula* spp. and *Boltenia echinata* (L.)] are common on shallow subtidal soft-bottoms of the White Sea. These multi-tier clusters develop on empty bivalve shells and stones scattered on the muddy bottom. Primary substrates, such as empty shells of the clam *Serripes groenlandicus* (Brugiere) and small stones (Yakovis et al., 2004), are usually covered by living barnacles and their empty shells (hereafter "dead barnacles"). Dead barnacles degrade slowly and often remain attached to the substrate. At the study site ascidian clumps occur on barnacles live and dead, but almost never on primary substrate (Yakovis et al., 2008). The

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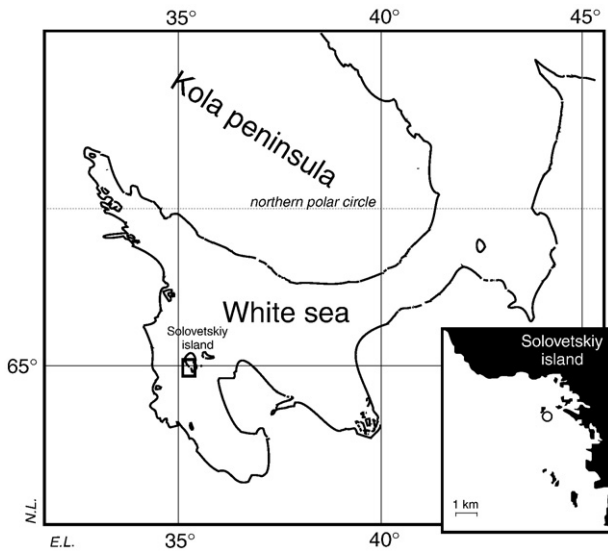


Fig. 1. Sampling site location (encircled).

clusters with various proportions of barnacles and ascidians co-occur at the same site. The diverse dependent assemblage includes various sessile (bryozoans, hydroids, red algae) and mobile (polychaetes, amphipods, gastropods and bivalves) organisms (Yakovis et al., 2004, 2005, 2007).

Empty substrates are initially colonized by barnacles, and ascidians are rarely found there (Yakovis et al., 2005). Most small barnacles are found on the primary substrate and conspecifics. Ascidians recruit to the surfaces of barnacle shells and conspecifics. The proportion of dead barnacles in a given size-class is greater in ascidian-dominated patches. One of the possible processes underlying this pattern is competitive exclusion of barnacles by ascidians (Yakovis et al., 2008). Ascidians also often grow inside the orifice and on the mobile plates of barnacle shells and thus may directly kill barnacles (Yakovis et al., 2008). Alternatively, ascidians may prefer the patches with declining barnacles, or there could be an unknown external process that negatively affects barnacles and favors ascidians.

Growth in barnacles often decreases in case of competition and thus is widely used to assess its intensity (Bertness, 1989; Bertness et al., 1999; Leonard, 2000; Lohse, 2002). Barnacles living in arctic and sub-arctic conditions develop annual rings of growth cessation on the outer shell surface (Bourget, 1980). We used vertical growth reconstructed from annual growth marks on the shell surface and dead:live ratios as a measure of the fitness of barnacles.

Unlike bivalves and polychaetes, ascidians are firmly attached to their substrates and we could not manipulate their density or presence by their exclusion (which destroys small patches) or by addition (because the manipulations attract crabs and other predators). Consequently, we regard the field observations on growth increments as the necessary first step to assess the potential negative effect of ascidians on barnacles. In present study we examined how the recent growth and dead:live ratios in the corresponding age classes of barnacles *Balanus crenatus* differ between the neighboring natural barnacle- and ascidian-dominated patches. The absence of the detectable correlation between the ascidian dominance and growth and survival of barnacles would suggest no effect of ascidians on barnacles (i.e., no competitive exclusion); the presence of the correlation, however, would require further experiments for evident conclusions.

## 2. Methods

### 2.1. Study site

Substrates with ascidians and barnacles were collected 100 m to the SW off the Solovetskiy island (Onega Bay, White sea) (65°01.2' N,

35°39.7' E, Fig. 1). Sea bottom landscapes are variable near the Solovetskiy archipelago with hard and mixed sediments predominating. The study site has a muddy bottom at a depth of 11–15 m. The bottom water temperature in July is 8 °C, and salinity varies between 24.4 and 27.6‰ (see Yakovis et al., 2005 and references therein).

### 2.2. Sampling and laboratory techniques

In July 2004 and 2005 SCUBA divers collected relatively large clusters of barnacles and ascidians (50 in total, with 1933 barnacles and 779 ascidians). The divers chose the clusters where the domination of either barnacle or ascidians was visually detectable. Later the patches were assigned either to ascidian-dominated (A) or barnacle-dominated (B) type based on the ratio of ascidian to barnacle biomass (A if greater or equal then 1, B if less then 1). Two areas separated by 30 m were sampled in 2004 (15 and 20 patches) and one in 2005 (15 patches) due to logistical constraints.

To identify the age of live and dead *Balanus crenatus* we counted the growth rings on each of the immobile undamaged shell plates. When growth rings were inconsistent among the plates, the number observed on the majority of plates was used. Growth increments (hereafter GI) were measured along the median of each plate and the length of the corresponding GIs averaged across the plates was used to quantify the individual growth.

To check the correspondence between the number of growth rings and the actual age, we reared barnacles in the field on initially clear clam shells and concrete blocks for 8 years 1998–2006 (see Yakovis et al., 2005). In July 1998–2002 at the site shown on Fig. 1 we added uncolonized dead shells of *Serripes groenlandicus* so that in 2004–2006 we could collect 2795 individuals of *Balanus crenatus* from 40 substrates with an exposure term (hereafter the time over which added substrates were available for recruitment) of 4–8 years. The age distribution of barnacles obtained from the analysis of growth rings then was matched to exposure term to check for consistency. The growth rings counted on the oldest individuals exactly matched the exposure term of substrates except for exposure term of 5 years, where barnacles with only 4 or less growth rings were found (Table 1). Given the single exception, we considered that the accuracy of age estimation from growth rings was sufficient for use in further analyses.

We determined the total wet weight of live barnacles and ascidians to the nearest milligram in each patch. Before weighing ascidians were pierced through branchial cavity and dried with filter paper to remove excess water. The biomass of conspecific neighbors was determined for each barnacle. We considered any pair of individuals as neighbors if the bases of their shells fused or if one of them grew on the other's shell surface.

Table 1

Distribution of the number of growth rings on the shells of barnacles *Balanus crenatus* reared in the field on initially uncolonized shells of *Serripes groenlandicus* with different exposure term

Number of growth rings	Exposure term, years				
	4	5	6	7	8
N.a.	1	2	3	0	4
0	186	284	129	129	237
1	21	92	55	159	3
2	23	105	18	12	5
3	181	468	14	6	6
4	5	71	50	9	5
5			59	32	11
6			248	50	26
7				45	21
8					20
Total	417	1022	576	442	338

N.a.-growth ring count is not available.

**Table 2**

Univariate results of ANCOVA testing the effect of Dominant FS (ascidians vs. barnacles) and interannual variation on relative length of growth increments of barnacles formed 1–3 years before sampling

Source of variation	df	1 year before sampling			2 years before sampling			3 years before sampling		
		F	p	$\eta_p^2$	F	p	$\eta_p^2$	F	p	$\eta_p^2$
Age	1	95.04	***	0.205	158.62	***	0.301	74.78	***	0.169
Neighbor Biomass	1	0.22	ns	0.001	7.93	***	0.021	11.79	***	0.031
Year	1	4.33	*	0.012	0.02	ns	0.000	5.03	*	0.013
Dominant FS	1	8.14	***	0.022	28.41	***	0.071	3.17	ns	0.009
Year × Dominant FS	1	1.48	ns	0.004	2.36	ns	0.006	4.05	*	0.011
Error	369									
Total	374									

Age and log-transformed Neighbour biomass used as covariates. Partial eta-squared ( $\eta_p^2$ ) used as a measure of effect size. ns = not significant; \* =  $p < 0.05$ ; \*\*\* =  $p < 0.001$ .

### 2.3. Data analysis

GI lengths formed during 1–3 years before sampling were analyzed for 375 barnacles of age classes 5+ ... 9+. GI lengths were expressed as the percentage of the shell height (hereafter “relative growth”) to remove size-dependent differences in growth rate of even-aged barnacles (e.g. Sukhotin and Pörtner, 2001). Relative growth proportions were arcsin-transformed ( $x' = 2 \arcsin(\sqrt{x})$ ) to normalize the distribution.

We compared relative growth of 5+...9+ barnacles from 50 A- and B-dominated patches (total 375 live barnacles: 302 from A and 73 from B) using the analysis of covariance (ANCOVA) with Dominant FS and Year as main effects, and barnacle Age and log-transformed [ $x' = \log(x+1)$ ] Neighbor biomass as covariates. We used Neighbor biomass to control for intraspecific effects because the average density of barnacles differed between A- and B-patches. Since we analyzed barnacles of different age classes simultaneously and took samples of even-aged barnacles only during the 2 subsequent years, the Year effect represents the differences between the pairs of years during which each given GI was formed (i.e. difference between 2003 and 2004 for GI that represents the year before sampling, the difference between 2002 and 2003 for the 2 years before sampling and so on). Data for the two sampling areas were pooled together. This procedure permitted an analysis of the separate effects of year, age and dominant FS on the relative growth of barnacles.

The ANCOVA assumption of homogeneity of regression slopes was met because no significant interactions were found between the categorical predictors and covariates. The assumption of homogeneity of variances was tested by examining a plot of residuals versus fitted values. We used partial eta-squared ( $\eta_p^2$ ) as a measure of effect size (Quinn and Keough, 2002). Unequal Ns Tukey's HSD test was used as a post-hoc test. Planned comparisons of relative growth in barnacle- vs. ascidian-dominated patches were performed on ANCOVA-adjusted means using Student's t-test. Means and standard deviations reported for this analysis were reverse angular transformed.

We used dead:live ratios to assess the mortality of barnacles in A- and B- dominated patches. Dead:live ratios are used by plant ecologists as an indirect measure of mortality (e.g. Spetich et al., 1999). For sessile species their value depends on preservation rate and mortality. We initially assumed that preservation rate of dead barnacle shells was roughly the same in A- and B-dominated patches. However, we only could underestimate dead:live ratios in A, at least for some age classes, because shells of juvenile barnacles preserve for a very short time on ascidian tunics, where we often observed settlers, and shells of older barnacles are often crushed by growing ascidians. In B, on the other hand, shells of dead barnacles preserve relatively well as they often stay cemented to the plates of live barnacles.

In A- and B-dominated patches, dead:live ratios were obtained separately for each age class where sample size exceeded 5 individuals (0+...9+ for barnacle-dominated patches and 0+...10+ for ascidian-dominated ones). We tested the resulting proportions for a difference

**Table 3**

Recent relative growth of barnacles from ascidian- and barnacle-dominated clusters

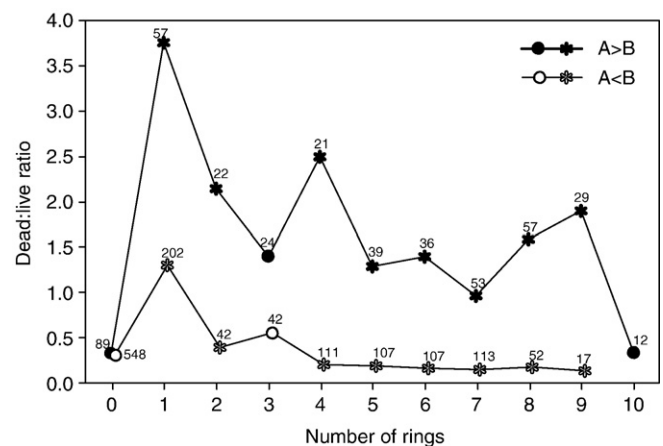
Growth increment	Dominant FS		Student's t
	barnacles	ascidians	
Sampled in 2004	N=193	N=54	
In 2003	13.0 ± 1.4	8.8 ± 1.1	***
In 2002	18.6 ± 1.7	9.9 ± 1.3	***
In 2001	12.9 ± 1.9	12.9 ± 1.5	ns
Sampled in 2005	N=109	N=19	
In 2004	9.9 ± 1.2	8.1 ± 1.1	ns
In 2003	16.9 ± 1.5	11.6 ± 1.3	*
In 2002	18.3 ± 1.7	13.1 ± 1.5	*

Relative growth increment lengths expressed as a percentage of shell height. ANCOVA-adjusted least-squares means ± standard deviations of relative growth increments' lengths (reverse arcsin-transformed values) computed at covariate means (Age=6.83, Neighbors=1.47). T-statistic computed on arcsin-transformed values. ns=not significant; \* =  $p < 0.05$ ; \*\*\* =  $p < 0.001$ .

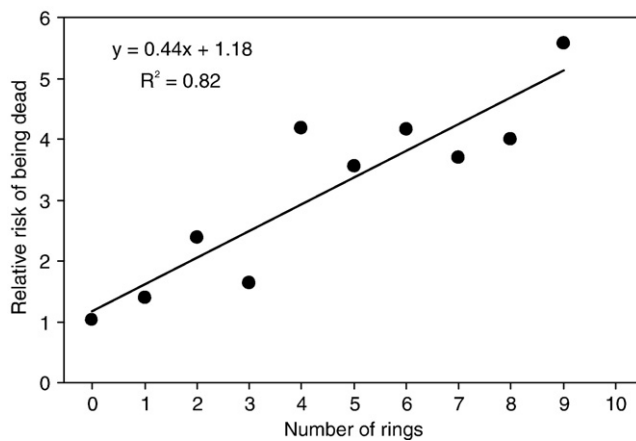
from 1:1 to assess the prevalence of either dead or live barnacles in A- and B-dominated patches. Dead:live ratios were used to compare mortality of barnacles between the two types of patches using the Fisher exact test. Dead:live ratios characterize the mortality over time. The competition pressure on an individual barnacle is changing through its life when its neighbors die. Hence we could not use neither neighbor biomass nor their number to estimate the effect of intraspecific competition on the barnacle mortality described by dead:live ratios. Relative risks of being dead (Simon, 2001) in ascidian- vs. barnacle-dominated patches were computed for age classes separately as  $r = p_a / p_b$ , where  $p_a$  and  $p_b$  were the percentages of dead individuals in A- and B-dominated patches, respectively. A linear regression was fitted to risk ratios. The assumptions of homogeneity of error variances were examined by plotting predicted vs. residual values.

### 3. Results

The primary substrates of A- and B-patches were empty shells of bivalves [*Serripes groenlandicus* ( $n=43$ ,  $S=39.8 \pm 12.8$  cm<sup>2</sup>), *Modiolus modiolus* (L.), ( $n=1$ ,  $S=41.3$  cm<sup>2</sup>)], the gastropod *Neptunea despecta* L. ( $n=1$ ,  $S=22.7$  cm<sup>2</sup>), and small stones ( $n=5$ ,  $S=23.5 \pm 15.7$  cm<sup>2</sup>). Patches occasionally carried several species of red canopy-forming algae [mostly *Phycodrys rubens* (L.), *Ptilota plumosa* (Huds.)], total biomass range 0–6.4 g·patch<sup>-1</sup>] that were attached mainly to ascidians and barnacles. Ascidians found in the patches were *Styela rustica* (L.), *Molgula retortiformis* (Verrill), *Styela coriacea* (Alder and Hancock) and *Boltenia echinata*, here listed in order of decreasing total biomass. In A-



**Fig. 2.** Dead:live ratio of *Balanus crenatus* in the patches dominated in terms of biomass by barnacles (A<B) and ascidians (A>B). Points are labeled with the sample size (number of ind.) for the corresponding ratio. Asterisks indicate significant differences between dead:live ratios in A<B and A>B patches for corresponding size class (Fisher's exact test). Data collected in 2004–2005 were used.



**Fig. 3.** Relative mortality risk for *Balanus crenatus* in ascidian- compared to barnacle-dominated patches estimated as the ratio of the percentages of dead barnacles in ascidian- and barnacle-dominated patches.

and B- dominated patches mean total biomass of live barnacles was  $10.4 \pm 7.2$  and  $45.2 \pm 22.1$  g·patch<sup>-1</sup> and mean total biomass of ascidians was  $29.1 \pm 11.9$  and  $5.2 \pm 7.2$  g·patch<sup>-1</sup>, respectively. Average density of barnacles in A- and B-dominated patches was  $0.27 \pm 0.34$  and  $1.05 \pm 0.85$  cm<sup>-2</sup>.

We used ANCOVA to assess the Dominant FS (A or B) effect on the relative growth of barnacles controlling for effects of Year, Age and Neighbor biomass (Table 2). Age affected relative length of all the growth increments examined (hereafter "GIs"). Neighbor biomass significantly influenced the GIs formed 2 and 3 years before sampling. The effect of Year was significant for GIs formed 1 and 3 years before sampling (GIs formed during 2003 vs. 2004 and 2001 vs. 2002). Recently formed GIs (1–2 years before sampling) were affected by Dominant FS. ANCOVA-adjusted means were significantly smaller in A patches than in B (Tukey's HSD test,  $p < 0.05$  and  $p < 0.01$ , respectively). There was a significant interaction between Year and Dominant FS for GIs formed 3 years before sampling, the differences of GI length were significant in barnacles sampled in 2005, but not in 2004 (Tukey's HSD test). ANCOVA-adjusted means for GIs formed in 2003 and 2002 were significantly smaller in A-patches than in B (Table 3, Student's t-test). For GIs formed 1–2 years before sampling the proportion of variance explained by the factors (Table 2) changed as follows: Age > Dominant FS > Year > Neighbor biomass > Year × Dominant FS interaction. For the 3-year-old GIs the order was similar, the only exception being that Dominant FS explained the least variance.

In A patches dead:live ratios differed significantly from 1:1 only for 0+ and 1+ barnacles ( $p < 0.01$ , Fisher's exact test, Fig. 2). In these patches, dead barnacles were more common than live barnacles. In B patches live individuals were more common than dead ones in age classes 4+...9+ (4+...8+ with  $p < 0.01$  and 9+ with  $p < 0.5$ , Fisher's exact test, Fig. 2). Dead:live ratios were significantly higher in A patches as compared to B for age classes 1+...2+ and 4+...9+ ( $p < 0.01$ , Fisher exact test, Fig. 2). Relative mortality risk in A patches compared to B for younger age classes of barnacles was close to 1. It increased with age ( $R^2 = 0.82$ ,  $F_{df=1,8} = 35.43$ ,  $p < 0.01$ ), so that 9+ barnacles from A patches were 5.57 times more likely to be dead than individuals of the same age in B (Fig. 3).

#### 4. Discussion

We found no evidence for the absence of negative influence of ascidians on barnacles. Barnacles grew slower and had lower survival in the patches with large ascidians compared to the patches dominated by barnacles. Thus we can not reject the hypothesis of the negative interactions between the two co-dominant FS, which still needs a direct experimental evidence.

To isolate the effect of ascidian domination, we corrected for intraspecific effects between barnacles. Under crowded conditions barnacles grow in height faster and have slimmer and longer shells than their conspecifics from sparsely populated areas (Barnes and Powell, 1950; Bertness et al., 1998). As soon as the observed density of live barnacles in A on average was lower than B, we controlled for the effect of live conspecific neighbors in the patch and compared it to the effect of local ascidian abundances.

We determined individual growth using the growth increments observed from the three subsequent years preceding the study. Because there is no method to determine the age of ascidians we could not estimate with certainty how long the patch had been colonized by them. Although some species of solitary ascidians can grow fast (Lambert, 1968; Gulliksen, 1972), in the White Sea *Styela rustica* weighing several grams can not develop in one year (V.V. Khalaman, unpublished data on long-term observations of tagged ascidians in nature). Therefore, if a patch bears large ascidians, it is likely that the barnacles in it have been influenced by those ascidians for several years at least. The more recent the growth increment the more likely it has been formed after the patch harbored adult ascidians. This is indirectly supported by the fact that Dominant FS influenced only the most recent GIs while Neighbors affected the older ones. Such a sequence of effects may be attributed to barnacle self-thinning coupled with the growth of ascidian biomass during the time in ascidian-dominated patches.

Dead:live ratios previously reported for the patches of barnacles and ascidians were size-based and did not include information on age (Yakovis et al., 2008). Age data allowed us to estimate mortality separately for age-classes and track how it changed with age. Greater mortality was observed in barnacles from A patches—this was indicated by the higher dead:live ratios registered for most of the age classes. Mortality risk was higher in A compared to B and this difference increased with age.

When assessing dead:live ratios we did not account for barnacle density in the patches. Intraspecific crowding, however, is frequently recognized as an important source of mortality for barnacle populations (Barnes and Powell, 1950; Connell, 1961; Bertness, 1989; Lopez and Gonzalez, 2003). Yet such mortality may be density-dependent only in periods of rapid growth (Connell, 1961; Lopez and Gonzalez, 2003). We rarely observed barnacles with signs of smothering by conspecifics and never observed live barnacles lifting the shells of one another off the surface, although such cases are common when competition for space is strong (Barnes and Powell, 1950; Connell, 1961). Consequently, in the patches of barnacles and ascidians the effect of crowding on mortality may be weak.

Our study demonstrated the difference in growth and demographic structure of barnacles between the patches where barnacles or ascidians dominated. The exact mechanism remains unknown, but we suggest several hypothetical scenarios. The first one implies the negative effect of ascidians on barnacles. The presence of epibionts often results in reduced growth or increased mortality of the host organisms (Wahl, 1989). Competition for food is possible between ascidians and barnacles, because the size ranges of the particles they consume overlap (Barnes, 1959; Tatián et al., 2004). Yet, recent data on food sources acquired from stable isotope ratio signatures suggest that sometimes cirripedes and ascidians have different diets (Dubois et al., 2007). Indirect interference may also be strong, since large ascidians may screen underlying barnacles from water currents. Barnacles feed most effectively in flowing water (LaBarbera, 1984) and local flow reduction might be critical for them. At our study site, the ascidian tunic often harbors several species of red canopy-forming algae (Yakovis et al., 2008) that may screen barnacles from currents (Barnes, 1955; Leonard, 2000). Growth generally occurs under favorable food conditions. Therefore, feeding interference and screening may inhibit growth and indirectly affect the survival of barnacles. Observations, however, suggest the direct influence of ascidians on barnacle survival. Ten percent of live barnacles with the

aperture longer than 3 mm have ascidians attached inside their orifice or on opercular plates (Yakovis et al., 2008). If they grow large enough, these ascidians can affect the feeding performance of their host and may eventually kill it by blocking its orifice.

The second hypothesis is that ascidian clumps can develop only in the patches where barnacles are declining due to some internal or external reasons. At the stage of larval substrate selection, however, solitary ascidians studied prefer surfaces of live barnacles rather than their empty shells (Young and Gotelli, 1988; Varfolomeeva et al., submitted for publication). The third hypothesis is that there is an external process operating at the patch scale that favors ascidians and negatively affects barnacles, like heterogeneous sedimentation or hydrodynamic conditions.

At the study site, *Serripes groenlandicus* shells and dropstones surrounded by mud are the only primary substrates available. The possible negative effect of ascidians on barnacles, which we can not reject, is important given that at our study site ascidians never occupy primary substrates and only live on barnacles and each other, dominating in 17% of all the patches (Yakovis et al., 2008). Successions where the juveniles of one species are facilitated by the other, but then these recruits grow up to become strong competitors are usual (Flores-Martinez et al., 1994; Callaway and Walker, 1997). In warmer localities ascidians with high growth rates often rapidly (within months) replace barnacles (Harms and Anger, 1983; Hatcher, 1998), and other sessile organisms (Kay and Keough, 1981; Russ, 1982). In the White Sea the succession takes at least several years yet the interaction likely also leads to the exclusion of barnacles at the level of an individual patch (Yakovis et al., 2005, 2008). However, the influence of ascidians does not lead them to space monopolization at larger scale, since patches with various proportions of barnacles and ascidians co-occur at the study site. Consistent with the pattern-process hypothesis (Watt, 1947), we expect that co-existence of barnacles and ascidians depends on the asynchrony of successional sequences in different patches. However, only further direct experiments may reveal the process leading to the replacement of the declining barnacles by ascidians at the patch scale.

## Acknowledgements

We give our hearty thanks to Alexandra Yakovis for her patient assistance in dismantling barnacle clusters. We thank numerous volunteers who helped us with fieldwork. We are grateful to the divers who returned with catch in any weather—Dmitry Tomanovskiy (Polar Institute for Fisheries and Oceanography, Murmansk) and Michael Fokin (Zoological Institute RAS, SPb). Our special thanks to Alexander Cherenkov and Nadezhda Cherenkova (Moscow State University) for technical support and accommodation. We are grateful to Mark C. Urban (National Center for Ecological Analysis and Synthesis) and Natalia Lentsman (St-Petersburg State University) for linguistic improvements. Martin Thiel (Universidad Católica del Norte, Coquimbo, Chile), Judi Hewitt (NIWA, Hamilton, New Zealand) and three anonymous referees provided valuable comments on the manuscript. The funding was provided by Russian Foundation for Basic Research (grants no. 05-04-48927A, 05-04-63041K, 06-04-63077K, 08-04-01373A, 08-04-10109K). [ST]

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