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Larval substrate preferences do not explain spatial distribution of ascidians in a multi-level facilitation cascade

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Abstract

Microhabitat associations in sessile invertebrates are largely determined by larval choices and early differential post-settlement mortality. Either process can have a broad community-wide impact when it regulates a cascade of foundation species, each facilitating multiple dependent taxa. On mixed sediments in shallow subtidal of Onega Bay (the White Sea, 65° N) cockles, barnacles and ascidians act as foundation species forming a multi-level facilitation cascade. Barnacles *Balanus crenatus* monopolize empty shells of the Greenland cockle *Serripes groenlandicus*, whereas ascidians (mainly *Styela rustica*) attach almost exclusively to barnacles and conspecifics. Field observations and experiments evidence that barnacles facilitate ascidians and suggest that individual patches shift from barnacle to ascidian dominance over time. Ascidian recruits are found on barnacles and almost never on *Serripes* shells, a pattern that may result either from substrate-specific larval settlement or from differential post-settlement mortality.

Here, we experimentally tested whether larval substrate preferences generate this pattern. In a laboratory experiment, fertilized *Styela* eggs were added to aerated seawater tanks containing *Serripes* shells with and without barnacles, and the distribution of ascidian juveniles was quantified after 10 days. Contrary to our hypothesis, settlement density on *Serripes* shells exceeded that on barnacles. This result rules out larval substrate selection as the primary mechanism and instead implicates substrate-specific post-settlement mortality of a secondary foundation species as the most likely driver of facilitation.

Introduction

The spatial structure of the marine benthic communities dominated by sessile organisms reflects variation in propagule supply as well as differential settlement and post-settlement processes, each influenced by multiple biotic and abiotic factors (Connell, 1985; Hunt and Scheibling, 1997; Underwood and Keough, 2001). Facilitation cascades (Altieri *et al.,* 2007) are sequences of interspecific interactions that arise when a strong facilitator (a primary foundation species) benefits another strong facilitator (a secondary foundation species), which in turn positively affects a suite of dependent taxa. Known multi-level facilitation cascades may include up to five or six hierarchical levels of foundation species (Thomsen *et al.,* 2016; Yakovis and Artemieva, 2017). The determinants of the space utilization pattern exhibited by a sessile foundation species in a facilitation cascade potentially have a broad community-wide impact because of the hierarchical indirect effects on multiple dependent taxa (Gribben *et al.,* 2019).

Planktonic larvae of various sessile benthic invertebrates actively select particular natural substrates for settlement (Ryland, 1962; Knight-Jones *et al.,* 1971; Buschbaum, 2001). In many systems, resulting settlement patterns often shape the spatial distribution of adults more strongly than differential post-settlement mortality (Grosberg, 1981; Hurlbut, 1991; McKinney and McKinney, 1993).

Barnacles and ascidians act as foundation species in benthic communities where they dominate (Dean, 1981; Bros, 1987; Fielding *et al.,* 1994; Monteiro *et al.,* 2002; Yakovis *et al.,* 2008; Yakovis and Artemieva, 2017). Barnacles frequently monopolize primary hard substrates, so that the rest of sessile organisms, including co-dominant solitary ascidians, attach primarily to barnacles and conspecifics (Dean and Hurd, 1980; Dean, 1981; Hatcher, 1998; Yakovis *et al.,* 2005, 2008; Yakovis and Artemieva, 2017). In the shallow subtidal of Onega Bay (the White Sea), epibenthic patches on mixed sediments are typically based on empty shells of the Greenland cockle *Serripes groenlandicus* (Mohr, 1786; hereafter *Serripes*). Barnacles *Balanus*

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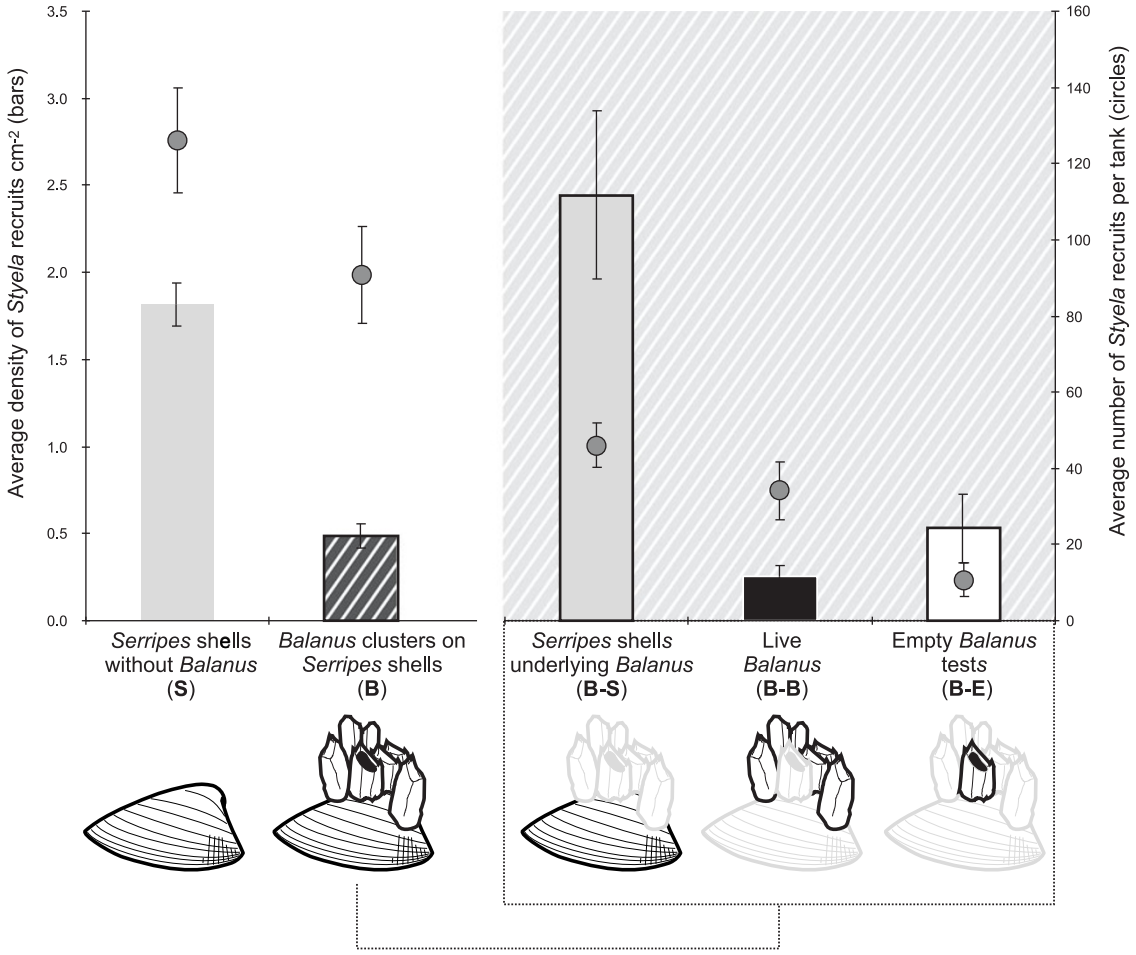


Figure 1. Average density (bars, left axis, ±S.E.) and average number of individuals per tank (circles, right axis, ±S.E.) of settled *Styela rustica* juveniles by substrate type. S – empty *Serripes groenlandicus* shells, B – *Serripes groenlandicus* shells with barnacles *Balanus crenatus* (substrates pooled). B-S – zones on *Serripes groenlandicus* shells in B not occupied by barnacles, B-B – live barnacles, B-E – empty barnacle tests. Settlement densities on S, B-S, and B-B were used in the analyses (see text for details).

crenatus Bruguière, 1789 (hereafter *Balanus*) exclusively dominate *Serripes* shells, whereas co-dominant solitary ascidians (mainly *Styela rustica* Linnaeus, 1767; hereafter *Styela*) attach to barnacles, their empty tests, and to each other (Supplementary Figure S1). At other sites in the White Sea (e.g. Kandalaksha Bay), however, in the absence of barnacles, *Styela* can form clumps directly on primary hard substrates such as shells or gravel (Yakovis *et al.,* 2008).

In Onega Bay, *Serripes, Balanus*, and *Styela* compose a multi-level facilitation cascade in which the presence of *Balanus* promotes *Styela* recruitment, and clean *Serripes* shells (without barnacles) exposed in the field for a year lack ascidian recruits (Yakovis and Artemieva, 2017). Given the diverse assemblages of dependent species associated with barnacles and ascidians (Yakovis *et al.,* 2008), the mechanism underlying barnacle facilitation of ascidians represents a key driver of the community structure and dynamics. Two alternative processes could explain the observed pattern: (i) larval substrate preferences of *Styela* larvae or (ii) substrate-specific post-settlement mortality of recruits. Here, we experimentally tested the first hypothesis. If larval preferences determine adult distribution, we predicted higher settlement density of *Styela* larvae on barnacles than on *Serripes* shells. Conversely, equal or higher settlement on *Serripes* shells would prompt post-settlement mortality as the principal mechanism.

Methods

In the summer of 2005, we collected 14 empty *Serripes* shells (hereafter S) and 14 empty *Serripes* shells with the convex side partially covered by adult *Balanus* (hereafter B) near the Solovetsky Islands in Onega Bay of the White Sea (65°01.180′ N, 35°39.721′ E, at 12 m depth, see Site 1 in Yakovis and Artemieva (2017)). Shells were cleaned of all macrobenthic organisms (except barnacles in B) and stored in aerated seawater tanks at +5°C. These empty *Serripes* shells, like most found in the field, had naturally eroded periostraca and were 5–8 cm long. Mean shell length did not differ between S and B (Student's t-test, $p = 0.136$, $n = 14$). There was a single substrate type in S (shell surface) and three substrate types in B (shell surface, hereafter B-S, live barnacles, hereafter B-B, and few empty barnacle tests, hereafter B-E). We only examined the convex sides of *Serripes* shells, as concave sides are typically buried in soft sediment in the field. Substrate surface areas were measured by wrapping substrates in thin aluminium foil and weighing the foil (Marsh, 1970).

In mid-September, during the annual breeding period of *Styela* in the White Sea, we randomly distributed the shells among seven replicate 20 L tanks with aerated seawater at +10°C. Two S and two B were placed on the bottom of each tank in alternating order, convex side upward (matching their typical orientation in the field).

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Mean (± S.E.) substrate areas per tank were 69 ± 4 cm^2 for S, 145 ± 14 cm^2 for B-B, 24 ± 5 cm^2 for B-S, and 21 ± 7 cm^2 for B-E.

Natural epibenthic patches on *Serripes* shells in the field are covered by fine sediment, except for the distal portions of live barnacles and their large flexible epibionts like ascidians and red algae (authors' personal observations). To reproduce this pattern, we added 100 ml of liquid silt (particle size ≤ 0.25 mm) to each tank 1 week after substrate placement, producing an unconsolidated sediment layer approximately 2 mm thick that covered all substrates, except the opercular plates and distal parts of B-B. After 24 hours, we added approximately 2500 fertilized *Styela* eggs to each tank during daylight hours (see Khalaman *et al.* (2008) for the details on the technique). Tanks were illuminated from above and maintained for 10 days under a 12:12 h light:dark cycle.

After 10 days, we removed the substrates, stained them with 0.1% methylene blue solution and counted all settled ascidians on each substrate type (S, B-B, B-S, and B-E; 1519 individuals in total; Supplementary Data S1). Previous laboratory experiments indicate that most *Styela* larvae settle within 2–3 days after fertilization (Khalaman *et al.,* 2008).

We compared settlement density (individuals per cm^2) between S and B-B using GLM ANCOVA (type III), with Substrate (S vs B-B) as a fixed factor, Tank as a random factor, and Substrate Area as a covariate. After pooling data by tank, we also compared settlement density within B shells between B-S and B-B using GLM ANCOVA (type III) with Substrate (B-S vs B-B) as a within-subject fixed factor and B-B/B-S substrate area ratio as a covariate. Empty barnacle tests (B-E) were excluded from statistical analyses because their surface area was too small for meaningful comparison; mean densities on B-E are reported descriptively in Figure 1. Variances were homogeneous (Cochran's *C*-test).

Calculations were performed in StatSoft STATISTICA software package version 8.0 (StatSoft, Inc., 2008). Means are reported ± S.E.

Table 1. Effect of substrate type (*Serripes groenlandicus* empty shells [S] vs live *Balanus crenatus* [B-B]) on the settlement rate of *Styela rustica*

Source of variation	SS	*df*	*F*	*P*
Tank (random, 7 levels)	0.97	6	1.67	0.212
Tank × Substrate (random)	1.23	6	2.12	0.126
Substrate × Substrate Area (fixed)	0.21	1	2.13	0.170
Substrate (fixed, 2 levels)	**2.15**	**1**	**22.29**	**<0.001*** **
Substrate Area (fixed, continuous)	0.28	1	2.92	0.113
Error	1.16	12		

GLM ANCOVA (type III). Significant effects highlighted in bold. *** $P < 0.001$

Table 2. Effect of substrate type (*Serripes groenlandicus* empty shells [B-S] vs live *Balanus crenatus* [B-B]) on the settlement rate of *Styela rustica* within the *Serripes* shells with *Balanus* (B)

Source of variation	SS	*df*	*F*	*P*
Between subject:				
B-S/B-B Substrate Area ratio (fixed, continuous)	2.38	1	5.10	0.074
Error	2.33	5		
Within subject:				
Substrate (fixed, 2 levels)	**14.75**	**1**	**38.06**	**0.002** **
Substrate × B-S/B-B Substrate Area ratio (fixed)	**3.36**	**1**	**8.68**	**0.032***
Error	1.94	5		

GLM ANCOVA (type III). Individual substrates pooled by tank. Significant effects highlighted in bold. * $P < 0.05$, ** $P < 0.01$

Results and discussion

Substrate type significantly influenced the settlement density of *Styela* recruits (Tables 1–2, Figure 1). Inconsistent with the natural distribution of juveniles and adults observed in the field (Yakovis *et al.,* 2008; Yakovis and Artemieva, 2017), *Styela* larvae clearly favoured cockle shells over barnacles. Settlement density was higher on S than on B-B (Table 1), and within B, higher on B-S than on B-B (Table 2). Mean settlement density was 1.8 ± 0.1 cm^{-2} on S and 2.4 ± 0.5 cm^{-2} on B-S, compared to only 0.3 ± 0.1 cm^{-2} on B-B. As in the field (Yakovis and Artemieva, 2017), *Serripes* shells provided less surface area than barnacles. Nevertheless, despite having less than half the available area, *Serripes* shells accumulated substantially more ascidian recruits (126 ± 14 individuals per tank) than live *Balanus* (34 ± 8 individuals per tank; Figure 1). These results clearly indicate that the scarcity of juvenile and adult *Styela* on *Serripes* shells in the field cannot be explained by larval substrate preferences.

Solitary ascidians often occur on barnacles rather than on adjacent relatively smooth primary substrates, both shortly after settlement and after longer exposure periods (Dean and Hurd, 1980; Young and Gotelli, 1988; Yakovis *et al.,* 2005). Young and Gotelli (1988) reported higher number *Styela plicata* recruits on barnacle tests than ceramic tiles after 2 weeks of field exposure; however, the design of that experiment did not allow separation of larval settlement from early post-settlement mortality, including potential predator effects.

While calcareous bivalve shells and barnacle tests seem chemically similar, differences in surface texture and wettability may help explain the observed ascidian settlement pattern. The surface of *Balanus* tests is markedly more complex, with numerous pits and crevices, whereas *Serripes* shells are comparatively smooth (Supplementary Figure S1). Ascidian larvae can respond to substrate roughness (Chase *et al.,* 2016) and avoid nano-folds compared to flat surfaces (Sakai *et al.,* 2024), yet there is no evidence that they actively discriminate among microtopographic features at the scale of 1 mm–1 cm. Also, larvae of many other sessile invertebrates that do exhibit such selectivity (e.g. sponges, corals, barnacles, bryozoans) preferentially settle in surfaces depressions rather than smooth surfaces (Walters and Wethey, 1996; Whalan *et al.,* 2015). Thus, although microtopographic complexity cannot be excluded as a contributing factor, the available evidence is limited and not entirely consistent.

Possible difference in substrate wettability may provide a more plausible explanation. Larvae of several ascidian species prefer less wettable (more hydrophobic) surfaces for settlement (Sensui and Hirose, 2025). Even eroded *Serripes* shells retain patches of periostracum on their convex surfaces, rich in conchiolin proteins (Supplementary Figure S1), which are likely more hydrophobic than calcified barnacle tests lacking a proteinaceous covering. A preference for less wettable surfaces could therefore promote *Styela* settlement on *Serripes* shells. In contrast, the barnacle *Balanus amphitrite* avoids intact periostracum when settling on bivalve shells (Scardino *et al.,* 2003), consistent with its preference for more wettable surfaces (Rittschof and Costlow, 1989).

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In our experiment, *Styela* larvae successfully settled on substrates covered with a 2 mm layer of unconsolidated silt, indicating a capacity to burrow into the sediment similar to that previously observed (though to a lesser extent) in coral larvae (Ricardo *et al.,* 2017). High sedimentation is often reported to reduce larval settlement (Hodgson, 1990; Te, 1992), but this effect may be masked in field studies by post-settlement mortality during prolonged exposure (Babcock and Davies, 1991). Sediment can cause abrasion, direct burial, and feeding inhibition (Moore, 1977) and represents an important source of juvenile mortality in ascidians (Young and Chia, 1984), although some species tolerate substantial siltation (Naranjo *et al.,* 1996). Consequently, sedimentation still can contribute to post-settlement mortality of *Styela* on *Serripes* shells. Yet, similar density of *Styela* juveniles on live barnacles and their empty tests in field experiments (Yakovis and Artemieva, 2017), together with our results, suggest that barnacle self-cleaning from sediment is not critical for *Styela* recruitment. Predation of *Styela* larvae by barnacles seems also unlikely, given that tropical barnacles consume the larvae of colonial ascidians but not the larvae of a solitary *Styela plicata* (Young and Gotelli, 1988).

The site selected for settlement by a benthic organism often maximizes subsequent growth and survival (Young and Chia, 1984; Buschbaum, 2001 and references therein). However, post-settlement mortality can decouple larval preferences from recruit distributions (Mizrahi *et al.,* 2014). *Styela* is common in the absence of co-dominant barnacles outside Onega Bay of the White Sea (Dybern, 1969; Khalaman, 2001; Yakovis *et al.,* 2008), and its larval preferences might have evolved primarily apart from the focal facilitation cascade. Yet, to match the recruitment patterns observed in the field, the higher settlement on *Serripes* shells must later be offset by substantially higher post-settlement mortality on shells (and thus higher survival on barnacles). Hierarchical facilitation may therefore buffer mismatches between larval behaviour and local selective pressures.

We suggest differential predation is a probable source of the expected contrast in ascidian survival between substrates, given the known strong consumer control of mobile fauna associated with the *Serripes–Balanus–Styela* system in the White Sea by shrimp and crabs (Yakovis and Artemieva, 2019, 2021). Particularly, predation on *Styela* in the White Sea is poorly studied, except that this species forms a subordinate component of a wolffish diet (Yershov and Khaitov, 2024). Juvenile solitary ascidians in general, however, commonly face strong predation pressure from gastropods, shrimp, crabs, sea urchins, and sea stars (Whitlatch and Osman, 2009; Dumont *et al.,* 2011; Giachetti *et al.,* 2022). The plicate surface of *Balanus* tests may provide an effective refuge against predators (like shrimp or gastropod grazers) compared with the smoother surfaces of cockle shells or stones (Young and Chia, 1984; Svane and Young, 1989; Walters and Wethey, 1991). Field caging experiments will be required to identify the precise mechanisms enhancing ascidian survival on barnacles and hence shaping the structure and dynamics of this multi-level facilitation cascade.

Supplementary material. The supplementary material for this article can be found at https://doi.org/10.1017/S0025315426101222.

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Data. The data supporting the findings of this study are available as supplementary material with this paper (Supplementary Data S1).

Ethical standards. The experiment was performed in accordance with local legislation concerning animal welfare. No approval from research ethics committees was required because the study involved an unregulated invertebrate species.

References

Altieri AH, Silliman BR and Bertness MD (2007) Hierarchical organization via a facilitation cascade in intertidal cordgrass bed communities. *The American Naturalist* **169**, 195–206. https://doi.org/10.1086/510603.

Babcock R and Davies P (1991) Effects of sedimentation on settlement of *Acropora millepora*. *Coral Reefs* **9**(4), 205–208. https://doi.org/10.1007/BF00290423.

Bros WE (1987) Effects of removing or adding structure (barnacle shells) on recruitment to a fouling community in Tampa Bay, Florida. *Journal of Experimental Marine Biology and Ecology* **105**, 275–296. https://doi.org/10.1016/0022-0981(87)90176-6.

Buschbaum C (2001) Selective settlement of the barnacle *Semibalanus balanoides* (L.) facilitates its growth and reproduction on mussel beds in the Wadden Sea. *Helgoland Marine Research* **55**, 128–134. https://doi.org/10.1007/s101520100070.

Chase AL, Dijkstra JA and Harris LG (2016) The influence of substrate material on ascidian larval settlement. *Marine Pollution Bulletin* **106**(1–2), 35–42. https://doi.org/10.1016/j.marpolbul.2016.03.049.

Connell JH (1985) The consequences of variation in initial settlement vs. post-settlement mortality in rocky intertidal communities. *Journal of Experimental Marine Biology and Ecology* **93**(1-2), 11–45. https://doi.org/10.1016/0022-0981(85)90146-7.

Dean TA (1981) Structural aspects of sessile invertebrates as organizing forces in an estuarine fouling community. *Journal of Experimental Marine Biology and Ecology* **53**, 163–180. https://doi.org/10.1016/0022-0981(81)90017-4.

Dean TA and Hurd LE (1980) Development of an estuarine fouling community: the influence of early colonists on later arrivals. *Oecologia* **46**, 295–301. https://doi.org/10.1007/BF00346255.

Dumont CP, Gaymer CF and Thiel M (2011) Predation contributes to invasion resistance of benthic communities against the non-indigenous tunicate *Ciona intestinalis*. *Biological Invasions* **13**, 2023–2034. https://doi.org/10.1007/s10530-011-0018-7.

Dybern BI (1969) Distribution and ecology of ascidians in Kviturdvikpollen and Vågsböpollen on the west coast of Norway. *Sarsia* **37**(1), 21–40. https://doi.org/10.1080/00364827.1969.10411143.

Fielding PG, Weerts KA and Forbes AT (1994) Macroinvertebrate communities associated with intertidal and subtidal beds of *Pyura stolonifera* (Heller) (Tunicata: Ascidiacea) on the Natal coast. *South African Journal of Zoology* **29**(1), 46–53. https://doi.org/10.1080/02541858.1994.11448326.

Giachetti CB, Battini N, Castro KL and Schwindt E (2022) The smaller, the most delicious: differences on vulnerability to predation between juvenile and adult of invasive ascidians. *Estuarine, Coastal and Shelf Science* **268**, 107810. https://doi.org/10.1016/j.ecss.2022.107810.

Gribben PE, Angelini C, Altieri AH, Bishop MJ, Thomsen MS and Bulleri F (2019) Facilitation cascades in marine ecosystems: a synthesis and future directions. *Oceanography and Marine Biology Annual Review* **57**, 127–168. https://doi.org/10.1201/9780429026379-3.

Grosberg RK (1981) Competitive ability influences habitat choice in marine invertebrates. *Nature* **290**, 700–702. https://doi.org/10.1038/290700a0.

Hatcher AM (1998) Epibenthic colonisation patterns on slabs of stabilised coal-waste in Poole Bay, UK. *Hydrobiologia* **367**, 153–162. https://doi.org/10.1023/A:1003228100220.

Hodgson G (1990) Sediment and the settlement of larvae of the reef coral *Pocillopora damicornis*. *Coral Reefs* **9**, 41–43. https://doi.org/10.1007/BF00686720.

Hunt HL and Scheibling RE (1997) Role of early post-settlement mortality in recruitment of benthic marine invertebrates. *Marine Ecology Progress Series* **155**, 269–301. https://doi.org/10.3354/meps155269.

Hurlbut CJ (1991) Community recruitment: settlement and juvenile survival of seven co-occurring species of sessile marine invertebrates. *Marine Biology* **109**, 507–515. https://doi.org/10.1007/BF01313517.

Khalaman VV (2001) Succession of fouling communities on an artificial substrate of a mussel culture in the White Sea. *Russian Journal of Marine Biology* **27**, 345–352. https://doi.org/10.1023/A:1013751403059.

Khalaman VV, Belyaeva DV and Flyachinskaya LP (2008) Effect of excretory–secretory products of some fouling organisms on settling and metamorphosis of the larvae of *Styela rustica* (Ascidiae). *Russian Journal of Marine Biology* **34**(3), 170–173. https://doi.org/10.1134/S106307400803005X.

Knight-Jones EW, Bailey JH and Isaac MJ (1971) Choice of algae by larvae of *Spirorbis*, particularly of *Spirorbis spirorbis*. In Crisp DJ (ed.), *Fourth European Marine Biology Symposium. European Marine Biology Symposia, 4*. London: Cambridge University Press, pp. 89–104.

Marsh JA (1970) Primary productivity of reef-building calcareous red algae. *Ecology* **51**, 255–263. https://doi.org/10.2307/1933661.

McKinney FK and McKinney MJ (1993) Larval behaviour and choice of settlement site: correlation with environmental distribution pattern in an erect bryozoan. *Facies* **29**(1), 119–131. https://doi.org/10.1007/BF02536924.

Mizrahi D, Navarrete SA and Flores AAV (2014) Uneven abundance of the invasive sun coral over habitat patches of different orientation: an outcome of larval or later benthic processes? *Journal of Experimental Marine Biology and Ecology* **452**, 22–30. https://doi.org/10.1016/j.jembe.2013.11.013.

Monteiro SM, Chapman MG and Underwood AJ (2002) Patches of the ascidian *Pyura stolonifera* (Heller, 1878): structure of habitat and associated intertidal assemblages. *Journal of Experimental Marine Biology and Ecology* **270**, 171–189. https://doi.org/10.1016/S0022-0981(02)00020-5.

Moore PG (1977) Inorganic particulate suspensions in the sea and their effects on marine animals. *Oceanography and Marine Biology Annual Review* **15**, 225–363.

Naranjo SA, Carballo JL and Garcia-Gomez JC (1996) Effects of environmental stress on ascidian populations in Algeciras Bay (southern Spain). Possible marine bioindicators? *Marine Ecology Progress Series* **144**, 119–131. https://doi.org/10.3354/meps144119.

Ricardo GF, Jones RJ, Nordborg M and Negri AP (2017) Settlement patterns of the coral *Acropora millepora* on sediment-laden surfaces. *Science of the Total Environment* **609**, 277–288. https://doi.org/10.1016/j.scitotenv.2017.07.153.

Rittschof D and Costlow JD (1989) Bryozoan and barnacle settlement in relation to initial surface wettability: a comparison of laboratory and field studies. *Scientia Marina* **53**(2-3), 411–416.

Ryland JS (1962) The association between Polyzoa and algal substrata. *Journal of Animal Ecology* **31**(2), 331–338. https://doi.org/10.2307/2145.

Sakai D, Sensui N and Hirose E (2024) Ascidian larvae discriminate nanoscale difference in surface structures during substrate selection for settlement. *Zoological Science* **41**(6), 564–569. https://doi.org/10.2108/zs240066.

Scardino A, de Nys R, Ison O, O'Connor W and Steinberg P (2003) Microtopography and antifouling properties of the shell surface of the bivalve molluscs *Mytilus galloprovincialis* and *Pinctada imbricata*. *Biofouling* **19**, 221–230. https://doi.org/10.1080/0892701021000057882.

Sensui N and Hirose E (2025) Ascidian larvae prefer hydrophobic substrates for settlement. *Zoological Science* **42**(5), 478–483. https://doi.org/10.2108/zs250022.

StatSoft, Inc. (2008) *Statistica for Windows (Data Analysis Software System), Version 8.0. Computer Program Manual, Quick Reference* Tulsa, OK: StatSoft, Inc.

Svane I and Young CM (1989) The ecology and behaviour of ascidian larvae. *Oceanography and Marine Biology Annual Review* **27**, 45–90.

Te FT (1992) Response to higher sediment loads by *Pocillopora damicornis* planulae. *Coral Reefs* **11**(3), 131–134. https://doi.org/10.1007/BF00255466.

Thomsen MS, Hildebrand T, South PM, Foster T, Siciliano A, Oldach E and Schiel DR (2016) A sixth-level habitat cascade increases biodiversity in an intertidal estuary. *Ecology and Evolution* **6**, 8291–8303. https://doi.org/10.1002/ece3.2499.

Underwood AJ and Keough MJ (2001) Supply-side ecology: the nature and consequences of variations in recruitment of intertidal organisms. In Bertness MD, Gaines SD and Hay ME (eds), *Marine Community Ecology*. Sunderland, MA: Sinauer Associates, 183–200.

Walters LJ and Wethey DS (1991) Settlement, refuges, and adult body form in colonial marine invertebrates: a field experiment. *The Biological Bulletin* **180**, 112–118. https://doi.org/10.2307/1542434.

Walters LJ and Wethey DS (1996) Settlement and early post-settlement survival of sessile marine invertebrates on topographically complex surfaces: the importance of refuge dimensions and adult morphology. *Marine Ecology Progress Series* **137**, 161–171. https://doi.org/10.3354/meps137161.

Whalan S, Abdul Wahab MA, Sprungala S, Poole AJ and de Nys R (2015) Larval settlement: the role of surface topography for sessile coral reef invertebrates. *PLoS One* **10**(2), e0117675. https://doi.org/10.1371/journal.pone.0117675.

Whitlatch RB and Osman RW (2009) Post-settlement predation on ascidian recruits: predator responses to changing prey density. *Aquatic Invasions* **4**(1), 121–131. https://doi.org/10.3391/ai.2009.4.1.13.

Yakovis E and Artemieva A (2017) Cockles, barnacles and ascidians compose a subtidal facilitation cascade with multiple hierarchical levels of foundation species. *Scientific Reports* **7**, 237. https://doi.org/10.1038/s41598-017-00260-2.

Yakovis E and Artemieva A (2019) Epibenthic predators control mobile macrofauna associated with a foundation species in a sub-Arctic subtidal community. *Ecology and Evolution* **9**, 10499–10512. https://doi.org/10.1002/ece3.5570.

Yakovis E and Artemieva A (2021) Effects of a trophic cascade on a multi-level facilitation cascade. *Journal of Animal Ecology* **90**, 2462–2470. https://doi.org/10.1111/1365-2656.13558.

Yakovis EL, Artemieva AV, Fokin MV, Grishankov AV and Shunatova NN (2005) Patches of barnacles and ascidians in soft bottoms: associated motile fauna in relation to the surrounding assemblage. *Journal of Experimental Marine Biology and Ecology* **327**(2), 210–224. https://doi.org/10.1016/j.jembe.2005.06.015.

Yakovis EL, Artemieva AV, Shunatova NN and Varfolomeeva MA (2008) Multiple foundation species shape benthic habitat islands. *Oecologia* **155**(4), 785–795. https://doi.org/10.1007/s00442-007-0945-2.

Yershov P and Khaitov V (2024) Long-term variations in the diet composition of Atlantic wolffish, *Anarhichas lupus marisalbi* (Zoarcoidei: Anarhichadidae), in Kandalaksha Bay, White Sea. Proceedings ZIN, **328**(4), 555–570. https://doi.org/10.31610/trudyzin/2024.328.4.555

Young CM and Chia F-S (1984) Microhabitat-associated variability in survival and growth of subtidal solitary ascidians during the first 21 days after settlement. *Marine Biology* **81**(1), 61–68. https://doi.org/10.1007/BF00397626.

Young CM and Gotelli NJ (1988) Larval predation by barnacles: effects on patch colonization in a shallow subtidal community. *Ecology* **69**(3), 624–634. https://doi.org/10.2307/1941011.

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