Substrate exploitation and resistance to biotic disturbance in the brachiopod *Terebratalia transversa* and the bivalve *Pododesmus macrochisma*

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ABSTRACT: To test the hypothesis that epifaunal bivalves are more resistant to biotic disturbance than brachiopods, I evaluated abundances and body size of the brachiopod *Terebratalia transversa* and the anomiid bivalve *Pododesmus macrochisma*, which co-occur in the San Juan Islands (Washington State, USA, eastern Pacific). The proportion of bare space correlated with intensity of biotic disturbance had negative effects and surface rugosity had positive effects on abundance of *T. transversa*. Both rugophilic settlement and post-settlement mortality of juveniles due to biotic disturbance restrict *T. transversa* to crevices and complex substrates formed by solitary ascidians and giant barnacles. Its juveniles are under-represented on flat substrates, implying lower survivorship than in crevices, where juveniles are common. Abundance of the byssally-cemented bivalve *P. macrochisma* is negatively affected by rugosity and does not decrease with increasing bare space. *P. macrochisma* size patterns do not differ between crevices and flat substrates. Flat valves and high post-settlement mobility probably increase its juvenile survivorship under grazing pressure. *T. transversa* is not able to re-attach after settlement and is thus less resistant to grazing effects than *P. macrochisma*. This study supports the hypothesis that brachiopods are more negatively affected by biotic disturbance than epibyssate bivalves. Although brachiopods can be less preyed upon by carnivorous predators than epibyssate bivalves, *T. transversa* is affected more negatively by grazing than *P. macrochisma*. The evolutionary decline of brachiopod abundance in shallow habitats may represent responses to a heavy pressure on juveniles by grazers that evolved during the Mesozoic.

KEY WORDS: Bivalve mollusk · Brachiopod · Disturbance · Grazing impact · Substratum · Subtidal marine macrobenthos

INTRODUCTION

Although some brachiopods from temperate and polar regions occupy open, non-cryptic substrates (Noble et al. 1976, Grange et al. 1981), present-day habitats usually harbor small-sized brachiopods that are restricted to cryptic environments (Logan 1975). The restriction of brachiopods to safe places or refuges in modern hard-bottom habitats is generally ascribed either to high carnivorous predation pressure (Harper & Wharton 2000, Aberhan et al. 2006, Gili et al. 2006), or to high competition pressure, owing to the evolution of mollusks and

other groups with superior abilities to compete for space and food (Thayer 1985, Bush et al. 2007, Novack-Gottshall 2007). The survivorship of brachiopods in present-day habitats thus may depend on abundance of prey and competitive refuges, which generally correlates with substrate complexity (Hixon & Menge 1991), and on efficiency in resource utilization and resistance to consumer pressure (Peck 1996, Peck et al. 2005). However, the terebratulid brachiopod *Terebratalia transversa*, which is a relatively common inhabitant of shallow, cool-temperate, rocky bottom habitats of the San Juan Islands (Washington State, USA, eastern Pacific), is

rarely preyed on. Sea stars, crabs, and predatory gastropods occupying either intertidal or subtidal habitats of the San Juan Islands consistently prefer mussels over *T. transversa* and this species can be partly unpalatable due to its toxic tissue (Mauzey et al. 1968, Thayer 1985). This brachiopod does co-occur with the epibyssate bivalve *Pododesmus macrochisma*, which is commonly attacked by predatory gastropods, sea stars and other predators (Mauzey et al. 1968, Spight et al. 1974, Schmitt 1987). Higher drilling frequencies of bivalves than brachiopods in past and present-day non-cryptic environments (Hoffmeister et al. 2004, Simões et al. 2007) also imply low predation pressure on brachiopods and counteract the hypothesis of negative effects of escalation on brachiopod ecology (Kowalewski et al. 2005, but see Leighton 1999).

However, it was hypothesized that grazing on juveniles and small-sized individuals rather than predation on adults can have negative effects on brachiopod ecology. High consumer pressure can still limit *Terebratalia transversa* (and brachiopods in other environments), due to negative effects of unselective grazing or its bulldozing side-effects. Vermeij (1977) has suggested that brachiopods are more negatively affected by grazing than epifaunal bivalves and Asgaard & Stentoft (1984) suggested that the restriction of micromorphic brachiopods to crevices and cryptic habitats can be related to the high grazing pressure in shallow environments (see also Asgaard & Bromley 1991). In addition, it also has been suggested that abundance of the large-sized brachiopod *Terebratulina septentrionalis* is negatively affected by incidental effects of strong grazing pressure (Noble et al. 1976, Witman & Cooper 1983, Logan et al. 1984, Collins 1991). This grazing hypothesis remains unexplored for brachiopods and epifaunal bivalves that co-occur within one habitat, and for large-sized brachiopods other than *T. septentrionalis* that live in different habitats. Therefore, in order to compare effects of grazing disturbance on abundance of the large-sized brachiopod *T. transversa* and co-occurring sessile epifauna, in this study I analyzed hard-bottom epifaunal communities of the San Juan Islands.

First, I evaluated whether abundance of *Terebratalia transversa* is more negatively affected by biotic disturbance (measured as proportion of bare space and coralline crusts) and more positively affected by the availability of crevices than abundance of the epibyssate bivalve *Pododesmus macrochisma*. Second, I assessed differences in responses to surface rugosity between juveniles and adults because grazing effects should preferentially affect juvenile and small-sized individuals (i.e. large-sized individuals can achieve refuge when they become less vulnerable to grazing).

Terebratalia transversa and the anomiid bivalve *Pododesmus macrochisma* are the most common representatives of brachiopods and sessile bivalves in hard-bottom habitats of the San Juan Islands. Manipulative experiments and observations have shown that brachiopods either do not settle on settlement panels, or are the last to colonize (Thayer 1977). Therefore, a non-manipulative approach based on measurements of percent cover and density of *T. transversa* and *P. macrochisma* sampled in natural substrates varying in surface rugosity and bare space was used here.

MATERIALS AND METHODS

Field sites and data. *Terebratalia transversa* mainly occupies rocky subtidal habitats exceeding 20 m in depth in the San Juan Islands and is less common on downward-facing surfaces of boulders and cobbles, and on vertical rock walls in intertidal habitats (Thayer 1977). The slope topography of San Juan Channel was substantially shaped by glaciers and is thus characterized by highly uneven topography with high substrate complexity, steep, rocky slopes, and large boulders. Habitats were subdivided here into 2 zones according to the presence of red algae. Shallow subtidal habitats included rocky bottoms with abundant foliose, fleshy and filamentous red algae, coralline red algae, and bryozoans. Deep subtidal habitats were characterized by rocky bottoms with hydroids, barnacles, ascidians, bryozoans, mollusks, and brachiopods.

In this study, rocky substrates larger than 25 cm^2 were sampled in: (1) intertidal and shallow subtidal habitats (<20 m in depth) of Mitchell Bay and Mosquito Pass (MB/MP) on the NW margin of San Juan Island, and (2) deep subtidal habitats of San Juan Channel (SJC, between 20 and 110 m in depth, Fig. 1). Intertidal habitats were sampled on a cobble beach in Mitchell Bay (MB1) in an approximately 100 cm thick zone near mean lower low water (MLLW). Rock wall surfaces reaching 100 cm^2 in area were photographed in the field. Undersides and upper sides of boulders and cobbles that were collected from meter-scale crevices under cliff walls were photographed separately when placed in a flow tank in the laboratory.

Small rocks (mainly cobbles) from subtidal habitats were sampled by a dredge at 7 sites. At least 20 rocks per site, with a surface area exceeding 25 cm^2, were randomly selected from the dredge and placed in a bucket filled with seawater (mean = 48 cm^2, maximum = 150 cm^2). An upper side of each rock was photographed in the laboratory after it was placed in a flow tank. The dredged rocks were sampled within 1 depth along a 50 to 100 m transect parallel to shore. Shallow subtidal habitats were represented by
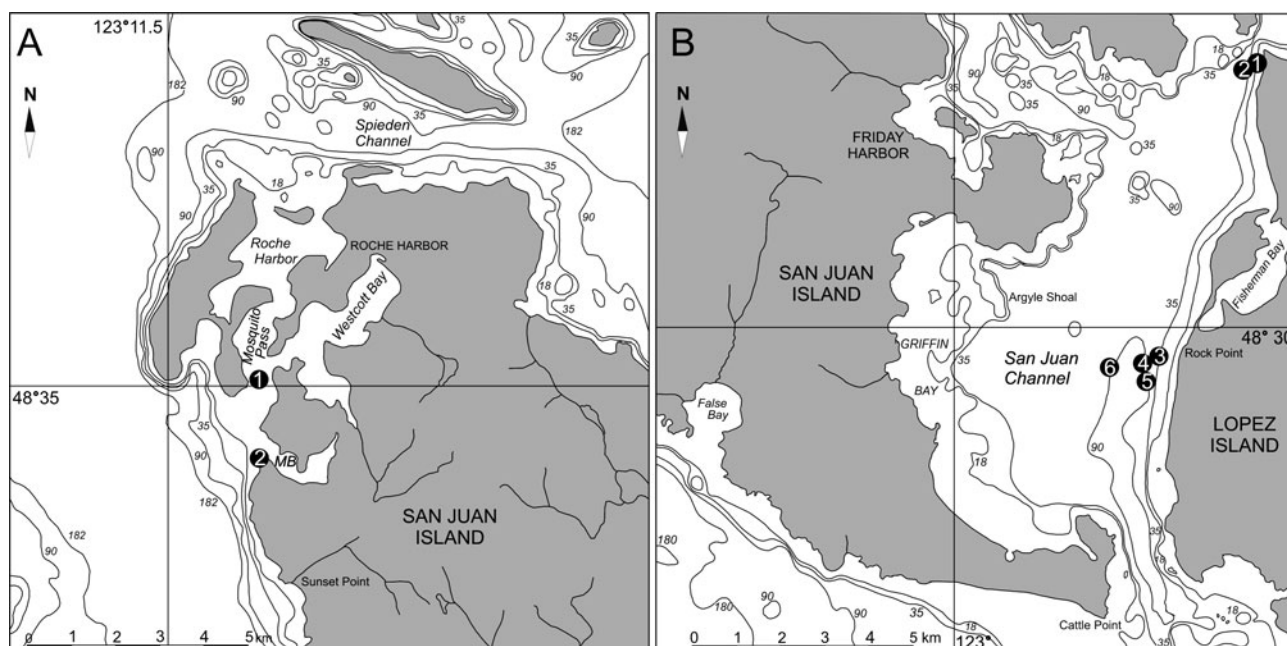
Fig. 1. Geographic location of (A) 2 sampling sites in intertidal and shallow subtidal habitats in Mosquito Pass (1) and Mitchell Bay (MB; 2), and (B) 6 sampling sites in deep subtidal habitats of San Juan Channel (San Juan Islands, Washington, USA)

1 dredged site (MB2, 13 to 17 m in depth) in the Mosquito Pass on the northern margin of the San Juan Island (Fig. 1A). Boulders and cobbles were dominated by coralline red algae, non-coralline red algae and sheet bryozoans associated with dense populations of the sea urchin *Strongylocentrotus franciscanus*. Small rocks from deep subtidal habitats were sampled by dredge at 6 sites on the eastern side of San Juan Channel along the western margin of Lopez Island (Fig. 1B). The sites SJ1 and SJ2 represented the shallowest sampled sites (22 and 46 m in depth), and small rocks were mainly occupied by *Pododesmus macrochisma* and small-sized barnacles *Balanus balanus* and *Balanus rostratus*. *Terebratalia transversa* was absent. The sites SJ3, SJ4 and SJ5 represented a bathymetric transect along a steep topographic slope near the Rock Point (50, 73 and 75 m in depth). Small rocks were dominated by small-sized barnacles, solitary ascidians, *P. macrochisma*, the suspension-feeding gastropod *Calyptraea fastigiata*, the blind limpet *Cryptobranchia concentrica*, and the brachiopod *T. transversa*. The deepest site sampled near the Rock Point (SJ6, 110 m in depth) was almost exclusively dominated by the giant acorn barnacle *B. nubilus*, commonly colonized by *T. transversa*. The sea urchin *Strongylocentrotus droebachiensis* is very abundant in deep subtidal habitats of San Juan Channel.

The population density of *Terebratalia transversa* and *Pododesmus macrochisma* was estimated by counting the number of individuals per 25 cm^2. Percent cover of encrusters, proportion of bare space and

coralline crusts, and surface covered by biofilms were estimated on digitized rocks with the ImageJ software. The percent cover of encrusters was estimated by drawing an outline along each organism and computing its enclosed area up to nearest 0.1 cm^2. The percent cover of all encrusters can exceed 100% because small-sized encrusters commonly coated other taxa attached to small rocks. The proportion of bare space was estimated by outlining bare rock. The mean of the area surveyed per site was 2100 cm^2, with a range of 620 to 3600 cm^2.

Percent cover of each of 28 sessile groups was estimated from photographs. These included the barnacles *Balanus balanus*, *B. rostratus,* and *B. nubilus*, the anomiid bivalve *Pododesmus macrochisma*, the vermetid gastropod *Petaloconchus* sp., the brachiopod *Terebratalia transversa*, sheet bryozoans, and 2 erect bryozoans (*Dendrobeania* sp. and 1 undetermined taxon, excluding the canopy-forming erect bryozoan *Bugula stolonifera*), 6 encrusting sponges (*Halichondria* sp., *Ophlitaspongia* sp., and 4 undetermined taxa), sabellariid, chaetopterid, serpulid, and spirorbid polychaetes, solitary and compound ascidians (*Pyura haustor*, *Boltenia villosa*, *Didemnum* sp., *Diplosoma* sp., *Chelyosoma* sp., *Metandrocarpa* sp.), 2 coral taxa, non-coralline and coralline red algae, and green algae.

Substrates without rugosity were characterized by flat or low-relief rocks lacking crevices (5 to 10 mm in depth). Substrates with rugosity were characterized by presence of cm-scale crevices (rocky irregularities and

aggregations of polychaetes, ascidians, and barnacles), with crevices attaining 5 to 10 mm in depth and diameter and with inter-crevice distance less than 10 to 20 mm. The proportion of bare space and of crusts of coralline red algae represents an indirect correlative measure of disturbance (see 'Discussion'). The bare space was treated as a continuous variable in generalized linear models (GLM) and as a categorical variable in multivariate analyses. Substrates were divided into 2 groups with less than or greater than 40% bare space. Attachment sites of *Terebratalia transversa* and *Pododesmus macrochisma*, their rugosity (i.e. a flat surface, or a crevice exceeding 5 mm in depth), and valve lengths of *T. transversa* and *P. macrochisma* individuals were recorded on small rocks dredged in deep subtidal habitats. Therefore, analyses of size patterns of *P. macrochisma* and *T. transversa* were restricted to the subset of samples and did not incorporate intertidal and shallow subtidal habitats.

Data analysis. Univariate and multivariate analyses were performed at 2 spatial extents, within 3 habitats, including (1) intertidal and shallow subtidal rocks, (2) intertidal and shallow subtidal rock walls, and (3) deep subtidal rocks; and within 5 sites nested within the deep subtidal habitat. Abundance data of *Terebratalia transversa* and *Pododesmus macrochisma* were analyzed as densities in univariate analyses. In multivariate analyses, abundance data were represented by percent covers of encrusters because sessile taxa are represented by solitary and colonial groups.

GLM less prone to assumptions of linear regression models were used to assess effects of rugosity and bare space on density of *Terebratalia transversa* and *Pododesmus macrochisma* within habitats and within deep subtidal sites. I evaluated whether 1 predictor variable (e.g. rugosity) did not explain any of the variation in abundance, beyond the variation explained by the second predictor variable (e.g. bare space). GLM are based here on the log link function (describing how the mean of the density depends on the predictor variable) and the quasi-Poisson variance function (describing how the variance of the density depends on its mean), which assumes that dispersion of individuals is not random (Kindt & Coe 2005). To assess relative predictive power of rugosity and bare space, their slopes (normalized to *Z*-scores to account for their different magnitude and dispersion) were compared within habitats and within sites. The amount of total deviance explained by GLM is comparable to the R^2 of a standard linear regression. GLM evaluating effects of rugosity and bare space on *T. transversa* and *P. macrochisma* used density as the response variable.

Univariate analyses based on means with 95% bootstrapped confidence intervals were used to evaluate: (1) whether percent cover of *Terebratalia transversa* and *Pododesmus macrochisma* differs between substrates with and without rugosity under constant proportion of bare space, and between substrates with low and high bare space under constant rugosity; and (2) whether *T. transversa* and *P. macrochisma* differ in size between crevices and flat surfaces.

To evaluate differences in overall community composition between substrates differing in the rugosity and bare space within 3 habitats and within 6 sites, I analyzed similarities (2-way analysis of similarities, ANOSIM) based on the Bray-Curtis coefficient. Percent covers of *Pyura haustor* and *Balanus nubilus* were removed from analyses evaluating effects of rugosity. In addition, non-metric multidimensional scaling (NMDS) based on Bray-Curtis similarities was used to examine differences in community composition and relationships between percent covers of encrusters within deep subtidal sites. I adopted the approach of Oksanen et al. (2005) to resolve the indeterminacy of scaling and orientation of axes in NMDS and to ordinate sample and taxon scores into 2-dimensional space. Two-way ANOSIM was performed with PRIMER software (Clarke & Warwick 2001), and GLM and NMDS with the R-language (R Development Core Team 2007).

RESULTS

Univariate analyses

In intertidal and shallow subtidal habitats, the effects of rugosity on *Terebratalia transversa* density were significantly positive both on small rocks and on rock walls (Table 1). The effects of bare space on *T. transversa* density were insignificant on small rocks and on rock walls (Fig. 2A,B, Table 1). The proportion of bare space had significantly positive effects on density of *Pododesmus macrochisma* in intertidal and shallow subtidal habitats with rock walls, and insignificant effects on small rocks (Fig. 2D,E, Table 1), and the effects of rugosity on *P. macrochisma* density were insignificant. In deep subtidal habitats, *T. transversa* decreased significantly in density with increasing bare space and with decreasing rugosity (Table 1, Fig. 2C). In contrast to *T. transversa*, the density of *P. macrochisma* decreased significantly with rugosity, but was not significantly affected by bare space in deep subtidal habitats (Fig. 2F).

Within-site effects of bare space on density of *Terebratalia transversa* were significantly negative in 2 deep subtidal sites (Table 1). The effects of rugosity were significantly positive in 2 deep subtidal sites. Within-site effects of bare space on density of *Pododesmus macrochisma* were highly variable but mostly

insignificant in 5 deep subtidal sites (Table 1). Although bare space decreases on topographically complex substrates, univariate analyses indicate that both bare space and rugosity had unique effects on density of *T. transversa* and *P. macrochisma,* and that *T. transversa* and *P. macrochisma* had different responses to rugosity and bare space.

Multivariate analyses

Two-way ANOSIM showed that the overall community structure was affected by between-substrate differences in rugosity and bare space (Table 2). *Terebratalia transversa* co-occurred with non-coralline red algae, the bryozoan *Dendrobeania* sp., and chae-

Table 1. *Terebratalia transversa, Pododesmus macrochisma.* Generalized linear models evaluating effects of rugosity and bare space on density at 2 spatial extents: within habitats and sites. Note that these within-site analyses were restricted to a subset of sites because sites SJ1 and SJ2 do not contain *T. transversa,* and site SJ6 is invariably characterized by presence of rugose substrates with dominance of *Balanus nubilus.* Slope values in bold correspond to significant results after Bonferroni correction

|	Explained deviance	Slope	SE	*t*	p
HABITAT					
Terebratalia transversa					
Intertidal - shallow subtidal walls	0.37				
Rugosity		**1.41**	0.31	4.48	<0.0001
Bare space		0.0002	0.2	0.001	0.99
Intertidal - shallow subtidal rocks	0.27				
Rugosity		**0.88**	0.34	2.58	0.012
Bare space		−0.4	0.29	−1.37	0.17
Deep subtidal rocks	0.33				
Rugosity		**0.87**	0.2	4.45	<0.0001
Bare space		**−0.82**	0.19	−4.35	<0.0001
Pododesmus macrochisma					
Intertidal - shallow subtidal walls	0.55				
Rugosity		−0.27	0.16	−1.71	0.09
Bare space		**0.67**	0.09	7.22	<0.0001
Intertidal - shallow subtidal rocks	0.09				
Rugosity		−0.36	0.22	−1.66	0.1
Bare space		0.28	0.17	−1.7	0.1
Deep subtidal rocks	0.03				
Rugosity		**−0.26**	0.1	−2.6	0.0099
Bare space		−0.07	0.12	−0.57	0.57
SITE					
Terebratalia transversa					
Site SJ3	0.18				
Rugosity		0.26	0.35	0.74	0.46
Bare space		−0.7	0.36	−1.93	0.061
Site SJ4	0.46				
Rugosity		**1.9**	0.69	2.74	0.008
Bare space		**−1.07**	0.38	−2.8	0.007
Site SJ5	0.41				
Rugosity		**0.99**	0.27	3.72	0.00045
Bare space		−0.73	0.36	−2.03	0.047
Pododesmus macrochisma					
Site SJ1	0.005				
Rugosity		0.02	0.17	0.09	0.93
Bare space		−0.06	0.2	−0.32	0.75
Site SJ2	0.009				
Rugosity		−0.17	0.55	−0.3	0.77
Bare space		−0.11	0.44	−0.25	0.81
Site SJ3	0.02				
Rugosity		0.09	0.22	0.41	0.68
Bare space		0.18	0.22	0.8	0.43
Site SJ4	0.2				
Rugosity		**−0.51**	0.15	−3.5	0.0009
Bare space		0.11	0.2	0.53	0.6
Site SJ5	0.18				
Rugosity		−0.33	0.3	−1.09	0.28
Bare space		−1.14	0.5	−2.29	0.026
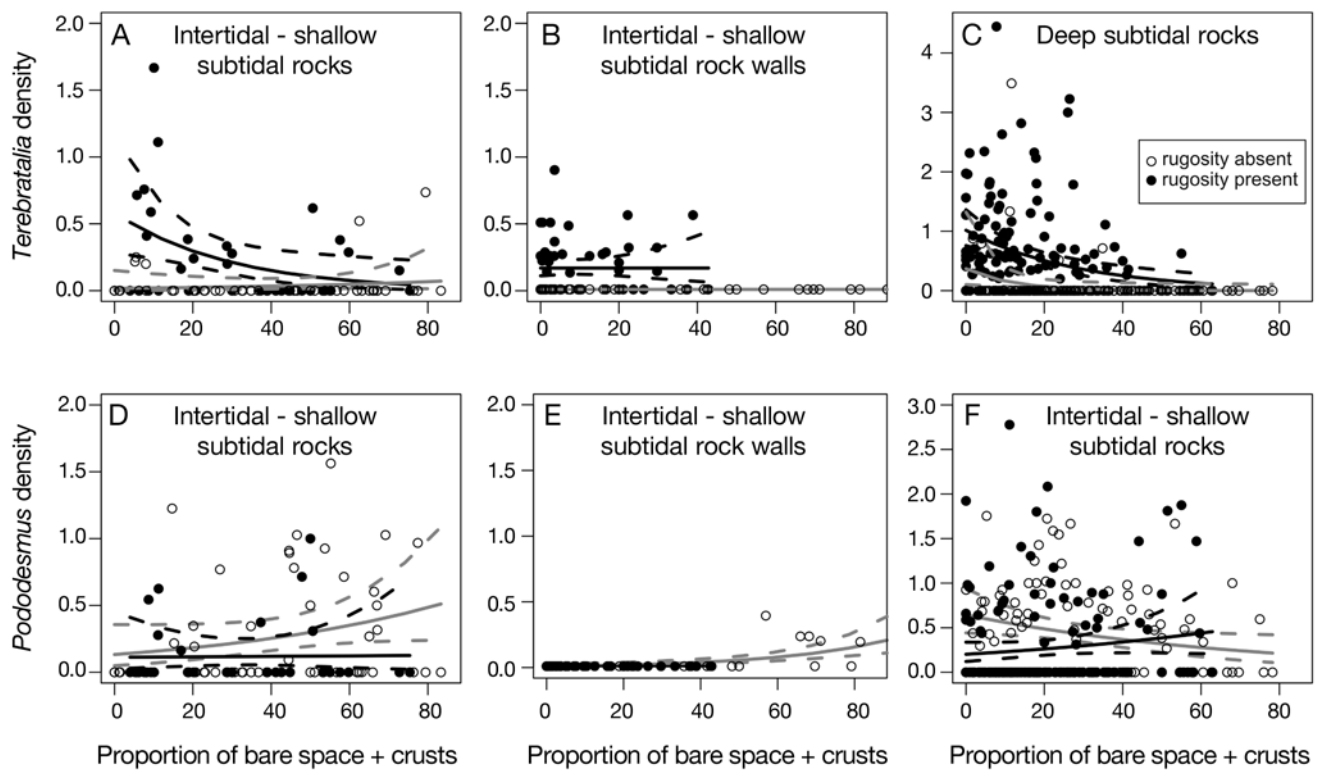
Fig. 2. (A–C) *Terebratalia transversa*, (D–F) *Pododesmus macrochisma.* Predicted slopes and 95% confidence intervals of the relationship between density (ind. per 25 cm^2) and bare space within 3 habitats, based on generalized linear models with the log link and the quasi-Poisson variance function. *T. transversa* generally declines in abundance with increasing bare space. Grey slopes correspond to substrates without rugosity and black slopes represent substrates with rugosity

topterids on rock walls with rugosity in intertidal habitats. Small-sized barnacles, sheet bryozoans, sponges, and *Pododesmus macrochisma* inhabited rock walls without rugosity and higher bare space (Fig. 3A,B). In intertidal and shallow subtidal habitats, *T. transversa* co-occurred mainly with sponges, the ascidian *Didemnum* sp., the bryozoan *Dendrobeania* sp., sheet bryozoans, and spirorbids on small rocks

with rugosity and low bare space in intertidal and shallow-subtidal habitats. Non-coralline red algae, chaetopterids, serpulids, and *P. macrochisma* attained the highest percent cover on small rocks with low rugosity and high bare space (Fig. 3C,D). In deep subtidal habitats, topographically complex substrates were mainly formed by solitary ascidians and giant barnacles that commonly surrounded *T. transversa* (Figs. 3E,F & 4A,B). In contrast, flat surfaces characterized by higher bare space were dominated by *P. macrochisma* and small-sized barnacles (Figs. 3E,F & 4C,D).

Two-way ANOSIM and NMDS of deep subtidal sites also demonstrated consistent within-site differences in community composition between substrates differing in rugosity and bare space (Table 2, Fig. 5). NMDS plots showed that *Terebratalia transversa* was associated with substrates with rugosity (mainly formed by *Pyura haustor* and *Balanus nubilus*) and low bare space, in contrast to *Pododesmus macrochisma*, which co-occurred mainly with small-sized barnacles and sheet bryozoans on substrates without rugosity (Fig. 5).

Table 2. Two-way analysis of similarities (ANOSIM) showing significant differences in community composition between substrates with and without rugosity, and with low and high bare space at 2 spatial extents. p-values in bold represent significant results after Bonferroni correction. p-values in italics represent results insignificant after Bonferroni correction

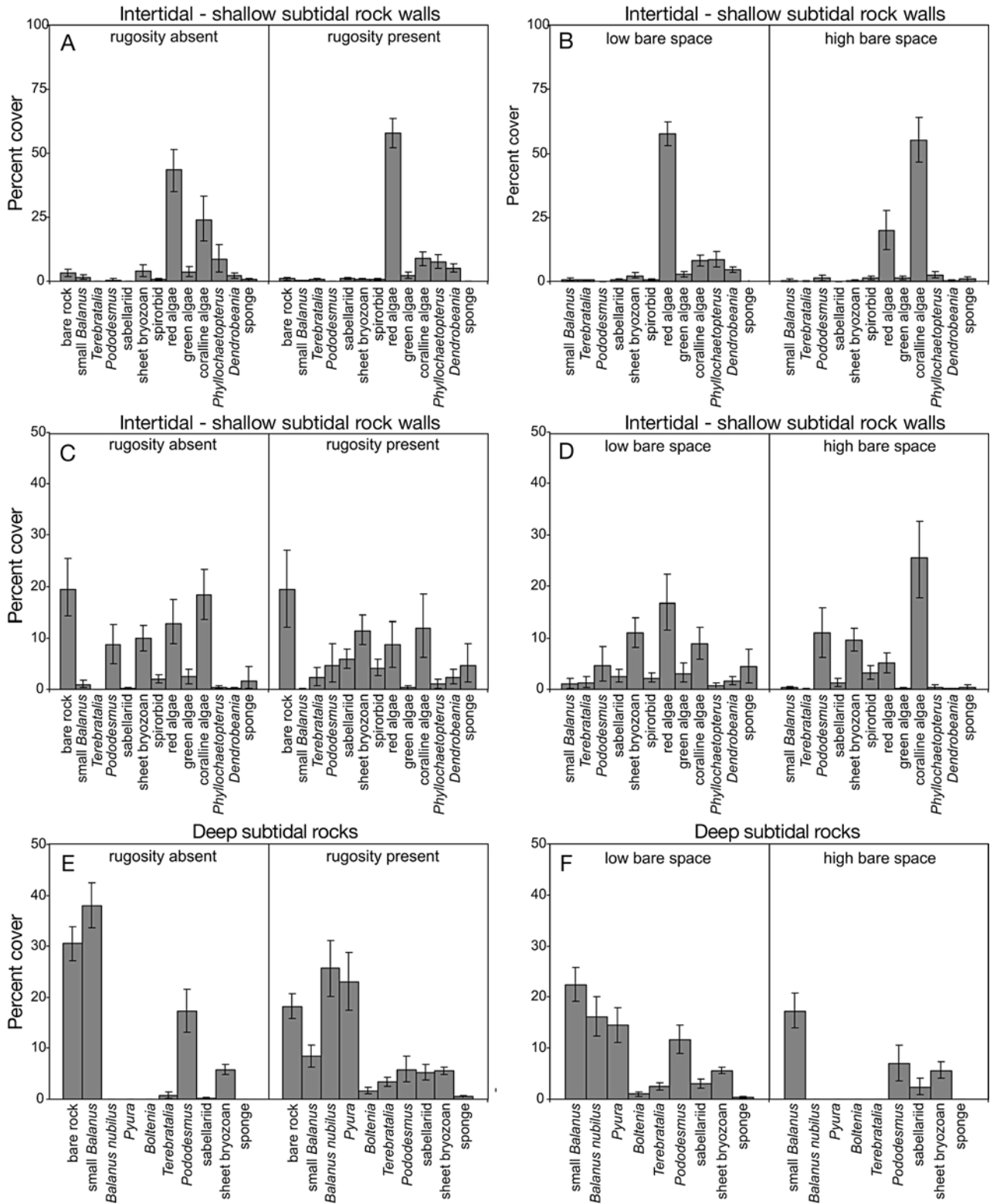| Habitat/site	Bare space ANOSIM *R*	p	Rugosity ANOSIM *R*	p
Intertidal - shallow subtidal walls	**0.42**	**0.002**	**0.15**	**0.002**
Intertidal - shallow subtidal rocks	**0.16**	**< 0.001**	**0.11**	**0.005**
Deep subtidal rocks	**0.15**	**0.001**	**0.39**	**< 0.0001**
Site SJ1	**0.42**	**0.0001**	**0.47**	**< 0.0001**
Site SJ2	*0.23*	*0.026*	*0.41*	*0.018*
Site SJ3	*0.08*	*0.21*	*0.1*	*0.05*
Site SJ4	**0.41**	**0.0073**	**0.57**	**< 0.0001**
Site SJ5	*0.23*	*0.034*	**0.51**	**< 0.0001**

Fig. 3. Differences in percent covers of sessile benthos between substrates differing in rugosity and bare space on: (A,B) intertidal and shallow subtidal rock walls, (C,D) intertidal and shallow subtidal rocks, and (E,F) deep subtidal rocks. *Terebratalia transversa* is more common on rocks with rugosity; *Balanus nubilus*, *Pyura haustor* are more common on low bare space; and *Pododesmus macrochisma* mainly co-occurs with small barnacles on rock walls and rocks without rugosity. Error bars are 95% bootstrapped confidence intervals
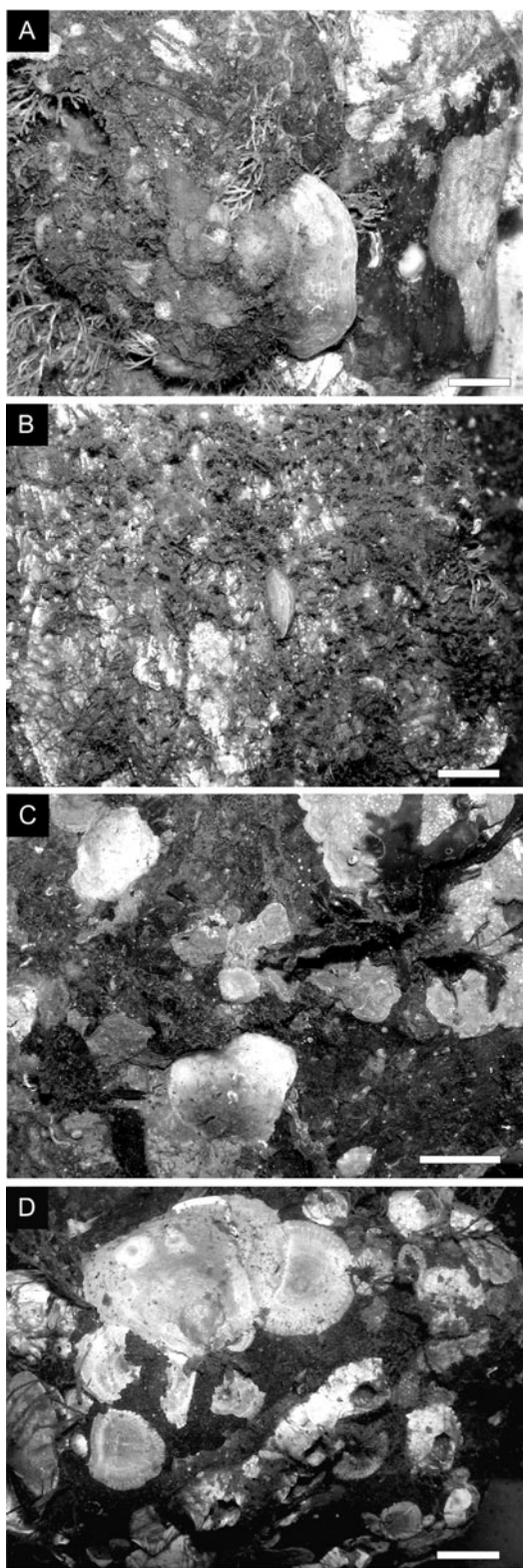
Fig. 4. (A,B) Deep subtidal rocks with rugosity formed by the ascidian *Pyura haustor* and the giant barnacle *Balanus nubilus*, and *Terebratalia transversa* inhabiting crevices, and (C,D) flat rocks with *Pododesmus macrochisma* and high bare space. Scale bars = 10 mm
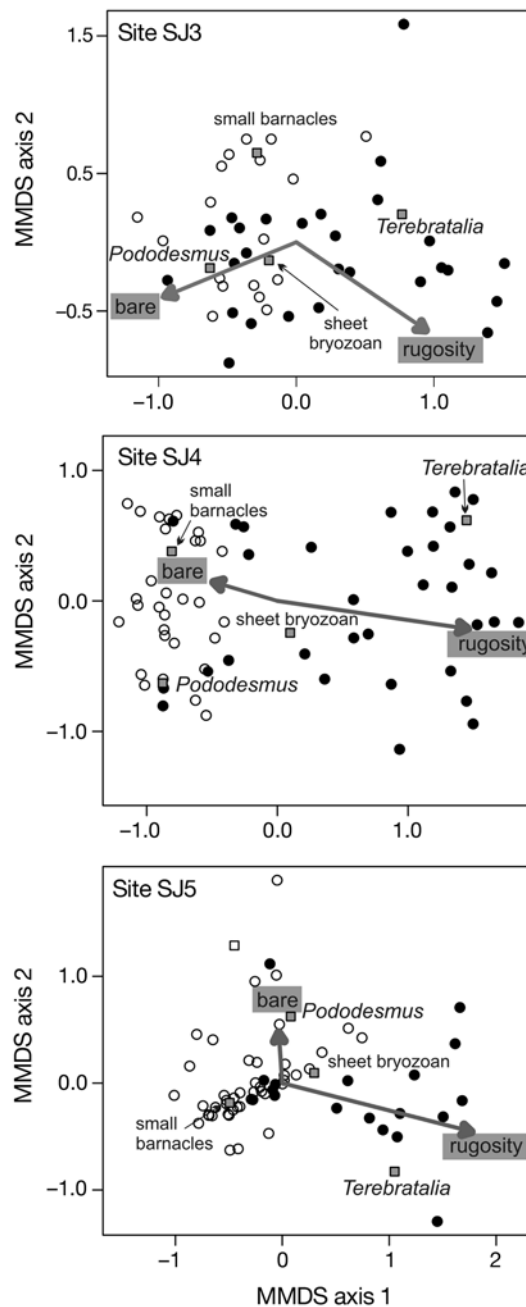

Fig. 5. Non-metric multidimensional scaling (NMDS) of 3 deep subtidal sites shows consistent differences in community composition between substrates with (●) and without rugosity (○). *Terebratalia transversa* occurs on rugose substrates with low bare space and *Pododesmus macrochisma* co-occurs with small barnacles on substrates with high bare space. Taxon scores were added to the Q-mode plot as weighted averages (▣). Vectors of rugosity and bare space were fitted into NMDS ordination with the fitting method of Oksanen et al. (2005) to approximate the direction of gradients in bare space and rugosity. The length of the vector approximates the correlation between the environmental variable and NMDS ordination. Stress values are smaller than 0.2. Note that percent covers of *Pyura haustor* and *Balanus nubilus* were not analyzed because they define surface rugosity

Size patterns

The comparisons of attachment sites and body size patterns in *Terebratalia transversa* and *Pododesmus macrochisma* were restricted to deep subtidal sites with more than 40 individuals. *T. transversa* was attached mainly to solitary ascidians (25%), sabellariid polychaetes (22%), rock surfaces (19%), giant barnacles (15%), and, less commonly, to conspecific shells (5%). *P. macrochisma* was predominantly attached to rock surfaces (90%). Based on non-overlapping 95% bootstrapped confidence intervals, *T. transversa* attained significantly lower mean shell size in crevices than on flat surfaces (Fig. 6A). Median shell size was also significantly smaller in crevices (10 to 22.4 mm) than on flat surfaces (21 to 27 mm) (Mann-Whitney *U*-test: site SJ3, p = 0.016, site SJ4, p = 0.00018, site SJ5, p = 0.014, site SJ6, p < 0.0001). Size-frequency distributions show that the larger shell size of *T. transversa* on flat surfaces than in crevices was related to higher proportion of juveniles and subadults attached to crevices (Fig. 6C). Flat surfaces were characterized by very low proportion of small-sized *T. transversa* individuals. In contrast to *T. transversa*, the median size of *P. macrochisma* was not smaller in crevices (26 to 46 mm) than on flat surfaces (22 to 39 mm, Fig. 6B).
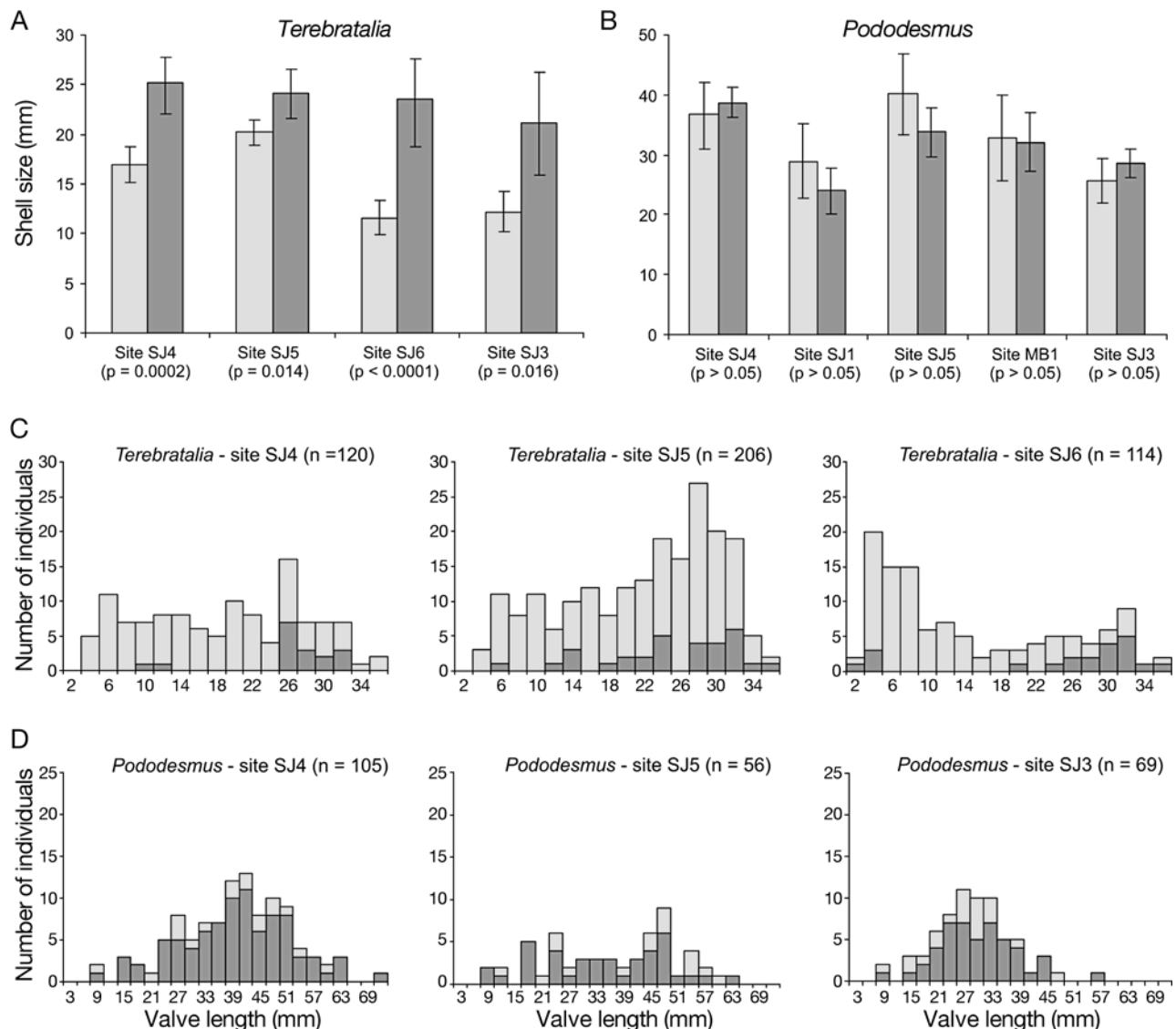

Fig. 6. (A) *Terebratalia transversa* attached to crevices (light grey bars) is consistently smaller than on flat surfaces (dark grey bars) in deep subtidal habitats. (B) Size differences between *Pododesmus macrochisma* attached to crevices and flat surfaces are insignificant. (C) Size-frequency distributions show that small-sized individuals of *T. transversa* were mainly attached to crevices (light grey bars) and rarely to flat surfaces (dark grey bars). (D) Size-frequency distributions of *P. macrochisma* do not differ between crevices and flat surfaces. p-values correspond to significance levels of Mann-Whitney *U*-test

Within deep subtidal sites, *P. macrochisma* thus did not show any consistent size differences in size-frequency distributions between substrates differing in the degree of rugosity (Fig. 6D).

DISCUSSION

Effects of rugosity and disturbance on abundance

Terebratalia transversa mainly utilized crevices within topographically complex substrates and its distribution patterns might partly be explained by varying availability of substrates with high rugosity. The substrate complexity can also decrease the biotic disturbance by inhibiting access of consumers to prey and can cause positive relationship between brachiopod abundance and substrate rugosity even when brachiopod larvae do not strongly prefer crevices as sites of settlement (Keough & Downes 1982, Holt 1984, Connell 1985, Menge et al. 1985, 1986, Petraitis 1990, Maldonado & Uriz 1998). GLM indicated that the presence of rugosity explains a significant amount of variation in abundance of *T. transversa* that is unexplained by bare space. Rugophilic settlement of *T. transversa* larvae may thus contribute to the spatial variation in the abundance of *T. transversa* and its higher abundance in crevices. Stricker & Reed (1985) found that larvae of *T. transversa* tend to settle in darkened, wrinkled regions of various substrates, showing photonegative and rugophilic behavior in a laboratory. In addition, larvae of other articulate brachiopods also exhibit selective settlement choices (Pennington et al. 1999), and, generally, photonegative and/or rugophilic behavior prior to settlement (Noble et al. 1976, Witman & Cooper 1983). In contrast to *T. transversa*, *Pododesmus macrochisma* was negatively affected by surface rugosity, implying contrasting settlement behavior and reduced ability in utilization of rugose substrates.

The proportion of bare space and of crusts of coralline red algae generally represents a measure of disturbance. The presence of crust-forming coralline red algae depends on presence of grazers that inhibit overgrowth of slow-growing crusts by fast-growing algae (Steneck et al. 1991, Sebens 1985). Bare rocks are often the consequence of the combined effects of biological and physical disturbance (Sousa 1980, Chapman 2002). In this study, within-site analyses controlled for the between-habitat variation in physical disturbance because deep subtidal sites are characterized by medium-energy conditions and the presence of muddy sediment among small rocks. In addition, low and insignificant relationships between rock size and bare space in both shallow (Spearman's rank correla-

tion coefficient, $r_S = -0.2$, p = 0.06) and deep ($r_S = -0.14$, p = 0.02) habitats suggest that the bare space (plus coralline crusts) resulted more from the intensity of biotic disturbance (i.e. predation, herbivory, and grazing) than physical disturbance (McGuinness 1987).

Controlling for the effects of rugosity in univariate and GLM analyses, *Terebratalia transversa* and *Pododesmus macrochisma* differed in response to biotic disturbance. *T. transversa* generally attained higher abundance with low bare space, suggesting that *T. transversa* was less resistant to biotic disturbance than *P. macrochisma*. Reduced abundance of *T. transversa* on rugose substrates with high bare space indicates that utilization of physical refuges such as crevices can reduce, but does not eliminate, post-settlement mortality of *T. transversa*. Even though small rocks and rock walls may provide some escape from biotic disturbance by reducing access to grazers (Sebens 1985, Knott et al. 2004, Bowden et al. 2006), substrates with crevices may still provide insufficient refuges under heavy biotic disturbance. In addition, multivariate analyses indicated that bare space positively affected abundances of other sessile taxa, such as small-sized barnacles.

The negative effects of grazers on *Terebratalia transversa* are also indicated by virtual absence of *T. transversa* on exposed intertidal and shallow subtidal substrates dominated by crusts of coralline red algae, which generally result from grazing (Lubchenco et al. 1984, Littler et al. 1995). In the San Juan Islands, both limpets and the chiton *Katharina tunicata* can exert a strong impact on community composition in intertidal habitats (Duggins & Dethier 1985, Steneck et al. 1991). Grazing by sea urchins is also one of the major causes of juvenile mortality of benthic invertebrates in subtidal habitats (Ebert 1977, Karlson 1978, Ayling 1981). The sea urchin *Strongylocentrotus droebachiensis* occurs in high abundances in deep subtidal sites of San Juan Channel and co-occurs with *T. transversa*. This species has a strong negative impact on grazing-susceptible species in the eastern Atlantic (Sebens 1985, Witman 1985, Briscoe & Sebens 1988, Lauzon-Guay & Scheibling 2007) and can be a candidate for grazing pressure on small-sized individuals of *T. transversa* in depths with rare chitons and limpets and without macroalgae.

Effects of rugosity and disturbance on size patterns

The differential response to biotic disturbance was supported by size-frequency distributions that imply differences in survivorship of juveniles of *Terebratalia transversa* and *Pododesmus macrochisma* between crevices and flat substrates. Although *T. transversa*

juveniles grow relatively rapidly (approximately 6 mm yr^{-1}), individuals larger than 10 mm are already sexually mature (Thayer 1977). The typical size of *P. macrochisma* at sexual maturity is poorly known but juveniles of other species of the genus *Pododesmus* are smaller than 20 mm (Yamaguchi 1998). Small-sized individuals of *T. transversa* were frequently under-represented on flat substrates, indicating higher juvenile mortality on flat surfaces than in crevices because juveniles and subadults on flat substrates should be more prone to grazing. Higher juvenile mortality on flat substrates thus might be caused by unselective grazing that mainly affects small-sized juvenile and subadult individuals (<10 mm) because the removal force is partly a function of the maximum cross-sectional area of the brachiopod shell and the attachment strength by pedicle partly increases with increasing pedicle diameter (Thayer 1975). Adults of *T. transversa* can become less vulnerable to grazing because individuals larger than 10 mm on flat substrates reach equally large or larger sizes than individuals attached to crevices. This supports the hypothesis that biotic disturbance is driven by grazing effects on juveniles and small-sized individuals rather than by predation on adults. However, other experiments and observations are needed to support the hypothesis that the higher abundance of large-sized brachiopods in crevices is related to effects of biotic disturbance and is not a pure consequence of rugophilic settlement preference.

Associational refuges of *Terebratalia transversa*

Although *Terebratalia transversa* generally did not dominate on substrates in terms of its percent cover, space limitation probably did not affect *T. transversa* because its abundance positively covaried with percent cover of other encrusters and its individuals were rather frequently attached to large and abundant habitat-modifiers such as *Pyura haustor* and *Balanus nubilus*. The close association of *T. transversa* with aggregations of *P. haustor* and *B. nubilus,* which form dense populations in deep subtidal habitats, indicates that the principal means of grazing avoidance in such habitats can be represented by associational refuges. *P. haustor* and *B. nubilus* are large and long-lived sessile invertebrates (Sherrard & LaBarbera 2005), and their high-density self-perpetuating aggregations can probably reduce grazing in comparison to areas where their population density is low. Juvenile solitary ascidians are negatively affected by grazing gastropods, algal overgrowth and high sedimentation, but *P. haustor* is predation- and grazing-resistant in the adult stage (Young & Chia 1984, Young 1986). Importantly,

this species provides refuge for other grazing-susceptible taxa such as the erect bryozoan *Bugula stolonifera* and the solitary ascidian *Boltenia villosa*. In subtidal habitats of the western Atlantic, *Bugula* is highly susceptible to predators and its survival is substantially enhanced in crevices (Walters 1992, Walters & Wethey 1996). *B. stolonifera* co-occurred with *T. transversa* and was commonly attached to *P. haustor* and *B. nubilus* in San Juan Channel, and was rare on substrates with high bare space. *B. villosa* was attached also almost exclusively to *P. haustor*, which possesses a thick leathery tunic with sediment inclusions and sharp microscopic spines around its siphons that provide defense mechanisms limiting the predatory snail *Fusitriton oregonensis* and other predators (Young 1985, 1986, 1989). The association of *B. villosa* with the invulnerable ascidian *P. haustor* represents an associational refuge not affected by foraging, even when its predator co-occurs in the same habitat (Young 1986). Therefore, high abundance of *T. transversa* individuals attached to *P. haustor* can also enhance its survival in predation-free sites.

Effects of juvenile ecology on distribution patterns

Although *Terebratalia transversa* can reach lower percent cover than *Pododesmus macrochisma* on rugose substrates, differences in their responses to rugosity and biotic disturbance indicate that they trade-off abilities to resist disturbance and to utilize complex substrates. In the adult stage, *T. transversa* and *P. macrochisma* have similar life habits because both are suspension feeders that feed on phytoplankton and other particles of similar size, are fixed by pedicle or calcified byssus to a firm substrate, and are unable to rotate in the adult stage (LaBarbera 1977, 1981). *T. transversa* is attached to a substrate with a pedicle that attains about 5 mm in diameter in the adult stage and does not require unlimited substrate area for attachment. *P. macrochisma* is attached to a substrate with stout, calcified byssus that forms a solid cylinder attaining about 10 mm in diameter in the adult stage. *P. macrochisma* requires a large flat area for attachment because the lower right valve has to lie flat against the substrate and the valve margins are mostly supported by the substrate to inhibit dislodgment (Bourget et al. 1994). The flat valves firmly attached to a surface along the whole attachment area can also explain its higher resistance to grazing pressure. Once dislodged from a substrate by disturbance, juvenile brachiopods are not able re-attach to their substrate and are thus very susceptible to grazing-induced post-settlement mortality. In contrast, juvenile *P. macrochisma* up to 10 mm in size can detach and

move from their substrate after early settlement (Yonge 1977, Yamaguchi 1998). This post-settlement mobility of byssally-cemented anomiids can substantially enhance their juvenile survivorship on hard substrates in comparison to brachiopods (Yamaguchi 1998).

It is possible that the differential response of pedunculate brachiopods and epibyssate mollusks to increased grazing on evolutionary time scales is related to the differences in their juvenile ecology because grazing on juveniles can represent a substantial source of abundance variations of sessile invertebrates in present-day benthic communities (Osman & Whitlatch 1995, 2004). Marine herbivores such as chitons, limpets and sea urchins, feeding on multicellular attached plants and able to excavate calcareous substrates, originated or substantially increased in abundance in hard-bottom communities during the Late Mesozoic, as did the diversity of nongeniculate coralline algae (Steneck 1983, Aguirre et al. 2000, Vermeij & Lindberg 2000). This change probably led to the increase in grazing effects that negatively affected survival of brachiopod juveniles, in contrast to epibyssate juvenile bivalves, which can move and re-attach after dislodgment. On long time scales, the escalation in grazing and bulldozing pressure on brachiopod juveniles might thus primarily contribute to brachiopod evolutionary decline in hard-bottom environments characterized by rocky boulders, metazoan reefs, and carbonate sea-floors. This is in contrast to the post-Paleozoic increase in predation pressure on adult sessile benthos that affected brachiopods only secondarily (Kowalewski et al. 2005).

CONCLUSIONS

Univariate and multivariate analyses showed that rugosity had positive effects and bare space had negative effects on abundance of the brachiopod *Terebratalia transversa*. GLM showed that both rugosity and bare space had unique effects on abundance of *T. transversa*, implying that both selective rugophilic larval settlement and post-settlement mortality owing to intense biotic disturbance restrict individuals of *T. transversa* to crevices. *T. transversa* was affected by biotic disturbance more negatively than the co-occurring epibyssate bivalve *Pododesmus macrochisma*. This supports the hypothesis that brachiopods are less resistant to biotic disturbance than epifaunal bivalves in hard-bottom habitats. Notably, although average percent covers of *T. transversa* are relatively low (<5%), its abundance increases towards structurally complex communities dominated by long-living solitary ascidians and giant barnacles.

Juveniles of *Terebratalia transversa* were underrepresented on flat substrates, implying their higher mortality there than in crevices. Adults of *T. transversa* were not larger in crevices than on flat substrates, indicating that adults became less vulnerable to disturbance. This supports the hypothesis that biotic disturbance negatively affected *T. transversa* mainly via grazing effects on juveniles and small-sized individuals. In contrast to *T. transversa*, flat valves in contact with substrate and high post-settlement mobility of *Pododesmus macrochisma* probably increased juvenile survivorship under intense biotic disturbance. *T. transversa* is not able to re-attach after larval settlement and is thus less resistant to grazing effects than the byssate bivalve *P. macrochisma*.

Although *Terebratalia transversa* is less preyed upon by carnivorous predators than *Pododesmus macrochisma*, it is affected more negatively by grazing on juveniles and small-sized individuals than *P. macrochisma*. This study thus supports the hypothesis that grazing negatively affects not only small-sized micromorphic brachiopods but also large-sized brachiopods, both in shallow and deep subtidal habitats, and thus the hypothesis that the decline in abundance of brachiopods on exposed substrates and preference of brachiopod larvae for cryptic habitats might be related to a heavy grazing pressure on juveniles in hard-bottom habitats during the Mesozoic.

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