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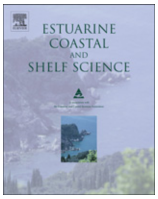

Effects of habitat structure and tidal height on epifaunal assemblages associated with macroalgae

Eva Cacabelos[a,*], Celia Olabarria[a], Mónica Incera[b], Jesús S. Troncoso[a]

[a] *Dpto. Ecoloxía e Bioloxía Animal, Facultade de Ciencias do Mar, Universidade de Vigo, Campus Lagoas-Marcosende, 36310 Vigo, Pontevedra, Spain*
[b] *Centro Tecnológico del Mar-CETMAR, Vigo, Spain*

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ABSTRACT

Patterns of distribution and abundance of epifauna often differ markedly among macroalgal species. The hypotheses tested were that (1) assemblages of mobile epifauna associated with *Laminaria ochroleuca* and *Sargassum muticum* differed because they have different structure, and (2) assemblages of mobile epifauna associated with *S. muticum* differed between heights on the shore because tidal height affects physical and biological conditions. We also investigated the effect of epiphytic biomass on the composition of epifaunal assemblages. Hypotheses were tested with measuring and manipulative experiments using natural and artificial algae, and by measuring uni- and multivariate assemblage descriptors. The results indicated that epifaunal assemblages associated with natural *L. ochroleuca* and *S. muticum* differed, but only differences in epifaunal densities were likely to be related to the structure of algae since all other variables did not clearly differ between the two algae. Although structure might play an important role, other factors need to be taken into account and further experimental tests are necessary. Epifaunal assemblages associated with *S. muticum* did vary depending on the height on the shore, but inconsistently over time in the case of natural algae. In addition, epifaunal densities of natural algae were positively related to biomass of epiphytes in both species. Time of sampling, epiphytic load and height on the shore were the most important factors in structuring epifaunal assemblages rather than complexity of the host algae.

1. Introduction

In rocky intertidal habitats, one of the most limiting resources for benthic organisms is space (Dayton, 1971). Some marine organisms, however, can act as foundation species (*sensu* Dayton, 1972), thereby increasing substrate heterogeneity and the area available for settlement. Biological substrates indeed have a major influence on the organization of shallow water communities by diversifying the spatial resources that can be used, by increasing the area available for colonisation by sessile species, and by providing refuges against predators and unfavourable environmental conditions (Monteiro et al., 2002). Previous studies have pointed out the important role that habitat-forming species can play in facilitating associated organisms (Stachowicz, 2001; Bruno et al., 2003). For example, marine macroalgae serve as both primary space holders in communities, competing for resources such as space, as well as a secondary substratum, acting as biological habitat structure (*sensu* Jones and Andrew, 1992; Chemello and Milazzo, 2002; Wikström and Kautsky, 2004) and providing suitable habitat for abundant and diverse organisms. There is evidence that different macrophytes support different assemblages of mobile epifauna (Taylor and Cole, 1994; Schreider et al., 2003; Vazquez-Luis et al., 2008), and this may be due to several biological factors such as life cycles, algal structure (*sensu* McCoy and Bell, 1991; Gee and Warwick, 1994), habitat complexity (Schreider et al., 2003), chemical defences (Wernberg et al., 2004) or physical factors (e.g. wave exposure or tidal height) (Chemello and Milazzo, 2002; Schreider et al., 2003).

Shape and structural complexity of macroalgae are important factors in determining patterns of abundance and size structure of associated epifaunal organisms. The most structurally complex algae harbour more abundant and diverse assemblages of invertebrates because among other effects, they provide a larger availability of surface for colonisation by fauna and epiphytic algae (Gee and Warwick, 1994; Chemello and Milazzo, 2002). In this context, quality and quantity of epiphytic load may play an important role by increasing the structural complexity of the habitat, determining habitat preferences for some invertebrates (Schneider and Mann, 1991; Martin-Smith, 1993; Schreider et al., 2003), and providing additional new resources (i.e. food, habitat) for invertebrates (Viejo, 1999; Jones and Thornber, 2010). Thus presence of epiphytes can influence strongly the structure of epifaunal assemblages (Attrill et al.,

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[*] Corresponding author.
E-mail address: cacabelos@uvigo.es (E. Cacabelos).

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2000). In addition, any factor related to different elevations on the shore may be also important in shaping patterns of abundance of epifaunal organisms. For example, height above sea level is important for many organisms on rocky shores, because it may affect physical conditions (e.g. desiccation levels, changes in water currents), availability of food, rate of predation or availability of recruits (Underwood, 1984; Martin-Smith, 1993; Schreider et al., 2003).

Spatial variability of epifaunal assemblages among and within habitats may be shaped by temporal variation at different scales ranging from weeks to months. Epifauna frequently undergoes strong temporal fluctuations, due to a range of physical and biological factors (e.g. Taylor, 1998; Jones and Thornber, 2010). Changes in several factors such as temperature, abundance of epiphytic algae, productivity, predation pressure, competition or recruitment are likely to influence the patterns of epifaunal abundance at different spatial and temporal scales (Taylor, 1998; Jones and Thornber, 2010).

Several papers have dealt with the role of marine macroalgae in structuring epifaunal assemblages, some of them comparing how different species of macroalgae influence the abundance, richness, and diversity of assemblages associated (e.g. Taylor and Cole, 1994; Chemello and Milazzo, 2002). Special attention has been only recently given to comparisons among native and invasive habitat-forming macroalgal species (Wernberg et al., 2004; Wikström and Kautsky, 2004; Schmidt and Scheibling, 2006; Harries et al., 2007; Vazquez-Luis et al., 2008; Gestoso et al., in press).

The semi-exposed low intertidal rocky shores of the Galician coast (north-western Spain) are generally dominated by large macroalgae such as *Laminaria ochroleuca* Bachelot de la Pylaie and *Sacchoriza polyschides* (Lightfoot) Batters (Cremades et al., 2004). Over the past decades, however, kelp beds have been progressively invaded by the invasive brown alga *Sargassum muticum* Yendo (Fensholt), forming dense stands that cover native algal species (Viejo, 1997; Sánchez and Fernández, 2005). *Laminaria ochroleuca* and *S. muticum* form dense forests and house a large number of epiphytes and associated invertebrates, and both species are currently common in the low intertidal habitat of the Galician coast, although *S. muticum* is also found in the mid intertidal area in smaller numbers.

This study focused on assemblages of mobile epifauna associated with *Laminaria ochroleuca* and *Sargassum muticum*. Both species have notable differences in structure; the invasive species being more complex than *L. ochroleuca*, with numerous secondary 3-dimensional branches coming from the primary ones (Arenas et al., 2002). In contrast, structure of *L. ochroleuca* is relatively simple (flat-blades), having long strap-like blades that are suspended above the substratum with a stipe that is firmly attached with a root-like holdfast. The stiff and upright stipes of *S. muticum* and *L. ochroleuca* also provide substrate for a number of macroalgae, being heavily colonised by filamentous algae and macrophytes in the study area. It is important to note that both species differ in various characteristics other than structural complexity, such as colour, surface texture and chemical contents of tissues. We attempted to avoid confounding any effects of these factors with influences in structure. Therefore, artificial mimics of both species were used to separate the effects of structural complexity from other characteristics intrinsic to the algae.

The main goal of this study was to analyse the composition and abundance of mobile epifaunal assemblages associated with two habitat-forming algae, *Laminaria ochroleuca* and *Sargassum muticum*. With measuring and manipulative experiments using natural and artificial algae, we tested the hypotheses that (1) epifaunal assemblages associated with *L. ochroleuca* and *S. muticum* on the low shore differed because they have different structure, and (2) epifaunal assemblages associated with *S. muticum* differed between heights on the shore because a seaweed's position may affect physical and biological conditions of associated epifauna. If this is the case, we would also expect that epifaunal assemblages associated with artificial *S. muticum* placed at two different heights on the shore would be different. In addition, we investigated the role of epiphyte loads on the composition of epifaunal assemblages associated with the two macroalgal species because differences in epiphytes load are likely to occur. Finally, we tested if patterns of abundance and composition of epifaunal assemblages associated with natural algae were consistent over time.

2. Material and methods

2.1. Study area

This study was carried out on the south region of the Galician coast (NW Spain), at mid and low heights on the shore (0.2–0.8 m above the lowest astronomical tide) of an intertidal area, Monte Lourido (42° 7′ 26″N; 8° 49′ 4″W), located on the southern shore at the entrance to Ria de Vigo. This area has rock platforms with numerous pools, and the subtidal and intertidal levels are invaded by *Sargassum muticum* (for more detailed description of the area, see Olabarria et al., 2009).

2.2. Sampling strategy

Natural *Sargassum muticum* and *Laminaria ochroleuca* algae of similar size (average fresh weights (±SE): *S. muticum* = 149.9 ± 58.9 g; *L. ochroleuca* = 87.78 ± 22.6 g, $F_{1,14} = 0.59$, $p = 0.455$) were sampled during low tide on two dates (6 May and 4 June, 2008) ($n = 4$).

Individuals of *Sargassum muticum* were collected at mid and low tidal heights on the shore, whereas individuals of *Laminaria ochroleuca* were collected at low height on the shore. Each alga including the holdfast was gently cut from the substratum with a scraper and immediately transferred into a plastic bag filled with formalin (10%). In the laboratory, mobile epifauna was washed off each alga through 0.5 mm sieves and algae were searched thoroughly for any remaining animals under binocular lens. Animals were fixed in 70% ethanol before being quantified and identified to the lowest taxonomic level feasible. In addition, epiphytes were scraped off the algae and then fixed in 70% ethanol before quantifying biomass. Dry weight of epiphytes was calculated after drying them for 48 h at 60 °C.

The density of each taxon (individuals per alga) was expressed as the number of animals per cm^2 of algal surface (Johnson and Scheibling, 1987). Surface area was estimated by submersing algae in oil of low viscosity (Johnson's Baby®). Assuming equal rates of absorption and retention of oil by algae, the surface area of each alga was proportional to the weight of oil required to cover it. Algae were bottled dry with paper towels, submersed in oil and shaken until oil stopped dripping. Then algae were weighed again, and the weight of oil calculated. Surface area was estimated using relationships between the weight of oil and the true surface area of *Sargassum muticum* and *Laminaria ochroleuca*. To calculate true surface area 10 randomly chosen individuals of each species were collected and scanned (150 dpi, HP Scanjet G4010 scanner) and then their surfaces were measured with ImageJ analysis software. The r^2 values derived from the linear regressions between surface areas and oil weights were 0.94 and 0.96 for artificial *L. ochroleuca* and *S. muticum*, and 0.99 and 0.98 for respective natural species. To evaluate the differences between the two species, the ratios weight/surface areas were calculated and analysed using one-way ANOVA. These ratios significantly differed between natural *S. muticum* and *L. ochroleuca* ($F_{1,14} = 5.39$, $p < 0.05$).

2.3. Test of hypotheses using artificial algae

Artificial units were created from brown polypropylene (Bio Models Co., USA) to mimic the natural "simple" (*Laminaria ochroleuca*) and "complex" (*Sargassum muticum*) species (Fig. 1). Algae were placed within natural mixed stands of their con-specifics and attached to the substratum with quick-drying cement (Weber.Tec Supercrono). Four "simple" algae were placed at low height on the shore and four "complex" algae were placed at two heights on the shore, mid and low level, from 28 March to 1 April. Previous studies suggested that colonisation of artificial algae by epifauna occurs within 1 month after being placed in the field (Edgar, 1991; Schreider et al., 2003), so artificial units were collected after one month, i.e. 6 May 2008. The artificial units, the associated fauna and their epiphytes were sampled using the same procedure as for natural algae. The procedure used to measure the surface of the artificial units was the same as for natural algae. In the case of these units, the ratio weight/surface differed significantly between both species ($F_{1,14} = 9.80$, $p < 0.01$).

2.4. Data analyses

2.4.1. Univariate analyses

Number of taxa, density of individuals and diversity (Shannon Wiener) of epifaunal assemblages were separately fitted to generalized linear mixed and generalized linear models using the lme and glm functions in R program, v 2.9.0 (The R Foundation for Statistical Computing, 2009). When appropriate, we fitted models using adequate error distributions and function links. Model selection was based on the protocol described by Zuur et al. (2009), with forward stepwise selection of variables based on the information-theoretic approach. Random effects were fitted by the restricted maximum likelihood method (REML), and optimal fixed structures were fitted through comparisons between nested models with the same random structure using ML estimations. Height on the shore (fixed, 2 levels, mid vs. low shore), Identity of species (fixed, 2 levels, *Sargassum muticum* vs. *Laminaria ochroleuca*) and Time (random, 2 levels, time 1 vs. time 2) were factors included in the different models. Height on the shore and Identity of species were fixed factors and Time was a random factor. Epiphytic biomass was also a covariate included in the initial models.

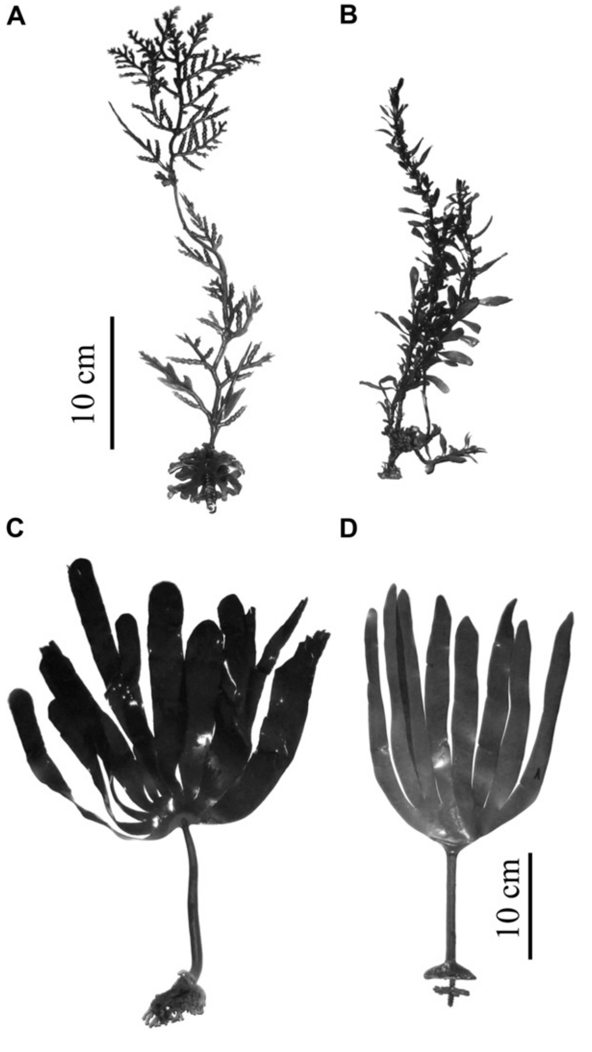

Fig. 1. Natural (b and c) and artificial (a and d) *Laminaria ochroleuca* (c and d) and *Sargassum muticum* (a and b) used in the experiments.

2.4.2. Multivariate analyses

Non-parametric permutational multivariate analysis of variance (PERMANOVA) was used to test hypotheses about differences of epifaunal assemblages. Factors were Height on the shore, Identity of species and Time (see univariate analyses). If appropriate, a posteriori multiple comparisons were used to test for differences between/within groups for pairs of levels of factors. Analyses of multivariate dispersion were also done to test for homogeneity of dispersions between Heights on the shore, Identity of algae and Time (PERMDISP, Anderson, 2004). The tests were based on 9999 unrestricted random permutations of data. In addition, responses of assemblages were visualised by non-metric multidimensional scaling (nMDS) on the basis of Bray–Curtis dissimilarity matrices on fourth-root transformed density data. The SIMPER procedure was used to identify the percentage contribution of each taxon to the Bray–Curtis dissimilarity between the averages of groups. Taxa were considered important if their contribution to percentage dissimilarity was ≥3%. Multivariate analyses were conducted using Primer v.6 and Permanova (Primer-E Ltd., Plymouth, UK).

3. Results

3.1. Epifauna associated with natural Sargassum muticum and Laminaria ochroleuca on low shore

Gastropods, malacostracans (mainly amphipods and isopods), nematodes and polychaetes accounted for more than 70% of the total number of individuals in *Sargassum muticum*, and for more than 80% in *Laminaria ochroleuca* (see Appendix for more details of fauna). Malacostracans were the dominant group in *S. muticum*, whereas polychaetes and gastropods were the dominant groups in *L. ochroleuca*. Although epiphytic biomass did not vary significantly between the two algae ($F_{1,14}$: 0.33, $p = 0.577$), it was positively related to density of epifauna. However, neither identity of algal species nor sampling time (Fig. 2) significantly affected the univariate biotic variables (see Table 1, showing only the optimal models for variables).

The composition of assemblages did vary between algal species, but this variation was inconsistent over time (PERMANOVA, Identity of species x Time, pseudo-$F_{1,12}$: 3.13, $p < 0.01$; Fig. 3a). This interaction was due to differences within algal species across sampling times (Pair-wise tests of factor Time: *Laminaria ochroleuca*: $t = 1.42$, $p(\text{MC}) = 0.106$; *Sargassum muticum*: $t = 1.78$, $p(\text{MC}) = 0.026$). There was not any heterogeneity in multivariate dispersion between algal species and times (PERMDISP, Identity of species, $F_{1,12}$: 0.125, $p(\text{perm}) = 0.76$; Time, $F_{1,12}$: 0.28, $p(\text{perm}) = 0.605$). Dissimilarity between algal species was 65%, with the

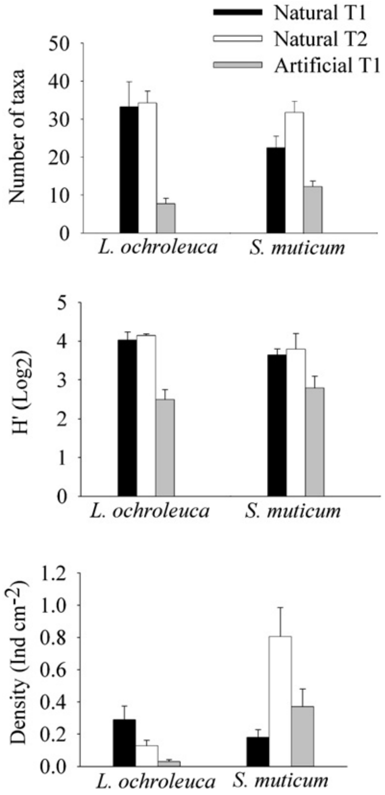

Fig. 2. Mean (+SE, $n = 4$) number of taxa, diversity (H′) and density of epifaunal assemblages associated with natural and artificial *Laminaria ochroleuca* and *Sargassum muticum* on the low shore at time 1 (=T1) and 2 (=T2). Grey bars indicate artificial *L. ochroleuca* and *S. muticum* on the low shore at time 1.

isopod *Dynamene bidentata*, the amphipod *Ampithoe* spp., insects and sabellid polychaetes being the taxa responsible for this dissimilarity (SIMPER analysis). The ophiuroid *Amphipholis squamata*, the polychaete *Platynereis dumerilii*, the gastropod *Gibbula umbilicalis* and caprellids were the most important taxa contributing to the dissimilarity between sampling times (54%, SIMPER analysis).

Table 1
Coefficients of the optimal linear mixed-effects models investigating how Identity of species, Time and Epiphytes influence diversity (H′), density (N) and number of epifaunal taxa (S) of natural *Sargassum muticum* and *Laminaria ochroleuca*. Coefficients and standard errors for fixed factors are indicated. $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$.

	Variable	MS	Value	SE	*F*	*p*-value
H′[a]	Intercept	1487.31	22.72	4.13	377.56	0.000***
	Identity of species	22.70	−4.73	2.66	1.83	0.203
	Epiphytes	3.22	-2.49×10^3	2.47×10^3	0.26	0.621
	Time	0.15			0.01	0.914
	Identity of species × Epiphytes	6.88	1.42×10^3	1.35×10^3	0.55	0.472
N[b]	Intercept	30.82	−2.97	0.59	385.36	0.000***
	Identity of species	0.25	0.48	0.38	0.96	0.348
	Epiphytes	6.23	8.15×10^2	3.56×10^2	24.08	0.000***
	Time	0.00			0.00	0.995
	Identity of species × Epiphytes	0.17	-2.10×10^2	1.95×10^2	0.67	0.429
S	Intercept	4669.05	40.51	6.54	83.02	0.000***
	Identity of species	240.14	−9.01	4.47	3.38	0.091
	Epiphytes	69.66	1.95×10^3	1.38×10^3	0.98	0.341
	Time	38.02			0.54	0.478

[a] x^3 transformed.
[b] Ln(x) transformed.

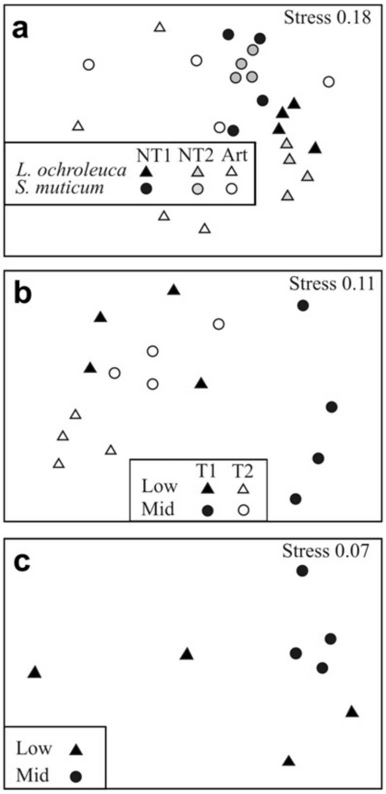

Fig. 3. Multidimensional scaling (MDS) plots of epifaunal assemblages of (a) natural (=N, at times 1 = T1 and 2 = T2) and artificial (=Art, at time 1) *Sargassum muticum* and *Laminaria ochroleuca* on low shore, (b) natural *S. muticum* placed on mid and low shores at times 1 and 2, and (c) artificial *S. muticum* on mid and low shores at time 1.

3.2. Epifauna associated with artificial *Sargassum muticum* and *Laminaria ochroleuca* on low shore

Gastropods were the dominant group in both species followed by malacostracans (see Appendix). There was a significant effect of the identity of the artificial algae on epifaunal density (Fig. 2; Table 2), with larger densities in *Sargassum muticum*. However, the number of taxa and the diversity were not significantly affected by identity of algal species or epiphytic biomass (Table 2). In fact, epiphytic biomass did not vary significantly between both artificial algae ($F_{1,14}$: 0.39, $p = 0.544$; Fig. 4).

The composition of assemblages did not vary between both algae (PERMANOVA, pseudo-$F_{1,6}$: 0.85, $p = 0.656$; Fig. 3a). Potential differences between algal types were masked by a strong variability within each algal type (i.e. average Bray–Curtis dissimilarity was

Table 2
Coefficients of the optimal generalized linear models investigating how Identity of species and Epiphytes influence epifaunal density (N) and number of epifaunal taxa (S) of artificial *Laminaria ochroleuca* and *Sargassum muticum*. Coefficients and standard errors for fixed factors are indicated. $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$.

	Variable	MS	Estimate	SE	*F*	*p*-value
N[a]	Intercept	44.59	−5.90	0.87	77.08	0.000***
	Identity of species	8.35	2.18	0.58	14.42	0.013*
	Epiphytes	1.00	5.83×10^2	4.52×10^2	1.73	0.246
S	Intercept	492.29	1.17	3.60	67.85	0.001***
	Identity of species	35.96	5.22	2.25	4.96	0.090
	Epiphytes	16.21	3.64×10^4	2.60×10^4	2.23	0.209
	Identity of species × Epiphytes	11.52	-1.76×10^4	1.30×10^4	1.59	0.276

[a] Ln(x) transformed.

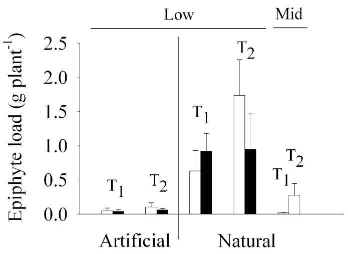

Fig. 4. Epiphyte load (+SE, $n = 4$) found on artificial and natural algae on low and mid shores at time 1 (=T1) and 2 (=T2). White bars indicate *Sargassum muticum* and black bars indicate *Laminaria ochroleuca*.

85% and 78% in *Laminaria ochroleuca* and *Sargassum muticum*, respectively). Dissimilarity between the two types of artificial algae was high (80%), with *Bittium reticulatum*, nematodes, *Rissoa parva*, barnacles and serpulids as the most important taxa (SIMPER analysis). However, several taxa such as serpulids, *Amphipholis squamata*, *Chrysallida* spp., *Gnathia* spp. and sipunculids were only found in the complex algae.

3.3. Epifauna associated with natural and artificial Sargassum muticum on mid and low shores

Malacostracans and gastropods were the dominant taxa on mid and low shores, with larger densities on the mid shore. Height on the shore was an important factor explaining variability in the density of individuals, number of taxa and diversity associated with natural individuals of *Sargassum muticum* (Fig. 5; Table 3). In general, these variables presented lower values on the mid shore (Fig. 5). Epiphytic biomass was also significant in explaining variability in the number of taxa, and the sampling time had an effect on the density of fauna (Table 3). Epiphytic biomass varied significantly between heights on the shore ($F_{1,14}$: 14.30, $p < 0.01$), with a greater biomass on the low shore (Fig. 4).

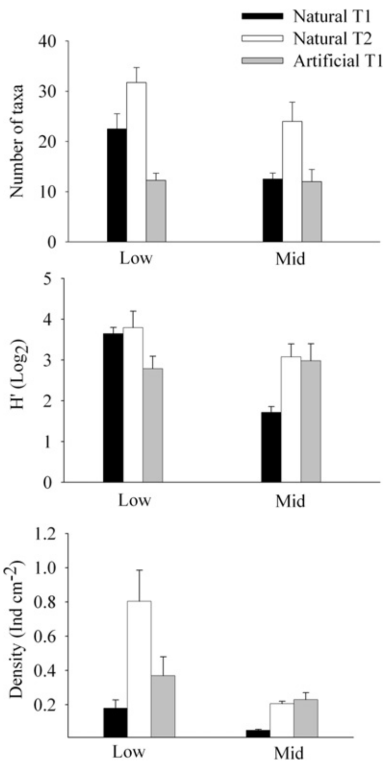

Fig. 5. Mean (+SE, $n = 4$) number of taxa, diversity (H′) and density of epifaunal assemblages associated with natural *Sargassum muticum* on mid and low shores at time 1 (=T1) and 2 (=T2). Grey bars indicate artificial algae of *S. muticum* on mid and low shores at time 1.

Table 3
Coefficients of the optimal linear mixed-effects models investigating how Height on the shore, Time and Epiphytes influence diversity (H′), density (N) and number of epifaunal taxa (S) of natural *Sargassum muticum*. Coefficients and standard errors for fixed factors are indicated. $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$.

	Variable	MS	Value	SE	*F*	*p*-value
H′	Intercept	38.23	5.75	0.84	53.78	0.041*
	Height	6.41	−1.85	0.44	18.41	0.001***
	Epiphytes	0.36	-3.3×10^3	1.8×10^3	1.03	0.331
	Time	0.90			2.59	0.136
	Height × Epiphytes	0.53	3.2×10^3	1.86×10^3	1.52	0.243
N[a]	Intercept	21.20	−0.42	0.83	7.91	0.21
	Height	1.68	−0.94	0.30	10.36	0.007**
	Epiphytes	0.19	119.23	97.81	1.16	0.302
	Time	3.87			23.86	0.000***
S	Intercept	1268.70	29.13	5.69	77.01	0.002**
	Height	142.13	−8.34	3.39	6.45	0.027*
	Epiphytes	166.13	-4.80×10^4	1.26×10^4	7.54	0.019*
	Time	13.55			0.62	0.450
	Height × Epiphytes	159.26	5.06×10^4	1.25×10^4	7.23	0.021

[a] Ln(x) transformed.

The composition of epifaunal assemblages varied significantly between shores, but inconsistently over time (PERMANOVA, Height × Time, pseudo-$F_{1,12}$: 3.93, $p < 0.01$; Fig. 3b). The interaction was mainly due to the magnitude of differences between heights on the shore across sampling times (i.e. average Bray–Curtis dissimilarity between mid and low shores was 67% and 55% at time 1 and 2, respectively). In fact, multivariate variability was significantly different among assemblages across times (PERMDISP, Time, $F_{1,12}$: 12.61, $p(\text{perm}) = 0.002$). The post-hoc comparisons indicated a greater heterogeneity at the second sampling time (PERMDISP, Time 1: 40.47 ± 1.35; Time 2: 31.96 ± 1.98 [Average ± SE]). The most important taxa contributing to dissimilarities between heights on the shore, for which an average dissimilarity of 61% was noted (SIMPER analysis), were *Hyale* sp., *Caprella* spp. and insects, In contrast, dexaminids and mytilids were the most important taxa contributing to a dissimilarity of 61% between sampling times (SIMPER analysis).

Gastropods were the most abundant group associated with artificial algae (Appendix). Neither height on the shore nor epiphytic biomass had significant effects on the univariate biotic variables (Fig. 5, Table 4). In fact, there was no significant variation of epiphytic biomass associated with *Sargassum muticum* algae placed on different shores ($F_{1,14}$: 1.24, $p = 0.308$; Fig. 4).

The composition of epifaunal assemblages associated with artificial algae varied significantly between heights on the shore (PERMANOVA, Height, pseudo-$F_{1,6}$: 1.91, $p < 0.05$; Fig. 3c).

Table 4
Coefficients of the optimal generalized linear models investigating how Height on the shore and Epiphytes influence density (N) and number of epifaunal species (S) of artificial *Sargassum muticum*. Coefficients and standard errors for fixed factors are indicated. $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$.

	Variable	MS	Estimate	SE	*F*	*p*-value
N	Intercept	0.26	0.39	0.19	13.69	0.021*
	Height	0.01	−0.11	0.12	0.74	0.438
	Epiphytes	0.08	2.98×10^2	1.72×10^2	4.56	0.100
	Height × Epiphytes	0.03	-1.29×10^2	0.98×10^2	1.72	0.260
S	Intercept	1176.13	10.82	1.55	74.48	0.000***
	Epiphytes	22.67	1.49×10^3	1.09×10^3	1.88	0.219

Multivariate variability was significantly different between assemblages located on different shores (PERMDISP, Height, $F_{1,6}$: 10.05, $p(\text{perm}) = 0.02$). The post-hoc comparisons showed a greater heterogeneity on mid shore (PERMDISP, low shore: 47.7 ± 2.31; mid shore: 32.81 ± 4.01, Average ± SE). SIMPER analysis revealed that dissimilarity between heights on the shore was 74%, and the main taxa responsible for this dissimilarity were the gastropods *Gibbula umbilicalis* (6%), *Bittium reticulatum* (5%), and *Barleeia unifasciata* (4%). *Gibbula umbilicalis* and *Hyale* sp. only occurred on the mid shore, whereas serpulids, the gastropod *Tricolia pullus* and the amphipod *Jassa* sp. were exclusively found on the low shore.

4. Discussion

Results indicated that the initial hypotheses were only partially supported. On one hand, epifaunal assemblages associated with natural *Laminaria ochroleuca* and *Sargassum muticum* differed, but these differences did not seem to be related to the structural complexity of algae. On the other hand, epifaunal assemblages associated with *S. muticum* did vary depending on the height on the shore; however, this variation was temporally inconsistent in the case of natural algae.

4.1. Influence of algal identity on the low shore

Similar to other studies, the results demonstrated that identity of the host algae was an important factor in structuring the epifaunal assemblages (e.g. Christie et al., 1998; Viejo, 1999; Kelaher, 2003; Wernberg et al., 2004; Wikström and Kautsky, 2007; Bates, 2009; Jones and Thornber, 2010). Differences between assemblages were due to both composition of taxa and density of individuals, influenced in this case by epiphyte load. In contrast, the number of taxa and diversity did not contribute to such differences. In the case of *Sargassum muticum*, previous studies found differences in epifaunal assemblages associated with this invasive alga and other native algae (e.g. Viejo, 1999; Wernberg et al., 2004; Buschbaum et al., 2006). These studies concluded that structure of epifaunal assemblages associated with *S. muticum* and other native algae differed, but differences were mainly due to different density of individuals and biomass rather than composition of species. Here, epifaunal assemblages varied between the two natural host algae, but such variation differed in magnitude over time. This specific fluctuation may be the result of changes in the physical and biological conditions of the environment such as water current, temperature, productivity or presence of predators (Edgar, 1992; Taylor, 1998; Viejo, 1999; Jones and Thornber, 2010).

Although epifaunal assemblages differed depending on the identity of algae, these differences only occurred in natural algae. Some taxa such as polychaetes and malacostracans were more abundant in natural *Laminaria ochroleuca* and *Sargassum muticum*, respectively. These results are in agreement with previous studies that indicated a larger abundance of small crustaceans in more complex algal habitats (Taylor and Cole, 1994; Wernberg et al., 2004). In contrast, Russo (1990) showed that complexity of algae was not a consistent predictor of number of individuals and species of amphipods. Similarly, Schreider et al. (2003) found no differences in abundance of amphipods between algae of different structural complexity. These authors suggested that although complexity was not important for various species of epifaunal amphipods, other attributes of habitat structure (e.g., heterogeneity *sensu* McCoy and Bell, 1991) might affect epifaunal densities. In addition, some studies have reported strong host specificity likely determined by specific chemical, structural and morphological characteristics of the algal species, host species identity being more important when abiotic conditions are stressful (see Bates and DeWreede, 2007). Lilley and Schiel (2006) found, for example, that the removal of a canopy of *Hormosira banksii* (Turner) Decaisne from a shore exposed to thermal stress had a significant influence on structure of associated biota. Other factors such as epiphytic load might also play an important role in determining the structure of epifaunal assemblages. This possible dependency might be related to different faunal strategies to exploit epiphytic algae. For example, epiphytes may play an important role by providing shelter and/or food for many taxa of epifauna (Schneider and Mann, 1991; Martin-Smith, 1993; Viejo, 1999; Schreider et al., 2003; Wikström and Kautsky, 2004). Bologna and Heck (1999) highlighted the trophic role of epiphytes over the increase in structural complexity, which appeared to be particularly important in increasing density of bivalves.

Within artificial algae only the total epifaunal density was affected by identity of host, and this fact may have different explanations. Firstly, that were the internal properties of the seaweeds (intrinsic characteristics such as food value) those which contributed to the distribution patterns of the natural seaweeds. Secondly, that structural complexity of algae did not play an important role in shaping composition and structure of epifaunal assemblages. This argument would not be in agreement with most previous studies that indicated morphological complexity as a key factor structuring associated benthic assemblages (e.g. Schreider et al., 2003; Wernberg et al., 2004; Schmidt and Scheibling, 2006). Thirdly, epiphytic algae were less abundant in artificial than in natural algae. This is an important point to take into account because patterns of distribution and abundance of epifauna may be related to the presence of epiphytic algae (see above). Finally, it is clear that the artificial units under sampled real assemblages (see Fig. 2). It is possible that our experiment was not run long enough to detect differences in epifaunal assemblages associated with these artificial algae. In fact, many of the studies of colonisation on artificial structures (e.g. reefs) were short term and had insufficient colonisation time, not being subjected to the same processes that natural communities (Hiscock et al., 2010). Despite the use of artificial units that more precisely imitated the shape of natural algae than those used in previous studies (Kelaher, 2003; Schreider et al., 2003; Mirto and Danovaro, 2004; Cole et al., 2007), assemblages colonising our units did not exactly resemble those of natural assemblages. Thus, gastropods were the dominant taxon in both types of artificial algae instead of polychaetes and malacostracans that were the dominant taxa in natural *Laminaria ochroleuca* and *Sargassum muticum*, respectively. This may be in part explained by differential dispersal abilities since, for example, gastropods show higher dispersal ability (Tuya et al., 2009) than amphipods and isopods (Christie et al., 1998; Tuya et al., 2009).

4.2. Influence of height on the shore on epifaunal assemblages

Variations in physical conditions afforded by different heights on the shore clearly play an important role in structuring the epifaunal assemblages of both natural and artificial *Sargassum muticum* algae. However, epifaunal assemblages differed between heights inconsistently across time in natural algae. Differences between assemblages were due to both composition and abundances of individuals and taxa. The number of taxa and individuals were larger in natural algae on the low shore. This was in agreement with other studies that indicated height on the shore as an important factor influencing epifaunal assemblages (Benedetti-Cecchi, 2001; Schreider et al., 2003; Davidson, 2005), showing that increased physical stress (e.g. aerial exposure or desiccation) become more important to the survival of species higher on the shore (Lilley and Schiel, 2006). Spatial variability of physical and biotic factors (i.e. rates of predation, availability of food, changes in water current, and different desiccation levels) may also cause variability in epifaunal assemblages (Bertness and Leonard, 1997; Schreider et al., 2003; Molina-Montenegro et al., 2005).

In addition, variability of intrinsic characteristics of natural individuals of *Sargassum muticum* (i.e. morphology, phenolic content) across the vertical gradient might also play an important role in determining the patterns of distribution and abundance of epifauna. Moreover, epiphytic biomass varied significantly between heights on the shore and it was an important factor explaining variation of number of taxa associated with natural *S. muticum* (see Section 3.3). Epiphytes might regulate number of taxa by providing food supply or by adding extra structural complexity to the habitat. The labile relationship between mobile epifauna and host algae has been often explained by an indirect relationship mediated by the presence of epiphytes (Johnson and Scheibling, 1987; Edgar, 1992; Viejo, 1999).

This study carried out at a local scale demonstrated that the two macroalgae supported diversified epifaunal assemblages. Analyses showed that the time of sampling, the epiphytic load and the height on the shore were the most important factors in explaining variability of epifaunal assemblages, although the mechanisms underlying were not clear and further experimental tests are necessary. In contrast, structural complexity of the algae seemed to be of minor importance for the structure of epifaunal assemblages. We suggest that a shift from *Laminaria ochroleuca* to *Sargassum muticum* dominance could have a major effect on patterns of abundance of associated mobile epifauna. The consequences of these changes are unknown, but they could include altered food webs as a result of changes in availability of food, grazing pressure on algal propagules and recruits, or changes in secondary production (see Viejo, 1999; Wernberg et al., 2004).

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Appendix

Taxa and density of individuals found in the different natural and artificial (=A) *Laminaria ochroleuca* (=L) and *Sargassum muticum* (=S) on the mid and low shores at time 1 and 2 (average ± SE, individuals per alga).

Species	ALLowT1	ASLowT1	ASMidT1	LLowT1	LLowT2	SLowT1	SLowT2	SMidT1	SMidT2
Phylum Cnidaria									
Class Hexacorallia									
Zoanthidea				2.00 ± 4.00			0.25 ± 0.50		0.75 ± 1.50
Phylum Platyhelminthes									
Class Turbellaria	0.25 ± 0.50				0.75 ± 0.96		1.25 ± 1.26		1.00 ± 0.82
Phylum Nematoda	0.50 ± 1.00	4.75 ± 6.60	1.25 ± 1.50	3 ± 21.20	36.50 ± 21.46	15.50 ± 17.02	6.75 ± 7.63		21.25 ± 16.82
Phylum Nemertea				0.50 ± 0.58	0.75 ± 0.96				2.00 ± 2.45
Phylum Annelida									
Class Oligochaeta	0.25 ± 0.50		0.25 ± 0.50		3.25 ± 3.30	0.75 ± 1.50			0.50 ± 1.00
Class Polychaeta									
Phylo sp.				0.50 ± 1.00		0.25 ± 0.50			
Spionidae				0.25 ± 0.50			0.25 ± 0.50		
Polydora spp.				0.25 ± 0.50	0.50 ± 1.00		0.25 ± 0.50		0.25 ± 0.50
Cirratullidae				1.00 ± 0.82	0.75 ± 0.50	0.25 ± 0.50	0.25 ± 0.50		0.25 ± 0.50
Capitella spp.				0.75 ± 0.50	0.25 ± 0.50				0.25 ± 0.50
Maldanidae				1.25 ± 2.50					
Phyllodocidae				1.25 ± 1.26	1.50 ± 1.91	0.25 ± 0.50	0.25 ± 0.50		0.50 ± 0.58
Aphroditoidea	0.50 ± 0.58	0.25 ± 0.50	0.25 ± 0.50	4.00 ± 2.00	4.25 ± 2.63	0.50 ± 0.58	0.25 ± 0.50		1.50 ± 2.38
Lepidonotus clava				0.75 ± 0.96	2.50 ± 1.91		0.25 ± 0.50		
Syllidae		0.25 ± 0.50	1.50 ± 1.29	26.75 ± 24.97	23.00 ± 9.76	1.50 ± 1.29	1.00 ± 0.82		1 ± 11.43
Nereidae						1.00 ± 1.41			
Micronereis variegata							0.25 ± 0.50	0.25 ± 0.50	2.00 ± 3.37
Perinereis cultrifera						0.25 ± 0.50			
Platynereis dumerilii					0.50 ± 0.58		0.25 ± 0.50		3.50 ± 2.08
Aberrantidae	0.25 ± 0.50	0.25 ± 0.50	0.25 ± 0.50	2.25 ± 1.50	1.00 ± 0.82	0.25 ± 0.50	0.25 ± 0.50		1.50 ± 2.38
Lumbrineridae				0.50 ± 1.00	0.25 ± 0.50				
Dorvilleidae					0.25 ± 0.50				
Sabellaria spp.	0.25 ± 0.50			2.25 ± 2.63	3.25 ± 2.75	0.50 ± 1.00			
Terebellidae	0.25 ± 0.50			0.75 ± 0.96	0.25 ± 0.50				1.25 ± 1.89
Sabellidae				9.00 ± 3.16	18.25 ± 10.69	1.00 ± 2.00	0.75 ± 0.96		1.75 ± 2.87
Serpulidae		1.00 ± 1.41							
Spirorbidae		0.25 ± 0.50		1.50 ± 3.00				0.50 ± 0.58	9.25 ± 15.17
Phylum Sipuncula		0.25 ± 0.50		1.00 ± 0.82					
Phylum Arthropoda									
Class Ostracoda		0.50 ± 1.00		2.50 ± 4.36	1.25 ± 0.96	1.25 ± 1.50	0.75 ± 0.96		18.75 ± 16.01
Class Cirripedia									
Balanomorpha	2.25 ± 1.71	1.75 ± 2.36	0.25 ± 0.50		0.25 ± 0.50				0.25 ± 0.50
Class Malacostraca									
Nannastacidae				0.25 ± 0.50	0.50 ± 0.58				
Apseudes spp.				0.50 ± 1.00	0.25 ± 0.50				
Tanais dulonguii				1.25 ± 1.50		1.75 ± 2.36			
Heterotanais oerstedii					0.25 ± 0.50				
Leptochelia dubia				0.25 ± 0.50	2.00 ± 3.37				
Anthura sp.	0.25 ± 0.50				1.25 ± 1.50	0.50 ± 1.00			

(*continued on next page*)

Appendix (*continued*)

Species	ALLowT1	ASLowT1	ASMidT1	LLowT1	LLowT2	SLowT1	SLowT2	SMidT1	SMidT2
Gnathia sp.		0.25 ± 0.50							
Cirolanidae	0.25 ± 0.50			0.25 ± 0.50		0.50 ± 1.00			
Sphaeromatidae		0.25 ± 0.50				0.25 ± 0.50			
Campecopea hirsuta		0.25 ± 0.50							
Dynamene bidentata	0.25 ± 0.50	0.25 ± 0.50	1.25 ± 1.26	1.75 ± 1.50	0.75 ± 1.50	30.50 ± 21.32	79.25 ± 86.72	68.25 ± 39.72	31.50 ± 15.15
Lekanesphaera levii			0.25 ± 0.50						
Idotea sp.									1.00 ± 1.41
Synisoma acuminatum								1.00 ± 0.82	
Munna koyeri				0.25 ± 0.50					2.75 ± 1.89
Amphipoda		0.25 ± 0.50		4.75 ± 8.22	0.75 ± 0.50	0.75 ± 0.96		1.25 ± 1.50	0.50 ± 0.58
Pereionotus testudo					0.25 ± 0.50				
Gitanopsis spp.								2.25 ± 3.20	
Amphilochus neapolitanus						0.75 ± 0.96		0.25 ± 0.50	
Peltocoxa damnoniensis									
Stenothoe monoculoides			0.50 ± 0.58	0.25 ± 0.50	1.00 ± 1.41	7.50 ± 7.59	5.50 ± 3.00	1.00 ± 1.41	5.75 ± 3.40
Hyale sp.			1.50 ± 2.38	1.00 ± 2.00		2.75 ± 0.96	22.00 ± 11.80		1.00 ± 1.41
Gammaridae					0.50 ± 1.00				
Melitidae		0.25 ± 0.50		0.50 ± 1.00	4.50 ± 7.14				
Elasmopus rapax					1.50 ± 1.73				
Apherusa spp.				0.75 ± 0.96		1.75 ± 2.36	1.25 ± 2.50	0.25 ± 0.50	18.75 ± 25.94
Dexaminidae		0.75 ± 1.50		3.25 ± 5.25	0.50 ± 0.58	2.00 ± 4.00	1.00 ± 0.82	0.25 ± 0.50	58.75 ± 112.86
Ampithoe spp.	0.50 ± 1.00	0.50 ± 1.00		9.75 ± 19.50	0.25 ± 0.50	6.75 ± 6.95	10.75 ± 11.44	1.25 ± 1.26	7.50 ± 4.51
Aoridae	0.50 ± 0.58			8.00 ± 12.78	4.00 ± 4.83		1.75 ± 0.96		0.75 ± 1.50
Leptocheirus sp.			0.25 ± 0.50						
Microdeutopus spp.		0.50 ± 1.00		0.75 ± 1.50					3.25 ± 2.36
Micropropotus maculatus		0.25 ± 0.50			0.75 ± 1.50	2.25 ± 2.63	3.25 ± 4.72		0.25 ± 0.50
Gammaropsis maculata				0.50 ± 1.00	3.25 ± 3.95				
Corophium spp.					0.75 ± 1.50	0.50 ± 0.58	0.25 ± 0.50		2.00 ± 1.63
Jassa spp.	0.25 ± 0.50	0.50 ± 0.58			7.75 ± 3.77	0.25 ± 0.50	1.00 ± 1.41	0.50 ± 0.58	
Podocerus sp.				2.50 ± 3.79	1.75 ± 2.87	0.25 ± 0.50			
Caprella spp.	0.25 ± 0.50	0.25 ± 0.50		0.50 ± 0.58	4.75 ± 2.99	12.75 ± 16.96	50.75 ± 16.15	2.25 ± 2.63	0.50 ± 0.58
Palaemonidae								1.00 ± 0.82	
Pilumnus hirtellus				0.25 ± 0.50	1.50 ± 0.58				
Class Insecta	1.00 ± 2.00	0.50 ± 1.00	5.25 ± 9.84	2.25 ± 4.50	0.25 ± 0.50	7.50 ± 13.03	2.00 ± 1.41	0.50 ± 1.00	29.25 ± 23.88
Phylum Chelicerata									
Class Arachnida									
Acarina	0.25 ± 0.50	0.50 ± 1.00	1.25 ± 0.50	2.75 ± 1.71	2.50 ± 1.73	3.00 ± 4.08	1.50 ± 1.00	0.25 ± 0.50	8.75 ± 3.86
Phylum Pycnogonida					0.25 ± 0.50	0.75 ± 1.50			
Achelia spp.				1.00 ± 0.82	3.50 ± 3.87	0.50 ± 1.00	0.25 ± 0.50		
Nymphon gracile					0.25 ± 0.50				
Ammotheidae									
Anoplodactylus sp.				0.25 ± 0.50	1.25 ± 1.89		0.25 ± 0.50		
Phylum Mollusca									
Class Polyplacophora									
Lepidochitona cinereus	0.25 ± 0.50	0.25 ± 0.50	0.25 ± 0.50			0.25 ± 0.50			1.25 ± 1.26
Acanthochitona fascicularis			0.50 ± 0.58	1.25 ± 1.50	0.75 ± 0.96				0.75 ± 0.96
Class Gastropoda									
Collisella tessulata		0.25 ± 0.50							
Tectura virginea									
Patella spp.	0.25 ± 0.50		0.25 ± 0.50						1.50 ± 1.73
Patina pellucidum				1.50 ± 0.58	2.50 ± 2.65				
Gibbula cinerea						0.25 ± 0.50			
Gibbula umbilicalis			3.00 ± 2.45	1.25 ± 1.26		0.75 ± 1.50	1.00 ± 1.41	2.75 ± 1.71	5.75 ± 5.62
Tricolia pullus	0.25 ± 0.50	0.75 ± 0.96		11.50 ± 13.48	1.25 ± 1.89	2.25 ± 3.30	0.75 ± 0.96	1.00 ± 1.15	2.50 ± 3.00
Littorina obtusata									0.25 ± 0.50
Littorina mariae								0.50 ± 1.00	
Littorina neritoides				0.25 ± 0.50			0.25 ± 0.50		
Littorina nigrolineata		0.25 ± 0.50		0.75 ± 1.50					
Hydrobia ulvae				0.25 ± 0.50	0.25 ± 0.50	4.25 ± 8.50			
Cingula trifasciata	0.25 ± 0.50	0.25 ± 0.50	0.75 ± 1.50						
Onoba semicostata				0.25 ± 0.50					
Alvania semistriata				1.50 ± 3.00	1.00 ± 0.82				
Rissoa parva	4.25 ± 5.32	2.25 ± 1.89	3.50 ± 5.07	6.50 ± 7.55	1.50 ± 2.38	2.25 ± 2.00	2.75 ± 1.89	2.75 ± 2.22	13.75 ± 13.74
Barleeia unifasciata	0.25 ± 0.50	1.00 ± 1.41	2.25 ± 3.86	4.50 ± 1.73	4.25 ± 4.99	12.50 ± 16.74	9.25 ± 8.06	1.25 ± 1.26	23.75 ± 12.12
Cingulopsis fulgida					0.25 ± 0.50		3.25 ± 4.57	0.25 ± 0.50	
Skeneopsis planorbis		0.25 ± 0.50	1.75 ± 1.50		0.25 ± 0.50				2.00 ± 2.16
Bittium reticulatum	0.75 ± 0.96	16.75 ± 19.21	4.25 ± 1.26	11.00 ± 10.98	0.25 ± 0.50	2.25 ± 2.63	2.50 ± 1.91	1.00 ± 1.15	1.75 ± 2.36
Caecum glabrum							0.25 ± 0.50		
Melanella eulimoides			0.25 ± 0.50	0.25 ± 0.50		0.25 ± 0.50	0.50 ± 1.00		
Buccinidae									
Ocenebrina aciculata				0.75 ± 0.96	0.50 ± 0.58		0.50 ± 0.58		2.75 ± 4.86
Philine scabra				0.50 ± 0.58					
Chrysallida spp.		0.25 ± 0.50							
Odostomia spp.						0.25 ± 0.50			
Elysia viridis									0.50 ± 1.00

Appendix (*continued*)

Species	ALLowT1	ASLowT1	ASMidT1	LLowT1	LLowT2	SLowT1	SLowT2	SMidT1	SMidT2
Limapontia sp.						0.25 ± 0.50			0.25 ± 0.50
Aeolidiidae							0.25 ± 0.50		
Class Bivalvia									
Mytilidae	0.25 ± 0.50	0.50 ± 0.58	0.75 ± 0.96	7.00 ± 5.72	10.50 ± 12.77	3.00 ± 3.56	3.50 ± 3.87	0.25 ± 0.50	21.00 ± 18.67
Lasaea rubra	0.25 ± 0.50	0.50 ± 0.58		0.75 ± 0.50	0.25 ± 0.50	0.25 ± 0.50	0.25 ± 0.50		0.50 ± 1.00
Venerupis sp.				0.25 ± 0.50					
Hiatella arctica					0.25 ± 0.50	0.25 ± 0.50	0.25 ± 0.50		
Phylum Echinodermata									
Class Asteroidea									
Asterina gibbosa					0.25 ± 0.50			0.25 ± 0.50	
Class Ophiuroidea									
Amphipholis squamata		0.75 ± 0.96	0.25 ± 0.50	7.25 ± 10.72	4.50 ± 4.12	0.50 ± 0.58	1.50 ± 2.38		8.75 ± 5.19
Class Holothurioidea				0.25 ± 0.50					
Phylum Chordata									
Class Ascidiacea									
Ciona intestinalis				0.25 ± 0.50					
Molgula sp.				1.25 ± 1.50	1.25 ± 0.50		0.25 ± 0.50		

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