

Combined effects of wrack identity and solar radiation on associated beach macrofaunal assemblages

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ABSTRACT: The ecological role of wrack as a habitat-forming species for beach macrofauna was investigated by experimental manipulation of 2 macroalgal species: *Laminaria ochroleuca* Bachelot de la Pylaie, 1824, and *Sargassum muticum* (Yendo) Fensholt. Both species are abundant in rocky bed communities, and commonly found shaping wrack patches on Atlantic sandy beaches in NW Spain. In beach ecosystems, this resource subsidy provides macroinvertebrates with accessible food, refuge and nursery in an otherwise inhospitable environment. Our analysis indicated a substantial shift in the dominant macrofauna, from wrack-dependent consumers in *L. ochroleuca* patches to terrestrial larval species in *S. muticum* patches. In addition, we examined *in situ* for the first time the direct impacts of changes in ambient solar radiation on the macroalgal biochemical content, and the consequent effects on wrack-associated macrofauna. During a 5 d experiment, cut-off filters were applied to generate treatments: P: photosynthetically active radiation (PAR) (400–700 nm), PA: PAR + UVA (320–700 nm), PAB (procedural control): PAR + UVA + UVB (280–700 nm), and C: control with no filter. Lack of natural radiation affected the biochemical content of the wrack and promoted differences in the associated macrofaunal composition; taxa assemblages among wrack patches exposed to C and PAB treatments were more similar compared to P or PA exposed patches. Our results indicated that changes in wrack nutritional quality and phenols caused by a moderate manipulation of the UVR had consequent effects on beach macrofauna looking for shelter, food or both. We suggest that in a scenario of global impacts, changes in the identity and fundamental biochemical traits of wrack can affect beach macrofaunal assemblages with unpredictable implications for coastal food-webs and ecosystem functioning.

KEY WORDS: Cut-off filters · Macrofaunal assemblages · Sandy beaches · Solar radiation · Wrack · *Laminaria ochroleuca* · *Sargassum muticum*

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INTRODUCTION

The accumulation of allochthonous organic debris, also known as wrack, is one of the most characteristic features in exposed beaches (Inglis 1989, Colombini & Chelazzi 2003). The lack of *in situ* primary production in sandy beaches means that wrack represents the main food resource for consumers. This resource subsidy serves as a fundamental refuge and nursery for several intertidal and upper shore species, includ-

ing semi-terrestrial (e.g. talitrid amphipods, cirrolanid isopods) and terrestrial (e.g. tenebrionid and staphylinid beetles) invertebrates (Colombini and Chelazzi 2003, Dugan et al. 2003). In temperate regions, most wrack is composed of large amounts of brown macroalgae from nearby productive rocky shore ecosystems (Orr et al. 2005, Lastra et al. 2008), and plays an important role in beach ecosystem functioning (Ince et al. 2007, Marczak et al. 2007, Spiller et al. 2010).

Several studies have started to resolve the effects of different wrack traits, such as identity, size, composition or nutritional contributions on beach macrofaunal communities (Crawley & Hyndes 2007, Olabarria et al. 2007, 2009, Rodil et al. 2008). For instance, beach-inhabiting consumers possess the capacity of exploiting different wrack species depending on the nutritional content (Adin & Riera 2003, Olabarria et al. 2009, Duarte et al. 2011). However, macroalgal traits such as shape and toughness may have a larger influential role on macrofauna behaviour than previously thought (Cruz-Rivera & Hay 2000, Van Alstyne et al. 2001). A recent study (Duarte et al. 2014) suggested that wrack physical features such as those that provide refuge against competition and desiccation, rather than chemical characteristics, might drive feeding preferences. Moreover, wrack patches constituting different macroalgal species may determine the patterns of algal-dependent macrofauna through the provision of more diverse habitat conditions (Crawley & Hyndes 2007, Rodil et al. 2008, Rossi et al. 2010, Taylor et al. 2010).

The position of beach ecosystems at the land–sea margin renders them highly vulnerable to climate change (Dugan et al. 2010), yet the consequences of global environmental impacts on these systems remain largely unexplored. Over the coming decades, global changes are expected to increase the exposure of marine organisms to damaging UV wavelengths, particularly UVB (280–320 nm), with far-reaching ecological consequences (Andrady et al. 2010). In temperate latitudes, although ozone losses are less severe, the magnitude and variation of UVR reaching Earth's ecosystems has not been stable since the mid 20th century due to anthropogenic-related changes in cloudiness and aerosol concentrations, with possible implications for climate change and ecosystems (Wild 2009, Mateos et al. 2013). Changes in UVR are not expected to have dramatic effects on inconspicuous beach macrofauna, since most of these species live buried in sand or use wrack as shelter (Brown & McLachlan 2002). However, algal biochemical composition (e.g. nutrients, pigments or phenols) can be affected by shifts in UVR, and we can use those changes in algal metabolic traits as indicators of the algal response to stress conditions (Figueroa et al. 2014). It has been demonstrated that shifts in the levels of UVR have direct effects on macrophytes with indirect consequences on consumers (Lotze et al. 2002, Swanson & Fox 2007, Rodil et al. 2015). Thus, shifts in natural incident UVR may affect wrack

macroalgal traits and degradation processes while stranded on the beach for days before being sand-buried or washed away. Beach macrofauna are likely to respond directly and immediately to a range of changes in environmental variables, including physical and chemical, since macrofaunal assemblages are structured mainly by habitat conditions (Defeo & McLachlan 2005). Therefore, changes in the incident UVR and/or UVR-induced changes on algal metabolic conditions may prompt measurable shifts on wrack-dependent macrofaunal assemblages.

Here, we performed a wrack experimental manipulation using 2 different species of brown macroalgae; the native *Laminaria ochroleuca* Bachelot de la Pylaie, 1824, and the non-indigenous *Sargassum muticum* (Yendo) Fensholt, 1955. Both species are easily found stranded on Atlantic beaches of the Iberian Peninsula. *S. muticum* is structurally and biochemically different than the co-occurring *L. ochroleuca*. Moreover, *S. muticum* is known to impact marine communities, replacing the functional role of native species in the ecosystem and by modifying habitat characteristics and food sources for consumers (Britton-Simmons 2004, Rodil et al. 2008). In order to gain insights into the potential effects of solar radiation modifications on beach macrofaunal assemblages, we manipulated the ambient UVR by using cut-off filters and examined the subsequent effects on the biochemical composition of wrack algae and associated macrofauna. We assessed whether 2 different algal species could promote different macrofaunal responses when combined with different UVR treatments. We hypothesized that the role of algal wrack as a refuge would be central in the response of macrofauna to UVR changes, since the capacity to provide protection and resources to macrofauna will vary between different wrack species.

MATERIALS AND METHODS

Study site, experimental design and setup

Playa Ladeira is an exposed sandy beach, about 2 km long and 130 m wide (low spring tide), located in the Corrubedo Natural Park (42° 34' 36" N, 9° 3' 20" W) in northwest Spain. This beach is influenced by a mesotidal ocean regime with a medium tidal range of ~3.5 m, and backed by a large and active dune system. On this beach, macrophyte wrack is very diverse and variable, with hetero-

geneous patches mainly composed of brown algae that are spread along the upper shore of the beach (Barreiro et al. 2011).

We designed a manipulative field experiment to test for UV-induced shifts on the biochemical traits (i.e. total nitrogen and carbon content, C/N ratio, organic matter, chlorophyll *a* and phenols) of 2 macroalgae. *Sargassum muticum* is a non-indigenous, structurally complex macroalgae with long primary branches bearing numerous terete secondary branches. In contrast, *Laminaria ochroleuca* is a native macroalgae, with simple long strap-like blades that stack up in layers in the sand. The day before starting the experiment, ~40 kg of *L. ochroleuca* (hereafter *Laminaria*) and *S. muticum* (hereafter *Sargassum*) were collected by hand from a nearby rocky intertidal area, taken to the laboratory, washed, and separated in wrack patches (16 patches per species) of similar weight (mean \pm SD; 1.0 ± 0.2 and 1.0 ± 0.3 kg wet wt for *Laminaria* and *Sargassum*, respectively) and volume (~5000 cm³).

At the field site, 4 replicated patches (20 \times 20 cm) for each of the 2 algal species and treatments were placed at the northern part of the beach between the highest mark of the drift line and the base of the dune parallel to the shoreline on 20 September 2013; altogether, 32 experimental wrack patches were established (see Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m531p167_supp.pdf). Each patch was placed ~2 m apart and assigned a treatment using a previously generated random distribution. All wrack patches were covered by a bird-net (1 cm mesh size) attached to the sand by aluminium pegs to prevent aeolian dispersion of the patches (Fig. S1), and left in place for 5 d. This time-gap was chosen because wrack, in natural conditions, loses exponentially most of its biomass within a few days, and most of the associated macroinvertebrates are early colonizers (Colombini & Chelazzi 2003, Rodil et al. 2008).

To modify the quality of the incident solar radiation, cut-off filters were suspended immediately (10 cm) above the wrack patches, supported over square polyethylene structures (4 legs buried 5 cm into the sand) (Fig. S1). In this way, 4 ambient solar radiation treatments were established: (1) photosynthetically active radiation (PAR) treatment (hereafter P) using Lee 226 filters to block radiation <400 nm (i.e. UVA and UVB), but allow for full transmission of PAR (400–700 nm), (2) PAR + UVA (320–700 nm) treatment (hereafter PA) using Lee 130 filters to block UVB radiation, (3) full sunlight (PAR + UVA + UVB [280–700 nm]) treatment (hereafter PAB) using

a commercial polyethylene food wrap film as a procedural control, which allowed penetration of full spectrum light (> 90 % for PAR, UVA, and UVB; previously tested), and (4) full sunlight with no filter as a control for filter artefacts (hereafter C). Radiation through the filters was recorded at noon (~12:00 h) with a HD 2012.2 radiometer (DeltaOHM) for PAR (400–700 nm), UVA (315–400 nm), and UVB (280–315 nm) on the first and last day of the experiment. Temperature (°C) and humidity (%) were recorded daily using electronic iButton® logger devices located within the wrack during the course of the experiment (n = 8; 4 UVR treatments, 2 algal species).

Biochemical composition of the macroalgae

After 5 d, 4 subsamples (± 5 g) of each replicated treated wrack were collected for biochemical analysis. Subsamples were dried (60°C, 48 h), ground to a fine powder and stored in a freezer (–20°C). Total organic matter (OM, %) was measured as the difference of dried seaweed before and after ignition (500°C, 4 h). Chlorophyll *a* (chl *a*, $\mu\text{g g}^{-1}$) was analysed following Lorenzen (1967). Total carbon (TC) and nitrogen (TN) content (%) were determined by combustion using a CHN analyser.

For analyses of phlorotannins (i.e. phenols), 4 subsamples (± 5 g) from each replicated treated wrack were excised, dried (60°C, 48h) and frozen (–60°C). Phenols were extracted with 70 % aqueous acetone (mg g^{-1}) and determined according to the Folin–Ciocalteu method (Singleton & Rossi 1965) using phloroglucinol (Sigma-Aldrich) as a standard agent.

Wrack-associated macrofauna

We retained all macrofauna by enclosing each wrack patch in individual plastic bags, which were then transported to the lab and stored in a freezer (–20°C). Macrofauna underneath each patch were sampled using a 10 cm diameter corer (3 cores per patch), penetrating 20 cm depth into the substratum. Sediment samples were sieved through a 1 mm mesh, placed in bags and preserved in 70 % ethanol. Control replicates were randomly taken 1 m away from patches and separated by 50 cm to measure the natural abundance of invertebrates in bare sediment (n = 16). All retained macrofauna was sorted, counted and identified to the lowest possible taxonomic grouping.

Statistical analyses

Changes in the wrack biochemical content (i.e. OM, chl *a*, phenols, TC, TN, C/N) and in the wrack-associated macrofauna (i.e. total abundance, abundance of specific taxa and species richness) were analysed using a 2-way ANOVA. Algae (A: *Laminaria* and *Sargassum*) and radiation (R: C, PAB, PA, P) were considered as orthogonal fixed factors. *A posteriori* comparisons of treatment factors were evaluated using Student–Newman–Keul's (SNK) tests ($p < 0.05$). The homogeneity of variances was evaluated with Cochran's test and data were transformed when necessary (see tables in the 'Results' section). Univariate statistical analyses were performed with WinGMVA 5.0 (Centre for Research on Ecological Impacts of Coastal Cities, University of Sydney).

A 2 factor non-parametric multivariate analyses of variance (PERMANOVA) was run to detect shifts in macrofaunal assemblages between the 2 algal species (A), while accounting for radiation (R). The Bray-Curtis coefficient was used on fourth root-transformed data to create the resemblance matrix (4999 permutations). Only significant effects ($p < 0.05$) were further investigated through pair-wise comparisons. PERMDISP was used to check whether data showed homogeneity in multivariate dispersion.

To ascertain how much of the overall change in the composition of the macrofaunal assemblages (i.e., species richness, macrofauna abundance and identity of species) in the wrack can be explained by the macroalgal biochemical content (log-transformed predictor variables), distance-based linear models (DistLM) were performed (Anderson et al. 2008). DistLM performs a partitioning in the variation in data matrices similar to regression, but it generates *p*-values by a permutation routine. Bray-Curtis similarity matrices were constructed after 4th-root transforming the data (4999 permutations). DistLM were fitted using the stepwise selection procedure and R^2 criteria (sequential test). Model parsimony was assessed by repeating the tests using Akaike information criterion (AIC) to retain or remove variables at each step. Distance-based redundancy analysis (dbRDA) was applied to visualize the position of the wrack fitted to the significant predictor variables and the main macrofaunal species (Anderson et al. 2008). A similarity percentage (SIMPER) analysis was performed to find the species with the highest contribution to the wrack assemblages. Multivariate analyses were performed with PRIMER 6+ PERMANOVA® (Anderson et al. 2008).

RESULTS

Solar radiation and microclimatic conditions

Filters successfully manipulated the light spectrum (Fig. 1), with significant differences ($p < 0.001$) among treatments for PAR ($F_{3,328} = 5909$), UVA ($F_{3,328} = 684746$), and UVB ($F_{3,328} = 1192609$). All cut-off filters allowed for > 90% transmission of PAR (Fig. 1a). C and PAB filters allowed for > 90% transmission of UVA and UVB (Fig. 1b,c). PA allowed for 80 and 40% transmission of UVA and UVB, respectively. P allowed for < 8% transmission of UVA and UVB (Fig. 1b,c).

Temperature was significantly higher in *Sargassum* (mean \pm SD; $26.6 \pm 5.1^\circ\text{C}$) than *Laminaria* ($24.8 \pm 3.7^\circ\text{C}$) patches ($F_{1,96} = 6.1$, $p < 0.05$), and in PA ($25.7 \pm 4.0^\circ\text{C}$) ($F_{3,96} = 6.04$, $p < 0.05$) compared to C ($23.5 \pm 3.5^\circ\text{C}$) and PAB ($24.5 \pm 3.5^\circ\text{C}$) treatment patches

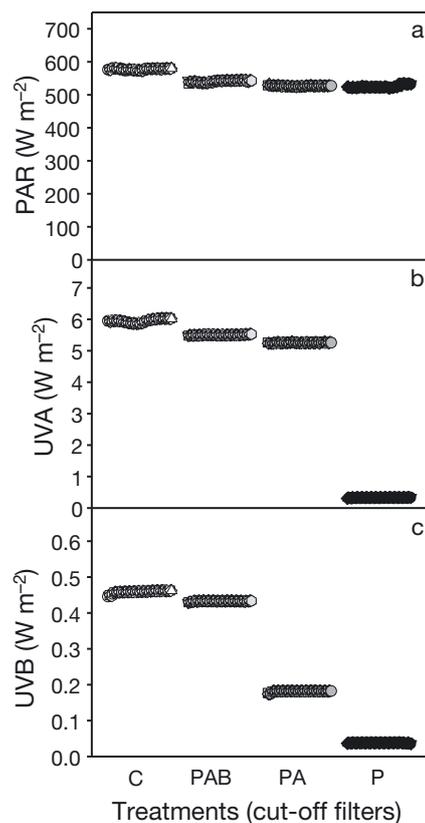


Fig. 1. Ambient and treatment solar radiations recorded simultaneously with a radiometer for (a) photosynthetically active radiation (PAR), (b) UVA and (c) UVB at solar noon time (~12:00 h), averaged from the first and last days, using periods of 3 minutes ($n = 83$). Radiation treatments: P (400–700 nm: blocks UVA + UVB radiation), PA (320–700 nm: blocks UVB radiation), PAB (full sunlight: 280–700 nm as a procedural control), and C (full natural sunlight with no filter as a control for filter artefacts)

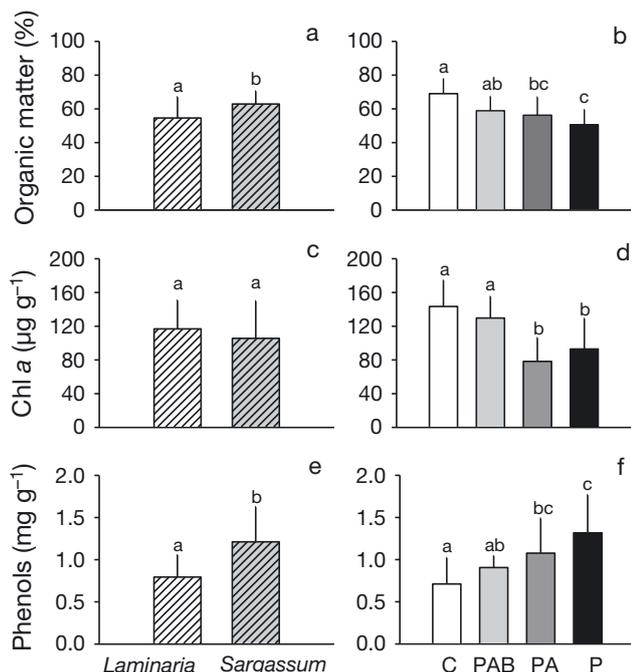


Fig. 2. Mean (+ SD) amount of (a,b) organic matter, (c,d) chlorophyll a, and (e,f) phenols in *Laminaria ochroleuca* and *Sargassum muticum* wrack patches ($n = 16$) subjected to radiation treatments: C, PAB, PA and P (see Fig. 1 legend for treatment descriptions) ($n = 8$). Data from panels b, d, and f were pooled from *Laminaria* and *Sargassum* wrack patches. Different letters represent significant differences

(Fig. S2a,b in the Supplement at www.int-res.com/articles/suppl/m531p167_supp.pdf). Temperature was not significantly different between PA and P treatments (SNK test; $p > 0.05$) (Fig. S2b). Temperature increased significantly ($F_{3,96} = 8.2$, $p < 0.05$) 48 h after setting the experiment (Fig. S2c). Humidity was significantly higher within *Laminaria* than *Sargassum* patches, but only in PA (mean \pm SD; $94.6 \pm 3\%$ vs. $57.1 \pm 21.3\%$, respectively) and P ($95.9 \pm 3.5\%$ vs. $86.8 \pm 7.0\%$, respectively) treatments (i.e. A:R interaction,

$F_{3,96} = 16.9$, $p < 0.001$) (Fig. S2d). There were significant humidity differences among wrack patches between the 1st ($92 \pm 6.8\%$) and 2nd ($95 \pm 3.3\%$) day of the experiment ($F_{3,96} = 2.9$, $p < 0.05$) (Fig. S2e).

Biochemical composition of the macroalgae

OM content differed significantly between the 2 algae (*Sargassum* > *Laminaria*, Fig. 2a), and over R treatments (Table 1). Wrack treated with P had the smallest OM content (Fig. 2b). The greatest chl a concentrations were found in control (C and PAB) patches (i.e. full radiation spectrum) (Table 1, Fig. 2c,d). Phenols varied significantly between the algae (*Sargassum* > *Laminaria*), and between radiation treatments (Fig. 2e), whereby wrack treated with P had the highest levels of phenols (Fig. 2f).

Nutrient content varied significantly between the 2 species of algae (Table 1). Although marginally non-significant, TC content varied between the algae (*Laminaria* > *Sargassum*, $p = 0.058$), and it was significantly smaller ($p < 0.001$) in wrack treated with filters than in controls (Fig. 3a). In control patches, TN content was significantly greater in *Laminaria* than in *Sargassum* (Fig. 3b), and the C/N ratio was significantly higher in *Sargassum* than *Laminaria* in C and PAB (Fig. 3c). C/N ratio significantly decreased in *Sargassum* when exposed to PA and P (Fig. 3c).

Wrack-associated macrofaunal assemblages

A total of 14 013 individuals from 20 taxa were identified (Table S1, SIMPER). The presence of wrack significantly ($p < 0.001$) increased the abundance of macrofauna ($F_{4,75} = 168.2$) and species richness ($F_{4,75} = 39.2$) compared to bare sediment.

Table 1. Summary of ANOVA for organic (org.) matter (%), chlorophyll a ($\mu\text{g g}^{-1}$), total carbon (%), total nitrogen (%), C/N ratio, and phenols (mg g^{-1}) for the 2 macroalgae (*Laminaria ochroleuca* and *Sargassum muticum*) and radiation treatments (C, PAB, PA, P [see Fig. 1 legend for definitions]). Significant results in italics (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$). + denotes marginally non-significant results ($0.1 < p < 0.05$)

Source	df	Org. matter (%)		Chl a ($\mu\text{g g}^{-1}$)		Total C (%)		Total N (%)		C/N ratio ^a		Phenols (mg g^{-1}) ^a	
		MS	F	MS	F	MS	F	MS	F	MS	F	MS	F
Algae (A)	1	1079.5	8.1**	1009.01	1.11	8.01	3.97 ⁺	0.37	5.8*	12	10.3**	0.33	21.7***
Radiation (R)	3	284.8	6.8**	7408.5	8.1***	30.1	14.9**	0.09	1.4	0.03	2.1	0.13	8***
A:R	3	20.5	1.4	1120.5	1.23	1.16	0.6	0.21	3.3*	0.04	3.2*	0.02	1.33
Residuals	24	51.3		911.2		2.02		0.065		0.01		0.02	
Cochran's test		C: 0.30 ($p > 0.05$)		C: 0.20 ($p > 0.05$)		C: 0.29 ($p > 0.05$)		C: 0.32 ($p > 0.05$)		C: 0.37 ($p > 0.05$)		C: 0.36 ($p > 0.05$)	

^a $\ln(x+1)$ transformed

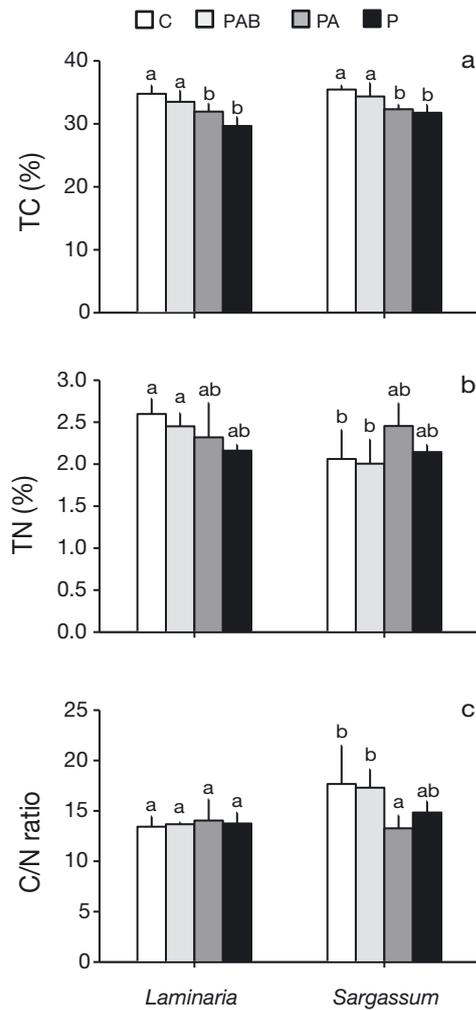


Fig. 3. Mean (+ SD, n = 4) amount of (a) total carbon content, (b) total nitrogen content, and (c) C/N ratio in *Laminaria ochroleuca* and *Sargassum muticum* wrack patches subjected to radiation treatments: C, PAB, PA, P (see Fig. 1 legend for treatment descriptions). Different letters represent significant differences

Total macrofaunal abundance was significantly larger in *Sargassum* than in *Laminaria* (Table 2, Fig. 4a), and in C compared with P treatments (SNK tests; $p < 0.01$) (Fig. 4b), and comprised mostly terrestrial larvae (> 80%) and talitrids (~ 3%) (Table S1 in the Supplement). Larval abundance was significantly larger (Table 2) in *Sargassum* than in *Laminaria* (Fig. 4c), and in C compared with P treatments (Fig. 4d) (SNK tests; $p < 0.01$). One dipteran species (family Anthomyiidae) in larval stage accounted for 70% of total number of individuals (Table S1), and tended to display larger abundances in *Sargassum* than in *Laminaria* ($p = 0.07$) (Table S2 in the Supplement). The rest of the terrestrial species did not vary significantly between algae or amongst R treatments (Table S2). The number of species was significantly larger in C patches made of *Laminaria* than in any other treatment (SNK test; $p < 0.05$) (Table 2, Fig. 5a). The majority of the wrack-associated species was represented by talitrids (Table S1). Talitridae abundance was significantly larger in *Laminaria* than in *Sargassum*, and in C than in PAB ($p < 0.05$), PA ($p < 0.01$), or P ($p < 0.05$) (SNK tests) (Table 2, Fig. 4e,f). *T. saltator*, *D. deshayesii*, and juveniles of both species were significantly (SNK tests; $p < 0.01$) more abundant in C patches of *Laminaria* (Fig. 5b,d, Table 3). The abundances of adult talitrids were also significantly larger in *Laminaria* than in *Sargassum* in PA treated patches (SNK tests; $p < 0.05$) (Fig. 5b,c). Significant differences in the number of talitrids between C and PAB patches (see Fig. 4e,f and Fig. 5b,c) indicate a possible filter artefact.

PERMANOVA distinguished significant differences between the macrofaunal assemblages of the 2 macroalgae (*Laminaria* vs. *Sargassum*: 30.3% dissimilarity) (Table 4), and among R treatments (Table 4). Thus, the dissimilarity between macrofaunal assemblages

Table 2. Summary of ANOVA for the total macrofauna, larvae and talitridae abundances, and species richness for the 2 macroalgae (*Laminaria ochroleuca* and *Sargassum muticum*), and radiation treatments (C, PAB, PA, P [see Fig. 1 legend for definitions]). No larvae: total abundance of all the individuals in adult stage. Significant results in italics (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$). + denotes marginally non-significant results ($0.1 < p < 0.05$)

Source	df	Macrofauna abundance									
		Total		Larvae		Talitridae ^a		No larvae		Species richness	
		MS	F	MS	F	MS	F	MS	F	MS	F
Algae (A)	1	260281	6.55*	329875	8.96***	6.36	14.6***	4118	4.02*	0.78	0.34
Radiation (R)	3	149328	3.8*	110692	3.01*	2.99	6.9***	4244	4.1*	12.1	5.2**
A:R	3	25128	0.6	40471	1.1	1.32	3.02+	2397	2.34	4.7	2.02
Residuals	24	39719		36817		1025		2.3			
Cochran's test		C: 0.25 ($p > 0.05$)		C: 0.27 ($p > 0.05$)		C: 0.35 ($p > 0.05$)		C: 0.37 ($p > 0.05$)		C: 0.27 ($p > 0.05$)	
^a Ln(x+1) transformed											

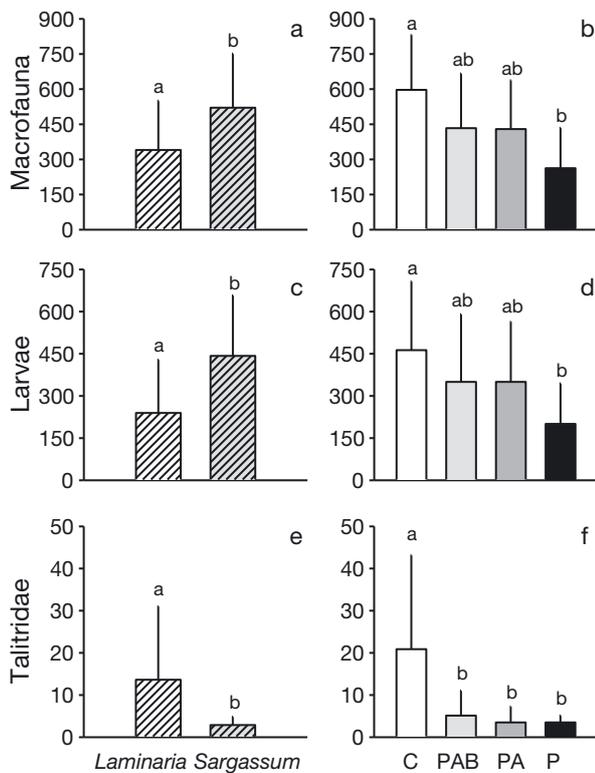


Fig. 4. Mean (+ SD) (a,b) macrofauna, (c,d) larvae, and (e,f) talitridae abundances in *Laminaria ochroleuca* and *Sargassum muticum* wrack patches ($n = 16$) subjected to radiation treatments: C, PAB, PA, P (see Fig. 1 legend for treatment descriptions) ($n = 8$). Panels b, d, and f are pooled data from *Laminaria* and *Sargassum* wrack patches. Different letters represent significant differences

in patches of *Laminaria* and those of *Sargassum* was greater in C than PA (~30%) and P treatments (~31%) (pair-wise tests, Table 4).

Influence of the algal biochemical composition on wrack macrofaunal assemblages

DistLM highlighted the association between species richness and the biochemical composition of the macroalgae (model explained 41.7% cumulative variation in species richness) (Table 5). A large part of the observed variation in species richness was significantly explained by OM and TN (Table 5), and macrofauna abundance was mainly explained by TC content (34.1%). DistLM and subsequent variation partitioning suggested that a significant part of the observed variation in wrack species assemblages was explained by the biochemical composition of the macroalgae (31%), including OM, TN, and phenols (Table 5).

Table 3. Summary of ANOVA for abundance of the main beach species (talitrids: *Talitrus saltator*, *Deshayesorchestia deshayesii*, and juveniles of both species) in wrack patches (*Laminaria ochroleuca* and *Sargassum muticum*), and radiation treatments (C, PAB, PA, P [see Fig. 1 legend for definitions]). All data were $\ln(x + 1)$ transformed. Significant results in italics (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$). + denotes marginally non-significant results ($0.1 < p < 0.05$)

Source	df	Macroinvertebrate beach species					
		<i>T. saltator</i>		<i>D. deshayesii</i>		Talitridae (juveniles)	
		MS	F	MS	F	MS	F
Algae (A)	1	5.04	14.5***	2.0	11.4**	2.96	10.7**
Radiation (R)	3	2.87	8.23***	0.77	4.4*	1.2	4.3*
A:R	3	1.1	3.1 ⁺	1.5	8.4***	0.92	3.3*
Residuals	24	0.35		0.18		0.28	

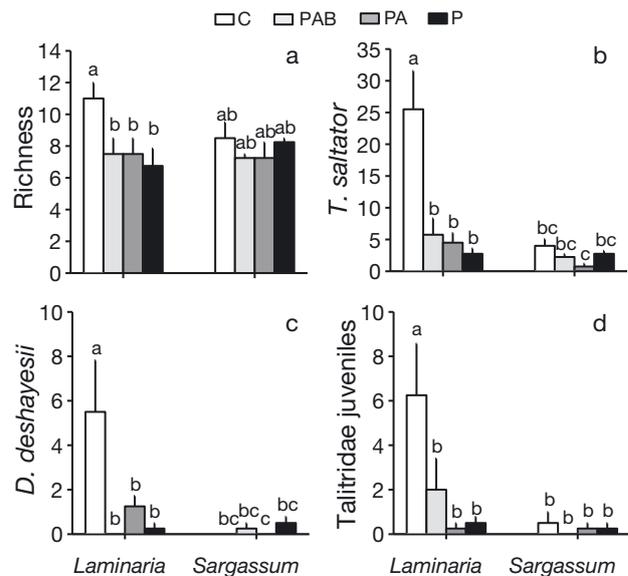


Fig. 5. Mean (+ SE, $n = 4$) (a) species richness, and (b,c,d) abundances of (b) *Talitrus saltator*, (c) *Deshayesorchestia deshayesii* and (d) juveniles of both species in *Laminaria ochroleuca* and *Sargassum muticum* wrack patches subjected to radiation treatments (C, PAB, PA, P [see Fig. 1 legend for treatment descriptions]). Different letters represent significant differences

The first 2 dbRDA axes captured most of the salient patterns in the fitted model with nearly 71% of the variability, and 21% of the total variation in the data cloud (Fig. 6). The ordination plot showed a separation of *Laminaria* from *Sargassum*, the latter being associated with high values of OM (Fig. 6a). The plot also showed a separation between controls (C and PAB) and radiation treatments (PA and P) (Fig. 6b). Controls were associated with high values of OM,

Table 4. Results of 2-factor permutational multivariate analysis of variance (PERMANOVA) on the abundance of the entire wrack assemblage (20 species) and *a posteriori* pair-wise analysis (MC = Monte Carlo tests) between macroalgal species (*Laminaria ochroleuca* and *Sargassum muticum*), and radiation treatments (C, PAB, PA, P [see Fig. 1 legend for definitions]). 4999 unrestricted permutations of raw abundance data. PERMDISP: homogeneity of dispersions. Significant results in italics (* $p < 0.05$)

Source	df	MS	pseudo- <i>F</i>	<i>p</i>
Algae (A)	1	1128.7	2.66	<0.05*
Radiation (R)	3	703.56	1.66	<0.05*
A:R	3	462.7	1.09	0.365
Residuals	24	424.4		
PERMDISP				
A	2, 32		1.543	0.224
R	4, 32		1.462	0.246
Pair-wise tests				
Groups	<i>t</i>	<i>p</i> (MC)	Dissimilarity (%)	
<i>L. ochroleuca</i> vs <i>S. muticum</i>	1.631	0.03*	30.3	
C vs PAB	1.831	0.06	28.5	
C vs PA	2.291	0.02*	30	
C vs P	1.754	0.05*	31	
PAB vs PA	0.478	0.774	28.5	
PAB vs P	0.461	0.825	29.5	
PA vs P	1.018	0.432	31.3	

and treated patches with TN (Fig. 6b). To determine the relationships between macrofaunal species and macroalgae exposed to R treatments, another dbRDA was performed (Fig. 7). The first 2 axes of this plot explained ~50 % of the relationship, and ~54 % of the total variability. *Anthomyiidae* sp1 was mainly associated with *S. muticum*, meanwhile talitrid amphipods and tylid isopods were associated with *L. ochroleuca* (Fig. 7a). Most species were found in control patches of both types of algae (Fig. 7b).

Table 5. Results of variation partitioning analysis (DistLM) quantifying the sequential effects (step-wise selection, 4999 permutations) of the specific contribution of the macroalgal biochemical content (OM: organic matter, %; TC: total carbon, %; TN: total nitrogen, %; and phenols, mg g^{-1} , all log-transformed) on the composition of the wrack macrofauna assemblages. Akaike information criterion (AIC) assessed model parsimony. Significant results in italics (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$)

Predictors	Species richness			Total abundance			Wrack species assemblage		
	R ²	SS	pseudo- <i>F</i>	R ²	SS	pseudo- <i>F</i>	R ²	SS	pseudo- <i>F</i>
OM	0.26	64.2	10.3**	–	–	–	0.11	1556.2	3.52**
TN	0.11	27.6	5.01*	–	–	–	0.1	1199.3	2.88*
TC	–	–	–	0.34	861.9	15.5***	–	–	–
Phenols	0.05	13.0	3.18	–	–	–	0.1	826.3	2.06*
Cumulative	0.42			0.34			0.31		
AIC		144.9			130.5			195.5	

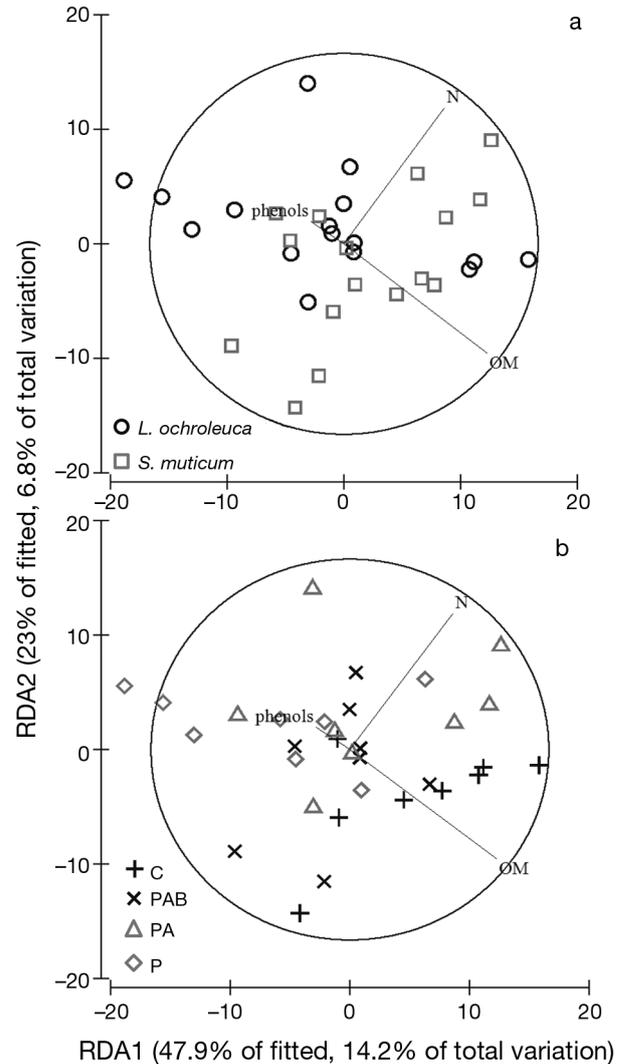


Fig. 6. dbRDA (distance-based redundancy analysis) ordination for the main wrack biochemical composition variables (N: total nitrogen, %; OM: organic matter, %; and phenols, mg g^{-1}) and (a) wrack macroalgae (*Laminaria ochroleuca* and *Sargassum muticum*), and (b) radiation treatments (C, PAB, PA, P [see Fig. 1 legend for treatment descriptions])

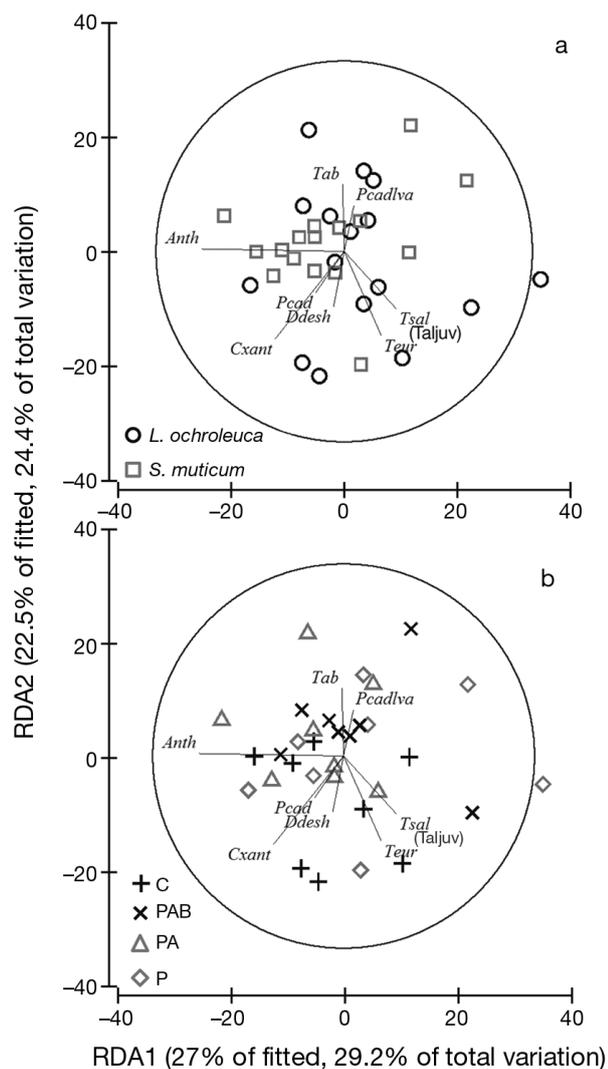


Fig. 7. dbRDA (distance-based redundancy analysis) ordination for the main macrofaunal species and (a) wrack macroalgae (*Laminaria ochroleuca* and *Sargassum muticum*), and (b) radiation treatments (C, PAB, PA, P [see Fig. 1 legend for treatment descriptions]). Macrofaunal species: Anth = Anthomyiidae sp1, Cxant = *Cafius xantholoma*, Ddesh = *Deshayesorchestia deshayesii*, Pcad = *Phaleria cadaverina*, Pcadlva = *P. cadaverina* larvae, Tab = Tabanidae sp1, Teur = *Tylos europaeus*, Tsal = *Talitrus saltator*, Taljuv = Talitrids in juvenile stage

DISCUSSION

In sandy beach ecosystems, the absence of conspicuous primary producers poses a large constraint for benthic organisms. Wrack made up of macroalgae comes loose from highly productive rocky-bed communities and is washed onto the otherwise low-productive beach, providing refuge and food for countless species, and subsidizing beach food webs

(Dugan et al. 2003, Crawley & Hyndes 2007, Ince et al. 2007, Spiller et al. 2010). We found that changes in the type of wrack subsidizing resources on beaches, and alterations of its basic biochemical traits due to moderate environmental manipulations affected associated macrofaunal assemblages.

Our short-term experiment showed that moderate changes in ambient radiation had significant effects on fundamental metabolic traits (OM and chl *a*), and secondary metabolism (phenols) of wrack macroalgae. OM and chl *a* diminished in wrack patches subjected to UVR treatments, and although wrack decomposition dynamics are mainly controlled by micro and meiofauna activity (Inglis 1989, Mews et al. 2006), solar radiation is also known to affect the degradation process of these specific detritus compounds (Vähätalo et al. 1998). Thus, the response of OM and chl *a* to our treatments may be related to a combination of changes in mineralization rates of organic matter, and modifications of bacterial activity affected by the lack of natural UVR; both aspects require further research. Importantly, UV-related changes of such labile compounds can affect the amount and quality of the food available to beach macrofauna (Rodil et al. 2015). Furthermore, brown macroalgae release protective substances via exudation, and indirectly as a consequence of stress conditions such as grazing or tissue degradation (Swanson & Druehl 2002, Koivikko et al. 2005). In our study, phenols were rapidly synthesized after 5 d of filter treatments. Excessive UVR is known to induce phenols in macroalgae (Pavia et al. 1997, Swanson & Fox 2007, Figueroa et al. 2014, Rodil et al. 2015), and recent studies also observed that phenols can be induced by only PAR (Steinhoff et al. 2012, present study). Therefore, it seems that the lack of UVR natural conditions, either above or below the ambient UVR range, affected the secondary metabolism of macroalgae. Eventually, UVR may affect the presence of wrack macrofauna and alter consumption patterns by increasing the concentration of defence chemicals in algae and thus decreasing algal palatability (e.g. Lotze et al. 2002, Swanson & Fox 2007).

Light environment is one of the main regulatory factors of macroalgal nutrient metabolism (Martínez & Rico 2008). We found additive effects of UVR and algae on TC content; TC content was similar between *S. muticum* and *L. ochroleuca*, and the lack of natural UVR (i.e. PA and P) diminished TC for both macroalgal species. We found interactive effects of radiation and algae treatments on nutrient quality-related variables; *L. ochroleuca* exhibited greater TN content than *S. muticum* in controls (C and PAB), but

it was similar under UVR filters. TN is considered to have a high nutritional value, ready to produce fundamental organic metabolites and promote growth, whilst TC has a structural role (Duarte 1992). Traditionally, the C/N ratio is considered an indicator of the physiological status of the algae, so a small C/N ratio suggests good conditions and high-quality food (Duarte 1992, Weykam et al. 1996, Figueroa et al. 2014). C/N is also considered a good predictor of decomposition rate for different types of plant detritus, with strong negative correlations between decomposition rates and C/N (Enríquez et al. 1993, Taylor et al. 2010). Detritus derived from *L. ochroleuca* (with its high TN content and low C/N) was probably more labile, nutritious, and rapidly degraded, thus providing a short-term food source that is readily available to opportunistic consumers (Penning et al. 2000, Taylor et al. 2010). A more refractory source of detritus, such as *S. muticum*, usually has a large C/N (Tenore et al. 1979, present study), and low decomposition rates (Rodil et al. 2008). The lack of UVB (PA) seemed to trigger the decomposition process of *S. muticum*. The beneficial role of natural levels of UVB on nutritional metabolism, growth and photosynthetic efficiency of macroalgae has been previously documented (Flores-Moya et al. 1999, Martínez & Rico 2008, Xu & Gao 2010).

Beach wrack plays a physical and a trophic role by providing valuable habitat conditions for macrofauna. Wrack casts shade, alters light, temperature and moisture regimes, and increases habitat complexity on bare sediment. Furthermore, wrack microclimatic conditions are considered a main factor affecting supratidal species (Colombini & Chelazzi 2003). In our study, temperature and humidity varied between the 2 algal species, with lower temperatures and higher humidity within *L. ochroleuca*. This is probably due to its simple structure, with long and wide, strap-like blades, that keep humidity and temperature to comfortable levels for beach species. Slight changes in these structural parameters can affect colonization processes (Rodil et al. 2008), particularly early colonizers such as sand-hoppers, which prefer moist, fresh wrack due to their susceptibility to desiccation (Marsden 1991). Wrack made of *S. muticum* generated different conditions in terms of humidity and temperature compared to *L. ochroleuca*. Our UVR treatments, including the procedural control, caused a significant change in the abundance of talitrids associated with wrack patches of both algal species. This response to treatments could be attributable to a combination of experimental filter artefact and high orientation sensitivity of sand-

hoppers to solar and local cues (Colombini et al. 2013).

Studies have documented the deleterious effects of invasive primary producers on the structure and functioning of diverse marine ecosystems (Britton-Simmons 2004, Monteiro et al. 2009, Taylor et al. 2010). *S. muticum* has the potential to alter the biodiversity of recipient beach systems (Rodil et al. 2008, Olabarria et al. 2010); thus, by including this non-indigenous species, we further tested for ecological effects of wrack identity on beach macrofaunal assemblages. The present study showed that large numbers of beach-inhabiting species, such as *T. saltator* and *D. deshayesii* were undoubtedly attracted by the presence of wrack made of *L. ochroleuca*, whilst *S. muticum* provided preferable nursery habitat for dipteran larvae. *S. muticum* is known to generate large amounts of refractory detritus composed of more structurally complex materials with slower decomposition rates, which offer a more long-lasting habitat to organisms that may use wrack for oviposition (Inglis 1989, Colombini & Chelazzi 2003, Rodil et al. 2008). However, macrofauna depends not only on macroalgal inputs for nursery, but also for food (especially amphipods) (Duarte et al. 2011, MacMillan & Quijón 2012). In a recent study, *T. saltator* showed a greater consumption of UV-treated *L. ochroleuca* compared to *S. muticum* (Rodil et al. 2015), which could explain the high abundances of talitrids within *L. ochroleuca* in the present study. Furthermore, Olabarria et al. (2009) previously suggested that *S. muticum* and *Cystoseira baccata* could be among the main wrack food sources for *T. saltator* in both juvenile and adult stages. However, the importance of *S. muticum* as a food source for wrack consumers is temporally variable and dependent on the availability of other indigenous wrack sources (Rossi et al. 2010). Many terrestrial species and larvae are common components in wrack communities that serve to extend and connect land and sea ecosystems (Orr et al. 2005, Rodil et al. 2008, Spiller et al. 2010). However, such a dramatic shift in dominant macrofauna from wrack dependent beach consumers to terrestrial species might have unpredictable implications for beach food webs and ecosystem functioning (Spiller et al. 2010). On temperate beaches that accumulate detached macroalgae, the main consumers, in terms of biomass, are talitrids (Colombini & Chelazzi 2003). These species play an important role in recycling detritus as nutrients that contribute substantially to maintaining coastal primary productivity (Colombini & Chelazzi 2003, Lastra et al. 2008). This process makes marine-derived energy and nutrients

available to other consumers, thus establishing a critical link between the marine and terrestrial ecosystems (Ince et al. 2007, Marczak et al. 2007, Spiller et al. 2010).

Incident solar radiation determines the climatic conditions of our habitats. However, the anthropogenic contribution to changes in the magnitude and variation of solar radiation is a documented phenomenon in temperate latitudes, with potential implications for both climate change and ecosystems (Wild 2009). The implications on beach ecosystems are far from being completely understood. In our study, macrofaunal assemblages were strongly related to wrack patches subjected to full ambient solar radiation, also with the greatest nutritional content and the lowest levels of grazer deterrents. Several studies have evaluated the deleterious effects of increasing UVR on marine benthic communities including macrophytes, consumers and their interactions (e.g. Pavia et al. 1997, Lotze et al. 2002, Swanson & Fox 2007, Rodil et al. 2015). We suggest that even small changes in ambient UVR may be capable of modifying the structural and nutritional status, and thus the ecological significance of beach wrack. Shifts in the availability and type of wrack species, and moderate variations in UVR can consequently affect wrack-associated macrofauna on beaches. These changes can eventually modify the natural energy flow between different trophic levels, resulting in reorganized beach food webs, and drive coastal ecosystems to unprecedented ecological conditions with unpredictable consequences.

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