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Cross-habitat impacts of species decline: response of estuarine sediment communities to changing detrital resources

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Abstract Food webs of many ecosystems are sustained by organic matter from other habitats. Human activities and climatic change are increasingly modifying the quality and supply of these resources, yet for most ecosystems it is unknown how the taxonomic composition of organic matter influences community composition. Along the coastline of Sydney, Australia, the once abundant habitat-forming macroalga, *Phyllospora comosa*, is now locally extinct. Shallow reefs are now primarily occupied by *Sargassum* sp. and, to a lesser extent, the kelp *Ecklonia radiata*. We experimentally manipulated the supply of *P. comosa*, *Sargassum* sp. and *E. radiata* to estuarine sediments to assess responses by macroinvertebrate communities to: (1) changing the identity of the dominant detrital resource; and (2) varying the ratio of input of different macrophytes. Estuarine sediments dosed with *P. comosa* supported greater abundances of macroinvertebrates than sediments receiving *Sargassum* sp. or the kelp *E. radiata*. Whereas plots receiving *Sargassum* sp. or *E. radiata* had fewer macroinvertebrates than controls, plots receiving a moderate (120 g dry weight per m^2) loading of *P. comosa* had more. Mixtures of detritus dominated by *P. comosa* supported similar macroinvertebrate communities to monocultures of the alga. Communities in sediments receiving detritus comprised of less than one-third *P. comosa* were, however, distinctly different. Our study provides evidence that the ecological ramifications of species decline can extend to spatially removed ecosystems, subsidised by allochthonous materials. Even prior to extinction of detrital sources, small changes in their provision of organic matter may alter the structure of subsidised communities.

Keywords Detritus · Extinction · Macroinvertebrates · *Phyllospora comosa* · Spatial subsidy

Introduction

Spatially distinct food webs are often linked through transfer of energy or nutrients. This occurs during the frequent transport of materials, energy, and organisms across ecosystem boundaries. This transfer of resources from a donor to a recipient habitat has been termed a spatial subsidy (Polis et al. 1997). Spatial subsidies are a major determinant of ecosystem functioning in terrestrial and aquatic systems, influencing all aspects of food web structure (Polis et al. 1997).

Spatial subsidies of detritus (dead organic matter) enable secondary productivity in ecosystems that have low or absent primary productivity (Polis et al. 1997). In environments with abundant primary producers, allochthonous detritus can also be the main carbon source (Cebrián and Lartigue 2004). Detritivores directly consume detritus (Findlay and Tenore 1982) or consume microorganisms

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(e.g. diatoms) stimulated by detrital break-down (Rublee 1982). The detritivores are then eaten by first order predators, and these, in turn, can fuel higher trophic levels (Melville and Connolly 2003).

Increasingly, human activities are disrupting transport of detritus across ecosystem boundaries. Climate change, habitat destruction, species introductions and pollution are leading to unprecedented rates of species extinction on global and local scales (Vitousek et al. 1997). This may produce changes in the quantity of detritus reaching a subsidised ecosystem. Changes in quality may also occur where the declining species is replaced with compensating taxa.

In the marine environment, little is known about how the qualitative value of detritus varies among sources. Many of the previous studies considering the spatial subsidy provided by detritus have focused on effects of altering the supply of a single source (e.g. Bishop and Kelaher 2007; Olabarria et al. 2007). Several studies have demonstrated effects of different kelp species on individual consumers (Duggins and Eckman 1994, 1997), but it is poorly understood how changes in the composition of detritus affect the structure of whole communities.

Decomposition studies have indicated that mixing of litter species commonly leads to non-additive effects on decay processes (e.g. Moore and Fairweather 2006). Our own recent research demonstrated non-additive effects on macroinvertebrates of mixing detrital sources, which were not easily predictable from constituent monocultures (Bishop and Kelaher 2008). Another consideration is that most aquatic macrophytes will suffer moderate changes in abundance long before they suffer complete extirpation or extinction. Thus, not only is it important to understand the ramifications of changing detrital species composition, but also more subtle changes in the ratio of constituents.

Here, we assess cascading effects of the local extinction of the habitat-forming macroalga *Phyllospora comosa* on the benthic communities of estuarine mudflats fuelled by detrital subsidies. This alga once occupied moderately exposed to exposed coasts throughout southeastern Australia (Fletcher 1984; Underwood et al. 1991). Today, the macroalga is conspicuously absent from the shallow subtidal reefs around urbanised Sydney (Coleman et al. 2008). The local extinction of *P. comosa*, coincident with the construction of large ocean sewage outfalls (Coleman et al. 2008), represents not only the loss of habitat for subtidal organisms that are associated with its dense canopies (~20 kg m^2 and up to 3 m in height) but also the loss of a detrital resource. Historic references from the 1950s indicate that *Phyllospora* used to be a major contributor to wrack in the Sydney area (Dr Isobel Bennett field notebook, MS9348 National Library of Australia). Although in some instances the loss of *P. comosa* has been accompanied by increases in the abundance of *Sargassum* spp. and, to a lesser extent, the kelp *Ecklonia radiata* (Coleman et al. 2008), it is unclear to what extent these species are redundant in their contribution to the detrital pathways of recipient environments. First, we assess whether monocultures of *P. comosa, Sargassum* sp. and *E. radiata* produce similar biomass-dependent effects on benthic communities. Second, we assess how a decreasing contribution of *P. comosa* and an increasing contribution of *Sargassum* sp., as would have occurred during the decline of *P. comosa*, influences the value of the mix as a spatial subsidy. By comparing the effects of detrital mixtures and constituent monocultures, we assess whether changes in the ratio of detrital resources have predictable impacts on soft sediment assemblages.

Materials and methods

Study site

We tested hypotheses about cascading effects of loss of *Phyllospora comosa* on benthic mudflat communities in Quibray Bay (34°01′29″S, 151°10′45″E), New South Wales (NSW), Australia. Quibray Bay is situated on the southern shore of Botany Bay, a 7-km-long and 5.5-km-wide embayment, approximately 15 km south of Sydney (see Bishop et al. 2007 for a full site description). The bay's extensive intertidal mudflats receive a year-round supply of refractory organic matter from adjacent mixed-species (*Posidonia australis, Zostera capricorni* and *Halophila ovalis*) seagrass beds and nearby *Avicennia marina* mangrove forests. During the summer months, when on-shore winds dominate, this refractory organic matter is supplemented by labile organic material from nearby rocky reefs. The donor rocky shores, situated on both the northern and southern entrances to Botany Bay, historically supported abundant populations of *P. comosa* (Coleman et al. 2008). Today, *P. comosa* is conspicuously absent and the shores are instead dominated by *Sargassum* spp., with lesser amounts of the small kelp *Ecklonia radiata* (M.A. Coleman, personal observation). *Sargassum* spp. now comprise the bulk of macroalgal detritus accumulating on Quibray Bay mudflats (Bishop and Kelaher 2008).

Experimental design

In spring (October–November) 2007, when on-shore winds are just starting to deposit macroalgal material on the Quibray Bay mudflat, we conducted two experiments to assess whether loss of *P. comosa* has cascading effects on soft sediment assemblages. A fully orthogonal experiment with the two factors, detrital identity (3 levels: *Phyllospora* *comosa*, *Ecklonia radiata*, and *Sargassum* sp.) and supply [3 levels: high (90 g dry weight), medium (60 g dry weight), low (30 g dry weight)], examined whether *Sargassum* sp. and *E. radiata* have similar density-dependent effects on macroinvertebrate assemblages and microphytobenthos as the lost resource, *P. comosa* (Table 1). A one-factor experiment, holding density of detritus constant (at 90 g dry weight per plot) examined changes to macroinvertebrate assemblages during the process of replacement of *P. comosa* by *Sargassum* sp. and in some instances, *E. radiata* (Table 1). The 'high' detrital loading was equivalent to a wet weight of approximately 2 kg per m^2, the density of wrack that might reasonably accumulate at our study site following a storm (M.J. Bishop, personal observation). In addition, we established control plots where the sediment was physically disturbed but detritus was not added. As per previous experiments demonstrating detrital impacts (e.g. Bishop and Kelaher 2007, 2008), we established seven plots per experimental treatment.

P. comosa [C:N ratio: 15.8 ± (1 SE) 0.4, $n = 2$], *E. radiata* (C:N ratio: 17.2 ± 0.1, $n = 2$) and *Sargassum* sp. (C:N ratio: 13.1 ± 0.2, $n = 2$) wrack for experimental additions was collected from shores south of Sydney. Wrack was dried (at 60°C to constant weight) and shredded (<2 mm diameter) prior to experimental addition. Shredding maximised the rate at which detritus was uptaken by the benthos, and was representative of the particulate form in which most detrital material is incorporated into estuarine sediments. Drying ensured equivalent biomasses of detrital constituents across replicates, and should not have introduced experimental artifacts because wrack deposited in the intertidal zone is naturally dried at low tide.

At a tidal height of MLW springs +0.4 m, we established 0.25 m^2 plots, separated by at least 1.5 m, to which detrital treatments were haphazardly allocated. Plots were marked with a single PVC stake such that they were open to vertebrate predators and the large mud whelk, *Pyrazus ebeninus*, a key determinant of microphytobenthic biomass and macroinvertebrate abundance and species richness in this particular estuarine system (see Bishop et al. 2007). We manipulated detritus at a small spatial scale because natural topographic features of mudflats such as mounds and depressions produce patchiness in the accumulation of detritus on the scale of metres (Kelaher and Levinton 2003).

Detritus was added to experimental plots at low tide, when the intertidal mudflat is exposed, by evenly hand-churning dried and shredded material into the top 0.05 m of sediments. This method has been used to successfully manipulate detrital quality and quantity at this and other sites (e.g. Kelaher and Levinton 2003; Bishop and Kelaher 2007, 2008). Trials with recalcitrant *Juncus* sp. detritus indicate that 80–90% of the material mixed into sediments is retained over a 1-month period. The physical disturbance of hand-churning does not detectibly influence either benthic invertebrate abundance (ANOVA: $F_{1,8} = 2.51$, $P = 0.26$) or assemblage composition (PERMANOVA: $F_{1,8} = 2.62$, $P = 0.25$). Nevertheless, to assess the impact of detrital manipulations, we compared benthic assemblages to those within the control plots that had been physically disturbed without introduction of detritus.

Table 1 (a) Identity and biomass treatments used to assess whether *Sargassum* sp. and *Ecklonia radiata* have similar density-dependent effects on macroinvertebrate assemblages as the lost resource, *Phyllospora comosa*. (b) Biomass compensation treatments used to assess whether replacement of *P. comosa* by *Sargassum* sp. and, in some instances, *E. radiata*, will impact macroinvertebrate assemblages if there is no overall change in the total supply of detrital material; $n = 7$ plots per treatment

Treatment ID	Dry weight of detritus added (g)			
	Phyllospora	*Sargassum*	*Ecklonia*	Total
(a) Identity and biomass				
A	30			30
B	60			60
C	90			90
D		30		30
E		60		60
F		90		90
G			30	30
H			60	60
I			90	90
(b) Biomass compensation				
C	90			90
F		90		90
I			90	90
J	60	30		90
K	60	20	10	90
L	30	60		90
M	20	60	10	90

We sampled soft-sediment communities in December 2007, 8 weeks after detrital addition. This duration of experiment was sufficiently long for changes in primary and secondary producers to occur and impacts of the physical disturbance of sediments to dissipate, yet brief enough that any short-term responses of organisms to labile sources would still be evident (see Bishop et al. 2007; Bishop and Kelaher 2007). The short duration of the experiment also enabled external inputs of macroalgae from surrounding areas to be controlled by fortnightly hand-removal from control plots as well as those receiving experimental additions (<250 g wet weight of algae removed per plot over the study period).

Macroinvertebrates were sampled by depressing a 100-mm-diameter core in the centre of each plot to a depth of 80 mm. Back at the laboratory, infaunal cores were passed through a 500-μm sieve, with the animals retained fixed in 7% formalin for later enumeration to species, or where this was not possible, morphospecies. The wet weight (following towel drying) of each of the two dominant taxa, *Tellina deltoidalis* and *Nephtys australiensis*, was determined for each sample. This enabled us to ascertain whether any difference in the abundance of these taxa among treatments was compensated for by differences in their size.

Statistical analyses

Nonmetric multidimensional scaling (nMDS; Field et al. 1982) produced two-dimensional ordinations comparing average assemblage structure between treatments receiving a single type of detritus and controls. Non-parameteric multivariate analyses of variance (PERMANOVA; Anderson 2001) on macroinvertebrate assemblages and analyses of variance (ANOVAs) on the total abundance and species richness of infaunal assemblages tested hypotheses regarding effects of changing detrital resources (Table 1). The PERMANOVAs were run on matrices of Bray Curtis dissimilarity, calculated among invertebrate samples using untransformed data. The PERMANOVAs partitioned sources of variation in a similar way to ANOVA and used unrestricted permutation of raw data to assess statistical significance. Most of the ANOVAs also used untransformed data, except in the few instances in which Cochran's *C* test indicated heterogeneous abundance data needing $\sqrt{(x+1)}$ transformation. Analyses were followed by post-hoc tests to identify those treatment means that differed significantly at $\alpha = 0.05$. In the case of ANOVAs, these were Student–Newman–Keuls (SNK) tests.

The SIMPER (similarity of percentages) routine of PRIMER (Plymouth Routines in Multivariate Ecological Research) identified species that were important discriminators among samples (dissimilarity to standard deviation ratio >1.3, Clarke 1993), and abundances of these species were further analysed to determine effects of detrital mixing and identity using ANOVAs. We also ran ANOVAs on the gastropod *P. ebeninus,* which is known to inhibit many other macroinvertebrate species (Bishop and Kelaher 2008).

In order to simultaneously test for differences between the control plots and those enriched with a single detrital source, and differences among enriched treatments attributable to effects of detrital identity and supply, we utilised asymmetrical PERMANOVA and ANOVA. These analyses involved partitioning components of variation through a number of subanalyses (see Winer 1971). First, we ran one-way analyses testing for differences among all ten treatments (nine different types of detrital monoculture and the control). Second, we ran two-way analyses, including only the enrichment treatments, testing for effects of detrital identity and supply. We then subtracted variation among enriched treatments from variation among all treatments to test for effects of enrichment that occurred irrespective of detrital identity.

We used the number and species richness of invertebrates present in the 90-g detrital monocultures to predict expected numbers and types of invertebrates in 90-g mixtures under the null hypothesis of additive effects of mixing. Specifically, we multiplied the average number of invertebrates present in a monoculture by its percent contribution to the total dry weight of detritus in the mixture. This was done for each detrital component of the mixture and the numbers, corresponding to each component, were summed. We compared expected to observed assemblages within mixtures to test for multiplicative effects.

Results

Across the 98 plots sampled, we collected 3,157 invertebrates representing 55 different species. Polychaetes were the most numerous group with the 19 species comprising 35% of the total animals collected. The next most important groups were bivalves (6 species, 31% of total abundance) and amphipods (7 species, 22% of total abundance). Gastropods, decapods, tanaids, isopods, nemerteans and oligochaetes accounted for relatively small proportions of total abundance and diversity. Across all treatments, populations of invertebrates were dominated by small size-classes of animals. Consequently, analyses of biomass revealed similar patterns to analyses of abundance and are not presented here.

Analysis of plots receiving only a single detrital source revealed large effects of the identity, but not the biomass of detritus on benthic assemblages (Tables 2 and 3; Figs. 1 and 2). Macroinvertebrate assemblages in plots receiving *P. comosa* differed from those in plots receiving *E. radiata* or *Sargassum* sp. (significant 'Identity' effect; Table 2), but could not be distinguished from assemblages within control plots (post-hoc tests for significant 'Among all treatments' effect; Table 2). Nevertheless, plots receiving a moderate (30 g) amount of *P. comosa* contained greater abundances of macroinvertebrates than un-enriched control plots. By contrast, plots receiving with *E. radiata* or 60 or 90 g of *Sargassum* sp. had fewer invertebrates than controls (Table 3; Fig. 2). Consequently, macroinvertebrate abundance, like assemblage structure, displayed a significant effect of detrital identity. Fewer invertebrates were found

Table 2 Asymmetrical PERMANOVA testing for effects on macroinvertebrate assemblages of sediment enrichment with three detrital identities. *Phyllospora comosa* (*P*), *Sargassum* sp. (*S*), *Ecklonia radiata* (*E*), at three supply levels: 30 g (*30*), 60 g (*60*), 90 g (*90*) dry weight of particulate detritus

Source	*df*	MS	*F*	*P*
Among all treatments	9	2,167	1.5	**<0.01**
Control vs. enriched	1	3,475	1.0	N/A[a]
Among enriched	8	2,004	1.4	**0.02**
Identity	2	3,447	2.5	**<0.01**
Supply	2	1,631	1.2	0.27
Identity × supply	4	1,469	1.1	0.38
Residual	60	1,414		
Post-hoc test				
Among all treatments		(30P = 60P = 90P = 30S = 90S = C) > (30E = 90E = 60S)		
Identity		P ≠ (E = S)		

Effects of detrital enrichment were compared against a single, unenriched, control (*C*) treatment. The analysis used a Bray Curtis matrix of dissimilarity among invertebrate samples. *P* values were calculated through unrestricted permutation of raw data (see Anderson 2001), $n = 7$. *P* values significant at $\alpha = 0.05$ are shown in bold

[a] Although the MS and *F*-ratio for this source of variation could be computed by partitioning sources of variation, it was not possible to determine the significance of the *F*-ratio

in plots with *Sargassum* or *E. radiata* than in those with *P. comosa* (Table 3; Fig. 2).

The difference among treatments in the total abundance of taxa was driven by the polychaete, *Nephtys australiensis,* which accounted for 11–14% of dissimilarity among treatments and the bivalve, *Tellina deltoidalis*, which accounted for 21–27% of dissimilarity (SIMPER). *N. australiensis* was 80% more abundant in plots with *P. comosa* than *E. radiata,* but pair-wise comparisons could not detect differences in its abundance among the other treatments (Table 3; Fig. 2). *T. deltoidalis* was twice as abundant in plots with *P. comosa* than in plots with the other detrital species (Table 3; Fig. 2). Whereas plots receiving moderate (30 g) amounts of *P. comosa* had greater abundances of *N. australiensis* than control plots (though not significantly so), their density of *T. deltoidalis* was 25% lower than in the control treatment. The keystone whelk, *P. ebeninus*, did not differ in abundance among treatments (Table 3).

Across all biomasses of detrital addition, there was no effect of detrital identity on macroinvertebrate species richness (Table 3; Fig. 2). Plots receiving detritus generally contained a similar species richness of macroinvertebrates as control plots.

Subtle differences in detrital composition, such as might be experienced during the decline of *P. comosa* populations, also influenced benthic assemblages. Among plots to which 90 g of detritus had been added, macroinvertebrate assemblages in plots with *P. comosa* alone were similar to those in plots with only *Sargassum*, or at least 60 g of *P. comosa* as part of a mixture, but differed from assemblages in the other plots with less than 30 g of *P. comosa* component (PERMANOVA: $F_{6,42} = 1.68$, $P = 0.01$; post-hoc tests: P ≠ E, P ≠ P30/S60, P ≠ P20/S60/E10). However, no significant difference was found in the abundance or species richness of macroinvertebrate assemblages among treatments (ANOVA; abundance: $F_{6,42} = 0.93$, $P = 0.48$; species richness: $F_{6,42} = 5.48$, $P = 0.53$; Fig. 3). On the contrary, multivariate patterns appeared to be driven by one taxon, the polychaete *N. australiensis* (ANOVA, significant treatment effect: $F_{6,42} = 2.93$, $P = 0.05$; Fig. 3).

Mixtures of detrital sources generally supported the types and numbers of macroinvertebrates that would be expected if effects of constituent monocultures were additive. Nevertheless, the treatment with 60 g of *P. comosa*, 20 g of *Sargassum* sp. and 10 g of *E. radiata* supported fewer macroinvertebrates than predicted from the additive model (Fig. 3a). Similarly, the mixture with 20 g of *P. comosa*, 60 g of *Sargassum* sp. and 10 g of *E. radiata* contained fewer *N. australiensis* than expected (Fig. 3b).

Discussion

Our experiments suggest that, along the east coast of Australia, loss of the macroalga *Phyllospora comosa* from rocky reefs will have cascading effects on spatially distinct soft-sediment ecosystems. Moderate dosing of estuarine sediments with *P. comosa,* once an important contributor of wrack, facilitated a greater abundance of macroinvertebrates than unenriched control plots. Neither the plots receiving *Sargassum* sp. nor those receiving *E. radiata,* the species that have replaced *P. comosa* on rocky shores, were

Table 3 Asymmetrical analyses of variance testing for effects on macroinvertebrate abundance and richness of sediment enrichment with three detrital identities. *Phyllospora comosa* (*P*), *Sargassum* sp. (*S*), *Ecklonia radiata* (*E*), at three supply levels: 30 g (*30*), 60 g (*60*), 90 g (*90*) dry weight of particulate detritus

Source	*df*	Macroinveretebrate abundance			Macroinveretebrate richness			*Nephyts australiensis* abundance			*Tellina delatoidalis* abundance			*Pyrazus ebeninus* abundance[a]		
		MS	*F*	*P*	MS	*F*	*P*	MS	*F*	*P*	MS	*F*	*P*	MS	*F*	*P*
Among all treatments	9	499	4.8	**<0.01**	8.8	1.7	0.11	16.7	1.1	0.36	201.5	3.2	**<0.01**	0.06	1.05	0.41
Control vs. enriched	1	454	0.9	0.37	16.5	2.1	0.18	6.7	0.4	0.56	617.4	4.1	0.08	0.05	0.82	0.39
Among enriched	8	505	5.4	**<0.01**	7.8	1.4	0.22	17.9	1.3	0.27	149.6	3.2	**<0.01**	0.06	0.97	0.47
Identity	2	1,556	8.3	**0.04**	12.9	1.9	0.27	50.3	3.6	**0.03**	420.4	8.9	**<0.01**	0.03	0.39	0.68
Supply	2	87	0.9	0.40	4.4	0.8	0.46	6.0	0.4	0.66	33.7	0.7	0.50	0.06	0.90	0.41
Identity × supply	4	188	2.0	0.10	6.9	1.2	0.30	7.7	0.6	0.70	72.1	1.5	0.21	0.08	1.29	0.29
Residual	60	103			5.2			14.8			52.5			0.06		
SNK test																
Among all treatments		30P > (60P = 90P = 30S = C) > (60S = 90S = 30E = 60E = 90E)									C > (P30 = P60 = P90) > (60E = 30S = 90S) > (30E = 90E = 60S)					
Identity		P > (E = S)						P > E, P = S, S = E			P > (E = S)					

Effects of detrital enrichment were compared against a single, unenriched, control (*C*) treatment, $n = 7$. *P* values significant at $\alpha = 0.05$ are shown in bold

[a] Data were squareroot $(x + 1)$ transformed prior to analysis

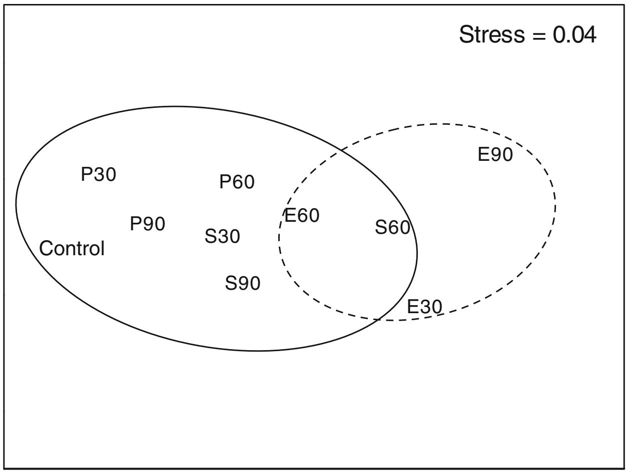

Fig. 1 nMDS ordination of mean macroinvertebrate assemblages present within plots to which *Phyllospora comosa* (*P*), *Ecklonia radiata* (*E*), *Sargassum* sp. (*S*) was added, at a dry weight of 30 g (*30*), 60 g (*60*), 90 g (*90*). *Control* denotes plots that were physically disturbed but did not receive detritus. *Circles* enclose groups of treatments that were statistically indistinguishable (at $\alpha = 0.05$), according to PERMANOVA analysis, $n = 7$

able to sustain the densities of fauna supported by plots with *P. comosa*.

Increasing the amount of *P. comosa* with which sediments were dosed from 30 to 60 g or 90 g decreased the abundance of macroinvertebrates in experimental plots. Whereas plots receiving 30 g of *P. comosa* contained more invertebrates than any of the other treatments, plots receiving greater amounts (60 or 90 g) of this detrital source contained similar numbers of invertebrates to control plots. In the plots receiving 60 or 90 g of *P. comosa*, it is possible that detrital mixing, through the stimulation of microbial processes, reduced sediment oxygen. Nevertheless, both control plots and those with higher *P. comosa* loads supported more invertebrates than the plots receiving 30, 60 or 90 g of the labile macroalgae, *E. radiata* or *Sargassum* sp. The greater number of macroinvertebrates in control plots than in plots with *E. radiata* or *Sargassum* sp. suggests that in this system there may be another source of labile detritus, perhaps phytoplankton, that was not considered here and which could help sustain benthic productivity in the absence of macroalgal sources.

Mixtures of detritus dominated by *P. comosa* supported similar macroinvertebrate communities to monocultures of the alga. Communities in sediments receiving detritus comprised of less than one-third *P. comosa* were, however, distinctly different. Thus, as *P. comosa* populations begin to decline, cascading impacts on estuarine sediments may be apparent long before the species becomes locally extinct. Recent poleward range expansion of the grazing sea urchin *Centrostephanus rodgersii* is reducing the abundance of *P. comosa* in Tasmania (Ling 2008). Further,

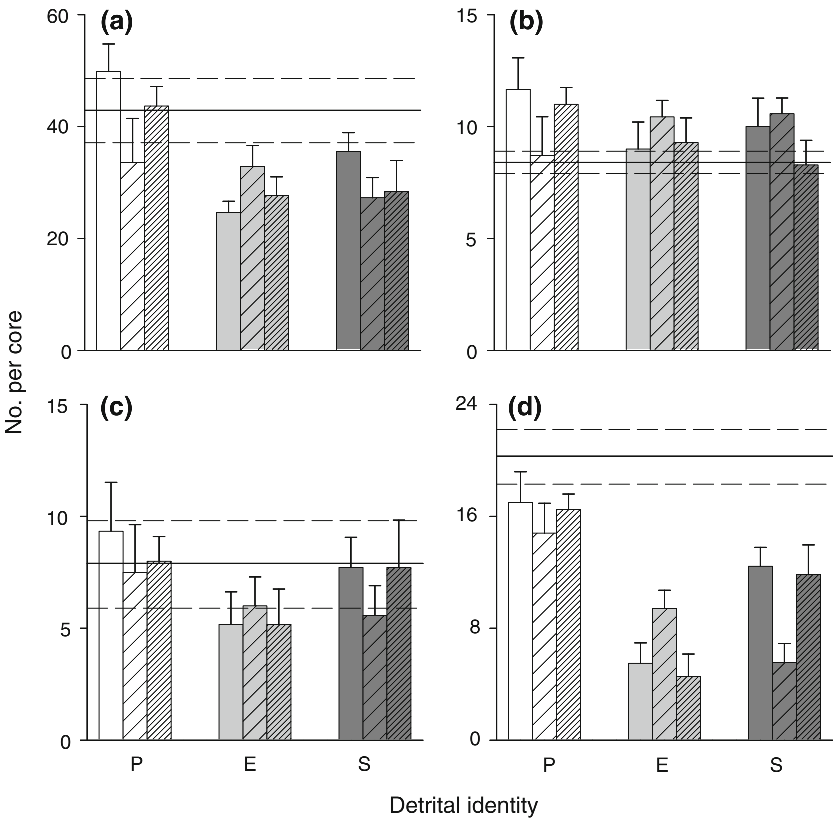

Fig. 2 Mean (+1 SE) of **a** total abundance and **b** species richness of macroinvertebrates, and abundance of the discriminating taxa, **c** *Nephtys australiensis* and **d** *Tellina deltoidalis* in cores of sediment collected from plots enriched with *Phyllospora comosa* (*P*; *white bars*), *Ecklonia radiata* (*E*; *light grey bars*) or *Sargassum* sp. (*S*; *dark grey bars*). Plots received either 30 g (*plain bars*), 60 g (*low density stripes*) or 90 g (*high density stripes*) of dried, shredded detritus, *n* = 7. The *solid line* denotes the mean abundance of macroinvertebrates in control plots that were physically disturbed but did not receive detritus; the *broken lines* indicated one standard error either side of this mean

competition with the introduced macroalga *Undaria pinnatifida* is limiting the ability of *P. comosa* to reestablish following natural die-back (Valentine and Johnson 2004). Such declines in this important habitat-forming alga may therefore have widespread consequences, extending to changes in soft-sediment systems.

In this study, mixing of detrital sources generally produced additive effects on benthic assemblages. However, the mixture containing 60 g of *P. comosa*, 20 g of *Sargassum* and 10 g of *E. radiata* supported approximately 25% fewer macroinvertebrates than predicted from its constituent monocultures, and the mixture of 20 g of *P. comosa*, 60 g of *Sargassum* and 10 g of *E. radiata* supported fewer nehpytids, *Nephtys australiensis*, than would be expected if effects of mixing were additive. Thus, consistent with results from our previous investigation of effects of detrital mixing (Bishop and Kelaher 2008), the present results support effects on macroinvertebrates of detrital species mixing that are dependent on detrital identity and, where non-additive, are generally antagonistic. Whereas in the previous study, which manipulated availability of detritus from *Sargassum* sp., the seagrass *Posidonia australis* and the grey mangrove *Avicennia marina*, synergistic effects were most apparent in mixtures containing *Sargassum* sp. (Bishop and Kelaher 2008), here effects were confined to treatments with *E. radiata*. If detrital heterogeneity is to be successfully incorporated into food web models, the processes by which these antagonistic and seemingly idiosyncratic effects arise will need to be understood.

Differences among plots in the abundance of macroinvertebrates were driven by two taxa. *Nephtys australiensis* was more abundant in plots with *P. comosa* than plots with *E. radiata*. The tellinid, *Tellina deltoidalis*, was more abundant in control plots than those to which detritus had been added, but among plots with detritus was more abundant in those with *P. comosa* than those with other sources. *N. australiensis* and *T. deltoidalis* display very different feeding modes: *N. australiensis* is thought to feed primarily as a predator on other invertebrates (Glasby et al. 2000); *T. deltoidalis* is a deposit feeder, collecting organic material and particles from surface sediments (Willan 1998; Ponder et al. 2000). The common response may be explained by the predator *N. australiensis* responding to resource driven increases in *T. delatoidalis*, a potential prey item.

Alternatively, each of these species, which have a planktotrophic larval phase (Willan 1998; Glasby et al. 2000; Ponder et al. 2000) may not recruit to areas with *E. radiata* detritus due to the alga's high phenolic content (~5.5% dry weight, as compared to 2.7% for *P. comosa* and 3–4% for *Sargassum* sp.; Steinberg 1989). Although Australian herbivores, which have experienced prolonged exposure to high phenolic concentrations, may be able to tolerate the phenolic concentrations found within *E. radiata* (e.g. Steinberg 1989; Steinberg and van Altena 1992),

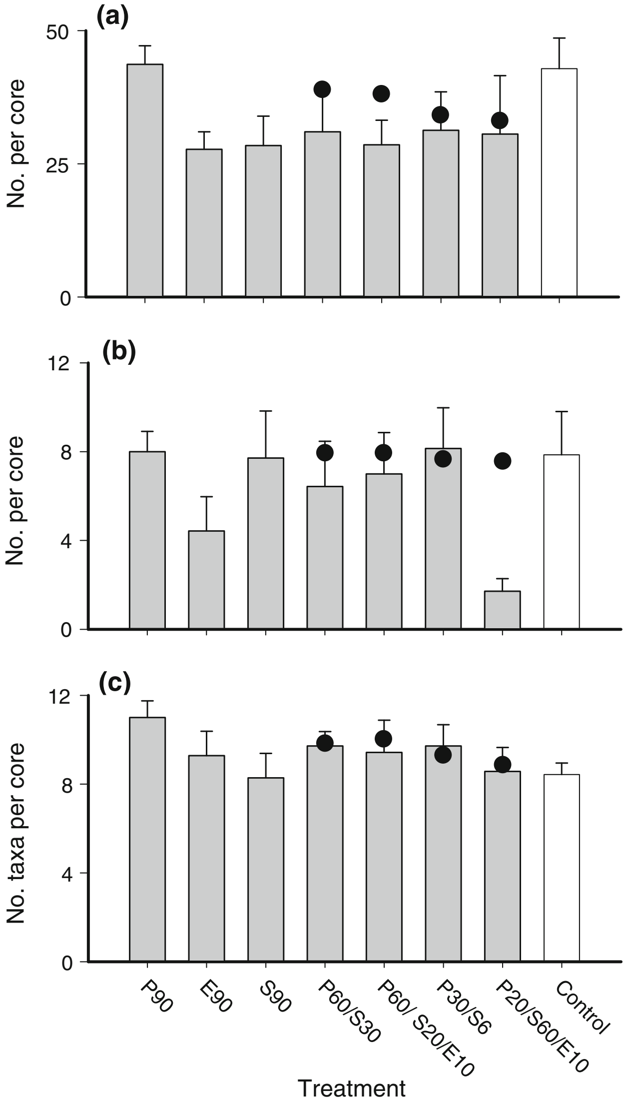

Fig. 3 Mean (+1 SE) of **a** total abundance of macroinvertebrates, **b** abundance of *Nephtys australiensis* and **c** species richness of macroinvertbrates in plots enriched with 90 g of *Phyllospora comosa* (*P*), *Ecklonia radiata* (*E*), *Sargassum* sp. (*S*), or mixtures of these. *Control* denotes plots that were physically disturbed but did not receive detritus, $n = 7$. *Black dots* denote the predicted abundance/species richness of macroinvertebrates in plots receiving detrital mixtures, under the assumption that detrital sources have additive effects

estuarine detritivores that are only periodically exposed to this material may be deterred by this material. The C:N ratios of the three detrital sources were similar (range 13.1–17.2) and are unlikely to have contributed to differences in benthic assemblages. The large mud-whelk, *Pyrazus ebeninus*, which has previously been demonstrated to have a large impact on benthic assemblage structure at our study site (Bishop and Kelaher 2008) did not differ among our experimental treatments and is therefore unlikely to have contributed to our results.

Our study considered impacts of particulate detritus to soft sediment systems which is consistent with most algae displaced from rocky reefs being highly fragmented by the time the detritus is incorporated into estuarine sediments. Where macroalgae wash up whole, the physical structure of the detritus may, however, further influence macroinvertebrate assemblages by providing refuges from predators and harsh abiotic conditions, altering the availability of light to primary producers and acting as a physical barrier to new settlers. The three species considered here, *P. comosa*, *Sargassum* sp. and *E. radiata*, differ markedly in their morphology. Whereas *P. comosa* can grow to 3 m and *E. radiata* to 2 m in length, *Sargassum* spp. are typically much smaller, <0.3 m in length. *P. comosa* has a thallus with long strap-like fronds, *E. radiata* has a large lamina with spines and *Sargassum* spp. are finely branched and leaf-like. These differences in morphology will further contribute to differences among the macroalgal species in their value as a resource on coastal beaches where they wash in as fresh, whole pieces.

P. comosa is just one of the many important detrital donors that are under threat as a result of human activities. In the marine environment, many other species of canopy-forming macroalgae are experiencing similar decline (Steneck et al. 2002; Airoldi and Beck 2007; Connell et al. 2008), and eutrophication is presently threatening seagrass (Duarte 2002). On the land, deforestation, agriculture and urbanisation are having major impacts on the types of detritus entering terrestrial food webs, and those of adjacent aquatic systems (Lake et al. 2000). Our study provides evidence that the ecological ramifications of decline and extirpation of habitat forming species will extend to spatially distinct ecosystems that are dependent on allochthonous materials to sustain their detritus-based food webs.

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