

Impacts of detritus from the invasive alga *Caulerpa taxifolia* on a soft sediment community

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ABSTRACT: Invasive primary producers can dramatically reorganize food webs through detrital subsidies. This study assessed (1) contributions of the invasive alga *Caulerpa taxifolia* to detrital resources of temperate Australian estuaries, and (2) effects of these contributions on sediment-dwelling invertebrates. In an invaded estuary, sampling of an intertidal shore indicated *C. taxifolia* fragments were consistently present in organic matter deposits and were particularly abundant following storms. Sampling of the alga across 6 invaded estuaries showed that the ratio of organic carbon to nitrogen (C:N) in fresh tissue varied between 7 and 16. To determine how *C. taxifolia* detritus influences benthic macrofaunal assemblages and whether this influence depends on the quantity and C:N ratio of *C. taxifolia* detritus, a manipulative field experiment was performed. On a sheltered intertidal mudflat, 0.25 m² plots of sediment were experimentally enriched with either a high (90 g DW) or low (30 g) loading of high C:N (14) or low C:N (7) *C. taxifolia* detritus. Experimental enrichment negatively affected the total abundance and species richness of macroinvertebrates relative to controls, and these effects increased with detrital loading. For some macrofauna, reducing the C:N ratio tended to exacerbate negative effects on abundances, whereas it moderated these effects for other species. Given that organic matter derived from invasive species can be transported beyond the distribution of live invaders, greater consideration should be given to the potential broad-scale effects of invasive primary producers on detrital pathways.

KEY WORDS: Detritus · *Caulerpa taxifolia* · Food quality · Invasion · Nitrogen content · Spatial subsidy

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INTRODUCTION

Detritus (i.e. decaying dedead organic matter) serves as an important source of energy and nutrients in many aquatic and terrestrial food webs (Polis & Strong 1996, Moore et al. 2004). Detritus is directly consumed by some detritivores (Findlay & Tenore 1982) or is the indirect source of nutrition for other organisms that consume microorganisms stimulated by detrital breakdown (Ruble 1982). Detritivores are in turn eaten by secondary consumers that fuel higher trophic levels (e.g. Chen & Wise 1999).

Detritus is frequently transported across ecosystem boundaries by water, wind or animals (see Polis et al. 1997). Hence, the detritus supporting a particular food web may come from autochthonous or allochthonous sources, which are of varying value to food webs (Moore et al. 2004). Refractory sources of detritus, which have a high carbon to nitrogen ratio (C:N), are composed of complex structural materials, providing more prolonged nutrition to slow growing consumers with powerful digestive mechanisms (Tenore et al. 1979). Detritus derived from less structurally complex biota with a high nitrogen content, termed labile

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sources, typically degrades rapidly and produces a short-term nutritional source to fast growing consumers (Tenore 1977). Although the C:N ratio of detritus can change during degradation (Anderson 1973, Suberkropp et al. 1976), the starting C:N ratio is a good predictor of decomposition rate (Enriquez et al. 1993).

Invasive primary producers are an increasingly large component of detrital pools (Kennedy & Hobbie 2004, Rodil et al. 2008) and have the potential to markedly alter their value. Many successful invaders have rapid individual growth, early maturity, a short life span, high fecundity, minimal structural defence and extensive dispersal capacity (Lodge 1993, Schaffelke et al. 2006). Consequently, invasive primary producers tend to generate large amounts of labile detritus with a low C:N ratio, which is more readily decomposed than is litter from native species (Vitousek et al. 1987, Ashton et al. 2005). Whereas small amounts of refractory detritus may fuel productivity, large quantities of labile detritus may induce sediment anoxia (Pearson & Rosenberg 1978). This phenomenon may be exacerbated in areas of nutrient enrichment where invasive primary producers, which tend to display plasticity in physiological traits (Callaway et al. 2003, Funk 2008), may acquire a much higher nitrogen content than in less enriched environments.

In general, the potential effect of organic material from invasive species on detrital pathways of nutrition is rarely considered. The first studies to address effects of invasive species on detritus considered only changes in the decomposition processes (e.g. Allison & Vitousek 2004, Kennedy & Hobbie 2004, Ashton et al. 2005). Recent studies have now begun to consider effects propagating through the food web to consumers (Levin et al. 2006, Rodil et al. 2008, Whitcraft et al. 2008, Casu et al. 2009). No studies have investigated whether effects are greater when the detrital material has come from a source growing in nutrient-enriched environments, where the invasive plant may rapidly assimilate nitrogen, making its detritus a more labile resource.

Caulerpa taxifolia (Vahl) C. Agardh is an invasive marine macroalga from the phylum Chlorophyta, of which 7 of the 9 orders contain introduced species (Schaffelke et al. 2006). The invasive alga earned notoriety from its proliferation in the Mediterranean (see Meinesz et al. 2001), but since 2000 has also established in 13 estuaries or coastal lakes of New South Wales (NSW), Australia. Research into *C. taxifolia* has focused largely on its range expansion (e.g. Meinesz et al. 2001) and effects of the live alga on local seagrass populations (Ceccherelli & Cinelli 1997, Ceccherelli & Sechi 2002, Holmer et al. 2009), epi- and in-fauna (Gollan & Wright 2006, Wright et al. 2007, Gribben et al. 2009, McKinnon et al. 2009) and fish assemblages

(York et al. 2006). Also, *C. taxifolia* also has the potential to markedly alter detrital pools. *C. taxifolia* easily fragments and can be transported large distances (Ceccherelli & Cinelli 1999, West et al. 2009), it contains the secondary metabolite Caulerpenyne that can deter some herbivores and limit fouling (Lemée et al. 1993, Amade & Lemée 1998). *Caulerpa* spp. are known to rapidly assimilate nitrogen from their environments (Chisholm & Moulin 2003, Lapointe et al. 2005).

This study provides the first assessment of the effects of detritus derived from *Caulerpa taxifolia*. An observational component documents the contribution of *C. taxifolia* to detrital resources of temperate Australian estuaries, whilst a detrital addition experiment assesses effects of *C. taxifolia* detritus to sediment communities. It is anticipated that (1) in an invaded estuary, *C. taxifolia* will be a temporally persistent, though proportionately variable, component of wrack deposits; (2) among invaded estuaries, the C:N ratio of the material deposited will be spatio-temporally variable; and (3) the quantity and initial quality of *C. taxifolia* detritus enriching sediments will determine the effect on infaunal assemblages. The detrital addition experiment thereby provides the first test of how plasticity in the traits of an invader (C:N ratio) can affect its consumers. Understanding effects of invasive species on detrital resources is critical, given the importance of this pathway in determining food web structure.

MATERIALS AND METHODS

Spatial and temporal variability in detrital quantity and quality. To determine whether in an invaded estuary *Caulerpa taxifolia* is a persistent component of wrack deposits and displays significant temporal variability in its contribution, monthly samples of wrack (dislodged macrophytic matter) were collected between February and July 2007 from the southern side of Botany Bay (33° 59' S, 151° 12' E), a large embayment, 15 km south of Sydney. On each sampling date, 5 replicate samples of wrack, floating in the shallow water of the intertidal zone (~mean low water [MLW], +0.4 to 0.6 m), were collected at each of 2 sites using a 250 × 190 mm dip net. The sites were 260 m apart and were not places where living *C. taxifolia* was growing. Each site was sampled on an incoming tide at ~0.5 m water depth. We chose to sample wrack on, rather than below, the sediment surface because the particulate nature of material incorporated into sediments makes it difficult to identify to species. We also expected that *C. taxifolia* in sediments would rapidly decompose, making the standing stock in sediments a poor metric of the contribution of *C. taxifolia* to detrital pathways. Observations of some larger *C. taxifolia* fragments in sedi-

ments in these and other sites around Botany Bay indicate that much of this material ends up in sediments.

In the laboratory, wrack samples were washed over a 6.7 mm sieve to remove sand and shell grit. In each sample, *Caulerpa taxifolia* was separated from other wrack components, dried at 60°C to a constant weight (DW), and weighed. The combined DW of the other detrital fractions was also determined to calculate the percentage contribution of *C. taxifolia* to the total detrital biomass. The temporal contribution of *C. taxifolia* to wrack deposits was then used to ascertain high and low loadings to be added to sediments in the manipulative field experiment, also conducted in this estuary (see 'Experimental manipulation of quantity and quality of detritus').

To ascertain how the C:N ratio of *Caulerpa taxifolia* varies across large spatio-temporal scales, *C. taxifolia* was collected from 6 estuaries where the alga is established: Pittwater (33° 35' S, 151° 19' E), Botany Bay (34° 00' S, 151° 14' E), St Georges Basin (35° 11' S, 150° 36' E), Lake Conjola (35° 16' S, 150° 30' E), Narrawallee Inlet (35° 18' S, 150° 28' E) and Burrill Lake (35° 24' S, 150° 27' E). Within each estuary, a 200 to 300 g sample of live *C. taxifolia* was randomly taken from at least 1 location, but more typically 2 to 3, separated by kilometres. Where possible, samples were collected from each location on multiple dates during the warm months (November to May; see Table 1). Each sample was dried at 60°C prior to transport back to the laboratory to avoid any changes in C:N ratio as a result of degradation. Upon return to the laboratory, each sample was ground into a fine powder using a ball mill. Total organic C and N of a ~0.2 g sub-sample were determined as a percentage using a CHN analyser (Leco TrueSpec CN). We ascertained the C:N ratio of live material as opposed to wrack, to minimise variability due to differences in the age of the material. A pilot study in Botany Bay indicated that the C:N ratio of fresh wrack samples washed up on shore was within the range found within live specimens collected from this estuary.

Experimental manipulation of quantity and quality of detritus. A field experiment investigating effects of *Caulerpa taxifolia* detritus on soft sediment macrofauna was done on an intertidal mudflat in Quibray Bay (33° 59' S, 151° 12' E), on the south side of Botany Bay (Bishop et al. 2007). The mudflat receives organic matter inputs from an adjacent *Avicennia marina* mangrove forest, intertidal and shallow subtidal seagrasses, and seasonally, from dense patches of *C. taxifolia* within and around the seagrass (S. L. Taylor pers. obs.). Experimental enrichments of *C. taxifolia* detritus were done at a tidal height of MLW neap + 0.4 m, in 0.25 m² sediment plots, separated by 1 m and marked with a PVC stake such that they were open to mobile

species. A small spatial scale was chosen for manipulation of *C. taxifolia* detritus because mudflats are typically 'patchy' in resources on a spatial scale of metres (Thrush 1991, Kelaher & Levinton 2003), with organic material tending to accumulate in depressions formed by bioturbation e.g. by sting rays.

The experiment had 5 treatments: 2 fully orthogonal factors, quantity and quality of *Caulerpa taxifolia* detritus, each with 2 fixed levels, and an unenriched control. The 2 levels of detrital quantity were high (90 g DW) and low (30 g DW). The high quantity was based on observations of *C. taxifolia* washed up on shores following severe storms in winter, the season in which there is also typically a reduction in *C. taxifolia* biomass (see 'Results'). The low quantity represented a deposit more likely to occur during normal weather periods. The 2 levels of detrital quality were nitrogen-rich (low C:N of 7.5 ± 0.3 , $n = 4$, from Silver Beach, NSW) and nitrogen-poor (high C:N of 13.9 ± 0.9 , $n = 4$, from Pittwater, NSW) *C. taxifolia* detritus. Two detrital qualities were used following evidence of differences in C:N ratios of *C. taxifolia* among and within NSW estuaries (see 'Results'). The 2 different quality types were harvested from live beds of *C. taxifolia*, dried at 60°C to constant weight and the quality determined using CHN analysis as described above. The control treatment did not receive any detritus but was otherwise treated identically to the *C. taxifolia* addition treatments. Seven plots were randomly assigned to each of the 5 treatments.

Caulerpa taxifolia was added to plots assigned to the addition treatments in a dried, shredded (<2 mm diameter) form. This was to represent natural wrack, which on mud flats experiences drying at low tide and often needs to be mechanically broken down before it can be incorporated into intertidal sediments. Drying the *C. taxifolia* before adding it to the plots also prevented significant decomposition from occurring between collection and the experiment, which would have led to heterogeneity in C:N ratio. When rehydrated in the sediment, the detritus was expected to break down and subsequently the C:N ratio would change, but the starting quality was constant for all replicates within a treatment. Experimental additions of detritus were performed by hand-churning the shredded *C. taxifolia* into the top few centimetres of experimental plots. Previous studies have shown this method of addition successfully manipulates detrital quantity at this and other sites (see Kelaher & Levinton 2003, Bishop & Kelaher 2008). Furthermore, trials with recalcitrant *Juncus* sp. detritus indicated that only 10% of the material mixed into sediments using this method is washed out over a 1 mo period (M. J. Bishop unpub.). To control for the physical disturbance of sediments associated with detrital addition, control plots received similar hand-

churning as detrital addition treatments. Undisturbed control plots were not included in the design because a previous study on the same mudflat found that in the absence of detrital enrichment, there is no significant difference in invertebrate communities between churned and undisturbed plots (Bishop et al. 2007).

After 7 wk, macroinvertebrates were sampled from each experimental plot using a 100 mm internal diameter corer depressed to a depth of 100 mm. Cores were washed through a 500 μm sieve and all fauna retained on the sieve were fixed in 8% buffered formalin and then transferred to 70% ethanol for enumeration and identification to either species level or, where this was not possible, morphospecies (Oliver & Beattie 1996).

Analyses. Two-way analysis of variance (ANOVA) tested for differences of *Caulerpa taxifolia* DW in wrack among sampling dates (monthly, February to July) and between the 2 study sites ($n = 5$). One-way ANOVA tested for differences in C:N ratio of *C. taxifolia* samples among the 19 collections made over a 5 mo period from 13 sites distributed across 6 estuaries ($n = 2$, see Table 1 for details of each collection). Samples collected from multiple sites within an estuary and from an estuary at multiple times were considered independent. Differences between these samples from within a single estuary were just as great as between samples that had come from different estuaries. Prior to each ANOVA, homogeneity of variances was tested using Cochran's *C* test, which was found to be non-significant for all tests. *A posteriori* Student-Newman-Keuls (SNK) tests identified significant differences among the means of treatments when ANOVA was significant.

Non-metric multidimensional scaling (nMDS) was used to produce a 2D ordination of macrofaunal assemblages present in cores of sediment collected from the field experiment. The ordination was based on a Bray–Curtis dissimilarity matrix (Bray & Curtis 1957) derived from untransformed data. Hypotheses about the effects of *Caulerpa taxifolia* detritus on infaunal communities were tested using 1-way non-parametric multivariate analyses of variance (PERMANOVA, Anderson 2001) on Bray–Curtis dissimilarity measures derived from untransformed data. The single factor, treatment, had 5 levels: the control plus the 4 experimental treatments. The SIMPER (Similarity of Percentages) routine in PRIMER version 5.2.7 (Primer-E) identified species that were important discriminators of macroinvertebrate assemblages among treatments (dissimilarity to SD ratio >1.3 , Clarke 1993).

One-way ANOVA was used to assess the effects of *Caulerpa taxifolia* detrital addition on the abundance and species richness of infauna as well as taxa identified by SIMPER as key species. As with the PERMANOVA, the single factor treatment had 5 levels.

Homogeneity of variances was confirmed using Cochran's *C* test, and SNK tests were used for a *posteriori* comparisons (as above).

RESULTS

Spatial and temporal variability in detrital quantity and quality

At each of the two sites in Botany Bay, *Caulerpa taxifolia* was present in wrack deposits at all 6 sampling times (February to July 2007). At one of the sites, the contribution of the alga to wrack deposits peaked in February (ANOVA: month \times site: $F_{5,48} = 5.64$, $p = 0.0004$; SNK, Site 1: March = April = July = May = June $<$ February), but at the other site, a peak was seen in June following winter storms, which coincided with the natural annual regression of *C. taxifolia* (SNK, Site 2: March = May = February = July = April $<$ June). At the first site, the contribution by weight of the alga to total wrack deposits remained $<1\%$, even during the February peak. At the second site, the June influx of *C. taxifolia* inflated the contribution of the non-native species from a baseline of $<1\%$ to $13 \pm 5\%$ of total wrack.

Sampling of *Caulerpa taxifolia* from 13 sites distributed across 6 estuaries revealed significant spatio-temporal variability in the C:N ratio of the alga (ANOVA: $F_{18,19} = 50.13$, $p < 0.0001$, Table 1). The highest C:N was 15.9 ± 0.0 at St Georges Basin, while the lowest C:N ratio of 7.2 ± 0.2 was recorded in Botany Bay.

Experimental manipulation of detritus quantity and quality

A total of 3568 invertebrates from 41 species were identified from the manipulative experiment. Polychaetes and gastropods were the 2 most diverse groups, contributing 12 and 11 different species, respectively. The sabellid polychaete *Euchone variabilis* constituted 57% of the total number of individuals sampled.

Infaunal assemblages in control plots were significantly different from those receiving *Caulerpa taxifolia* detritus (PERMANOVA: pseudo- $F_{4,30} = 9.86$, $p < 0.001$; Fig. 1). There was a clear effect of quantity of detritus, but no significant effect of the quality of *C. taxifolia* detritus on macroinvertebrate assemblages (pairwise tests: [90 g, low C:N = 90 g, high C:N] \neq [30 g, low C:N = 30 g, high C:N] \neq Control; Fig. 1).

The abundance of macroinvertebrates was reduced significantly in plots enriched with 90 g of detritus and also, but to a lesser extent, in plots enriched with 30 g of detritus (ANOVA: $F_{4,30} = 25.0$, $p < 0.001$; Fig. 2a).

Table 1. *Caulerpa taxifolia*. Spatio-temporal variation of total organic C:N ratio (means \pm SE) in algae sampled from different locations in 6 New South Wales estuaries (n = 2)

Estuary	Location	Date	C:N ratio
Pittwater	Church Point	Nov 06	14.0 \pm 0.04
Botany Bay	Quibray Bay	30 Jan 07	13.8 \pm 0.04
	Silver Beach	15 Mar 07	9.7 \pm 0.29
	Kurnell	29 Mar 07	7.5 \pm 0.20
	Silver Beach	27 Apr 07	7.2 \pm 0.25
	Kurnell	02 May 07	7.6 \pm 0.13
St Georges Basin	Basin View	22 Nov 06	11.6 \pm 0.21
	Pattimores Lagoon	23 Nov 06	11.9 \pm 0.08
	Island Point	27 Feb 07	13.1 \pm 0.05
	Basin View	27 Feb 07	15.9 \pm 0.02
	Basin View	14 Mar 07	12.0 \pm 0.05
Lake Conjola	West Conjola	22 Nov 06	10.5 \pm 0.25
	Caravan Park	23 Nov 06	9.4 \pm 0.66
	West Conjola	28 Feb 07	12.9 \pm 0.83
	Berringer	01 Mar 07	12.2 \pm 0.30
Narrawallee Inlet	Site 1	01 Mar 07	9.9 \pm 0.19
	Site 2	01 Mar 07	10.3 \pm 0.08
Burrill Lake	SW Arm	28 Feb 07	11.2 \pm 0.12
	Burrill Lake South	28 Feb 07	11.9 \pm 0.67

The quality of the detritus (low versus high C:N) had no discernable effects on macroinvertebrate abundance (Fig. 2a). Macroinvertebrate species richness was reduced significantly by the addition of 90 g of either low or high C:N detritus (ANOVA: $F_{4,30} = 6.0$, $p < 0.01$), whereas the 30 g additions had no significant effects on richness (Fig. 2b).

SIMPER analyses identified 4 taxa—the polychaetes *Euchone variabilis* and *Nephtys australiensis*, the gastropod *Salinator fragilis* and a gammarid amphipod morphospecies — as good discriminators of macro-

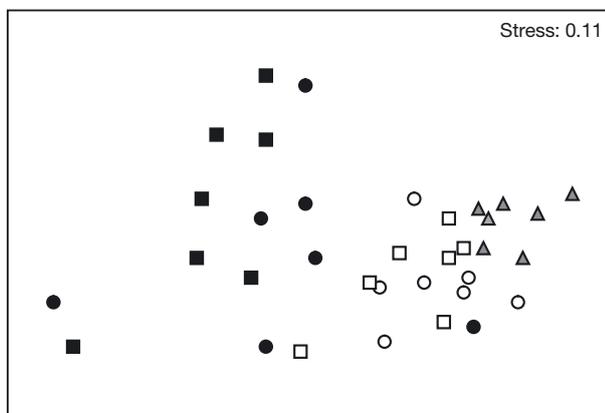


Fig. 1. *Caulerpa taxifolia*. Non-metric multidimensional scaling comparing macrofaunal assemblages between plots receiving high (90 g, ■, ●) or low (30 g, □, ○) loading of *C. taxifolia* detritus, and unenriched control plots (▲). Detritus C:N ratio received in enriched plots: 13.9 \pm 0.9 (high, ○, ●) and 7.5 \pm 0.3 (low, □, ■) (n = 7)

faunal assemblages among treatments. Patterns for total macroinvertebrate abundance were driven primarily by the numerically dominant polychaete *E. variabilis*, which showed the same significant reduction in abundances with increases in quantity of detritus, but no significant effect of detrital quality (ANOVA: $F_{4,30} = 18.4$, $p < 0.001$). There was, however, a non-significant trend for numbers of *E. variabilis* to be reduced more by the lower quality detritus in the 90 g addition treatments (Fig. 2c). Patterns for the gammarid amphipod were essentially the same as those for *E. variabilis*, with abundances decreasing with increasing quantity of detritus (ANOVA: $F_{4,30} = 4.5$, $p < 0.01$; Fig. 2d). SNK tests could not, however, resolve any differences among the 30 g low or high quality detritus and the 90 g high quality treatment (Fig. 2d).

Abundances of the polychaete *Nephtys australiensis* were reduced significantly by the addition of 90 g of high quality detritus (ANOVA: $F_{4,30} = 10.8$, $p < 0.001$; Fig. 2e). Again, *a posteriori* comparisons of means could not unequivocally discriminate differences among the other treatments, but there was a clear trend for high quality detritus to have the most negative impact on abundances of *N. australiensis* for both the 30 and 90 g additions (Fig. 2e). Detrital additions had no significant effects on abundances of the gastropod *Salinator fragilis* (ANOVA: $F_{4,30} = 1.1$, $p > 0.30$). Interestingly the pattern among treatments for *S. fragilis* was the opposite of that for the other taxa, with means of all detrital addition treatments being greater than the unenriched control (Fig. 2f).

DISCUSSION

The alteration of detrital food webs by the organic material of invasive plants has received little attention. Siphonous green seaweeds, such as *Caulerpa taxifolia*, *C. racemosa* and *Codium fragile* ssp. *fragile* are highly successful invaders of aquatic ecosystems. Due to their high productivity and rapid growth, these species have the potential to contribute significantly to organic matter supply. This study demonstrated that the invasive alga *C. taxifolia* provides a temporally persistent source of organic matter to spatially subsidize estuarine soft-sediments. Its contribution to wrack resources was highly variable and, following a storm event in winter, when live *C. taxifolia* biomass can regress

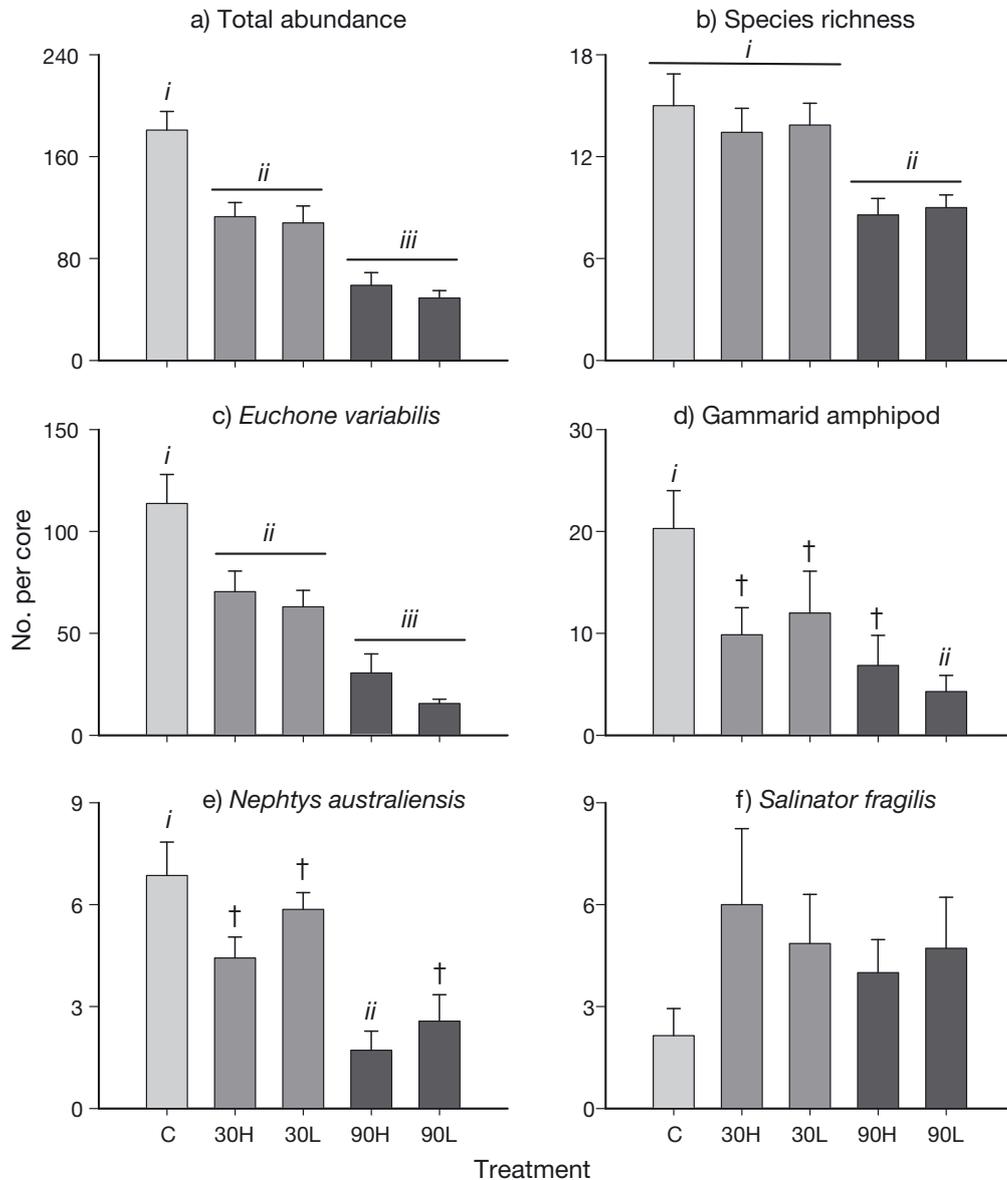


Fig. 2. *Caulerpa taxifolia*. Abundances of macroinvertebrates (means \pm SE). (a) Total abundance, (b) species richness and (c–f) taxon specific abundance in control plots (C, grey bars) and plots receiving either 30 g (30, light grey bars) or 90 g (90, dark grey bars) of *C. taxifolia* detritus. C:N ratios = 13.9 ± 0.9 (high, H) and 7.5 ± 0.3 (low, L) ($n = 7$). Treatments that differ significantly (Student-Newman-Keuls [SNK] test at $\alpha = 0.05$) are marked *i*, *ii*, *iii*. † = SNK unable to resolve differences among treatments

(Glasby et al. 2005), was as high as $13 \pm 5\%$. Furthermore, the enrichment experiment indicated that such pulses of *C. taxifolia* wrack influence negatively on the abundance and species richness of macroinvertebrate populations.

Both low and high loadings of sediment with *Caulerpa taxifolia* wrack reduced the overall abundance of macroinvertebrates relative to unenriched control plots. The magnitude of negative effects increased with the volume of *C. taxifolia* material added. Negative responses of invertebrate communities to

organic enrichment have also been seen following addition of large volumes of some other types of wrack to estuarine sediments, presumably due to sufficient stimulation of microbial processes to deplete sediment oxygen (Rossi 2006). The negative effects of *C. taxifolia* on macroinvertebrates were, however, far greater than those previously observed following the addition of other detrital sources to Botany Bay sediments. The addition of 90 g of litter from the eelgrass *Zostera capricorni* or from a mixture of sources including the strap weed *Posidonia australis*, the alga *Sargassum* sp.

and the mangrove *Avicennia marina* did not reduce macroinvertebrate abundance over a similar 2 mo period (Bishop et al. 2007, Bishop & Kelaher 2008). Other algal sources (*Ecklonia radiata*, *Sargassum* sp., or *Phyllospora comosa*) reduced abundances by only 10 to 30% (Bishop et al. 2010), not the 70% seen here following loading with *C. taxifolia*. In the present study, the reduction of abundances in experimental plots receiving *C. taxifolia* were unanticipated as plots never exhibited any evidence of surface anoxia, such as black patches or the presence of white, sulphur-reducing bacteria.

Secondary metabolites may have contributed to the negative effects of *Caulerpa taxifolia* detritus. The abundance of almost all invertebrate taxa decreased following addition of *C. taxifolia* detritus to plots, but one species showed a slight increase in numbers. Even opportunistic taxa such as capitellids and oligochaetes did not display their paradigmatic proliferation following organic enrichment (cf. Pearson & Rosenberg 1978, Beukema 1991). Only the gastropod *Salinator fragilis*, a surface dwelling grazer, was more abundant in enriched than control plots. On the surface of the sediment, *S. fragilis* would be less exposed to *C. taxifolia* detritus than infaunal taxa and may, in fact, have benefited from the alga as a result of the negative influence of *C. taxifolia* on competitors. Studies examining the nutritional quality of macroalgal detritus have emphasized the inhibitory role of secondary metabolites on detritivores (Hanson & Tenore 1981, Enriquez et al. 1993, Duggins & Eckman 1997). Amade & Lemée (1998) found degraded caulerpenynes in seawater can still inhibit larval recruitment of sea urchins; however, the capacity for caulerpenynes to influence the structure of detritivore communities has not been directly assessed and more research is needed in this area.

Like other foliose green macroalgae, *Caulerpa taxifolia* rapidly absorbs nutrients from the water column, but it also has the ability to fix nitrogen from its substrate (Chisholm et al. 1996, Ceccherelli & Cinelli 1997, Chisholm & Moulin 2003). It was predicted that the C:N ratio of live *C. taxifolia* would vary in space and time, presumably in response to environmental nutrient availability and therefore, the detritus emanating from these sources would also be of differing quality. Predictions were also made that more labile *C. taxifolia* detritus, of lower C:N ratio, would exacerbate the negative effects of the high quantity treatment by further stimulating microbial productivity and sediment anoxia. Sampling of 6 estuaries revealed that the alga's C:N ratio ranged from 7 to 16, which greatly exceeded variation amongst other wrack contributors (e.g. *Avicennia marina* C:N ratio: 26.3 ± 0.1 , $n = 2$; *Posidonia australis*: 23.0 ± 0.1 , $n = 2$; *Zostera capricorni*: 22.8 ± 0.3 , $n = 2$; Bishop & Kelaher 2008, B. P. Kelaher unpubl.).

The manipulative experiment confirmed *Caulerpa taxifolia* detritus significantly affected abundances of certain macrofauna regardless of whether its C:N ratio was at the lower or higher end of the range. At the high detrital loading of 90 g, there was a weak trend for a greater abundance of *Euchone variabilis* in plots with high rather than with low C:N detritus as predicted under the hypothesis of exacerbation of anoxic effects. But at the low detrital loading of 30 g, no difference in the abundance of *E. variabilis* was evident between quality treatments. The predatory polychaete *Nephtys australiensis* displayed the opposite pattern, with a weak indication of greater abundance in the low rather than the high C:N treatment. Increasing the nitrogen content of detritus tends to accelerate decomposition processes (Tenore et al. 1979, Mann 1988) and hence promote secondary production (Findlay 1982, Levinton & Stewart 1988). Nevertheless, it was the predator not the detritivore that appeared to benefit from more labile detritus. This may reflect the top-down force of predation offsetting any bottom-up effect of the labile detritus on detritivore abundance.

In the present study, the effect of the initial quality of *Caulerpa taxifolia* detritus was much weaker (and never statistically significant) than the effect of quantity. It is important to note, however, that each of the estuaries from which *C. taxifolia* was collected were relatively oligotrophic (Scanes et al. 2007). In eutrophic estuaries, where there is greater nitrogen availability, it is possible that even lower C:N ratios of *C. taxifolia* may be observed. Lower C:N ratios could exacerbate negative effects of high detrital loading by stimulating excessive bacterial metabolism that depletes sediments of oxygen. In other ecosystems, the starting C:N ratio of detritus is a key determinant of decomposition rate (Enriquez et al. 1993).

Coastal marine food webs are being dramatically altered through the shift in species composition (see Byrnes et al. 2007). There are now over 277 introduced macroalgal species, globally, several of which are considered among the world's 100 most invasive species (Williams & Smith 2007). Our results, in combination with those of recent studies (Rodil et al. 2008, Rossi et al. 2010), indicate that some introduced macroalgae can have broad-scale impacts on benthic communities by modifying detrital subsidies. It is likely that many other invasive macrophytes will produce similarly large impacts for several reasons. (1) According to the enemy release hypothesis, introduced plants should experience a decrease in regulation by herbivores due to the absence of their natural grazers (Keane & Crawley 2002). Hence, a higher proportion of introduced biomass than that of the native species may enter the detrital food web. (2) A recent review has shown that several families of algae contribute disproportionately

to the number of invasive macroalgal species (Williams & Smith 2007). Among these are several families well known to contain unique chemical faunal deterrents (e.g. Caulerpaceae, Codiaceae, Fucaeeae, Ceramiaceae).

Overall, this study demonstrates that invasive algae can impact communities that support productive detrital food webs of estuaries. Future efforts to manage aquatic or terrestrial invasive species and their influences should not only consider the impacts of live plants, but also the dead organic material from invasive species that can be transported across ecosystem boundaries, potentially well beyond the point of invasion.

Acknowledgements. This research was funded by an ARC Discovery Grant to B.K., a Hermon Slade Foundation Grant to B.K. and M.B. and a NSW AMSA student award to S.T. We thank B. Taylor, J. van den Broek and E. Wilke for assistance with field work and P. Gibson, R. Laird and B. Loudon for collecting *Caulerpa taxifolia* samples. R. Creese and 3 anonymous reviewers provided useful comments on the manuscript.

LITERATURE CITED

- Allison SD, Vitousek PM (2004) Rapid nutrient cycling in leaf litter from invasive plants in Hawaii. *Oecologia* 141:612–619
- Amade P, Lemée R (1998) Chemical defence of the Mediterranean alga *Caulerpa taxifolia*: variations in caulerpenyne production. *Aquat Toxicol* 43:287–300
- Anderson JM (1973) The breakdown and decomposition of sweet chestnut (*Castanea sativa* Mill.) and beech (*Fagus sylvatica* L.) leaf litter in two deciduous woodland soils. II. Changes in carbon, hydrogen, nitrogen and polyphenol content. *Oecologia* 12:275–288
- Anderson MJ (2001) A new method for non-parametric multivariate analysis of variance. *Austral Ecol* 26:32–46
- Ashton IW, Hyatt LA, Howe KM, Gurevitch J, Lerdaun MT (2005) Invasive species accelerate decomposition and litter nitrogen loss in a mixed deciduous forest. *Ecol Appl* 15:1263–1272
- Beukema JJ (1991) Changes in composition of bottom fauna of a tidal-flat area during a period of eutrophication. *Mar Biol* 111:293–301
- Bishop MJ, Kelaher BP (2008) Non-additive, identity-dependent effects of detrital species mixing on soft-sediment communities. *Oikos* 117:531–542
- Bishop MJ, Kelaher BP, Alquezar R, York PH, Ralph PJ, Skillebeck CG (2007) Trophic cul-de-sac, *Pyrazus ebeninus*, limits trophic transfer through an estuarine detritus-based food web. *Oikos* 116:427–438
- Bishop MJ, Coleman MA, Kelaher BP (2010) Cross-habitat impacts of species decline: response of estuarine sediment communities to changing detrital resources. *Oecologia* 163:517–525
- Bray JR, Curtis JT (1957) An ordination of the upland forest communities of southern Wisconsin. *Ecol Monogr* 27: 325–349
- Byrnes JE, Reynolds PL, Stachowicz JJ (2007) Invasions and extinctions reshape coastal marine food webs. *PLoS ONE* 2:e295
- Callaway RM, Pennings SC, Richards CL (2003) Phenotypic plasticity and interactions among plants. *Ecology* 84: 1115–1128
- Casu D, Ceccherelli G, Sechi N, Rumolo P, Gianluca S (2009) *Caulerpa racemosa* var. *cylindracea* as a potential source of organic matter for benthic consumers: evidences from stable isotope analysis. *Aquat Ecol* 43:1023–1029
- Ceccherelli G, Cinelli F (1997) Short-term effects of nutrient enrichment of the sediment and interactions between the seagrass *Cymodocea nodosa* and the introduced green alga *Caulerpa taxifolia* in a Mediterranean bay. *J Exp Mar Biol Ecol* 217:165–177
- Ceccherelli G, Cinelli F (1999) The role of vegetative fragmentation in dispersal of the invasive alga *Caulerpa taxifolia* in the Mediterranean. *Mar Ecol Prog Ser* 182: 299–303
- Ceccherelli G, Sechi N (2002) Nutrient availability in the sediment and the reciprocal effects between the native seagrass *Cymodocea nodosa* and the introduced rhizophytic alga *Caulerpa taxifolia*. *Hydrobiologia* 474:57–66
- Chen B, Wise DH (1999) Bottom up limitation of predaceous arthropods in a detritus-based terrestrial food web. *Ecology* 80:761–772
- Chisholm JRM, Moulin P (2003) Stimulation of nitrogen fixation in refractory organic sediments by *Caulerpa taxifolia* (Chlorophyta). *Limnol Oceanogr* 48:787–794
- Chisholm JRM, Dauga C, Ageron E, Grimont PAD, Jaubert JM (1996) 'Roots' in mixotrophic algae. *Nature* 381:382
- Clarke KR (1993) Non-parametric multivariate analyses of changes in community structure. *Aust J Ecol* 18:117–143
- Duggins DO, Eckman JE (1997) Is kelp detritus a good food for suspension feeders? Effects of kelp species, age and secondary metabolites. *Mar Biol* 128:489–495
- Enriquez S, Duarte CM, Sand-Jensen K (1993) Patterns in decomposition rates among photosynthetic organisms: the importance of detritus C:N:P content. *Oecologia* 94: 457–471
- Findlay SEG (1982) Effect of detrital nutritional quality on population dynamics of a marine nematode (*Diplolaimella chitwoodi*). *Mar Biol* 68:223–227
- Findlay S, Tenore K (1982) Nitrogen source for a detritivore: detritus substrate versus associated microbes. *Science* 218:371–373
- Funk JL (2008) Differences in plasticity between invasive and native plants from a low resource environment. *J Ecol* 96: 1162–1173
- Glasby TM, Creese RG, Gibson PT (2005) Experimental use of salt to control the invasive marine alga *Caulerpa taxifolia* in New South Wales, Australia. *Biol Conserv* 122:573–580
- Gollan JR, Wright JT (2006) Limited grazing pressure by native herbivores on the invasive seaweed *Caulerpa taxifolia* in a temperate Australian estuary. *Mar Freshw Res* 57:685–694
- Gribben PE, Wright JT, O'Connor WA, Doblin MA, Eyre B, Steinberg PD (2009) Reduced performance of native infauna following recruitment to a habitat-forming invasive marine alga. *Oecologia* 158:733–745
- Hanson RB, Tenore KR (1981) Microbial metabolism and incorporation by the polychaete *Capitella capitata* of aerobically and anaerobically decomposed detritus. *Mar Ecol Prog Ser* 6:299–307
- Holmer M, Marabá N, Lamote M, Duarte CM (2009) Deterioration of sediment quality in seagrass meadows (*Posidonia oceanica*) invaded by macroalgae (*Caulerpa* sp.). *Estuaries Coasts* 32:456–466
- Keane RM, Crawley MJ (2002) Alien plant invasions and the enemy release hypothesis. *Trends Ecol Evol* 17:164–170
- Kelaher BP, Levinton JS (2003) Variation in detrital enrich-

- ment causes spatio-temporal variation in soft-sediment assemblages. *Mar Ecol Prog Ser* 261:85–97
- Kennedy TA, Hobbie SE (2004) Saltcedar (*Tamarix ramosissima*) invasion alters organic matter dynamics in a desert stream. *Freshw Biol* 49:65–76
- Lapointe BE, Barile PJ, Littler MM, Littler DS (2005) Macroalgal blooms on southeast Florida coral reefs. II. Cross-shelf discrimination of nitrogen sources indicates widespread assimilation of sewage nitrogen. *Harmful Algae* 4: 1106–1122
- Lemée R, Pesando D, Durand-Clément M, Dubreuil A, Meinesz A, Guerriero A, Pietra F (1993) Preliminary survey of toxicity of the green alga *Caulerpa taxifolia* introduced into the Mediterranean. *J Appl Phycol* 5:485–493
- Levin LA, Neira C, Grosholz ED (2006) Invasive cordgrass modifies wetland trophic function. *Ecology* 87:419–432
- Levinton JS, Stewart S (1988) Effects of sediment organics, detrital input, and temperature on demography, production, and body size of a deposit feeder. *Mar Ecol Prog Ser* 49:259–266
- Lodge DM (1993) Biological invasions: lessons for ecology. *Trends Ecol Evol* 8:133–137
- Mann RN (1988) Production and use of detritus in various freshwater, estuarine, and coastal marine ecosystems. *Limnol Oceanogr* 33:910–930
- McKinnon JG, Gribben PE, Davis AR, Jolley DF, Wright JT (2009) Differences in soft-sediment macrobenthic assemblages invaded by *Caulerpa taxifolia* compared to uninvaded habitats. *Mar Ecol Prog Ser* 380:59–71
- Meinesz A, Belsher T, Thibaut T, Antolic B and others (2001) The introduced green alga *Caulerpa taxifolia* continues to spread in the Mediterranean. *Biol Invasion* 3:201–210
- Moore JC, Berlow EL, Coleman DC, de Ruiter PC and others (2004) Detritus, trophic dynamics and biodiversity. *Ecol Lett* 7:584–600
- Oliver I, Beattie AJ (1996) Invertebrate morphospecies as surrogates for species: a case study. *Conserv Biol* 10:99–109
- Pearson TH, Rosenberg R (1978) Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. *Oceanogr Mar Biol Annu Rev* 16:229–311
- Polis GA, Strong DR (1996) Food web complexity and community dynamics. *Am Nat* 147:813–846
- Polis GA, Anderson WB, Holt RD (1997) Towards an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. *Annu Rev Ecol Syst* 28: 289–316
- Rodil IF, Olabarria C, Lastra M, Lopez J (2008) Differential effects of native and invasive algal wrack on macrofaunal assemblages inhabiting exposed sandy beaches. *J Exp Mar Biol Ecol* 358:1–13
- Rossi F (2006) Small-scale burial of macroalgal detritus in marine sediments: effects of *Ulva* spp. on the spatial distribution of macrofauna assemblages. *J Exp Mar Biol Ecol* 332:84–95
- Rossi F, Olabarria C, Incera M, Garrido J (2010) The trophic significance of the invasive seaweed *Sargassum muticum* in sandy beaches. *J Sea Res* 63:52–61
- Rublee PA (1982) Seasonal distribution of bacteria in salt marsh sediments in North Carolina. *Estuar Coast Shelf Sci* 15:67–74
- Scanes P, Coade G, Doherty M, Hill R (2007) Evaluation of the utility of water quality based indicators of estuarine lagoon condition in NSW, Australia. *Estuar Coast Shelf Sci* 74:306–319
- Schaffelke B, Smith JE, Hewitt CL (2006) Introduced macroalgae: a growing concern. *J Appl Phycol* 18:529–541
- Suberkropp K, Godshalk GL, Klug MJ (1976) Changes in the chemical composition of leaves during processing in a woodland stream. *Ecology* 57:720–727
- Tenore KR (1977) Growth of *Capitella capitata* cultured on various levels of detritus derived from different sources. *Limnol Oceanogr* 22:936–941
- Tenore KR, Hanson RB, Dornseif BE, Wiederhold CN (1979) The effects of organic nitrogen supplement on the utilization of different sources of detritus. *Limnol Oceanogr* 24:350–355
- Thrush SF (1991) Spatial patterns in soft-bottom communities. *Trends Ecol Evol* 6:75–79
- Vitousek PM, Walker LR, Whiteaker LD, Mueller-Dombois D, Matson PA (1987) Biological invasion by *Myrica faya* alters ecosystem development in Hawaii. *Science* 238: 802–804
- West EJ, Davis AR, Barnes PB, Wright JT (2009) The role of recreational activities in creating fragments of invasive *Caulerpa taxifolia*. *J Exp Mar Biol Ecol* 376:17–25
- Whitcraft CR, Levin LA, Talley D, Crooks JA (2008) Utilization of invasive tamarisk by salt marsh consumers. *Oecologia* 158:259–272
- Williams SL, Smith JE (2007) A global review of the distribution, taxonomy and impacts of introduced seaweeds. *Annu Rev Ecol Evol Syst* 38:327–359
- Wright JT, McKenzie LA, Gribben PE (2007) A decline in the abundance and condition of a native bivalve associated with *Caulerpa taxifolia* invasion. *Mar Freshw Res* 58: 263–272
- York PH, Booth DJ, Glasby TM, Pease BC (2006) Fish assemblages in habitats dominated by *Caulerpa taxifolia* and native seagrasses in south-eastern Australia. *Mar Ecol Prog Ser* 312:223–234

Editorial responsibility: Laura Airoidi,
Ravenna, Italy

Submitted: June 14, 2010; Accepted: October 27, 2010
Proofs received from author(s): December 9, 2010