Consistencies over regional scales in assemblages of mobile epifauna associated with natural and artificial plants of different shape

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Abstract

Epifaunal invertebrates associated with natural habitat types (wide-leaved and narrow-leaved *Sargassum*) and artificial habitat types (filamentous and foliose artificial plant units (APUs)) were investigated at paired sites nested within three tropical locations. Differences in species richness, faunal productivity and species composition between natural and artificial habitats were considerably less than differences between locations and differences between the two APU types. Location effects were consistent amongst all habitat types, indicating that APUs provide a valuable tool for monitoring the marine environment, particularly given low variability between samples collected at scales <1 km. Moreover, faunal productivity showed little variation within habitat and location, a result that supports the hypothesis that resource ceilings restrict epifaunal population growth to predictable levels. Species exhibited varying levels of host specificity between locations. At Brook Island and Fantome Island sites, the guild of ampithoid amphipod species present was host specific, occurring on natural *Sargassum* plants but largely absent from APUs; however, many of the same species occurred on APUs at Great Palm Island sites.
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1. Introduction

Aquatic vegetated habitats are widely perceived to differ trophodynamically from those in the terrestrial realm because of a paucity of species and individuals that directly consume

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macroscopic plants (Field, 1983; Klumpp et al., 1989). Thus, terrestrial food webs are often seen to be primarily fuelled by direct herbivory on leaf material, whereas aquatic food webs are suggested to be driven more by detrital, planktivorous or epiphytic production (Hatcher, 1983; Crossland et al., 1984; Newell, 1984; Mann, 1988; Klumpp et al., 1989; Cebrian, 1999). Two possible consequences of these basic differences between realms are: (i) a greater level of specialisation and host specificity amongst terrestrial invertebrates because of coevolution between grazers and plant defence mechanisms (see Hay, 1991), and (ii) relatively high densities and species richness of invertebrates associated with individual plants in the marine environment because of the variety of alternate food resources (Edgar, 1983).

The degree of host specificity amongst marine invertebrates, and the level of reliance on food resources external to the host plant, have been directly assessed in the present study by deploying artificial plants for colonisation. When faunas associated with inert structures are directly compared with faunas associated with plants of similar shape then faunal elements that utilise natural host plants as a food resource should be distinguishable. While such comparisons have been made by several workers (e.g. Myers and Southgate, 1980; Russo, 1990; Edgar, 1991a), previous studies have typically included only one artificial and one natural habitat type, hence differences in structural material may have been confounded with differences in morphology. In the present study, mobile epifaunal invertebrates associated with two artificial habitats exhibiting extremes of shape are compared with faunas inhabiting natural *Sargassum* plants of two different shapes. This comparison includes assessment of variation within as well as between natural and artificial morphotypes. The null hypothesis tested is that variation between natural plants of different physical structure does not differ from, and overlaps, the variation between artificial plants of different physical structure. In order to produce results with some generality, comparisons have been made at three island locations spanning 60 km distance.

2. Methods

Two types of artificial plant units (APUs) were placed in the field 6 weeks prior to 17 and 18 July 1996, the sampling dates when substrata (both APUs and natural plants) were collected with colonised invertebrates. APUs used were: (i) 50 g tufts of 100 mm long tanikalon rope fibre tied at the base to mimic filamentous algae such as *Halopteris* or *Chlorodesmis*, as used in other studies (Edgar, 1991a,b, 1993), and (ii) 10 flat polyethylene sheets 50 mm long by 10 mm wide tied at the base to mimic foliose (flat-bladed) seaweeds such as *Zonaria* or seagrasses such as *Enhalus*, *Cymodocea* or *Thalassia*. These two morphotypes were chosen to represent extremes in the range of natural plant shapes—fine filamentous algae with thousands of individual strands versus sheet-like foliose algae. Four replicate APUs of each type were placed 1–10 m apart at two tropical sites (0.1–1 km apart) nested within three inshore island locations (5–60 km apart) off the Queensland coast. The locations were Brook Island (146°17′E, 18°09′S), Great Palm Island (146°35′E, 18°41′S) and Fantome Island (146°31′E, 18°41′S, Schaffelke and Klumpp, 1997). APUs were tied to bricks and placed just below low water mark adjacent to natural *Sargassum* plants inshore from fringing reefs. The same general habitat type was present at all locations—inshore flats composed of a mosaic of sand, sparse seagrass and rocks with *Padina* spp. and *Sargassum* spp.

Invertebrates associated with APUs and natural *Sargassum* plants (four replicates) were sampled by detachment of APUs from bricks and plants from rock, and enclosure of these in plastic bags. Two morphotypes of *Sargassum* were collected—wide-leaved plants with 5–6 mm wide thalli (predominantly *Sargassum fissifolium* (Mert.) J. Ag.), which were collected at the two Great Palm Island sites, the two Brook Island sites and one Fantome Island site, and narrow-leaved plants with 1 mm wide thalli (*Sargassum baccularia* (Mert.) C. Ag.), which were collected at one Fantome Island site and two Brook Island sites. Both morphotypes were collected whenever locally present; however, this occurred only at Brook Island. Contents of bags were preserved using formalin and returned to the laboratory, where invertebrates were extracted by washing samples over a stacked series of sieves (0.5, 0.71, 1, 1.4, 2, 2.8, 4, 5.6 and 8 mm), as described by Edgar (1990). Material retained on each sieve was sorted under a dissecting microscope. Animals were counted after separation into species groups, and host plant material was weighed after drying at 60 °C for 48 h.

Estimates of the total productivity of invertebrates in samples were made because such estimates are approximately proportional to total community metabolism (i.e. total respiration and consumption as well as production; Edgar, 1993). Faunal biomass and estimated productivity were calculated using numbers of animals in each sieve size–class and protocols described by Edgar (1990). Briefly, faunal biomass of invertebrates was estimated by assuming that the ash-free dry weight (AFDW) of individuals was equal to the mean AFDW of animals in the same sieve size–class. Estimates of the daily productivity of benthic invertebrates were calculated using biomass estimates for each animal and the equation $P = 0.0049B^{0.80}T^{0.89}$, which relates daily macrobenthic productivity P (µg per day) to ash-free dry weight B (µg) and water temperature T (°C). Although water temperature during the season of sampling was ≈23 °C, estimated productivity (P_{20}) was calculated assuming a temperature of 20 °C to provide an index of community metabolism that is consistent with earlier studies (Edgar, 1993). P_{20} data can be converted to in situ productivity data at 23 °C by multiplying by 1.13 (assuming that temperature varies with an exponent 0.89; Edgar, 1990).

Number of individuals, number of species, estimated faunal biomass and estimated productivity data were analysed using nested ANOVA, with islands and sites (nested within islands) considered random factors and habitat type (foliose APU, filamentous APU and natural *Sargassum*) an orthogonal fixed factor. Brook Island data for wide-leaved *Sargassum* plants were excluded to maintain a balanced design in ANOVAs. Abundance, biomass and estimated productivity data were log transformed to normalise variances. Tests and variance associated with each of the ANOVA components were calculated using the model of expected mean squares described in Table 1 (see Searle et al., 1992).

Macrofaunal data were analysed using cluster analysis and multi-dimensional scaling (MDS), as run by SYSTAT (Wilkinson, 1987) and PRIMER (Carr, 1996) programs, in order to produce the best graphical depictions of faunal similarities between sites. For these analyses, the data matrix showing total abundance of species at each site was double root-transformed and then converted to a symmetric matrix of biotic similarity between pairs of sites using the Bray–Curtis similarity index. Species collected in only one sample or with fewer than five individuals recorded were excluded from similarity analyses. The similarity matrix was agglomeratively clustered using average linkage. These procedures follow the recommendations of Faith et al. (1987) and Clarke (1993) for data matrices with

Table 1
Expected mean squares derived using ANOVA with three habitat types, three islands, two sites nested within each island and four replicates

Source	d.f.	Expected mean squares
Habitat (H)	2	$\sigma_e^2 + 4\sigma_{HS(I)}^2 + 8\sigma_{HI}^2 + 24\sigma_H^2$
Island (I)	2	$\sigma_e^2 + 12\sigma_{S(I)}^2 + 24\sigma_I^2$
Site (S(I))	3	$\sigma_e^2 + 12\sigma_{S(I)}^2$
Habitat × island	4	$\sigma_e^2 + 4\sigma_{HS(I)}^2 + 8\sigma_{HI}^2$
Habitat × site	6	$\sigma_e^2 + 4\sigma_{HS(I)}^2$
Residual (e)	54	σ_e^2

numerous zero records. The usefulness of the two-dimensional MDS display of relationships between sites is indicated by the stress statistic, which if < 0.1 indicates that the depiction of relationships is good, and if >0.2 that the depiction is poor (Clarke, 1993).

A probability function that graphically describes dispersion of replicate samples within different locations and habitat types was calculated using MDS two-dimensional co-ordinates and SYSTAT (Wilkinson, 1987). Because calculations were based on the reduced two-dimensional MDS data set, the 95% calculated confidence contours were conservative compared to differences between groups in multi-dimensional space. SIMPER analysis was also used to identify species that typified the different habitat types and contributed substantially to average similarity between habitat groups (Clarke, 1993).

3. Results

3.1. Total abundance, biomass and productivity

A total of 38,726 invertebrates belonging to 242 species were collected from the major habitat types examined during the study. The filamentous APUs attracted considerably more individuals and approximately the same number of species as natural *Sargassum* plants, while over an order of magnitude fewer animals were associated with the foliose APUs (Table 2, Fig. 1). The greater total number of invertebrates collected from filamentous APUs than natural plants was due primarily to many more isopods and gastropods associating with APUs, whereas ampithoid amphipods were disproportionately abundant on natural plants. The number of species of most taxonomic groups collected from filamentous APUs was similar to the number collected from natural *Sargassum* plants.

The total number of individuals, biomass and estimated productivity of invertebrates associated with *Sargassum* plants increased with the biomass of plants, but not in a 1:1 manner. Plants weighing 5 g possessed a mean of 280 animals compared to a mean of 370 animals on 10 g plants. Patterns were most clearly defined for the relationship between plant biomass and invertebrate productivity ($R^2 = 0.32$; cf. 0.30 for invertebrate biomass and 0.18 for invertebrate abundance), with this relationship depicted in Fig. 2a. Invertebrates associated with plants of 2 g had an estimated productivity of 0.5 g per day compared to an estimated macrofaunal productivity of 1 g per day for plants of 10 g. Because of the lack

Table 2
Number of species and total number of individuals collected from different habitat types for different taxonomic groups

Taxon	Species			Numbers		
	Sargassum	Filamentous APU	Foliose APU	*Sargassum*	Filamentous APU	Foliose APU
Anemones	3	2	1	20	11	1
Ctenophores	1	0	0	14	0	0
Platyhelminthes	6	2	0	9	15	0
Nemerteans	3	4	2	7	9	3
Echiurans	0	1	0	0	5	0
Polychaetes	31	30	12	347	493	29
Pycnogonids	5	2	0	18	9	0
Insects	1	1	1	26	18	1
Cumaceans	3	3	1	159	286	2
Tanaidaceans	5	5	2	1802	1306	36
Ampithoid amphipods	8	6	6	3590	1116	82
Other gammaridean amphipods	33	37	21	1529	5128	165
Caprellid amphipods	4	4	0	44	11	0
Isopods	16	18	12	1824	14009	291
Mysids	1	2	0	4	5	0
Shrimps	3	5	1	26	183	2
Crabs	3	3	1	21	22	2
Pagurids	1	1	1	1	2	2
Chaetognaths	1	1	0	16	25	0
Chitons	1	0	1	2	0	1
Gastropods	43	49	15	1089	4826	54
Ophiuroids	4	3	3	16	6	6
Total	176	179	80	10564	27485	677

of 1:1 correspondence between macroalgal biomass and faunal variables (Fig. 2b), faunal data could not be readily standardised with respect to plant weight for analyses.

Differences in number of species between samples reflected total abundance of animals collected and island location more than habitat type (Fig. 1). For a given number of individuals, Brook Island samples from all three habitat types included relatively few species while Great Palm Island samples were disproportionately rich in species. *Sargassum* plants with high densities of animals typically possessed a similar number of species to the filamentous APUs with lowest invertebrate densities, except at Great Palm Island where natural habitats possessed a richer fauna than the artificial habitats with comparable animal densities (Fig. 1).

Number of species (Fig. 3), number of individuals (Fig. 4) and estimated productivity (Fig. 5) of faunas associated with natural plants varied considerably between island locations, but showed low levels of variation between sites. Comparable patterns were observed for each of the three habitat types, with higher values consistently recorded at Great Palm Island than at Fantome Island. Patterns of variation in faunal biomass were almost identical to those for productivity, so have not been figured.

Much of the variation in productivity between locations disappeared when estimated productivity values were divided by the biomass of the host plant. Although this
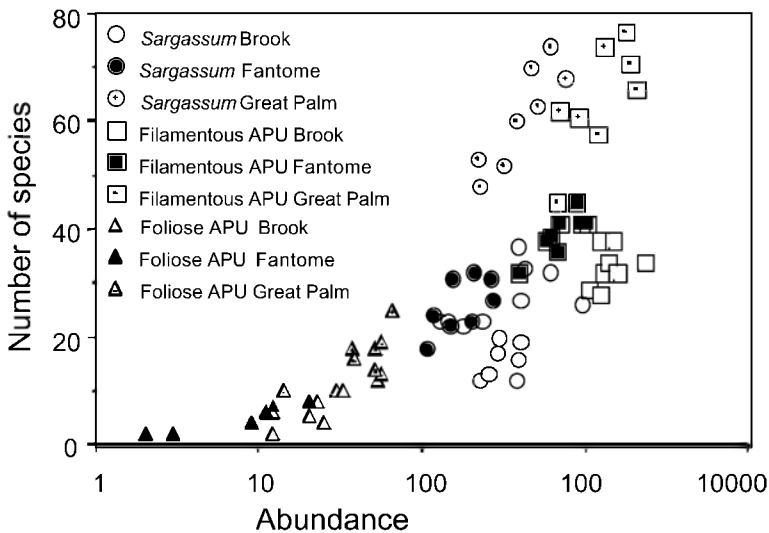
Fig. 1. Scattergram relating abundance of invertebrates associated with different habitat types and number of species.

transformation introduces error because of a lack of 1:1 correspondence between plant biomass and faunal productivity (Fig. 2b), weight specific productivity data are presented here to allow direct comparison with previous studies (Edgar, 1993). After standardisation, estimated productivity of epifauna associated with _Sargassum_ plants possessed a mean ($\pm$S.D.) of 149 ($\pm$76) μg g^{-1} per day at Brook Island, 151 ($\pm$7) μg g^{-1} per day at Great Palm Island and 176 ($\pm$4) μg g^{-1} per day at Fantome Island. The estimated productivity ($\pm$S.D.) of filamentous APUs was 103 ($\pm$31), 76 ($\pm$7) and 40 ($\pm$9) μg g^{-1} per day at Brook Island, Great Palm Island and Fantome Island, respectively.

Significant differences were detected in all faunal variables between habitat types and between island locations, but not between sites within each island (Table 3). Species richness and productivity data also exhibited significant interactions between habitats at different islands; however, in the case of productivity data, this outcome was largely due to exceptionally low variation between habitats at different sites, with zero variance calculated for this interaction term (Table 3). Variance in species richness data was overwhelmingly due to the factors 'habitat' and 'island'. Abundance, productivity and biomass data showed high levels of variance between habitat types, a moderate level of variance between islands and between replicates, and extremely low variance between sites or for interaction terms. Two interaction terms (habitat $\times$ island) were significant, although the variance estimates were low relative to other terms.

3.2. Faunal composition

All of the species most abundantly associated with _Sargassum_ plants also occurred commonly on filamentous APUs, with the exception of the ampithoid amphipod _Sunampithoe_
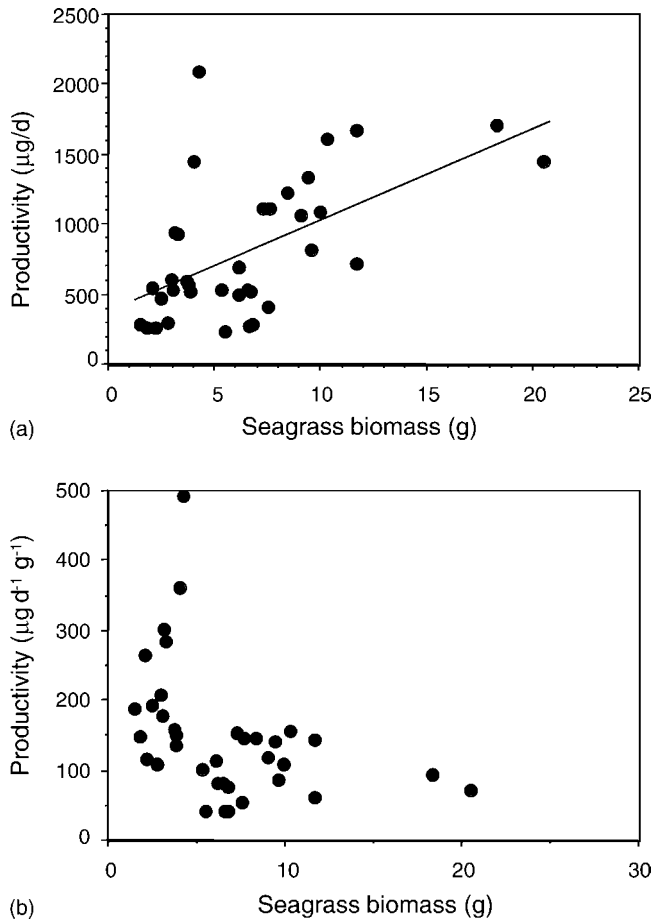
Fig. 2. (a) Scattergram showing relationship between estimated invertebrate productivity (P; μg per day) and biomass of host *Sargassum* plant (B; g). Regression of best fit ($P = 386 + 65B$; $r^2 = 0.32$, $P < 0.001$) has also been shown. (b) Relationship between invertebrate productivity per gram plant and plant biomass.

pelagia (Table 4). The melitid amphipod *Mallacoota* cf. *subcarinata* showed a contrasting pattern, occurring in extremely high densities on filamentous APUs but being collected on only two occasions from natural plants. In general, species that were commonly collected in one habitat type were also collected in other habitat types; however, the relative abundances of species varied substantially between habitats in some cases.

Samples collected at different sites on the same island showed few differences within habitat type, with the exception of the foliose APUs, which exhibited considerable stochastic variation as a consequence of low population sizes. Cluster analysis (Fig. 6) and MDS (Fig. 7) both indicated that foliose APU samples from Brook Island and Fantome Island were distinctly different from faunal samples collected at other sites and habitats, and that faunal variation between sites was negligible compared to other sources of variation. The
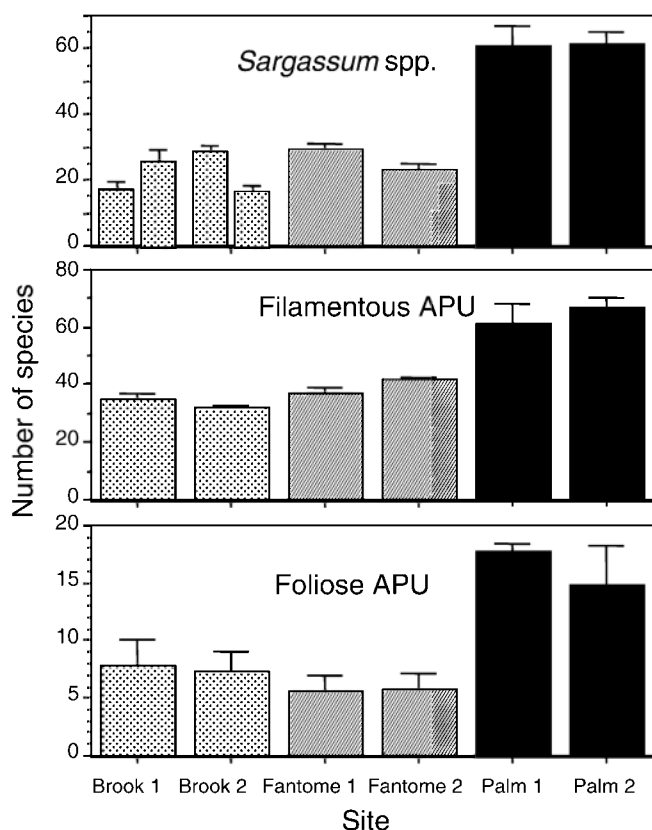
Fig. 3. Total number of species (±S.E.) associated with natural *Sargassum* plants and APUs collected from two sites at each of three locations. Note different scales on *Y*-axes. Two species of *Sargassum* were collected at each of the Brook Island sites.

next major dichotomies in the cluster analysis were between habitats collected at Great Palm Island and habitats collected at the other two islands (Fig. 6), and then between habitats collected at Brook Island and habitats collected at Fantome Island. Between island variation was therefore considerably greater than variation between filamentous APU and natural *Sargassum* habitat types.

Because foliose APUs contributed most of the faunal variation between samples and dominated MDS patterns, MDS was rerun with the foliose APU data set removed. Results for the replicate samples are shown in Fig. 8. Wide-leaved and narrow-leaved *Sargassum* morphs showed few differences in associated faunas, with general overlap in patterns for the Fantome Island samples despite different morphotypes having been collected at the two sites. Filamentous APUs each showed very tight groupings of replicate samples within location; nevertheless, samples from Great Palm Island showed marginal overlap with faunas associated with natural *Sargassum* plants.

Ampithoid amphipods comprised the major faunal component that was disproportionately abundant on *Sargassum* plants compared to APU habitats (Table 5). Four of the five
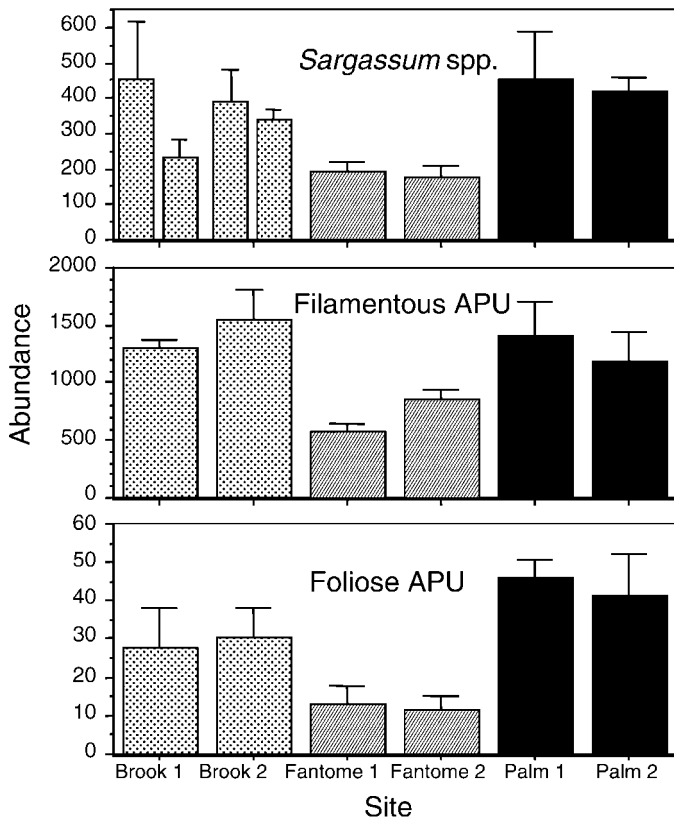
Fig. 4. Total number of animals (±S.E.) associated with natural *Sargassum* plants and APUs collected from two sites at each of three locations.

species that occurred abundantly on *Sargassum* at Brook Island and exhibited highest levels of dissimilarity between *Sargassum* and APUs in the SIMPER analysis were ampithoid species. Three of these amphipods (*S. pelagia, Ampithoe* sp. 1 and *Cymadusa* sp. 1) were also amongst the five most important *Sargassum* indicator species at Fantome Island. Surprisingly, these amphipods did not exhibit the same patterns at Great Palm Island, with most ampithoid species occurring more abundantly on APUs than on natural habitats at that location. The level of dissimilarity between habitats was generally much lower for species at Great Palm Island than at the other two locations, with the suite of species at Great Palm Island showing very little habitat specificity.

4. Discussion

Filamentous APUs provided a habitat for marine invertebrates that was difficult to distinguish from natural *Sargassum* plants—other than a relative paucity of ampithoid
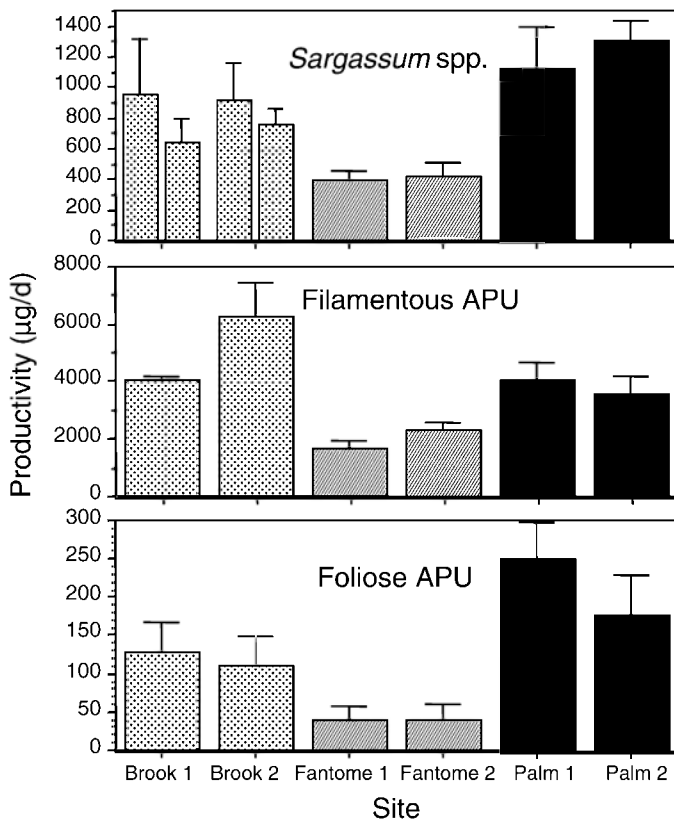
Fig. 5. Estimated productivity (±S.E.) of invertebrates associated with natural *Sargassum* plants and APUs collected from two sites at each of three locations.

amphipods—with variation between foliose and filamentous APU habitat types greater than variation between filamentous APUs and natural plants. Regional factors at >1 km geographic scales overwhelmingly influenced species richness, productivity and species composition of macrofaunal communities, and these factors exerted themselves in a similar manner amongst the different habitat types. Previous studies have also shown that APUs attract most elements of the mobile invertebrate fauna in their near vicinity (Myers and Southgate, 1980; Russo, 1990; Edgar, 1991a), and that assemblages associated with APUs are sensitive to local variation in environmental conditions (Edgar, 1991b). Artificial seagrass, artificial seaweed and artificial habitat units, including those used in the present study, clearly provide a valuable tool for monitoring the marine environment (Costello and Thrush, 1991).

The greatest benefit in using APUs over sampling natural habitats is the extremely low level of variation between replicates. The small standard errors of means, which extended to study sites 1 km apart in the present study, translates into high power for subsequent statistical tests (Edgar, 1991a). This is particularly the case for species richness and, to

Table 3
Results of ANOVA with site nested within island location and habitat as an orthogonal fixed factor

Factor	d.f.	Species			Abundance			Biomass			Productivity		
		MS	F	σ^2	MS	F	σ^2	MS	F	σ^2	MS	F	σ^2
Habitat	2	8290	15.42*	323.0	95.05	221.31***	3.94	87.46	55.96**	3.58	86.00	69.20**	3.53
Island	2	4962	257.93***	205.9	6.24	147.38**	0.26	14.77	116.32**	0.61	10.98	136.07**	0.45
Site (island)	3	19	0.51	0	0.04	0.14	0	0.13	0.22	0	0.08	0.18	0
Habitat × island	4	538	7.30*	58.0	0.43	4.10	0.04	1.56	5.23	0.16	1.24	7.43*	0.13
Habitat × site	6	74	1.95	9.0	0.10	0.35	0	0.30	0.52	0	0.17	0.37	0
Residual	54	38		37.7	0.30		0.30	0.57		0.57	0.45		0.45

Variance estimates for each factor (σ^2) were calculated using the design described in Table 1. Variance estimates <0 were equated with 0 (see Snedecor and Cochran, 1967).

  * $0.05 > P > 0.01$.

  ** $0.01 > P > 0.001$.

  *** $P < 0.001$.

Table 4
Total numbers of the 10 species collected in greatest abundance from three habitat types, with ranking within each habitat type shown in parenthesis

Species	Group	*Sargassum*	Filamentous APU	Foliose APU
Leptochelia longimana Shiino	Tanaidacean	1691 (1)	1221 (5)	32 (5)
Sunampithoe pelagia (Milne Edwards)	Amphipod	1431 (2)	8 (82)	2 (31)
Ampithoe sp.	Amphipod	909 (3)	509 (11)	16 (9)
Sphaeromatid sp.	Isopod	842 (4)	6668 (2)	28 (6)
Cymadusa sp. 1	Amphipod	745 (5)	282 (15)	9 (14)
Ianiropsis sp.	Isopod	693 (6)	6789 (1)	229 (1)
Cymadusa sp. 2	Amphipod	460 (7)	292 (14)	52 (2)
Podocerus sp.	Amphipod	356 (8)	470 (12)	0
Eatoniellid sp. 1	Gastropod	246 (9)	1800 (3)	1 (51)
Elasmopus sp.	Amphipod	227 (10)	724 (7)	34 (3)
Gammaropsis sp.	Amphipod	99 (16)	51 (39)	34 (3)
Lembos sp.	Amphipod	7 (78)	2 (115)	22 (7)
Bittium sp.	Gastropod	77 (19)	150 (25)	18 (8)
Aora sp.	Amphipod	70 (22)	162 (22)	15 (10)
Mallacoota cf. *subcarinata* (Haswell)	Amphipod	2 (118)	1458 (4)	2 (31)
Tricolia sp.	Gastropod	210 (11)	974 (6)	5 (21)
Hyale sp.	Amphipod	49 (27)	707 (8)	3 (27)
Paradexamine cf. *churinga* Barnard	Amphipod	90 (18)	587 (9)	4 (24)
Eatoniellid sp. 2	Gastropod	210 (11)	543 (10)	5 (21)

a lesser extent, faunal density and faunal production, because these variables possess a complex relationship with plant size. Plants of different sizes collected in the field could not be simply standardised by dividing by plant biomass or surface area (see Fig. 2b).

The concordance in patterns of invertebrate production between natural habitats and APUs at different locations provides empirical support for the 'production ceiling hypothesis' (Edgar, 1993; Edgar and Aoki, 1993), which suggests that the production, consumption and respiration of mobile epifaunal assemblages are predictable and that they vary primarily with levels of light and associated primary production. When productivity data were divided by habitat weight—a questionable procedure (see above), but one which allows comparison with other studies—the estimated productivity of *Sargassum* faunas was close to constant at all sites ($150 \, \mu g \, g^{-1}$ per day). This value was also similar to values previously recorded at other sites in northern Queensland ($90-160 \, \mu g \, g^{-1}$ per day; Edgar, 1993). Weight specific productivity values for filamentous APUs at Brook Island ($103 \, \mu g \, g^{-1}$ per day) and Great Palm Island ($76 \, \mu g \, g^{-1}$ per day) were also within the range of values for this habitat type in clear shallow water world-wide ($50-110 \, \mu g \, g^{-1}$ per day; Edgar, 1993), while the value at Fantome Island was marginally lower than this range ($40 \, \mu g \, g^{-1}$ per day). The Fantome Island APUs were placed at low water mark, and may have been affected by tidal emersion.

The consistency in faunal productivity data between sites and habitats indicates a key role for environmental effects in structuring macrofaunal assemblages. Predation has been suggested to exert a major influence on epifaunal communities in macrophyte beds (see, e.g. Orth et al., 1984; Edgar and Aoki, 1993), and presumably greatly affects individual species; however, predatory impact was unlikely to have substantively influenced total invertebrate
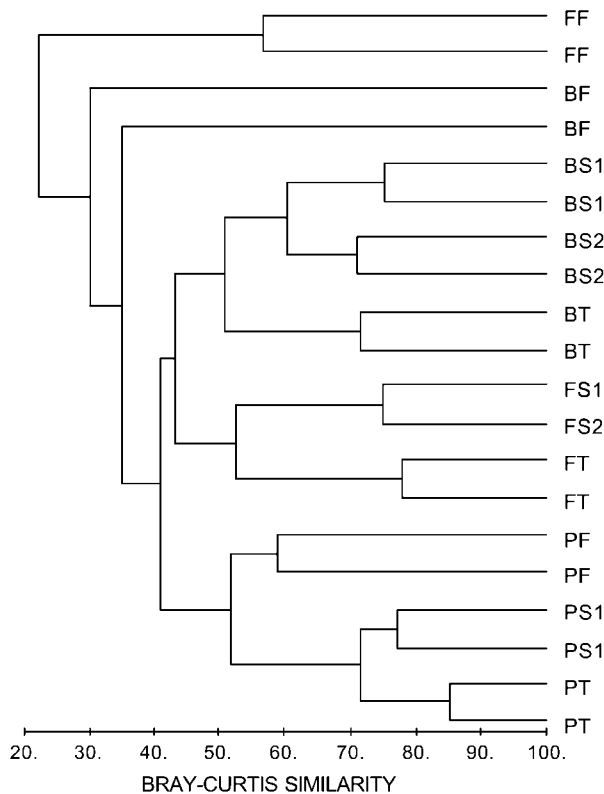
Fig. 6. Results of cluster analysis showing relationships between mean abundance of faunas associated with different habitats at different sites. To remove effects of different population sizes, data were standardised by the total abundance of each sample. Replicate data have been aggregated as mean density of species per habitat at each site. First digit of label represents site (B: Brook; F: Fantome; P: Great Palm) and succeeding digit(s) habitat type (F: foliose APU; S1: wide-leaved *Sargassum.*; S2: narrow-leaved *Sargassum*; T: filamentous tanikalon APU).

productivity in the present study because predation presumably varied between sites that exhibited consistent levels of faunal productivity. If predators substantively influence invertebrate productivity and, for example, fishes that preferentially pick invertebrates from broad-leaved plants such as *S. fissifolium* and the foliose APUs were disproportionately abundant at one site, then low productivity estimates should be encountered at that site for those particular habitat types. Such patterns were not evident. The only deviations from constant productivity in all samples were proportionate differences between habitat types, and location declines in overall productivity from Great Palm Island to Brook Island to Fantome Island.

The lack of consistent faunal deficiencies on artificial compared with natural habitats sampled, apart from reduction in some ampithoid amphipod species, indicates that few of the invertebrates associated with marine plants are directly reliant on host plant tissue or a microflora mediated by chemical compounds released by the host plant. Negligible
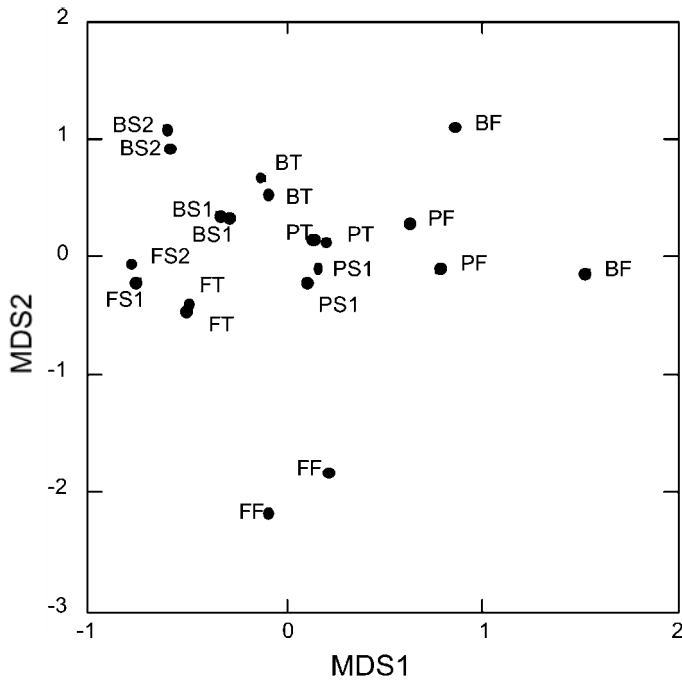
Fig. 7. Results of MDS showing relationships between mean abundance of faunas associated with different habitats at different sites. Data were standardised by the total abundance of species per habitat at each site. First digit of label represents site (B: Brook; F: Fantome; P: Great Palm) and succeeding digit(s) habitat type (F: foliose APU; S1: wide-leaved *Sargassum*.; S2: narrow-leaved *Sargassum*; T: filamentous APU). The stress statistic associated with the plot is 0.16.

detrital material was noticed on plants collected, hence invertebrates presumably were either suspension-feeders, fed away from the host plant, or consumed diatoms and other periphytic plant material associated with the surface of host plants. Previous experiments with APUs indicates that the timing of invertebrate colonisation corresponds with the development of a periphytic film of algae on APUs (Russo, 1988; Edgar, 1991a), and that few invertebrates settle on APUs in dark environments where primary production is limited (Edgar, 1991b). The 6 weeks period available for invertebrates to colonise APUs in the present study should have been sufficient for a stable associated invertebrate community to develop (Edgar, 1991a).

One notable outcome of the present study was the disparity between host specificity of invertebrates at Great Palm Island, where none of the common species was highly specific to either natural or artificial plants, and at the other two island locations, where several of the same invertebrate species were highly host specific. The Great Palm Island fauna also possessed a number of other distinctive characteristics in species composition, faunal productivity and species richness despite its close proximity to the Fantome Island sites (7 km), and the distance of these locations from Brook Island (60 km). Several important physical variables differed between locations, for example greater waver exposure and
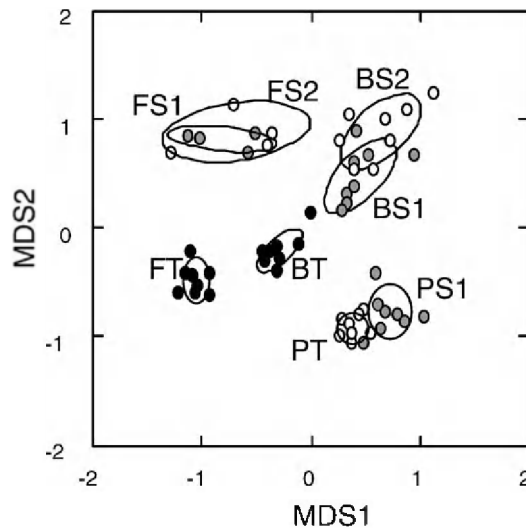
Fig. 8. Results of MDS showing relationships between faunas associated with each replicate habitat at different sites. Contour plots indicate 95% confidence intervals associated with habitat/sites. First digit of label represents site (B: Brook I; F: Fantome I; P: Great Palm I) and succeeding digit(s) habitat type (S1: wide-leaved *Sargassum*.; S2: narrow-leaved *Sargassum*; T: filamentous APU). The stress statistic associated with the plot is 0.18.

marginally deeper water depth at Great Palm Island; however, any hypothesis to explain the observed differences in host specificity would be highly speculative because of the limited replication of location. We nevertheless note that the Great Palm Island location, which possessed the most generalist fauna, also had highest species richness, contrary to predictions developed in the terrestrial environment that animals assume narrower niches as species packing increases (see, e.g. Diamond, 1975).

The observed disparity in host specificity between locations highlights the importance of conducting investigations at more than one site. If only the Great Palm Island sites had been investigated, then no substantive differences between natural and artificial plants would have been identified, and none of the common invertebrates could be considered trophically atypical. By contrast, if only Brook and Fantome Island sites had been investigated then we would have concluded that ampithoid amphipods comprised a major difference between natural and artificial habitat types, and that this amphipod family was atypical in the sense that members probably fed directly on the host plant in contrast to the majority of epifaunal species, which utilised external food resources. Such a conclusion would question the generality of the numerous studies on grazing invertebrates that use ampithoid amphipods as model species (e.g. Edgar, 1983; Hay et al., 1987; Duffy and Hay, 1991, 1994). If ampithoids differ markedly from most other mesograzers in their dietary habits, then considerable care is required in extrapolating from studies of ampithoids to mesograzers in general. Future studies that investigate why particular macrofaunal species can occupy a narrow range of habitat types at one site and a wide range of habitats elsewhere should prove interesting.

Table 5
The most characteristic five species in natural *Sargassum* and filamentous APU habitats at each location

Species	Brook Island			Fantome Island			Great Palm Island		
	$\bar{D}$	Mean density		$\bar{D}$	Mean density		$\bar{D}$	Mean density	
		Plant	APU		Plant	APU		Plant	APU
Species disproportionately abundant on *Sargassum*									
Sunampithoe pelagia	2.59	82.4	0.1	2.06	12.4	0		1.8	0.9
Ampithoe sp.	2.29	41.4	1.1	1.07	7.6	7.6		23.3	54.9
Cymadusa sp. 2	1.60	27.5	10.0		1.6	13.3		0.9	13.3
Pereionotus thomsoni (Stebbing)		0.8	0	1.48	5.3	0	0.66	2.6	0.1
Cymadusa sp. 1	1.19	41.5	11.0	0.91	3.3	0.8		6.9	23.5
Cymodoce sp.	1.11	8.9	3.4		0	0		1.0	0.1
Podocerus sp.		17.8	46.9	1.04	3.8	0		5.1	11.9
Leucothoe sp.		0	0		0	0	0.64	7.0	0.4
Syllid sp.		0.8	1.0		0	1.8	0.61	2.5	0.1
Exogone sp.		0.1	0.3		0.9	0.9	0.52	6.3	2.4
Cymadusa sp. 3		0.1	0		0	0.1	0.49	3.4	1.8
Species disproportionately abundant on filamentous APUs									
Sphaeromatid sp.	3.27	37.9	632.9	1.94	7.0	91.9		22.5	108.8
Ianiropsis sp.	3.29	26.0	441.3		0	0.3	1.22	34.6	407.1
Eatoniellid sp. 1	2.08	1.8	45.0	2.38	5.3	141.6		21.9	38.4
Mallacoota cf. *subcarinata*		0	3.3	3.83	0.3	179.0		0	0
Eatoniellid sp. 2		0.4	3.6	2.17	0	15.1		0.5	1.4
Tethygeneia sp.		1.8	3.8	2.07	0	12.6		0.5	1.4
Bittium sp.	1.68	0.5	10.4		2.5	27.8		1.4	2.1
Tricolia sp.	1.67	10.6	98.8		0	0		5.1	23.0
Hyale sp.		0.1	3.4		0	0	1.27	6.0	85.0
Eatoniellid sp. 3		0	0		0	0	0.94	0	13.0
Macrobrachium sp.		0.3	3.0		0.1	2.8	0.82	1.3	16.3
Paradexamine cf. *churinga*		0.8	0		0.1	1.1	0.75	9.5	72.3

Characteristic species were identified as those exhibiting highest levels of dissimilarity between habitat types, as assessed using SIMPER analysis. The level of dissimilarity between groups ($\bar{D}$) is shown for the five most important species at each location, as is mean abundance on *Sargassum* plants and filamentous APUs at all locations.

Acknowledgements

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