

Measurement of the carrying capacity of benthic habitats using a metabolic-rate based index

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Abstract. Carrying capacities of grazed habitats are typically expressed as numbers or biomass of animals per unit area; however, such parameters are appropriate only when the body size of animals is constant because consumption and other metabolic-rate based parameters such as respiration and production are proportional to body mass raised by a power of ≈ 0.75 rather than 0 or 1. Habitat carrying levels are therefore better expressed in the form of an index of total community consumption by summing the body masses of individual animals after they have been scaled using a biomass exponent of ≈ 0.75 . A parameter scaled in this way, P_{20} , varied in a predictable manner when calculated for the mobile epifaunal assemblages associated with rope fibre habitats placed at marine and estuarine sites; P_{20} showed no significant difference between 17 shallow, clear-water sites worldwide, but declined consistently when photosynthesis was reduced. P_{20} also did not vary significantly when calculated for the mobile epifaunal communities associated with four *Amphibolis antarctica* seagrass habitats in Australia ($\bar{x} = 100 \mu\text{g} \cdot \text{g}^{-1} \cdot \text{day}^{-1}$), and reached but did not significantly exceed a ceiling of $\approx 280 \mu\text{g} \cdot \text{g}^{-1} \cdot \text{day}^{-1}$ for *Sargassum* plants. These results are consistent with the hypothesis that the production of shallow-water epifaunal communities of grazers is constrained by resource ceilings which can be quantified using metabolic-rate based indices. If this “production ceiling” hypothesis is correct then diffuse competition is generally more important than predation or environmental disturbance in restricting the growth of mobile epifaunal populations.

Key words: Carrying capacity – Competition – Epifauna – Macrofauna – Macrophytes

tions; however, the biological implications of one sample of mixed species having greater faunal abundance or biomass than another are often unclear. Faunal abundance and biomass analyses are also confounded by animal size-distribution patterns; abundance comparisons predominantly incorporate information from the smallest species which are generally much more abundant than larger animals, whereas biomass comparisons primarily involve the largest species in a sample, in some cases only a single fortuitously collected individual. An alternative set of indices based on the general empirical finding that production, respiration, ingestion, etc. all vary with body mass raised by a power of ≈ 0.75 (Lavigne 1982; Peters 1983) remain unexamined, but may prove more useful than abundance or biomass in community studies. Such metabolic-rate based indices do not appear to be generally biased by either small or large species because the abundance of animals (N) has been found in community studies to show an overall decline with body mass (B) which corresponds to the increase in production, i.e. $N \propto B^{-0.75}$ (Peters and Wassenberg 1983; Marquet et al. 1990); consequently, the total production of communities of small animals per unit area is approximately equal to the production of communities of large animals. More importantly, metabolic-rate based indices are approximately proportional to major ecological attributes of communities, viz. total community production, respiration and consumption. In this study a metabolic-rate based index has been used to quantify community consumption for mobile invertebrate assemblages associated with marine algae and seagrasses. The study has dual aims, a general aim to investigate whether metabolic-rate based indices are potentially valuable, and a specific aim to investigate processes in epifaunal grazer communities.

Surfaces submersed in sunlit marine environments are rapidly colonised by a diverse array of small, mobile macro-invertebrates belonging to a variety of taxonomic groups, most notably amphipods, isopods, gastropods and polychaetes (Gunnill 1983; Virnstein and Curran 1986; Russo 1988; Edgar 1991a, 1992a). Almost all the

Statistical analyses of animal communities frequently compare the total abundance or total biomass of samples. Abundance and biomass parameters are easy to measure and are clearly useful when dealing with popula-

invertebrates in these assemblages are generalist feeders which prefer periphyton (i.e. diatoms, fine filamentous algae, protozoans, bacteria and particulate organic matter) to the host macroalga or seagrass itself (Norton and Benson 1983; Morgan and Kitting 1984; Orth and Van Montfrans 1984; Brawley and Fei 1987; Klumpp et al. 1989; Preston and Moore 1990; Sullivan and Moncreiff 1990). Mobile epifauna have considerable ecological importance as they provide the major trophic linkage in inshore reef and seagrass environments between primary producers and fishes (Quast 1971; Kikuchi 1980; Klumpp et al. 1989). The interaction between epifauna and fishes may also have reciprocal importance; fish and decapod predators are generally considered to play a principal role in regulating epifaunal numbers (Heck and Orth 1980; Orth et al. 1984).

As a consequence of the perceived importance of predators to benthic invertebrates, the dynamics of benthic communities are largely investigated and discussed in terms of fluctuations in predation pressure (e.g. Nelson 1979; Nelson et al. 1982; Edgar 1983; Kneib 1992). The evidence for an overriding role of predators in structuring benthic communities is, however, largely circumstantial, as it results from the observations that mobile macrofauna are predominant amongst the gut contents of fishes and decapods and that fishes and decapods are extremely abundant in inshore habitats, and from field and laboratory experiments where fishes, crabs and shrimps have been found to negatively influence the abundances of particular macrofaunal species (Wiltse et al. 1984; Jensen and Jensen 1985; Leber 1985; Kneib 1988). Caging experiments with fish and decapod predators nevertheless rarely produce unequivocal results, with epibenthic predators sometimes positively influencing the abundances of particular invertebrate species (Wilson 1989), having no influence (Bell and Westoby 1986; Russo 1991; Edgar and Robertson 1992), or having a variable influence on different species (Young et al. 1976; Young and Young 1978). Alternative hypotheses which need to be considered when investigating macrofauna are that abiotic factors (temperature, salinity, physical disturbance etc.) regulate population numbers, or that numbers are limited by insufficient food resources.

"Food limitation" hypotheses remain to be adequately tested in macrophytic habitats, partly because of the perception that macroalgae and seagrass occur in large quantities in inshore habitats so are unlikely to be limiting (Heck and Orth 1980). The quality of macrophytes as food resources compared to diatoms and filamentous algae is, however, probably low (Norton and Benson 1983; Morgan and Kitting 1984; Orth and Van Montfrans 1984). Methodological difficulties have also hindered studies of food limitation amongst benthic invertebrates because the diversity of benthic assemblages and the difficulties in quantifying the production and quality of the variety of foods available to benthic species make it virtually impossible to directly compare the consumption of mesograzers with the production of food. Food limitation hypotheses are therefore best investigated by looking at the accuracy of inferred predictions. A prediction which follows if mobile epifaunal species

are food limited is that, because species feed on an overlapping range of food items and recover quickly from disturbance by reproducing and recruiting rapidly (Moore 1977; Gunnill 1983; Imada and Kikuchi 1984; Edgar 1990c), total community consumption should be maintained as a result of diffuse competition at resource ceilings except in situations where severe disturbance has occurred recently (<1 month). The prediction that resource ceilings related to primary production are widespread for mobile epifaunal assemblages has been investigated here by comparing values of P_{20} , a metabolic-rate based parameter approximately proportional to total community food consumption, at a heterogeneous range of locations. In order to remove microhabitat variability, rope fibre habitats (RFHs) of constant morphology were initially used as substrata. Faunal assemblages associated with RFHs do not differ qualitatively from natural assemblages as they contain almost all mobile epifaunal species found on adjacent habitats (Edgar 1991a). P_{20} is predicted to vary little between sunlit sites but decline when a deficiency in light or nutrients limits algal photosynthesis; slight variation in assemblage P_{20} is nevertheless expected between sites because of residual variation in the general body mass versus production regression (Edgar 1990a) and differences in the degree of localised shading. By way of contrast, predation and abiotic disturbance hypotheses predict a high level of variation in P_{20} between sites because the severity and frequency of environmental disturbance (wave turbulence, temperature and salinity variation, etc.) and predation all differ substantially between the sites investigated. If species compete for space rather than primary production, P_{20} should be independent of declining levels of light.

Similar predictions can also be made in natural habitats because seagrasses and macroalgae possess few direct grazers, with the majority of animals in shallow habitats feeding on periphyton; if the "production ceiling" hypothesis is correct then relatively little variation in community P_{20} should occur between shallow, sunlit macrophytic habitats, providing that the physical and chemical structure of the substrata and plant density (degree of self-shading) remain constant.

Methods

Sampling protocol

In order to minimize variation between samples due to substratum morphology, standardized rope fibre habitats (RFHs) which mimic filamentous algae were placed at sites in Japan, Scotland, Kosrae (Federated States of Micronesia) and subantarctic Heard Island, and at a number of locations in Australia (see Table 1). Four RFHs were placed at each site except for the four south-west Tasmanian sites (Edgar 1991b), where two replicates only were placed. The 17 sites listed in Table 1 include all shallow-water sites at which I have placed RFHs, with the exception of two upstream sites with little visible light in the Bathurst Harbour estuary (Edgar 1991b). Sites were chosen to include as wide a range of habitats and biogeographical regions as possible. One additional "outgroup" site, an oligotrophic subalpine lake, was also sampled. Each artificial algal habitat consisted of a ≈ 50 g clump of Tanikalon rope fibre (Tanikalon Chemical Industries Ltd, Okayama, Japan) which was tied

Table 1. Locations where rope fibre habitats were deployed, and natural *Amphibolis antarctica* and *Sargassum* spp. plants sampled

Habitat and site	Depth (m)	Sample date	Reference
Rope fibre habitats			
Seagrass bed			
<i>Heterozostera tasmanica</i> , Seven Mile Beach, W.A. (29° 11' S 114° 53' E)	3	20 Jun 87	Edgar (1990b)
<i>H. tasmanica</i> , Cliff Head, W.A. (29° 31' S 114° 59' E)	1	20 Jun 87	Edgar (1990b)
<i>H. tasmanica</i> , Rhyll, Vic (38° 28' S 145° 17' E)	0	3 Aug 90	
<i>Amphibolis antarctica</i> , Seven Mile Beach, W.A. (29° 11' S 114° 53' E)	1	20 Jun 87	Edgar (1990b)
<i>A. antarctica</i> , Cliff Head, W.A. (29° 31' S 114° 59' E)	1	20 Jun 87	Edgar (1990b)
<i>Enhalus acoroides</i> , Kosrae, F.S.M. (5° 17' N 162° 59' E)	0	28 Oct 90	
Macroalgal bed			
<i>Durvillaea antarctica</i> , Breaksea I., Tas (43° 20' S 145° 58' E)	1	16 Feb 89	Edgar (1991b)
<i>Carpoglossum confluens</i> , Sarah I., Tas (43° 20' S 146° 00' E)	1	16 Feb 89	Edgar (1991b)
<i>C. confluens</i> , Farrell Pt, Tas (43° 21' S 146° 05' E)	1	16 Feb 89	Edgar (1991b)
<i>Sargassum patens</i> , Tomioka, Japan (32° 32' N 130° 02' E)	3	26 Mar 88	Edgar (1991a)
<i>Laminaria</i> spp., Millport, Scotland (55° 45' N 4° 57' W)	5	24 Jul 88	
Intertidal Rockpool			
Seven Mile Beach, W.A. (29° 11' S 114° 53' E)	0	20 Jun 87	Edgar (1990b)
Atlas Cove, Heard Island (53° 02' S 73° 21' E)	0	21 Feb 88	
Coral reef			
Tafansak, Kosrae, F.S.M. (5° 22' N 163° 02' E)	4	28 Oct 90	
Unvegetated habitat			
Rock, Celery Top I., Tas (43° 23' S 146° 08' E)	1	16 Feb 89	Edgar (1991b)
Sand, Seven Mile Beach, W.A. (29° 11' S 114° 53' E)	3	20 Jun 87	Edgar (1990b)
Sand, Cliff Head, W.A. (29° 31' S 114° 59' E)	2	20 Jun 87	Edgar (1990b)
Freshwater lake			
Rock, Pine Lake, Tas (41° 44' S 146° 43' E)	1	3 Jul 91	
<i>Sargassum</i> habitats			
Tomioka, Japan (32° 32' N 130° 02' E)	3	6 Jun 88	Edgar and Aoki (1993)
Wentworth Reef, Qld (16° 31' S 145° 32' E)	2	11 Aug 81	
Magnetic Island, Qld (19° 08' S 146° 53' E)	2	14 Aug 81	
Slade Point, Qld (21° 05' S 149° 13' E)	2	16 Aug 81	
Yeppoon, Qld (23° 07' S 150° 44' E)	1	17 Aug 81	
Myora Light, North Stradbroke Island, Qld (27° 28' S 153° 24' E)	0	12 Sep 81	
Minniewater, N.S.W. (29° 47' S 155° 18' E)	1	27 Jul 81	
Halifax Point, N.S.W. (32° 44' S 152° 09' E)	1	25 Jul 81	
Fancy Point, Tas (43° 13' S 147° 21' E)	1	20 Nov 80	Edgar (1983)
<i>Amphibolis antarctica</i> seagrass habitats			
Cliff Head, W.A. (29° 31' S 114° 59' E)	1	3 May 86	Edgar (1990c)
Seven Mile Beach, W.A. (29° 11' S 114° 53' E)	1	5 May 86	Edgar (1990c)
Rottneest Island, W.A. (32° 00' S 115° 33' E)	1	10 Jan 91	
Ventnor, Vic. (38° 31' S 145° 08' E)	3	28 Feb 90	

to a brick or the seabed and retrieved with associated animals after 1–3 months submergence (Edgar 1991a). Experiments conducted in Japan (Edgar 1991a) indicated that the length of submergence, when greater than 1 month, did not greatly affect the faunal production parameter investigated (P_{20} , described below); the estimated total production (P_{20}) of epifauna associated with RFHs in Japan did not differ significantly between habitats submerged for 24 [88 ± 30 (SD) $\mu\text{g} \cdot \text{g}^{-1} \cdot \text{day}^{-1}$] and 57 (93 ± 21 $\mu\text{g} \cdot \text{g}^{-1} \cdot \text{day}^{-1}$) days.

Mobile epifaunal assemblages associated with RFHs were sampled by enclosing individual RFHs underwater in plastic bags and adding buffered formalin ($\approx 5\%$ v/v) to the contents of the bags as soon as possible after collection (within 30 min). In the laboratory, the fauna was extracted by pouring the content of each bag onto the top of a nested series of sieves, 0.5, 0.71, 1.0, 1.4, 2.0, 2.8, 4.0, 5.6, 8.0 mm (Edgar 1990a). Each sieve was shaken in turn in a bucket of water to allow animals smaller than that sieve size to pass through, and the content of the bucket then poured onto the next smallest sieve. Animals retained on each sieve were identified and counted under a binocular microscope. Animals on the largest sieve were weighed after drying at 60° C for 2 days. Large (≥ 8 mm sieve

size) decapod and fish species using the RFHs as refuges were excluded from analyses.

Although it was difficult to sample macrophytes of constant morphology over a large geographic range, limited sampling of natural beds of the seagrass *Amphibolis antarctica* and macroalgae (*Sargassum* spp.) was also carried out. Five replicate 0.125×0.125 patches of *A. antarctica* were collected at each of four Australian sites, and five replicate *Sargassum* spp. plants collected at eight sites along an eastern Australian latitudinal transect (Table 1). Mobile epifauna collected in samples was extracted and processed in a similar way to RFH-associated assemblages, with the dry weight of the host plant determined by drying at 60° C for 2 days. Seven Mile Beach and Cliff Head seagrass plants were collected in May 1986, the only month during a seasonal study (Edgar 1990c) when *A. antarctica* plants were distinguished from co-occurring *Amphibolis griffithii* plants at Seven Mile Beach.

Measurement of community production

Food production and consumption within habitats have not been directly determined in this study; however an arbitrarily selected

parameter P_{20} ($\mu\text{g} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$), estimated daily macrofaunal production at 20°C ($= \sum a_i \cdot 0.0705 \cdot B_i^{0.80}$, where a_i is the number and B_i the mean ash-free dry weight (μg) of animals retained on sieve i ; Edgar 1990a), has been calculated for faunal assemblages sampled. If thin species such as capitellid polychaetes or caprellid amphipods are not common, P_{20} can be calculated using the mean weights of animals retained on different sieves as listed in Table III of Edgar (1990a) by simply multiplying the abundances of animals collected on sieve sizes 0.5, 0.71, 1, 1.4, 2, 2.8, 4, 5.6 with the constants 0.923, 1.92, 3.94, 8.19, 17.0, 35.5, 73.8, $154 \mu\text{g} \cdot \text{day}^{-1}$ and summing the data. P_{20} is based on the regression $P = 0.0049 \cdot B^{0.80} \cdot T^{0.89}$, where B is body mass (μg) and T is temperature ($^\circ\text{C}$), a relationship deduced in an empirical analysis of the effect of body mass on macrofaunal production (Edgar 1990a). The biomass exponent used in the equation (0.80) is close to 0.75, the general value calculated for allometric biomass/production relationships in a variety of terrestrial and aquatic studies (McNeil and Lawton 1970; Humphreys 1979; Lavigne 1982). P_{20} is suggested to be approximately proportional to the level of community food consumption because food ingested is closely related to production and varies with body weight raised to a similar power (Cammen 1980; Peters 1983). If almost all utilizable food resources within a habitat are being consumed, P_{20} should also be approximately proportional to the carrying capacity.

Production was calculated for an arbitrarily standardized temperature of 20°C to eliminate the metabolic effects of temperature on production between sites; this introduces an assumption that primary production shows a corresponding metabolic relationship to temperature, i.e., that the increased consumption which occurs as temperature increases is accommodated by a corresponding increase in the production of food resources. If this assumption is not justified then P_{20} should vary with water temperature.

Results

No significant variation in P_{20} was detected between any of the 17 shallow, clear-water marine sites at which

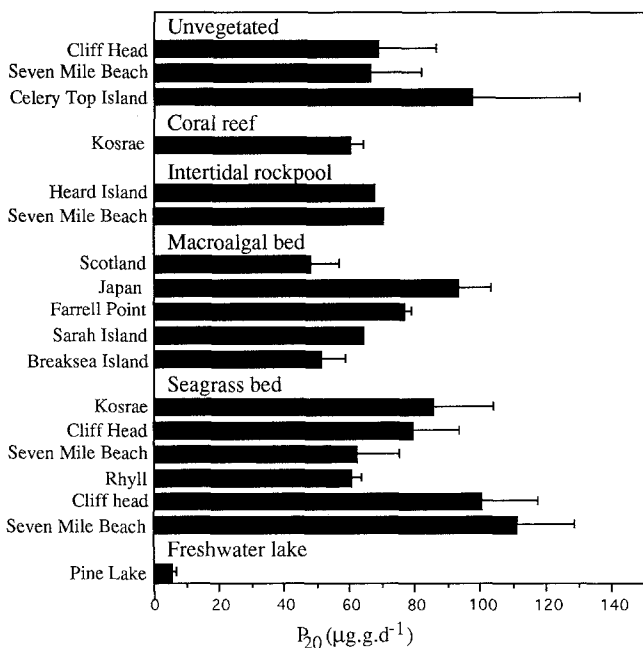


Fig. 1. P_{20} values (+SE bars) for faunas associated with 50 g rope fibre habitats (RFHs) submerged for ≈ 8 weeks in a variety of shallow marine (and one freshwater) habitats. The four Heard Island samples were amalgamated before sorting, with single RFHs collected from the rock pool at Seven Mile Beach and macroalgal habitat at Sarah Island because other replicate RFHs were lost due to wave action

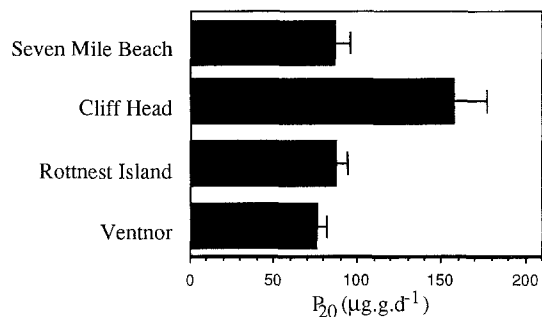


Fig. 2. P_{20} values (g^{-1} seagrass dry weight; +SE bars) for faunas (>0.5 mm sieve size) associated with *Amphibolis antarctica* collected in shallow water (<3 m) at four sites

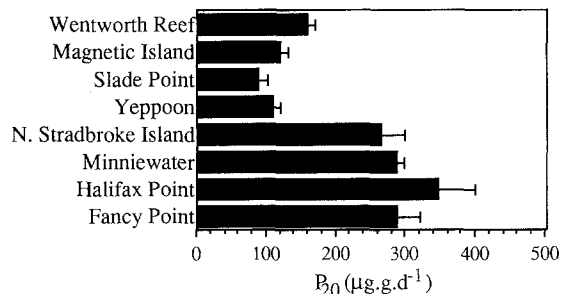


Fig. 3. P_{20} values (g^{-1} macroalgal dry weight; +SE bars) for faunas (>0.5 mm sieve size) associated with various species of *Sargassum* collected in shallow water (<3 m) along a latitudinal transect down the east coast of Australia

RFHs were placed (1-way ANOVA, $df=16/36$, $F=1.22$, $P=0.303$), although total faunal abundance ($F=4.35$, $P<0.001$) and biomass ($F=2.01$, $P=0.041$) both showed significant variation between sites (Fig. 1). P_{20} of RFH-associated assemblages did, however, decline when photosynthesis was limited; it was found to be much lower at a 15-m-deep site at Heard Island ($\bar{x} = 5.7 \mu\text{g} \cdot \text{g}^{-1} \cdot \text{day}^{-1}$) and at 5 m depth in turbid water at Rhyll ($\bar{x} = 28.9 \mu\text{g} \cdot \text{g}^{-1} \cdot \text{day}^{-1}$), and was 90% lower than the shallow marine values for the outgroup assemblage inhabiting nutrient-deficient Pine Lake (Fig. 1).

Epifaunal P_{20} did not vary significantly between sites for the samples of *Amphibolis antarctica* described in Table 1 (Fig. 2; ANOVA, $df=3/16$, $F=2.14$, $P=0.135$). However, a significant seasonal decline in P_{20} did occur at Cliff Head (ANOVA, $df=11/11$, $F=15.99$, $P<0.001$; Edgar, unpublished data) during an extended seasonal period when the water became turbid (Edgar 1990c). No significant variation in P_{20} was detected between years or seasons at the nearby, clearer-water Seven Mile Beach site during the same period (ANOVA, $df=11/11$, $F=1.80$, $P=0.172$; Edgar, unpublished data). P_{20} values for faunas associated with *Sargassum* varied over a four-fold range at the eight examined sites (Fig. 3).

Discussion

Resource limitation in benthic habitats

The results of statistical analyses for the RFH- and *Amphibolis antarctica*-associated assemblage data are consis-

tent with the food limitation hypothesis but not with the alternative hypotheses. Epifaunal assemblages are therefore more likely to be limited primarily by a lack of food resources than by other factors. Factors such as predator abundance (which varied from no observable fish at Celery Top Island to > 3 fish/m² on the Tafansak coral reef), water temperature, wave turbulence, salinity and surrounding habitat type appear to have relatively little influence on P_{20} . While the data presented here on the relationship between light and P_{20} are limited, P_{20} showed a strong and consistent negative correlation with light at Breaksea Island, Sarah Island, Farrell Point and Celery Top Island, and two other locations in the tannin-stained Bathurst Harbour estuary (as described in Edgar 1991b). P_{20} decreased with depth and with distance upstream in this estuary, and also during the winter period when tannin-stained surface water created a deep halocline. P_{20} was found to be an order of magnitude lower than indicated in Fig. 1 on occasions when no light was visible. Some of the variation in P_{20} which is shown in Fig. 1 can also be attributed to localised decreases in ambient light, although this variation in shading between the shallow sites could have caused a maximum of only a halving in P_{20} . The lowest P_{20} values were found at sites where the artificial habitats were shaded by either *Amphibolis* fronds (Seven Mile Beach and Cliff Head), kelps (Breaksea Island, Heard Island and Millport) or large overhanging rocks (Breaksea Island).

The variation in epifaunal P_{20} between the different *Sargassum* sites was much larger than for the other habitat types and possibly reflects morphological and chemical variation between species of *Sargassum*. Epifaunal P_{20} , when expressed per unit biomass of algae, also varied during the life-cycle of *Sargassum*; P_{20} increased fourfold during the annual growth cycle of *Sargassum verruculosum* and *Sargassum bracteolosum* at Fancy Point, Tasmania (see Edgar 1983), and also during the growth period for *Sargassum varians* at Tomioka, Japan (Edgar and Aoki 1993). If, as suggested, the epifaunal carrying capacity of plants is limited by periphyton production, this result is expected because young *Sargassum* plants possess high levels of secondary metabolites which inhibit the production of diatoms, protozoa and bacteria (Sieburth 1968; Hornsey and Hide 1974; Ryland 1974; Al-Ogilby and Knight Jones 1977). It is notable that P_{20} reached and stabilised at $\approx 280 \mu\text{g} \cdot \text{g}^{-1} \cdot \text{day}^{-1}$ for these three *Sargassum* species, the same level as recorded at three other sites during the latitudinal transect. This level possibly represents the carrying capacity of *Sargassum* on occasions when periphyton is not greatly inhibited by exudates.

Additional support for the hypothesis that quantifiable resource ceilings limit the abundance of epifauna is provided by experiments in which the recovery of partially-defaunated assemblages was monitored in field microcosms (see Edgar and Aoki 1993). After defaunation, the total P_{20} of macrofauna within microcosms rapidly converged on control P_{20} values of $\approx 5 \text{ mg} \cdot \text{day}^{-1}$, regardless of whether the microcosms were set up with *A. antarctica* as a substratum in Australia, or with *Sargassum varians* as a substratum in Japan. Faunal abundance varied significantly in these analyses.

Utility of metabolic-rate based indices

The low level of variation in epifaunal P_{20} between sites (Fig. 1) was unexpected given the inherent differences between species in their production/biomass relations (Edgar 1990a), and the potential variability in P_{20} introduced by factors, largely unexamined, such as the degree of localised shading and nutrient availability. While the ANOVA of the RFH assemblage data showed no significant difference in P_{20} between sites, this result would presumably have changed if the power of the statistical analysis had been increased, for example, by increasing the number of replicates and decreasing the number of sites. Despite this qualification, it remains difficult to conceive of any other nontrivial community parameter which varies over only a twofold range amongst such a diversity of marine environments. Faunal species composition, the prevalence of predators and water temperature had little effect on P_{20} at the sites examined, whereas light, biomass of seagrass debris and biomass of live seagrass material all have substantial and highly significant effects on macrofaunal production as calculated using metabolic-rate based indices (Edgar 1990b, 1991c). The closer correspondence found between environmental parameters and P_{20} than with faunal abundance or faunal biomass indicates that metabolic-rate based community indices warrant further investigation. If accurate predictions of P_{20} can be coupled with predictions of the size-distribution of assemblages for unexamined sites, then predictions of faunal biomass and abundance can also be made.

Because of the preliminary nature of this study, accurate predictions of the variation in P_{20} could not be made prior to the field work for rigorous hypothesis testing. For future work, P_{20} is predicted to vary over a twofold range for habitats of constant physical and chemical structure at sites with high light levels, but to decline when light is reduced.

Whether metabolic-based production and consumption indices are useful for calculating carrying capacities for communities other than those associated with macrophytes remains to be determined. Mobile macrofaunal assemblages may possess particular characteristics which make them unusually suitable for investigating hypotheses involving metabolic-rate based indices. Many epifaunal species have the reproductive capacity to double population numbers in a week (see, for example, Imada and Kikuchi 1984; Fredette and Diaz 1986). Hence, in contrast to the non-equilibrium state of many other assemblages, mobile epifaunal assemblages should recover rapidly from any environmental disturbance and are more likely to maintain total consumption at close to equilibrium levels. Moreover, the food resources of epifaunal grazers (and detritivores) are localised, so what is not eaten by one animal is available to others. By contrast, food available to suspension feeders is not locally contained because an unknown but generally large proportion of food accessible to these assemblages will not be ingested by animals but will drift through and out of the system. Accurate predictions of the carrying capacities of suspension feeding assemblages may therefore prove difficult, perhaps impossible.

The species richness of epifaunal assemblages (shallow-water RFHs used in this study contained between 21 and 95 macrofaunal species) also allows total production to be estimated with a relatively high degree of accuracy (Edgar 1990a). If a single species was to dominate an assemblage and had a production-rate which differed by a factor of 2 from that predicted using the general equation described in Edgar (1990a), then the estimate of total community production would be out by a similar factor. If many species occur in a sample and they have an equitable distribution, then it is likely that each species with a production rate higher than predicted will be approximately counterbalanced by a species with a rate lower than predicted.

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References

- Al-Ogilby SM, Knight-Jones EW (1977) Anti-fouling role of antibiotics produced by marine algae and bryozoans. *Nature* 265:728–729
- Bell JD, Westoby M (1986) Abundance of macrofauna in dense seagrass is due to habitat preference, not predation. *Oecologia* 68:205–209
- Brawley SH, Fei XG (1987) Studies of mesoherbivory in aquaria and in an unbarricaded mariculture farm on the Chinese coast. *J Phycol* 23:614–623
- Cammen LM (1980) Ingestion rate: an empirical model for aquatic deposit feeders and detritivores. *Oecologia* 44:303–310
- Edgar GJ (1983) The ecology of south-east Tasmanian phytal animal communities. II. Seasonal change in plant and animal populations. *J Exp Mar Biol Ecol* 70:159–179
- Edgar GJ (1990a) The use of the size-structure of benthic macrofaunal communities to estimate faunal biomass and secondary production *J Exp Mar Biol Ecol* 137:195–214
- Edgar GJ (1990b) The influence of plant structure on the species richness, biomass and secondary production of macrofaunal assemblages associated with Western Australian seagrass beds. *J Exp Mar Biol Ecol* 137:215–240
- Edgar GJ (1990c) Population regulation, population dynamics and competition amongst mobile epifauna associated with seagrass. *J Exp Mar Biol Ecol* 144:205–234
- Edgar GJ (1991a) Artificial algae as habitats for mobile epifauna: factors affecting colonization in a Japanese *Sargassum* bed. *Hydrobiologia* 226:111–118
- Edgar GJ (1991b) Distribution patterns of mobile epifauna associated with rope fibre habitats within the Bathurst Harbour estuary, south-western Tasmania. *Estuar Coast Shelf Sci* 33:589–604
- Edgar GJ, Aoki M (1993) Resource limitation and fish predation: their importance to mobile epifauna associated with Japanese *Sargassum*. *Oecologia* 95:122–133
- Edgar GJ, Robertson AI (1992) The influence of seagrass structure on the distribution and abundance of mobile epifauna: pattern and process in a Western Australian *Amphibolis* bed. *J Exp Mar Biol Ecol* 160:13–31
- Fredette TJ, Diaz RJ (1986) Life history of *Gammarus mucronatus* Say (Amphipoda: Gammaridae) in warm temperate estuarine habitats, York River, Virginia. *J Crust Biol* 6:57–78
- Gunnill FC (1983) Seasonal variations in the invertebrate faunas of *Pelvetia fastigiata* (Fucaceae): effects of plant size and distribution. *Mar Biol* 73:115–130
- Heck KL, Orth RJ (1980) Seagrass habitats: the roles of structural complexity, competition and predation in structuring associated fish and macroinvertebrate assemblages. In: Kennedy VS (ed) *Estuarine perspectives*. Academic Press, New York, pp 449–464
- Hornsey IS, Hide D (1974) The production of antimicrobial compounds by British marine algae. I. Antibiotic-producing marine algae. *Brit J Phycol* 9:353–361
- Humphreys WF (1979) Production and respiration in animal populations. *J Anim Ecol* 48:427–453
- Imada K, Kikuchi T (1984) Studies of the reproductive traits of three caprellids (Crustacea: Amphipoda) and their seasonal fluctuations in the *Sargassum* bed. *Publ Amakusa Mar Biol Lab* 7:151–172
- Jensen KT, Jensen JN (1985) The importance of some epibenthic predators on the density of juvenile benthic macrofauna in the Danish Wadden Sea. *J Exp Mar Biol Ecol* 113:9–21
- Kikuchi T (1980) Faunal relationships in temperate seagrass beds. In: Phillips RC, McRoy CP (eds) *Handbook of seagrass biology: an ecosystem perspective*. Garland STPM, New York, pp 153–173
- Klumpp DW, Howard RK, Pollard DA (1989) Trophodynamics and nutritional ecology of seagrass communities. In: Larkum AWD, McComb AJ, Shepherd SA (eds) *Biology of seagrasses: a treatise on the biology of seagrasses with special reference to the Australian region*. Elsevier, Amsterdam, pp 394–457
- Kneib RT (1988) Testing for indirect effects of predation in an intertidal soft-bottom community. *Ecology* 69:1795–1805
- Kneib RT (1992) Population dynamics of the tanaid *Hargeria rapax* (Crustacea: Peracarida) in a tidal marsh. *Mar Biol* 113:437–445
- Lavigne DM (1982) Similarity in energy budgets of animal populations. *J Anim Ecol* 51:195–206
- Leber KM (1985) The influence of predatory decapods, refuge, and microhabitat selection on seagrass communities. *Ecology* 66:1951–1964
- McNeill S, Lawton JH (1970) Annual production and respiration in animal communities. *Nature* 225:472–474
- Marquet PA, Navarrete SA, Castilla JC (1990) Scaling population density to body size in rocky intertidal communities. *Science* 250:1125–1127
- Moore PG (1977) Organization in simple communities: observations on the natural history of *Hyale nilssoni* (Amphipoda) in high littoral seaweeds. In: Keegan BF, Ceidigh PO, Boaden PJS (eds) *Biology of benthic organisms*. Pergamon, New York, pp 443–451
- Morgan MD, Kitting CL (1984) Productivity and utilization of the seagrass *Halodule wrightii* and its attached epiphytes. *Limnol Oceanogr* 29:1066–1076
- Nelson WG (1979) An analysis of structural pattern in an eelgrass (*Zostera marina* L.) amphipod community. *J Exp Mar Biol Ecol* 39:231–264
- Nelson WG, Cairns KD, Virnstein RW (1982) Seasonality and spatial patterns of seagrass-associated amphipods of the Indian River Lagoon, Florida. *Bull Mar Sci* 32:121–129
- Norton TA, Benson MR (1983) Ecological interactions between the brown seaweed *Sargassum muticum* and its associated fauna. *Mar Biol* 75:169–177
- Orth RJ, Van Montfrans J (1984) Epiphyte-seagrass relationships with an emphasis on the role of micrograzing: a review. *Aquat Bot* 18:43–69
- Orth RJ, Heck KL, Van Montfrans J (1984) Faunal communities in seagrass beds: a review of the influence of plant structure and prey characteristics on predator-prey relationships. *Estuaries* 7A:339–350
- Peters RH (1983) *The ecological implications of body size*. Cambridge University Press, Cambridge

- Peters RH, Wassenberg K (1983) The effect of body size on animal abundance. *Oecologia* 60:89–96
- Preston A, Moore PG (1990) Observations on the feeding habits of the commoner animals associated with *Cladophora algida* (Huds.) Kütz. in rockpools. *Glasgow Nat* 21:523–535
- Quast JC (1971) observations on the food of kelp fishes. In: North WJ (ed) *Biology of kelp beds (Macrocystis pyrifera) in California*. Beih Nova Hedwigia 32:541–579
- Russo AR (1988) Detritus and epibiota on artificial substrata: the possible role of food in structuring Hawaiian epiphytal amphipod communities. *Int Rev Ges Hydrobiol* 73:319–325
- Russo AR (1991) Do predatory fishes affect the structure of an epiphytal amphipod assemblage on a protected algal reef in Hawaii? *Hydrobiologia* 224:185–192
- Ryland JS (1974) Observations on some epibionts of gulf-weed *Sargassum natans* (L.) Meyen. *J Exp Mar Biol Ecol* 14:17–25
- Sieburth JM (1968) The influence of algal antibiosis on the ecology of marine organisms. *Adv Microbiol Sea* 1:63–94
- Sullivan MJ, Moncreiff CA (1990) Edaphic algae are an important component of salt marsh food webs: evidence from multiple stable isotope analyses. *Mar Ecol Prog Ser* 62:149–159
- Virnstien RW, Curran MC (1986) Colonization of artificial seagrass versus time and distance from source. *Mar Ecol Prog Ser* 29:279–288
- Wilson WH (1989) Predation and the mediation of intraspecific competition in an infaunal community in the Bay of Fundy. *J Exp Mar Biol Ecol* 132:221–245
- Wiltse WI, Foreman KH, Teal JM, Valiela I (1984) Effects of predators and food resources on the macrobenthos of salt marsh creeks. *J Mar Res* 42:923–942
- Young DK, Young MW (1978) Regulation of species densities of seagrass-associated macrobenthos: evidence from field experiments in the Indian River estuary, Florida. *J Mar Res* 36:569–593
- Young DK, Buzas MA, Young MW (1976) Species densities of macrobenthos associated with seagrass: A field experimental study of predation. *J Mar Res* 34:577–592