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Resource limitation and fish predation: their importance to mobile epifauna associated with Japanese *Sargassum*

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Abstract. The possibility that resource limits constrain the growth of mobile epifaunal populations associated with *Sargassum patens* plants was investigated by placing plants and associated animals into field microcosms which excluded fish predators, and then comparing faunal abundance and size-structure changes in different microcosm treatments with field populations. Four different microcosm treatments were set up: two treatments containing defaunated plants inoculated with caprellid amphipods, and two control treatments with natural faunas. The estimated secondary production of faunas enclosed in all microcosm treatments rapidly settled on a constant value (5 mg/day) which was similar to that determined in experiments conducted in Western Australia using the same microcosms but for faunas associated with a seagrass rather than a macroalga. These results support the hypothesis that the secondary production of epifaunal communities associated with macrophytes is constrained by quantifiable food resource ceilings. Predation by the most common fish species in the area, the wrasse *Halichoeres tenuispinis*, did not appear to alter macrofaunal production in the *S. patens* bed; however, it did greatly affect the faunal size-structure by eliminating most of the larger animals. The majority of epifaunal animals ≥ 2.0 mm sieve-size were consumed by *H. tenuispinis*, while negligible numbers of 0.5-mm sieve-size animals were captured. We postulate that food resource ceilings and predatory size-selectivity are widespread phenomena, affecting epifaunal populations at a variety of locations. Predation is predicted to generally increase rather than decrease faunal abundance because the consumption of each large invertebrate by a predator frees sufficient resources to feed several smaller individuals.

Key words: *Sargassum patens* – *Halichoeres tenuispinus* – Competition – Predation – Macrofauna

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Mobile macrofaunal assemblages of peracarid crustaceans, gastropods, polychaetes, platyhelminths, pycnogonids and a variety of other groups occur ubiquitously in coastal environments. In contrast to the extensive literature on processes operating within megafaunal and sessile invertebrate communities (e.g. Dayton 1971; Paine 1976; Lubchenco and Menge 1978), the relative importance of different biotic (e.g. predation, competition, mutualism) and abiotic (e.g. disturbance, temperature, salinity, organic loading) factors in structuring mobile macrofaunal communities remains poorly understood. This situation needs to be remedied as a matter of priority in view of the trophic importance of the group; the majority of demersal fishes, for example, consume mobile epifauna rather than feeding directly on plant or detrital material, sessile epifauna or the large, conspicuous invertebrates (Kikuchi 1966, 1980; Quast 1971; Pollard 1984; Klumpp et al. 1989).

A major reason for the lack of field experiments involving mobile macrofauna is the difficulty in establishing a suitable experimental protocol. Exclusion and inclusion cages, the most successful tools used to determine functional relationships within other marine communities, often produce ambiguous results when applied to mobile epifauna. Predation has been recognized to significantly affect epifaunal numbers both positively (e.g. Kneib and Stiven 1982; Wilson 1989) and negatively (e.g. Summerson and Peterson 1984; Aoki 1988) in particular studies, but not in others (Choat and Kingett 1982; Russo 1991; Edgar and Robertson 1992), and to have an effect which varies substantially between different macrofaunal species (e.g. Young and Young 1978; Leber 1985). Caging artifacts, a frequent source of problems even for studies of sessile faunas (Dayton and Oliver 1980), are particularly severe in investigations of mobile epifauna (Virnstein 1978) because slight changes in environmental conditions can lead to rapid faunal emigration (DeWitt and Levinton 1985). This problem is compounded in subtidal macrophyte beds because shading of host macrophytes and the consequent reduction in primary production are impossible to avoid in cages with overhead panels. Another factor which can contribute to

the misinterpretation of caging results is that the rate of movement of macrofauna and meiofauna through cage walls is frequently ignored, possibly because it is assumed to be negligible. The turnover of epifauna nevertheless exceeds 30% per day in many habitats (Howard 1985, 1987; Virnstein and Curran 1986; Frid 1989; Edgar 1992). If prey are not confined within cages in such habitats then, unless predation rates are greater than turnover (a situation which would cause natural populations to crash), any loss of animals due to predation should be quickly compensated for by immigrating individuals, and any difference found between caged and uncaged habitats is more likely to result from an experimental artifact than from a predation effect. If prey are confined within cages then light and water flow are necessarily restricted, potentially causing additional artifacts.

In the present study we utilise exclusion microcosms coupled with field observations in an attempt to separate the relative effects of fish predation and resource limitation on epifaunal assemblages associated with *Sargassum*. We recognise that predation pressure is not the only environmental parameter to differ inside compared with outside field microcosms; however, microcosms were considered more useful than open cages with rapid faunal turnovers. Microcosms were primarily used to investigate the hypothesis that the growth of epifaunal populations is principally restricted by a lack of periphytic food and that resource ceilings can be quantified using metabolic-rate based indices (see Edgar 1993); a prediction of this hypothesis is that epifaunal assemblages will not show increased production when released from fish predation, providing that the substratum and light regime do not change. The approach used to study fish predation has been deductive rather than inductive. Data on consumption rates and prey size-selectivity for the most common fish in the study area, the wrasse *Halichoeres tenuispinis* (Günther), have been related to prey abundance so that the impact of *H. tenuispinis* on epifaunal prey can be directly calculated. Other fishes at the site should have a low impact on epifauna compared to *H. tenuispinis*. The next two most common fishes, the wrasses *Pteragogus flagellifera* (Valenciennes) and *Pseudolabrus japonicus* (Houttuyn), occurred at only $\approx 10\%$ of the densities of *H. tenuispinis* and fed predominantly on epifauna associated with the foliose turfing algae rather than *Sargassum* (G. Edgar and M. Aoki unpublished data). Diving observations indicated that *H. tenuispinis* fed within the *Sargassum* canopy rather than close to the reef substratum.

Methods

Epifaunal sampling

Seasonal changes in epifaunal populations associated with *Sargassum patens* C. Agardh plants were monitored in a bed at 3 m depth off the eastern shore of Magarisaki, Tomioka Peninsula, West Kyushu, Japan (32°32′N, 130°02′W). Within this bed *S. patens* forms a canopy above a patchy mosaic of foliose turfing algae (primarily *Gelidium* sp. and *Plocamium* sp.). The site is the same as that described by Aoki (1988), Aoki and Kikuchi (1990) and Edgar (1991). Mean daily water temperatures recorded at the nearby Amakusa Marine Biological Laboratory ranged from 12.5° C (±0.3° C SD) in mid February 1988 to 20.4° C (±0.9° C) in early June 1988.

At monthly intervals between 12 February 1988 and 6 June 1988, a diver detached replicate *Sargassum* plants from the rocky substratum and carefully placed the plants into individual plastic bags. Four replicate plants were collected on 12 February and 18 March, five replicates on 6 May and six replicates on 13 April and 6 June. Formalin was added to the bags within 30 min of collection. In the laboratory, the fauna was extracted by pouring the content of each bag through a nested series of eight sieves ranging in size from 0.5 mm to 5.6 mm (see 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 contents of the bucket then poured onto the next smallest sieve. The animals retained on each sieve were identified and counted under a binocular microscope. The weight of the macroalgal host plant was also determined after drying at 60° C for 2 days.

The estimated biomass of the fauna in each sample was calculated using the number of animals in each sieve size-class and sieve size/mean biomass values listed separately for caprellids and general fauna in Table III of Edgar (1990a). Secondary productivities of samples were estimated using water temperatures, the numbers and biomass of animals in each sieve size-class and the general equation $P = 0.0049 \cdot B^{0.80} T^{0.89}$ (Edgar 1990a).

The density of *Sargassum patens* plants was estimated by throwing 15 quadrats (1 m^2) into the study area on 9 May 1988, and counting the number of plants within each quadrat.

Microcosm (fish exclusion) experiment

Microcosms used to study changes in population numbers of epifaunal species in the absence of fish predators were the same as used in previous experiments in Western Australia (Edgar 1990b); they consisted of 300-mm-long 160-mm-diameter perspex tubes with the ends covered by 300 μm Nytal mesh which was held in place by stainless steel hose clamps. *Sargassum* plants with associated faunas were enclosed within the microcosms underwater, the microcosms being arranged in groups of six on perforated plastic trays (520 × 310 × 70 mm). Each group of six microcosms was held together by placing a tray on the top as well as the bottom of tubes, and then attaching rubber straps between the two trays to draw the trays with the tubes between together. After the groups of six microcosms were placed between trays, they were slowly dragged behind a boat to scallop culture lines set 1 km south-east of the study site, where they were suspended below securely anchored culture ropes at 3 m water depth. Microcosms could not be set up at the study site because wave action made it impossible to securely anchor the microcosms above the rocky substratum there. The scallop culture lines were exposed to a greater fetch but were over deeper water (8 m) than the collection site, so the total wave energy striking the microcosms was slightly less at the former site. Seawater flowed into and out of the microcosms, albeit in a restricted manner, throughout the study. The sides and bases of the trays were perforated with large gaps, and the 300 μm Nytal mesh was cleaned by scrubbing every 2 weeks and replaced after 2 months.

Two microcosm treatments were set up on 12 February 1988: "control-1" microcosms, which contained *Sargassum* plants detached from the reef with natural associated faunas, and "defaunated-1" microcosms, which contained *Sargassum* plants which had been defaunated and then inoculated with a multispecific assemblage of 20 adult caprellids. Plants were defaunated by being placed for 30 min into deoxygenated seawater which had been previously boiled, cooled and then aerated with CO_2. The caprellids were collected from the *S. patens* bed and also a *Sargassum horneri* C. Agardh bed adjacent to the study site where they were more abundant (Imada and Kikuchi 1984). The relative abundances of different caprellid species placed into defaunated microcosms was

estimated from a sample of 101 caprellids that were collected as inoculants but not used.

The epifauna and host plants within four replicate microcosms of each treatment were collected after 1 month, and six replicates after 2 month and 4 month, on the same days as field samples (with the same number of replicates) were collected. The faunas within each microcosm were extracted and counted using the same methods as for field samples.

On 13 April 1988, an additional experiment was commenced with two treatments: "control-2" microcosms, which contained *Sargassum* plants detached from the reef with natural associated faunas, and "defaunated-2" microcosms, which contained defaunated *Sargassum* plants inoculated with 10 mature individuals of *Caprella monoceros* Mayer. The methods used for setting up this experiment were the same as used for the longer running experiment. Six replicates of each treatment were collected on 6 June 1988. Individual microcosms for the various treatments were randomly intermingled on trays.

At the start of the experiments, microcosms for all treatments were sub-divided equally into two sets: one set of microcosms contained a nitrogen addition (slowly dissolving granules of NH_4NO_3 enclosed in perforated plastic capsules) and the other lacked this nitrogen source. This additional treatment was set up to test the hypothesis that the senescence of plants within the *Sargassum patens* bed in May was caused by a deficiency in accessible nitrogen in the natural environment. A rapid spring decline in dissolved nitrate concentrations from ≈ 3 to ≈ 0.4 µM occurs annually off Tomioka (Amakusa Marine Biological Laboratory, unpublished data). No significant differences in plant biomass or epifaunal population parameters within microcosms were found between the nitrogen addition and control treatments, so this experiment has not been discussed further.

Predation

The wrasse *Halichoeres tenuispinis* was visually censused on 18 February, 8 March, 19 April and 27 May 1988 using a belt transect method. A diver swam up and down a 100-m-long transect line which was permanently placed through the study area, and recorded the number of fishes sighted within 2 m of the line during each pass. Three censuses were made on each survey date, between 11.30 and 12.00 a.m., 1.30 and 2.00 p.m. and 3.30 and 4.00 p.m. The area censused thus totalled 3×400 m^2 during each sampling day.

Fish were collected for dietary analysis on 9 May 1988 during five half-hour periods between 6 a.m. and 9 a.m., and at 11 a.m. and 3 p.m. Approximately 12 specimens of *H. tenuispinis* were collected in each sample. *Halichoeres tenuispinis* were concealed in nocturnal refuges under sand by 6 p.m., so could not be captured at this time. Specimens were collected by a diver herding fishes into a set gillnet constructed with two mesh sizes, 7 and 45 mm. Fish were preserved using buffered formalin after underwater removal from the net.

In the laboratory, the sex and total length of each fish were recorded. The gut contents were removed and the identity and abundance of each prey item determined under a dissecting microscope. For two abundant prey species which remained well-preserved in the gut for relatively long periods, the caprellid amphipod *Caprella monoceros* and gammarid amphipod *Pereionotus thomsoni*, the size-frequency distributions of intact consumed prey were also determined. The length of head capsules of 174 *C. monoceros* and the total length of 68 *P. thomsoni* were recorded using a graticule in the eyepiece of the microscope; these measurements were related to the corresponding measurements for animals in different sieve size-classes, as recorded from monthly samples of *Sargassum* epifauna, thus allowing the prey to be allocated to sieve size-classes.

When observed underwater from distances > 2 m, *H. tenuispinis* did not appear to be disturbed by the diver. This wrasse could be seen to peck at individual prey items in the *Sargassum* canopy; consequently the mean number of prey consumed by *H. tenuispinis* per day was deduced by multiplying the total daily number of pecks which fish made at prey with the proportion of pecks which successfully resulted in prey capture. The success of pecks was determined by relating the mean number of prey in guts during the early morning, i.e. before any prey had been egested, with the mean cumulative number of pecks made by fish up to that time.

The number of pecks made at hourly intervals through the day was determined by divers watching individual fish underwater on 9 May 1988, and recording the number of pecks made at *Sargassum* plants during 15-min intervals. Rather than chasing fish, single fish were watched for pecking activity until they disappeared from view, and then another fish was immediately selected as the target of observations. Between two and seven ($\bar{x} = 4$) 15-min counts were undertaken during each hour interval from 6 a.m. to 6 p.m. Sunrise and sunset occurred at 5:26 a.m. and 7:08 p.m., respectively.

In order to calculate the impact of *H. tenuispinis* on different size-classes within the epifaunal community, an estimate of the growth rates as well as the standing stock of epifauna was necessary. This was done using the general relationship $P = 0.0049 . B^{0.80} . T^{0.89}$, where P is secondary production, B body mass and T temperature (Edgar 1990a), as a logistic equation to determine the growth of a generalized invertebrate at 20° C. An animal of 15.68 µg body mass, the minimum size of animals retained by the 0.5-mm sieve (Edgar 1990a), is calculated using this equation to have a daily production of 0.64 µg at 20° C, and will thus have a mass of 16.32 µg after 1 day. Continuing with this calculation of daily increments, the animal will be 40.0 µg after 24 days, and thus have just reached the minimum size to be collected by the 0.71-mm sieve (39.6 µg). (The periods which this generalized animal takes to grow through the different sieve size-ranges have been included in Table 5 as the turnover rate.)

Results

Microcosm (fish exclusion) experiment

Sargassum patens plants were found on 9 May 1988 to occur in densities (± SE) of 51 (± 3) m^{-2}. This density value has been assumed in plant biomass and faunal abundance calculations to have remained constant during the study. By using a constant value, fluctuations between months in plant density data which were due to sampling error were not incorporated into calculations of faunal density; the general annual decline in plant density from February to May (≈15% for the years 1986–1988; M. Aoki, unpublished data) was often less than the measured variation between neighbouring months.

The mean biomass of sampled plants doubled between February and early June (Fig. 1), but then declined

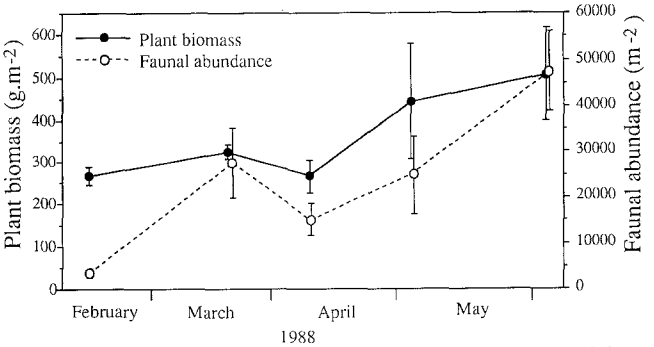

Fig. 1. Monthly mean changes (± SE) in plant biomass *(solid dots and line)* and faunal abundance *(open dots, dashed line)* during the period of study

Table 1. Mean (± SD) abundance, biomass and estimated production of epifaunal assemblages within four experimental microcosm treatments set up in Japan and two microcosm treatments set up in Western Australia (Edgar 1990b)

	Abundance	Biomass (mg)	Production (mg/day)
Japan			
Control-1	2000 ± 904	308 ± 151	6.65 ± 3.34
Control-2	1127 ± 327	276 ± 49	5.11 ± 0.89
Defaunated-1	1930 ± 489	221 ± 96	5.30 ± 2.05
Defaunated-2	1457 ± 481	212 ± 60	4.74 ± 1.28
Western Australia			
Control	995 ± 402	320 ± 64	4.60 ± 0.91
Defaunated	869 ± 105	235 ± 20	3.95 ± 0.23

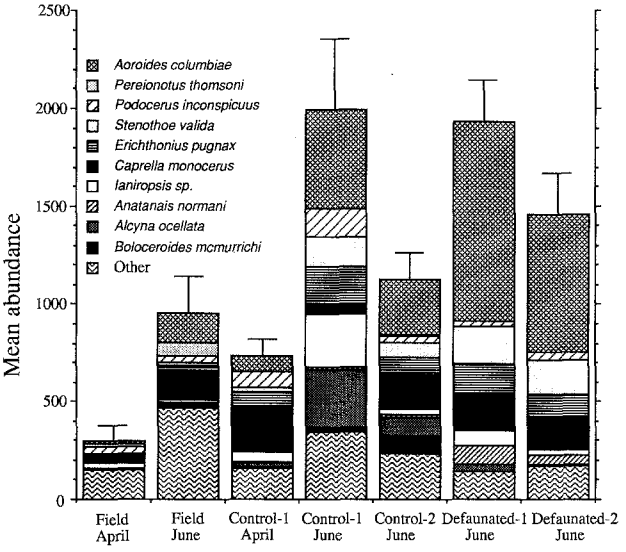

Fig. 2. Densities per plant of the most common species in the field in April and June and in various microcosm treatments. *SE bars* for total abundance are shown above *columns*. Densities of animals in defaunated-1 microcosms in April have not been shown as they were very low ($\bar{x} = 115 \pm 14$) animals

to negligible (< 20 g/m^2) levels at the end of June (M. Aoki and G. Edgar unpublished data). Much of the *S. patens* population detached and floated away from the study site during June, with the remaining plants senescing *in situ*.

The density of epifauna associated with *Sargassum* increased an order of magnitude between February and June (Fig. 1). Approximately half of this increase occurred during the first month. The decline in faunal abundance between March and April shown in Fig. 1 was probably an artifact of sample variability, being caused by the low biomass of sampled plants in April rather than indicating a real population decline in that month.

A number of epifaunal species infiltrated through the 300-μm mesh of the microcosm tubes. At the conclusion of the experiment, the number of species in defaunated tubes was only slightly (but significantly) lower than the number in control tubes. A mean (± SD) of 28 ± 4 species were collected in both defaunated-1 and defaunated-2 microcosms on 6 June, compared with 38 ± 4 and 35 ± 5 in the control-1 and control-2 microcosms, respectively. Despite this entry of species into microcosms, and total population numbers in control tubes being comparable to total numbers in defaunated tubes at the conclusion of the experiment (Table 1, Fig. 2), the abundances of different species varied consistently between microcosm treatments. A number of species which were common in the control tubes, e.g. the mollusc *Alcyna ocellata* and anemone *Boloceroides mcmurrichi,* were rarely if ever present in defaunated tubes. On the other hand, the amphipod *Aoroides columbiae,* the most abundant species in microcosms, was much more abundant in defaunated than control treatments (two-way ANOVA, month of commencement × defaunation treatment, $df = 1/20$, $F = 28.5$, $P < 0.001$). Thus, higher population sizes of infiltrating species in defaunated microcosms approximately counterbalanced the abundances of species present only in control microcosms. There was, however, a slight difference between the total abundances of animals in different treatments on 6 June (Table 2), with lowest numbers in the control-2 microcosms. No significant differences were found between the estimated faunal biomass or estimated secondary production of the assemblages in different treatments (Tables 1 and 2). Total faunal biomass and secondary production each rose within microcosms to constant levels, independently of which species were numerically dominant (Fig. 3). These levels were similar to those found using the same microcosms but different faunas and plant substrata in experiments conducted in Western Australia (Tables 1 and 2). Total epifaunal abundances in microcosms, on the other hand, differed significantly between the experiments conducted in Australia and in Japan.

Population increases within microcosms were much more rapid during the warmer April to June period than

Table 2. Mean-square values (treatments/residuals) from ANOVAs comparing the abundance, estimated biomass and estimated secondary productivity of faunas in Control-1, Control-2, Defaunated-1 and Defaunated-2 microcosms in Japan on 6 June 1988, and control and defaunated microcosms placed in the field for 2 mo in Australia (Edgar 1990b)

Experiment		Abundance	Faunal biomass	Productivity
Japan study	3/20	0.395/0.123*	0.165/0.133	0.076/0.124
Western Australian study	1/10	0.023/0.064	0.256/0.030*	0.057/0.022
Combined studies	5/30	0.664/0.103***	0.177/0.099	0.177/0.090

Data were log transformed to remove heteroscedasticity
* $0.05 > P > 0.01$; *** $P < 0.001$

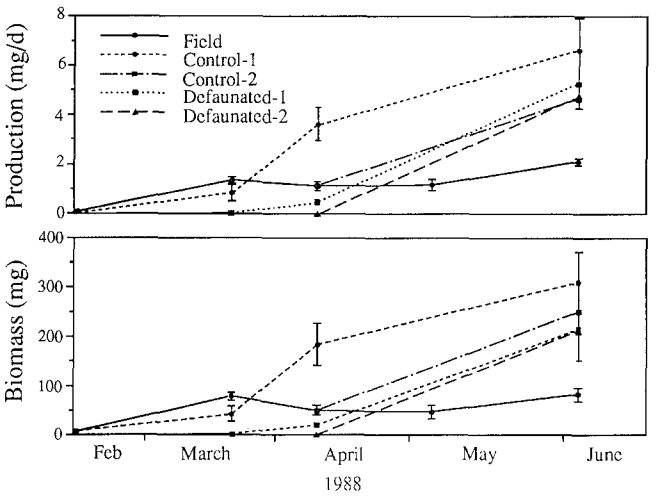

Fig. 3. Monthly mean changes in the estimated biomass and daily production of faunas in the field and in the various microcosm treatments. *SE bars* are shown

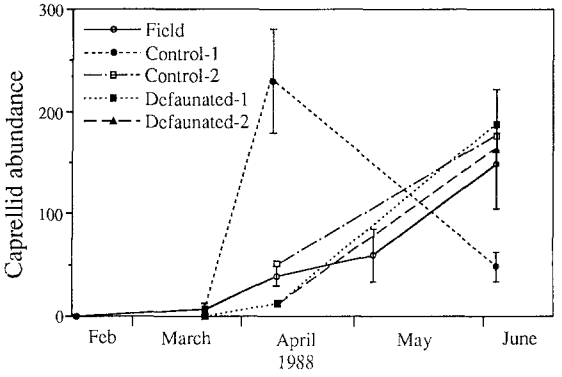

Fig. 4. Monthly mean changes in the abundance of *Caprella monoceros* in the field and in the various microcosm treatments. *SE bars* are shown

Table 3. Mean abundances of various caprellid species in Control-1 microcosms placed in the field on 12 February 1988 and retrieved on 9 March, 12 April and 6 June 1988

Species	9 March	12 April	6 June
C. danilevskii Czerniavski	11.8±16.3	2.5± 3.6	0
C. tsugarensis Utinomi	3.0± 5.4	9.0± 11.3	0
C. okadai Arimoto	0.5± 1.0	0	0
C. monoceros Mayer	6.8±12.2	174 ±149	47.7±34.9
C. kominatoensis Takeuchi	0.3± 0.5	38.0± 62.1	0
C. penantis Leach	0.3± 0.5	3.8± 3.8	7.0± 5.4
C. decipiens Mayer	14.3±27.2	67.0± 49.2	13.3±23.7
C. subinermis Mayer	1.5± 1.7	0.3± 0.4	0
C. scaura Templeton	1.3± 1.5	3.0± 4.9	0.9± 1.0
C. verrucosa Boeck	0.5± 0.6	5.5± 4.7	0

from February to April; only 450 animals were collected per defaunated microcosm after the 2-month period from February to April, whereas 4,800 animals were collected after the 2-month period from April to June. When data for the four microcosm treatments sampled in June are combined, the total abundance (N), estimated biomass (B; mg) and estimated production (P; µg/day) of animals within microcosms were all significantly correlated with the dry weight of plant material (W; g) contained within tubes ($n=24$; $N=722+159$ W, $r^2=0.64$, $P<0.001$; $B=139+19.1$ W, $r^2=0.39$, $P<0.001$; $P=2537+499$ W, $r^2=0.58$, $P<0.001$).

The number of caprellids in microcosms differed greatly between replicates, as is indicated by the high standard deviation in numbers in control-1 microcosms (Table 3). Abundances of species after 2 month tended to be either extremely low (0, 1 or 2), with no recruitment presumably having occurred, or high (26–363). Numbers within any microcosm therefore probably depended on the survival abilities of different caprellid species and whether sufficient individuals of a species had been initially introduced for that species to reproduce. The only caprellid consistently found to enter microcosms was *Caprella penantis;* other caprellids were absent from many tubes.

A number of caprellid species, notably *Caprella danilevskii, C. tsugarensis, C. okadai* and *C. kominatoensis,* had poor survival rates in microcosms (Table 3). *C. monoceros* and *C. decipiens,* on the other hand, showed rapid increases in population numbers (Table 3, Fig. 4). In the microcosms in which they were reproducing, *C. monoceros* increased two orders of magnitude in abundance within 2 months. The numbers then declined, so that at the conclusion of the experiment *C. monoceros* was significantly less abundant in the longest-running (i.e. control-1) treatment than in other treatments (Fig. 4; 1-way ANOVA, $df=3/20$, $F=5.25$, $0.01>P>0.001$; SNK test, $\alpha=0.05$).

The size-distributions of epifaunal species within microcosms generally differed from the population size-distributions in the field. All of the abundant amphipod and isopod species in the field, including the four most common and widespread species shown in Fig. 5, had field size-distributions heavily skewed to small body size. A number of non-peracarid species, including the common anemone *Boloceroides mcmurrichi* (Fig. 5), had size-frequency modes in the intermediate sieve size range rather than being skewed to small body size.

The size-distributions of species within microcosm were not greatly affected by treatment (Fig. 5). The larger size-classes of crustaceans were several times less abundant in the field than within all types of microcosm. By contrast, field populations of non-crustacean species often had similar size-distributions to microcosm populations.

Predation

The labrid *Halichoeres tenuispinis* was not observed in the study area on 18 February, and increased in abundance from March to April, occurring in densities (± SD) of 0.23 ± 0.06 m^{-2}, 0.72 ± 0.15 m^{-2} and 0.63 ± 0.44 m^{-2} on 8 March, 19 April and 27 May, respectively. A total of 90 *H. tenuispinis* was collected for dietary analysis on 9 May. No consistent differences in either the number or

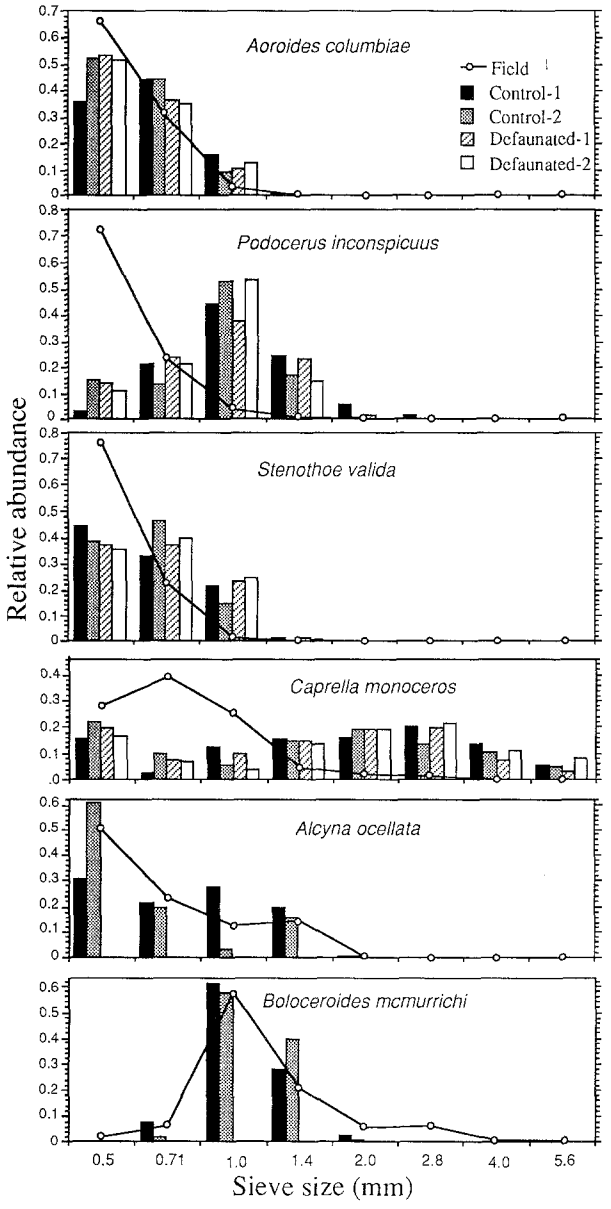

Fig. 5. The relative abundance in different size-classes of six epifaunal species in the field and in four microcosm treatments on 6 June 1988. The four amphipod species were the most common species collected in all replicate samples, while the mollusc *Alcyna ocellata* and anemone *Boloceroides mcmurrichi* were the most common non-crustacean species collected. The two non-crustacean species were very rare in the defaunated treatments ($\bar{x} < 1$ per microcosm), so these treatments were not shown

species of prey consumed by *H. tenuispinis* could be detected for fish of different sizes or sexes within the size-range examined (53 to 100 mm total length); consequently, the diets of *H. tenuispinis* have not been separated by size or sex in analyses.

The abundance of different prey in the gut of *H. tenuispinis* was significantly correlated with the field abundances of species associated with *S. patens* plants ($n = 24$, $r_s = 0.70$, $P < 0.001$; Table 4), indicating that the wrasse was not highly selective as a predator for particular species. However, while gut contents generally reflected prey availability, substantial variation was found between relative abundances in the field versus in the gut for particular taxa (Table 4). Wrasses predominantly fed on crustaceans, molluscs and, to a lesser extent, polynoid polychaetes, with negligible numbers of platyhelminths, anemones and polychaetes (except polynoids) being consumed.

Halichoeres tenuispinis was extremely size-selective as a predator, consuming disproportionately high numbers of large sieve-size prey. While only the consumption of *Caprella monoceros* and *Pereionotus thomsoni* by *H. tenuispinis* has been quantified, the results shown in Fig. 6 were typical of the size-distributions of prey consumed by fish (G. Edgar personal observations). Although the size-frequency distributions of *C. monoceros* and *P. thomsoni* shown in Fig. 6 differ, they indicate similar underlying patterns of selectivity for prey of particular body mass. The ingestion of *C. monoceros* at 0.5 and 0.71 mm body size was probably incidental to the selected prey; juvenile *C. monoceros* remain attached to the maternal parent for up to 18 days after liberation from the brood pouch (Aoki and Kikuchi 1991), hence the small caprellids ingested by *H. tenuispinis* were probably eaten along with the parent. Moreover, caprellids at 5.6 mm sieve-size have similar mean biomasses to gammaridean amphipods at 2.8 mm sieve-size (both 2.3 mg, Edgar 1990a), so if relative abundance had been plotted against biomass rather than sieve size, then the maximum size of *P. thomsoni* consumed would have been only slightly less than for *C. monoceros*.

The number of prey in the guts of *H. tenuispinis* was zero just before dawn but rapidly rose throughout the morning (Fig. 7). Prey numbers in the gut gradually declined during the afternoon due to fewer animals being ingested than egested. Ingested prey passed through to the end of the gut by 10 a.m., and would have first been egested about this time. *Halichoeres tenuispinis* fed most actively early in the morning. The maximum number of pecks at prey were observed to occur around 8 a.m., with a gradual decrease in pecking activity during the rest of the day, apart from a slight, non-significant, increase at 3 p.m. (Fig. 7). Fish were estimated to peck an average of 362 times per day. The number of prey consumed at any time in the morning was almost identical to the mean number of pecks made by fishes up to that time multiplied by a factor of 0.35 (Fig. 7). Therefore, for every 100 pecks made by fishes, ≈ 35 resulted in the successful capture of prey. Assuming that this success rate did not change during the afternoon, a mean of 127 ($= 362 \times 0.35$) prey were consumed per fish per day.

Calculations of the estimated predatory impact of *H. tenuispinis* on different size-classes of epifauna associated with *Sargassum patens* are shown in Table 5. The size preference of *H. tenuispinis* for *C. monoceros* (Fig. 6) is assumed in these calculations to apply also to other caprellids, and the size preference for *Pereionotus thomsoni* to apply to all other taxa.

While the calculations shown in Table 5 may include considerable error, it is clear that *Halichoeres tenuispinis* has a negligible impact on the smallest epifaunal size-class examined (0.5 mm) but is the major source of

Table 4. Densities (per g dry weight of algae; ±SE) of common taxa associated with *Sargassum patens* on 6 May 1988, with relative abundances (%) shown in parentheses

Taxon	Field densities (g^{-1})	Relative abundance in fish guts (%)
Ericthonius pugnax (Dana)	0.9±0.5 (2.0)	7.2±1.6
Gammaropsis japonica (Nagata)	1.3±0.6 (2.8)	1.8±0.6
Ischyrocerus sp.	1.4±0.9 (3.0)	13.0±2.0
Ampithoe ?kava Myers	1.2±0.4 (2.7)	2.7±0.8
Tethygeneia rostrata (Gurjanova)	0.9±0.3 (2.0)	1.8±0.5
Podocerus inconspicuus (Stebbing)	1.2±0.4 (2.6)	4.0±1.2
Paradexamine micronesica Ledoyer	3.4±1.3 (7.4)	3.2±1.0
Aoroides columbiae Walker	2.4±0.9 (5.1)	0.3±0.3
Pereionotus thomsoni (Stebbing)	4.0±1.0 (8.7)	7.2±2.0
Other gammaroidean amphipods	1.7±0.4 (3.7)	4.9±1.7
Caprella monoceros	6.7±1.8 (14.5)	41.2±3.6
C. decipiens	0.7±0.4 (1.5)	0.8±0.6
Other caprellid amphipods	1.3±0.6 (2.7)	1.1±0.4
Other crustaceans	1.2±0.6 (2.6)	0.8±0.1
Hiloa megastoma (Pilsbry)	2.6±0.7 (5.6)	1.5±1.5
Cantharidus callichroa (Phillipi)	2.9±0.5 (6.3)	0.9±0.4
Alcyna ocellata Adams	3.2±0.7 (6.9)	4.3±2.3
Other molluscs	1.0±0.3 (2.1)	0.4±0.2
Platynereis dumerillii (Audouin & Milne-Edwards)	2.8±1.1 (6.1)	0
Other polychaetes	1.1±0.4 (2.4)	2.6±0.8
Ctenoplana sp.	2.4±1.5 (5.2)	0
Platyhelminth sp. 1	10.7±0.2 (1.4)	0
Boloceroides mcmurrichi (Kwertniewski)	1.1±0.2 (2.3)	0
Other taxa	0.1±0.1 (0.2)	0.2±0.1

Mean relative abundances (%) of taxa in the guts of *Halichoeres tenuispinis* (±SE), as calculated from the total abundances of animals in the different sampling periods, are also shown

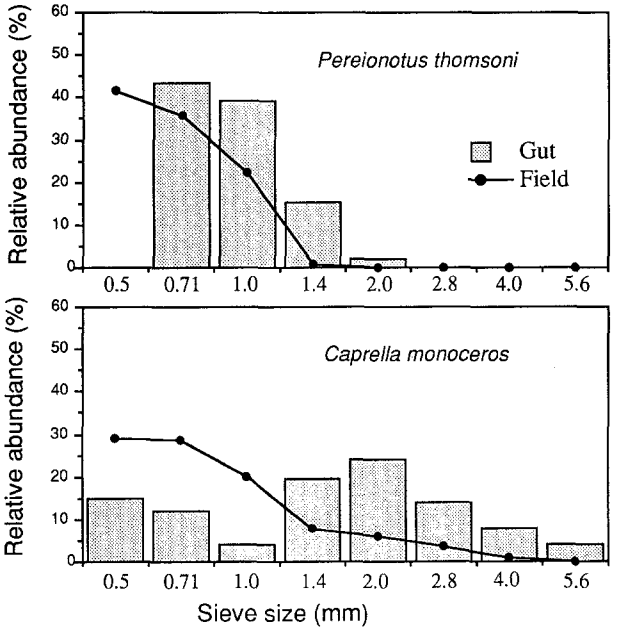

Fig. 6. The relative abundances in different sieve size-classes of the amphipods *Pereionotus thomsoni* and *Caprella monoceros* in the guts of *Halichoeres tenuispinis* on 9 May 1988 *(grey columns)* and in the field on 6 May 1988 *(solid dots and line)*

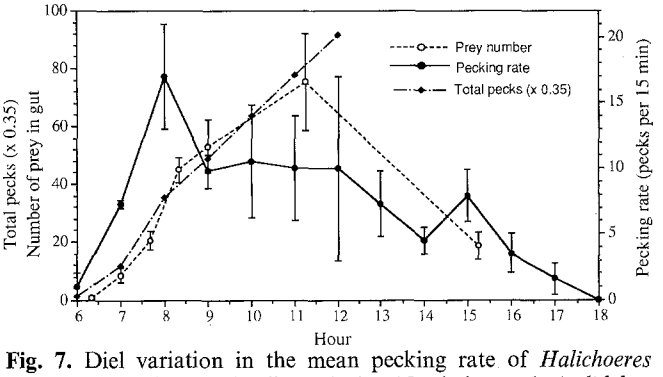

Fig. 7. Diel variation in the mean pecking rate of *Halichoeres tenuispinis*, as observed by divers during 15-min intervals *(solid dots and line)*, the cumulative number of feeding pecks made by *H. tenuispinis* during the first 6 h of the day *(diamonds, dot-and-dash line)*, and diel changes in the number of prey found in fish guts *(open symbols, dashed line)*. *SE bars* are shown

mortality to animals >2.0 mm sieve size. Very few crustaceans >1.4 mm sieve size would escape being consumed by fish; most animals not eaten by fish in any of the larger size-classes would not die from other causes but progress to the next size-class and then be captured by fish.

Discussion

Resource limitation and competition

The most interesting result of our microcosm experiment was that the total estimated secondary production of faunas within microcosms all rose quickly to a constant level which was independent of treatment, and that this level was similar to the level deduced for different faunas in experiments conducted in Western Australia (Tables 1 and 2). We consider that, rather than resulting from chance, assemblages within tubes probably reached a resource ceiling which was proportional to total faunal

Table 5. Estimated rates of consumption by *Halichoeres tenuispinis* of epifauna in different sieve size-classes

	Sieve size (mm)					
	0.5	0.71	1.0	1.4	2.0	2.8
Turnover rate (day)						
Caprellids	18	20	22	27	29	35
Other taxa	24	30	35	44	50	64
Field densities of prey (m^{-2})						
Caprella monoceros	928	908	632	266	234	133
Total caprellids	1184	1174	970	418	306	173
Pereionotus thomsoni	429	960	666	72	12	0
Non-caprellid epifauna	8434	5384	1590	806	102	20
Number of prey consumed ($m^{-2}d^{-1}$)						
Caprella monoceros	4.6	3.7	1.2	6.1	7.4	4.3
Total caprellids	4.9	3.9	1.3	6.4	7.8	4.5
Pereionotus thomsoni	0	1.9	1.7	0.7	0.1	0
Non-caprellid epifauna	0	20.6	18.5	7.2	1.0	0
Proportion of epifauna consumed (%)						
Caprella monoceros	8	8	4	61	91	113
Total caprellids	7	7	3	41	74	91
Pereionotus thomsoni	0	6	9	58	38	
Non-caprellid epifauna	0	11	40	39	49	
All epifauna	2	10	26	40	68	82

Turnover rate is the mean period which a macrofaunal species will take to grow through each sieve size-class at 20° C as calculated from the general equation of Edgar (1990a). Field densities of prey are densities of macrofauna associated with *Sargassum* plants (51 plants m^{-2}) on 6 May 1988, with the exception of *Pereionotus thomsoni* for which data from 13 April, 6 May and 6 June have been amalgamated because of small sample size in the larger size-classes. Number of prey consumed of type i (T_i) = $127 \times 0.63 \times d_i \times p_{ij}$ where d_i is the abundance of prey i in fish guts relative to the total consumed (Table 4) and p_{ij} is the proportion of prey type i which was consumed for each sieve size-class j (see Fig. 6). This calculation assumes that the density of fish was 0.63 m^{-2}, with each fish consuming 127 prey per day. The relative numbers of *Caprella monoceros* in different sieve size-classes consumed by *H. tenuispinis* were used in calculations of the rate of consumption of total caprellids, and the relative numbers of *Pereionotus thomsoni* used for all other epifauna. Proportion of epifauna consumed is the estimated proportion of animals in each size class which was consumed by *H. tenuispinis* (=number of prey consumed × turnover rate/field densities)

production (see Edgar 1993). Experimental evidence to support this hypothesis is that: (i) the ANOVA used had reasonable power, as shown by the highly significant difference in animal abundance between all treatments [animal abundance had a low coefficient of variation (=0.3) similar to production], and would be expected to detect minor differences between treatments if estimated production of faunas in different treatments were not converging on similar values, (ii) no single species was dominant in terms of biomass or production within any treatment, so the results were not caused by individual species reaching specific resource ceilings, and (iii) population numbers of species capable of passing through the microcosm mesh were negatively affected by the abundances of prexisting species within the microcosms. The most common species in microcosms, *Aoroides columbiae*, for example, occurred in twice the numbers in defaunated compared to control microcosms, although it presumably entered all types of microcosms in similar numbers. Even more pronounced differences in particular species between panially defaunated and control microcosms were documented in the Western Australian experiments (Edgar 1990b).

Only one measured parameter, biomass of host algae, was found to be highly correlated with faunal production within microcosms. Although our experiment did not address the possibility that epifaunal assemblages are limited by restricted physical space, and no data are available on the levels of autotrophic production within microcosms, we consider that food limitation is the most parsimonious explanation for the convergence of epifaunal production estimates and the correlation of production with quantity of host substrata. It is difficult to conceive of any other potentially limiting resource which is proportional to the biomass of plant material and is utilised in a manner approximately proportional to the sum of body masses raised to the power 0.8 (Edgar 1993) by species as divergent in life-histories as amphipods, gastropods and polychaetes. Space is unlikely to have limited total production if processes occurring in the Japanese experiments were similar to those in Western Australia because epifaunal production was found to be much lower in shaded compared to unshaded microcosms in Western Australia even when the biomass of host substrata was kept constant (Edgar 1990b).

Moreover, if space was limited in microcosms then, because antagonistic interactions associated with interference competition occur on much shorter time-scales than interactions associated with exploitative competition, particular highly-competitive species would be expected to rapidly eliminate others from the microcosms. Only one species, the benthic ctenophore *Ctenoplana* sp., could have been eliminated from microcosms by direct competition; all of the other species recorded in the field from February to June survived in microcosms for 4 month. A number of species, most notably the amphipod *Caprella monoceros*, declined in density within microcosms in the last 2 months of the experiment, the period when competition for food would presumably have been most intense. While we suggest that exploitative competition was more important than interference competition in microcosms, we cannot rule out the possibility that interference competition affected the composition of the faunal assemblage. *Caprella monoceros* or *C. decipiens*, for example, may have actively prevented other caprellids which were common in adjacent habitats from settling amongst *S. patens* in the field, and may also have been directly responsible for the poor survival rates of *C. danilevskii*, *C. tsugarensis*, *C. okadai* and *C. kominatoensis* in microcosms. *Caprella monoceros* has been reported to act belligerently towards other caprellids (Aoki and Kikuchi 1991).

The theoretical reasons for total secondary production of epifauna being proportional to primary production and being largely independent of the particular species present are presented in an associated paper (Edgar 1993). Briefly, total community production is postulated to be proportional to total community ingestion which,

when many species are present and virtually all food is utilized, is also approximately proportional to primary production. Consequently, manipulating the faunal composition should not cause great changes to overall secondary production or consumption, providing that the assemblage has sufficient species to utilise almost all of the food produced and that the physical aspects of the environment remain unchanged. By way of contrast, animal abundance and biomass would not be expected to remain constant in microcosms with different faunas because these parameters depend partly on the size-structure of the species present, i.e., whether secondary production is partitioned amongst a few large animals or many small animals.

If this "production ceiling hypothesis" is correct then the lack of a significant difference between the estimated faunal biomass of assemblages in the various microcosm treatments was largely due to the close relationship between faunal biomass and productivity ($P \propto B^{0.80}$). Faunal abundance shows a much lower correlation with secondary productivity, thereby providing an explanation for the significant differences in animal abundance between treatments (Table 2). If assemblage *"a"* has animals equal in abundance but double the body dimension of animals in assemblage *"b"*, then the estimated biomass of assemblage *"a"* is approximately 8 times, and the estimated productivity 5 times, that of assemblage *"b"*.

The production ceiling hypothesis involves several assumptions. It applies only to species-rich communities which have not been recently subjected to catastrophic disturbance, and secondary production is not predicted to be constant, for example, amongst assemblages with differing light levels or water temperatures. Fortuitously, the experiments conducted in Western Australia and Japan were concluded in seasons with similar water temperatures (20° C) and microcosms were placed at similar depths (2–3 m).

Given that epifaunal production in microcosms is restrained by resource ceilings, it remains to be shown whether these ceilings also apply in the field or whether other factors (e.g. predation, disturbance) prevent population numbers from attaining such high levels. The production of epifauna associated with field plants of average size ($\approx$10 g dry weight) in June (2.4 mg.day^{-1}) was approximately half the level recorded in microcosms (5.6 mg.day^{-1}). This discrepancy is expected, providing that the majority of animals graze on diatoms and other periphyton rather than on the host *Sargassum* plant, because the surface area available to periphyton on the microcosm surface (1910 cm^2) was approximately equal to that on the enclosed plant ($\bar{x} \approx 2000$ cm^2, as calculated from the geometric dimensions and component shapes). Periphyton would therefore have been as abundant on the mesh and perspex surfaces of microcosm tubes as on the plant substrata, with the microcosm and macroalgal surfaces each supporting epifaunal productivities of $\approx$1 μg.cm^{-2}.day^{-1}. Extrapolation to the *y*-axis of the regression relating plant biomass to faunal production indicates that epifaunal production of 2.5 mg.day^{-1} occurs when no plant material is present in microcosms. The assumption that the epifaunal assemblage consisted largely of periphyton grazers is based on almost all of the common species associated with *S. patens* being abundant on artificial substrata where periphyton is the only major food source available (Edgar 1991), and on other studies where epifaunal amphipods and molluscs have been shown to feed predominantly on surficial microalgae and detritus and small epiphytic algae (e.g. Nagle 1968; Zimmerman et al. 1979; Caine 1980; Van Montfrans et al. 1982; Norton and Benson 1983; Kitting 1984; Brawley and Fei 1987). Of the 18 species listed in Table 4, only *Ampithoe ?kava, Pereionotus thomsoni* and *Caprella decipiens* were not commonly found in association with artificial habitats placed in the *S. patens* bed (Edgar 1991). *Ampithoe ?kava* belongs to a family of amphipods with many *Sargassum*-consuming members (Hay et al. 1990; Duffy 1990), so may differ from most other collected species in feeding predominantly on the host plant.

The prediction that epifaunal production is approximately constant for plants with similar morphology, providing that water temperature and levels of illumination do not vary greatly, can be tested by investigating temporal changes in the *Sargassum patens*-associated assemblage. Faunal production did not significantly vary between months during the period from March to June if an increase in water temperature is not incorporated into production calculations [i.e. the parameter P_{20} (Edgar 1993) is used, one-way ANOVA, $df = 3/17$, $F = 3.1$, $P > 0.05$]. The justification for testing the production ceiling hypothesis with temperature not incorporated into production calculations is that faunal population structure remains steady as temperature rises because the increased growth rates of animals in different size-classes are compensated for by corresponding increases in primary production (Edgar 1993).

The prediction that the faunal productivities of *Sargassum* plants at other sites are similar to the levels estimated at Magarisaki during the latter stages of the annual *Sargassum* growth cycle (i.e. $\approx$240 μg.g^{-1}.day^{-1} for plants at 20° C) has been examined in Australia with the results given in the associated paper (Edgar 1993). Estimated faunal production of *Sargassum* plants at four Australian sites did not differ significantly from 240 μg.g^{-1}.day^{-1}, whereas at a further four sites faunal productivities were significantly less than this value, possibly due to host plants being in early growth stages at these locations.

Large seasonal fluctuations in epifaunal abundances have been reported in macrophyte beds throughout the world. At all sites exhibiting such fluctuations, apart from the Cliff Head site in Western Australia where abundance decreased during a period of high water turbidity (Edgar 1990b), cycles in total animal abundance approximately corresponded with seasonal fluctuations in the biomass or surface area of plant substrata (e.g. Hagerman 1966; Mukai 1971; Nelson 1979b; Edgar 1983; Norton and Benson 1983; Scheibling and Johnson 1987). For most of these assemblages, epifaunal density minima occurred during the winter months, and there was a lag of 2 or 3 months following the start of plant biomass recovery before epifaunal populations rebounded. This lag may be caused by the relatively slow growth rates of animals during the cooler months when plant

biomass is low, or by fish predators which can best control the numbers of epifauna when prey are present in low densities. Fish predators selectively remove the larger reproductive invertebrates (see below), so would most inhibit the growth of epifaunal populations when the number of mature animals is already low. A more likely explanation for the lag is that young, rapidly growing plants produce large quantities of polyphenolics and other inhibitory compounds which curtail the productivity of periphytic food resources. The population sizes of bacteria, diatoms and protozoans are all known to be reduced by toxic secondary metabolites-released by macrophytes (Hornsey and Hide 1974; Langlois 1975; Al-Ogilby and Knight-Jones 1977; Harrison 1982; Harrison and Durance 1985). These secondary compounds are concentrated and have greatest antibiotic activity in young, actively-growing tissue of *Sargassum* plants (Sieburth and Conover 1965; Sieburth 1968; Ryland 1974).

Predation

While food resource limits were inferred to be the major determinant controlling the production of the epifaunal assemblage associated with *Sargassum,* fish predation appears to have had a considerable influence on individual species. Our results consistently indicated that the major effect of predation was to channel secondary production towards the smaller size-classes: (i) calculations of fish consumption rates showed that most animals in sieve size-classes ≥ 2.0 mm would be consumed by fishes, whereas few small (< 1.0 mm) animals would meet a similar fate before reaching the larger size-classes, (ii) the size-distributions of common peracarid crustacean species were similar to each other in the field, with most individuals in the smallest two sieve size-classes and very low proportions of larger individuals, (iii) the size-distributions of crustacean species within microcosms (i.e. in the absence of fish predators) differed considerably between species, but all had much higher proportions of large animals than in the field, and (iv) the size-distributions of species not consumed by fishes (e.g. the anemone *Boloceroides mcmurrichi*) differed little between microcosms and the field.

A number of speculative predictions can be made if the size-selective predation and production ceiling hypotheses are combined. As fish predation increases: (1) the size-structure of the epifaunal assemblage should shift towards the smaller size-classes, (2) species not eaten by fishes due to unpalatability, crypsis or small size should become proportionately more abundant, and (3) total epifaunal abundance should increase because, with the removal of each large invertebrate by a predator, sufficient food resources become available to feed several smaller animals. The results of our study support these predictions.

The first prediction is consistent with the differences in epifaunal size-distributions between field and microcosm (Fig. 5). The level of predation also differed between months in the field, as did the size-frequency distributions of most epifaunal species. Predation pressure exerted by fishes at Magarisaki was low in February and March, the period when *Halichoeres tenuispinis* was absent or occurred in low densities within the study area, and increased to high levels by mid-April. The relative abundance of large-sized epifauna reflected this seasonal change in predation pressure; $\approx 20\%$ of the fauna was > 1.0-mm sieve size between February and April, but only 6% of the fauna grew to this size in May or June. Moreover, a high proportion of the large-sized fauna in May and June but not February, March or April consisted of species not consumed by fish. Individual species which grew to a large size and were preferred prey of fishes showed very pronounced changes in population size-structures during the study. The proportion of *Caprella monoceros* in the field which was > 1.0 mm sieve size was 59% in March, 49% in April, 22% in May and 7% in June. *C. monoceros* in microcosms were primarily > 1.0-mm sieve size in June.

Epifaunal species not captured by fishes increased in numbers very rapidly during the spring period of intense predation pressure. The populations of *Platynereis dumerillii, Ctenoplana* sp., *Boloceroides mcmurrichi* and Platyhelminth sp. 1 all increased by approximately an order of magnitude between April and June, while the population numbers of common crustacean species remained relatively constant. The only crustacean amongst the species listed in Table 4 to show a rapid population increase was *Aoroides columbiae,* the smallest of the common amphipods. *A. columbiae* matured at 0.5 mm sieve size and did not grow above 1.0 mm sieve size, even when protected from predators in microcosms (Fig. 5). An additional amphipod species, *Ceinina japonica* Stephensen, which was not listed in Table 4 because of its rarity in May, also showed a huge increase in population numbers between April (25 m^{-2}) and June (1850 m^{-2}). *C. japonica* bores through the axes of *Sargassum* plants (Stephensen 1933), so would rarely if ever be captured by fishes. There was a significant negative correlation overall between fish selectivity for prey (defined as the proportional abundance of the various species in fish guts divided by the proportional abundance of animals associated with *Sargassum,* both as shown in Table 4) and the magnitude of the change in population density between April and June (Spearman rank correlation $r_s = 0.50$, $n = 15$, $P = 0.02$; molluscs were excluded from this analysis because they have pelagic larval stages and breed discretely rather than continuously, so for life-history reasons particular molluscs may not have been able to increase in numbers).

The third prediction, that faunal abundance increases with increasing predation pressure, is counter-intuitive but agrees with our finding that faunal abundance rose during the period from March to June when predation levels increased and faunal biomass remained constant. Analogous findings have been made in studies of soft-bottom habitats, where decreases in total macrofaunal numbers and shifts in faunal size-distributions towards larger sizes occurred after the exclusion of predators (Reise 1978; Kent and Day 1983; Wilson 1989).

Similarities between our results and those of other studies in seagrass, macroalgal and soft-sediment habitats suggest that the size-selective predation and produc-

tion ceiling hypotheses may have wide generality for benthic communities. Theoretical considerations (Schoener 1971; Pyke et al. 1977; Hughes 1980) and field studies (e.g. Wallerstein and Brusca 1982) both indicate that large marine predators, particularly fishes, decapod crustaceans and cephalopods, select the largest accessible prey which can be conveniently handled. Because these predators are abundant throughout the world, they would be expected to skew faunal size-distributions towards small sizes in a wide variety of habitats. This is not to suggest that individual predators are not constrained by maximum prey sizes, as they clearly are (e.g. Elner and Hughes 1978; Griffiths and Seiderer 1980; Joyce and Weisberg 1986); however, the total predatory impact on a macrofaunal community will rarely depend on a single predatory species but on a variety of predators with overlapping prey size ranges which encompass the largest individual in the community.

Although a number of exceptions exist, size-selective aspects of predation are often ignored in studies of mobile benthos. Along with artifactual problems, this lack of interest in size-selectivity is possibly a major reason for conflicting conclusions reached by different workers regarding the importance of fish predation to mobile benthos. In many studies, particularly single-species studies in which comparatively large prey are investigated, predation has been shown to have a major controlling influence on prey numbers (e.g. Van Dolah 1978; Jensen and Jensen 1975; Kneib 1985). In another set of studies, much lower densities of benthic invertebrates have been found in predator exclusion treatments when compared with open treatments (Nelson 1981; Kneib and Stiven 1982; Virnstein et al. 1983; Wilson 1989). These somewhat contradictory results have been traditionally reconciled by invoking the "intermediate predator hypothesis", which postulates that cages exclude large predators which are capable of controlling the numbers of smaller invertebrate predators such as shrimps, crabs, and nereid and nephtyid polychaetes, and, because these small predators become abundant in cages, the densities of the majority of macrofaunal species which are prey to the small predators decline. Our production ceiling/size-selective predation hypothesis provides an alternative explanation by postulating that the consumption of food resources by larger animals rather than direct predation is the proximate cause of the decline in small animals in cages. The two hypotheses are not, however, mutually exclusive, and it is likely that neither provides a comprehensive explanation for patterns of faunal abundance within cages. Until appropriate tests have been made which evaluate the accuracy of conflicting predictions arising from the two hypotheses, we suggests that both the intermediate predator and production ceiling/size-selective predation hypotheses be considered equally plausible before interpreting caging results.

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