

Density, biomass and productivity of animals in four subtidal rocky reef habitats: the importance of small mobile invertebrates

Richard B. Taylor*

Leigh Marine Laboratory and School of Biological Sciences, University of Auckland, PO Box 349, Warkworth, New Zealand

ABSTRACT: Density, biomass and productivity of animals >0.5 mm were estimated in 4 shallow subtidal rocky reef habitats in temperate northeastern New Zealand. The main objective was to determine the relative contributions of mobile epifauna (0.5–10 mm) and megafauna (>10 mm) to the flux of materials on the reef. The habitats surveyed were (1) *Carpophyllum plumosum* var. *capillifolium* forest (Phaeophyceae: Fucales), (2) *Ecklonia radiata* forest (Phaeophyceae: Laminariales), (3) urchin barrens, and (4) articulated coralline algal turf flats. Epifauna comprised >99.5% of individuals in each habitat. Epifauna dominated biomass (>86%) in the finely structured *Carpophyllum* forest and turf flats, where they contributed >97% of total secondary productivity. Although lower in the other 2 habitats, the epifaunal contribution to total secondary productivity was still ~78% on the scale of the entire reef. These results show that epifauna are major contributors to the flux of materials in rocky reef habitats, and should therefore be included in trophic models of these systems. Consumption by fish could only account for ~26% of epifaunal production, with the fate of the remainder unknown. Estimated annual secondary productivity within the *Carpophyllum* forest and turf flats habitats (100 to 115 g AFDW m⁻² yr⁻¹) was higher than literature values for a range of soft sediment habitats, and was exceeded only by 2 other hard-bottom communities.

KEY WORDS: Biomass · Epifauna · Kelp forest · New Zealand · Rocky reef · Seaweed · Secondary productivity

INTRODUCTION

Temperate rocky reefs are inhabited by large numbers of small crustaceans, gastropods and polychaetes, but the extent to which these epifaunal organisms contribute to the flux of materials on rocky reefs is unclear. Previous quantitative studies (Miller et al. 1971, Newell et al. 1982) have focussed on larger animals such as echinoids, lobsters and fish (hereafter 'megafauna'; >10 mm long), and microorganisms (bacteria). However, epifauna (0.5 to 10 mm long) are also likely to be important consumers, producers and nutrient recyclers. They are extremely abundant on many ben-

thic substrata (e.g. Choat & Kingett 1982, Holbrook & Schmitt 1989, Taylor & Cole 1994), have high metabolic rates (Edgar & Moore 1986), and are productive enough to support large populations of small predatory fishes (e.g. Simenstad et al. 1977, Moreno & Jara 1984, Edgar & Moore 1986, Jones 1988, Holbrook et al. 1990).

Energy flow studies at the ecosystem level on rocky reefs have been carried out at St Margaret's Bay in Nova Scotia (Miller et al. 1971), and at the Cape Peninsula in South Africa (Field et al. 1977, Velimirov et al. 1977, Newell et al. 1982, review of Branch & Griffiths 1988). The flux measured in these studies is productivity, the rate at which organic matter is produced per area per time (i.e. a function of population density and the growth rates of individuals). Rates of production are informative because they are the rates at which organic matter is made available to higher trophic lev-

*Present address: Institute of Marine Sciences, University of North Carolina at Chapel Hill, 3431 Arendell St., Morehead City, North Carolina 28557, USA.
E-mail: rbtaylor@mail.clis.com

els, and they also reflect the relative importance of organisms as consumers and nutrient recyclers, as rates of all these metabolic processes scale to body mass with a power of ~ 0.75 (Peters 1983). The Canadian and South African studies largely ignored the potential contribution of epifauna, but Edgar & Moore (1986) show that, as a result, a major pathway may have been neglected. Edgar & Moore applied a literature-derived annual production:biomass ratio to biomass estimates for seaweed epifauna in the Cape Peninsula kelp forest, and calculated that productivity of seaweed epifauna in the mediate zone of the kelp forest comprises about 60% of the value given by Newell et al. (1982) for larger animals offshore. The relative contribution of the epifauna may be even greater elsewhere, because the dominance of large suspension feeders (such as mussels) in the South African kelp beds is not typical of subtidal rocky reefs in other parts of the world (Edgar & Moore 1986).

There appear to be 3 main reasons why epifauna have received less attention than the megafauna. First, epifauna are less conspicuous than larger animals such as echinoids, fish, and lobsters. Second, they are more difficult to sample quantitatively from the structurally diverse habitats found on rocky reefs. Third, the diversity of epifaunal assemblages generally precludes the calculation of productivity for each species using conventional methods such as cohort analysis. However, the recent method of Edgar (1990) makes it possible to estimate assemblage-level productivity simply by washing samples through a stack of sieves with geometrically decreasing mesh sizes, and counting the number of individuals trapped on each sieve. Edgar gives an equation that predicts the body mass of individuals on each sieve, and another equation that predicts productivity as a function of body mass and water temperature. The latter equation is based on a compilation of literature-derived data for individual species and is surprisingly precise (log body weight and log water temperature account for 94% of variation in log productivity). The error involved in predicting the productivity of individual species using such methods can be high, but tends to cancel out in assemblage-level estimates (Edgar 1990). Brey (1990) found that a similar allometric method generated assemblage-level estimates that were within 11% of values obtained using cohort-based methods for 3 of the 4 benthic communities he examined.

In this paper I quantify the density, biomass and productivity of reef-dwelling animals >0.5 mm sieve size in 4 habitats characteristic of shallow subtidal rocky reefs in temperate northeastern New Zealand. The main objective is to determine the relative contributions of epifauna and megafauna to secondary productivity on the reef.

The study was done in the Cape Rodney to Okakari Point Marine Reserve, which has been under legal protection since 1975 (Gordon & Ballantine 1976). Habitats within the reserve have been categorised and described by Ayling (1978). These habitats occur on hard substrata along the exposed northeastern coast of New Zealand (Choat & Schiel 1982), and Ayling's scheme is broadly adhered to in the following introduction of habitats surveyed in this study.

(1) *Carpophyllum plumosum* var. *capillifolium* forest (hereafter '*Carpophyllum* forest'). This finely structured fucalean seaweed grows to a height of 0.5 to 1.5 m, and forms dense monocultural stands on shallow (0 to 5 m depth) sandstone platforms. Most of the bedrock is occupied by densely intertwined *C. plumosum* var. *capillifolium* holdfasts. This habitat is a component of Ayling's (1978) 'shallow broken rock', which is typically dominated by several species of the endemic New Zealand genus *Carpophyllum*.

(2) *Ecklonia radiata* forest (hereafter '*Ecklonia* forest'). Dense, 1 to 1.5 m tall stands of the stipitate kelp *E. radiata* are a characteristic feature of rocky reefs in northern New Zealand (Choat & Schiel 1982, Schiel 1988). A variety of substrata including red turfing algae and encrusting corallines are found beneath the canopy of *Ecklonia* forests (Schiel 1988). The shallow area chosen for this study did not appear to have been affected by the mass mortality of *E. radiata* that occurred in deeper waters during the summer of 1992–93 (Cole & Babcock 1996).

(3) Urchin barrens. Also known as 'rock flats' (Ayling 1978), 'coralline flats' (Ayling 1981), or 'barren grounds' (Lawrence 1975), this habitat typically forms a zone at 5 to 10 m depth (Choat & Schiel 1982), and is defined by high densities of the echinoid *Evechinus chloroticus* and a suite of grazing gastropods that together eliminate almost all erect seaweeds, leaving a layer of crustose coralline algae (Ayling 1981, Andrew & Choat 1982).

(4) Coralline algal turf flats (hereafter 'turf flats'). In this habitat (termed 'sediment covered rock flats' by Ayling 1978), articulated corallines form uniform beds on flat rock. The turf traps and stabilises a 10 to 20 mm thick layer of sand, and also accumulates detritus. The turbinid gastropod *Cookia sulcata* and the sponge *Polymastia* sp. are the only conspicuous invertebrates. High densities of juvenile carangid, mullid, and sparid fishes are associated with this habitat, feeding on small animals in the turf (Choat & Kingett 1982).

In the following text, reference is often made to the structural complexity of the 4 habitats. The *Carpophyllum* forest and turf flats are considered to be finely structured on a scale relevant to epifauna due to the dense narrow fronds of the dominant plants (Taylor & Cole 1994). The *Ecklonia* forest is considered to be a

less structurally complex environment for epifauna since the fronds of the dominant alga are much wider and flatter (Taylor & Cole 1994), although the red algal understory species provide some fine structure. The urchin barrens are held to be the least complex habitat, as the dominant macroalgae (crustose corallines) mould to the bedrock and project very little tissue into the water column.

METHODS

Density, biomass and productivity of all mobile animals larger than 0.5 mm sieve size were surveyed within permanent plots set up in 4 subtidal habitats at sites in the Cape Rodney to Okakari Point Marine Reserve, northeastern New Zealand (36° 16' S, 174° 47' E). The habitats are listed in Table 1; together they occupy ~71% of exposed bedrock in the reserve (Ayling 1978). Their depths ranged from 2 to 9 m.

Within each habitat, 200 to 400 m² of seafloor was delimited using small floats tied to stainless steel pegs that were cemented into the bedrock. One to eight plots (irregular polygons) were set up in each habitat, with the number of plots depending on the patchiness of the habitat. The area within each plot was measured by trilateration amongst the pegs. All sampling and censuses were done within these plots by a diver during daylight hours. Within each habitat, sampling effort was distributed amongst plots in proportion to plot area (i.e. if a plot occupied 25% of the area of a habitat, then it received 25% of the sampling effort for that habitat). Quadrats were placed haphazardly within plots.

Sessile animals such as anemones, sponges, ascidians and bryozoans were uncommon, and were not considered except as substrata for epifauna.

Epifauna. Epifauna were sampled from virtually all substrata present (see Table 2).

Animals on sponges and erect seaweeds were sampled by enclosing their individual host organisms in a large plastic bag that had a 0.2 mm mesh drainhole clamped into one corner. *Ecklonia radiata* plants were

divided into 3 size classes (stipe length <50 mm, 50 to 200 mm, >200 mm) and were sampled complete with holdfast. *Carpophyllum plumosum* var. *capillifolium* stipes were divided into 2 size classes (length <500 mm, ≥500 mm), and were cut off 10 mm above their holdfasts. Entire sponges were removed by slicing them off at the base with a knife.

Animals on substrata such as *Carpophyllum plumosum* var. *capillifolium* holdfasts (after the stipes were removed), coralline turf, bare rock/coralline paint, and rock beneath the echinoid *Evechinus chloroticus* were sampled from within a sealed circular area of 100 mm diameter (7.85×10^{-3} m²) using a suction sampler with 0.2 mm mesh collecting bag attached (Taylor et al. 1995). The suction sampler was also used to sample sand from within a 50 mm internal diameter (1.96×10^{-3} m²) plastic pipe corer. Bedrock in the *Carpophyllum* forest was 'terraced' such that there were many coralline paint-covered vertical faces, each ~0.1 m high and 1 to 4 m long. The suction sampler was used to vacuum animals from 0.1 m wide sections of those faces.

Five replicate samples were taken of each substratum, except for *Carpophyllum plumosum* var. *capillifolium* stipes (n = 10 for each size class), and rock beneath *Evechinus chloroticus* (n = 10).

Epifauna inhabiting *Ecklonia radiata* and *Carpophyllum plumosum* var. *capillifolium* plants were removed from their hosts by washing in dilute formalin (Taylor & Cole 1994). Sponge-dwelling amphipods were individually removed from within their host using a scalpel and forceps (under a dissecting microscope). Samples from all substrata were preserved in 5% formalin, with Rose Bengal vital stain added to *E. radiata* and coralline turf samples. Samples were later washed through a log-series of sieves (8, 5.6, 4, 2.8, 2, 1.4, 1, 0.71, and 0.5 mm mesh sizes) to size-fractionate the animals (Edgar 1990). Megafaunal individuals encountered were dealt with separately (see next section). Epifaunal individuals trapped on each sieve were identified to coarse taxonomic levels and counted, and their biomass and productivity were estimated using the general equations of Edgar (1990).

Table 1. Habitats surveyed for density, biomass and productivity of animals >0.5 mm sieve size. Percent coverage of subtidal rock in the Cape Rodney to Okakari Point Marine Reserve, New Zealand, is from Ayling (1978), except for the *Carpophyllum* forest, which occupied part of Ayling's 'shallow broken rock' habitat (the figure given is my estimate)

	<i>Carpophyllum</i> forest	<i>Ecklonia</i> forest	Urchin barrens	Turf flats
Coverage of subtidal rock in reserve (%)	~5	29.8	31.4	5.1
Location	Knot Rock	Martins Rock	Waterfall Crest	Goat Is. Bay
Depth (m)	2-4	8-9	6-8	8
Plots (n)	8	1	1	5
Total area of plots (m ²)	231.6	380.9	400.9	196.0

Table 2. Extents of substrata sampled for epifauna

Substratum	<i>Carpophyllum</i> forest	<i>Ecklonia</i> forest	Urchin barrens	Turf flats
<i>E. radiata</i> (<50 mm stipe length)		9.6 plants m ⁻²		
<i>E. radiata</i> (50–200 mm stipe length)		1.9 plants m ⁻²		
<i>E. radiata</i> (>200 mm stipe length)		6.5 plants m ⁻²		
<i>C. plumosum</i> stipes (<500 mm length)	207.9 stipes m ⁻²			
<i>C. plumosum</i> stipes (≥500 mm length)	137.3 stipes m ⁻²			
<i>C. plumosum</i> holdfast	76.8 % cover			
Coralline turf	5.2 % cover	44.0 % cover		100 % cover
<i>Ceramium</i> sp. (red alga)		3.1 plants m ⁻²		
<i>Polymastia</i> sp. (sponge)		0.15 sponges m ⁻²		0.85 sponges m ⁻²
Beneath <i>Evechinus chloroticus</i>			4.0 <i>E. chloroticus</i> m ⁻²	
Sand		2.5 % cover		
Bare rock/coralline paint	14.4 % cover	47.0 % cover	100 % cover	
Vertical rock faces	0.26 m m ⁻²			

Results were scaled to account for the prevalence of each substratum, estimated using 0.25 m² quadrats for *Carpophyllum plumosum* var. *capillifolium* stipes in the *Carpophyllum* forest, and 1 m² quadrats for *Ecklonia radiata*, *Ceramium* sp. (red alga) and *Polymastia* sp. (sponge) in the *Ecklonia* forest (n = 10). Total counts were made of *Polymastia* sp. in the turf flats. Percent cover of substrata on flat surfaces (e.g. bare rock/coralline paint) was estimated by recording substratum type under points of a 1 m² grid laid over plots in each habitat using measuring tapes. The total distance of vertical rock faces within the *Carpophyllum* forest was measured with a tape, so that numbers of animals in suction samples taken from a 0.1 m width of rock face could be scaled to per m² of substratum. Extents of the various substrata are given in Table 2. Total cover sampled was less than 100% in 2 habitats. In the *Carpophyllum* forest the remainder consisted of transient sand (2.5%) and cobbles (1.0%), neither of which held appreciable numbers of epifauna (pers. obs.). In the *Ecklonia* forest, the remainder was *E. radiata* holdfasts (6.0%) that were sampled with the rest of the plant and scaled to plant density, and *Ancorina* sp. sponges (0.5%) that harboured negligible numbers of epifauna (pers. obs.).

Mega fauna. Animals longer than 10 mm were censused *in situ*. Sizes of gastropods, hermit crabs and echinoids were measured directly using vernier calipers, but lengths of more mobile animals such as fish and larger decapods had to be estimated visually. Within each habitat, total counts were made of spiny lobsters (*Jasus edwardsii*) and large fish (excluding pelagic species), the latter replicated 2 to 4 times on separate days. Smaller, cryptic fish (mostly blennioids) and large brachyuran crabs (mostly *Plagusia chabrus*) were censused within 5 × 1 m strip transects (n = 10). Echinoids (*Evechinus chloroticus*), gastropods (trochids, turbinids and neogastropods) and hermit crabs

(Paguroidea) were censused within 1 m² quadrats, except in the urchin barrens, where highly abundant individuals of the gastropods *Cantharidus purpureus*, *Cellana stellifera* and *Trochus viridis* were censused within 0.25 m² quadrats (n = 10). In the turf flats habitat, total counts were made of all invertebrates >40 mm (mostly the large gastropod *Cookia sulcata*; these individuals were not considered when found in the 1 m² quadrats). Biomass and productivity of megafaunal individuals encountered during sampling for epifauna (mainly cryptic blennioid and gobioid fish and gastropods found on seaweed plants) were estimated as described below, and scaled per m² of seabed according to the extent of the substratum, as described earlier for epifauna.

Biomass and productivity values were expressed as ash-free dry weight (AFDW), the difference between animal (shell-free) dry weight (after drying to constant weight at 80°C) and inorganic weight [after incinerating the dry tissue at 500°C for 12 h (most megainvertebrates) or 24 h (fish), or after boiling it for 1 h in 10% w/v NaOH (echinoids) (Crisp 1984)].

Biomasses were estimated using length-weight relationships determined from animals collected outside the study sites. Fish length-wet weight equations were taken from Taylor & Willis (1998). Coefficients for length-AFDW equations for megainvertebrates are given in Table 3.

Growth in length of individual fishes was estimated using the von Bertalanffy growth formula (VBGF):

$$L_t = L_{\infty}(1 - e^{-K(t-t_0)}) \quad (1)$$

where L_t = length at age t , L_{∞} = asymptotic length, K = the von Bertalanffy growth constant, and t_0 = the theoretical age at length zero. L_{∞} and K were taken from the literature wherever possible (compiled in Taylor & Willis 1998). When such data were unavailable for a species, they were estimated using regression equa-

Table 3. Equations relating ash-free dry weight (AFDW) to linear body dimension for megainvertebrates, and the von Bertalanffy growth parameters L_{∞} and K where available. $W' = aL^b$, where $W' = \text{AFDW (g)}$, and $L = \text{linear body dimension (mm)}$. Taxa: B = brachyuran crab, E = echinoid, G = gastropod, HC = hermit crab, SL = spiny lobster. Linear body dimensions: AL = aperture length, CL = carapace length, CW = carapace width, D = test diameter, H = height (axis of the spire), L = length (tip of spire to outermost point of aperture), SL = shell length, W = width (perpendicular to the axis of the spire). The correction factor of Snowdon (1991) is a scaling factor used to derive an arithmetic mean from the geometric mean predicted by the length-weight power curve after back-transforming a least squares regression on log-log data. Sources: (1) West (1991); (2) Hartley (1978); (3) Walker (1981); (4) Saila et al. (1978)

Taxon	Linear body dimension	a	b	Correction factor of Snowdon (1991)	Coeff. of determination (r^2)	n	Length range (mm)	L_{∞} (mm)	K	Source for L_{∞} and K
<i>Buccinum</i> spp. (G)	AL	3.964×10^{-5}	2.9096	1.0664	0.818	16	11–23			
<i>Calliostoma punctulatum</i> (G)	H	7.116×10^{-6}	3.4078	1.0116	0.992	20	12–32	37	0.71	(1)
<i>Cantharidus purpureus</i> (G)	H	1.774×10^{-5}	2.7903	0.9923	0.909	20	7–25	19	2.60	(2)
<i>Cellana stellifera</i> (G)	L	2.149×10^{-6}	3.3899	1.0178	0.971	21	13–40	40	0.84	(2)
<i>Cookia sulcata</i> (G)	L	2.153×10^{-5}	2.9192	1.0090	0.994	23	18–85			
<i>Dicathais orbita</i> (G)	AL	8.596×10^{-6}	3.2809	1.0701	0.941	23	16–50			
<i>Evechinus chloroticus</i> (E)	D	6.550×10^{-4}	2.1835	0.9907	0.987	17	13–95	92	0.16	(3)
<i>Jasus edwardsii</i> (SL)	CL	7.551×10^{-4}	2.5291	0.9933	0.985	20	50–188			
<i>J. edwardsii</i> (SL) (male)	CL							187	0.09	(4)
<i>J. edwardsii</i> (SL) (female)	CL							117	0.16	(4)
<i>Maoricolpus roseus</i> (G)	L	8.111×10^{-6}	2.5174	1.0036	0.910	18	56–76			
Paguroidea (HC)	SL	7.208×10^{-5}	2.2261	1.1590	0.556	18	13–45			
<i>Plagusia chabrui</i> (B)	CW	1.162×10^{-4}	2.9224	1.0339	0.984	21	8–58			
<i>Trochus viridis</i> (G)	W	9.473×10^{-8}	4.8496	1.0067	0.916	22	14–23	20	2.44	(2)
<i>Turbo smaragdus</i> (G)	W	1.747×10^{-5}	3.0695	0.9721	0.991	20	7–31			

tions in Taylor & Willis (1998), with L_{∞} estimated as a function of the lower length value given for adult individuals in Ayling & Cox (1982), and wet weight at L_{∞} then used to predict K . Growth in length was converted to growth in AFDW using length-wet weight relationships from Taylor & Willis (1998), and a wet weight-AFDW conversion factor of 0.202, estimated by drying and ashing single individuals of 18 fish species ranging in size from 0.61 to 4600 g wet weight (Taylor 1997). This procedure estimated the average annual growth of fish. Seasonality of growth was accounted for by using a seasonally oscillating form of the VBGF:

$$L_t = L_{\infty} [1 - e^{-K(t-t_0) + \frac{CK}{2\pi} \sin 2\pi(t-t_s)}] \quad (2)$$

where C = the amplitude of the oscillation and t_s = phase (Pauly & David 1981). Eq. (2) cannot be used to estimate growth in length directly, since an individual fish of given length is unlikely to be of the exact age specified by the equation. Instead, a multiplier is required that expresses, for any given time of the year, the seasonal growth rate relative to the annual average growth rate. This multiplier is equal to the slope of the seasonal VBGF divided by the slope of the ordinary VBGF. The derivative of length with respect to time in the seasonally oscillating VBGF (Eq. 2) is:

$$\frac{dL_t}{dt} = KL_{\infty} [1 + C \cos 2\pi(t - t_s)] e^{-[K(t-t_0) + \frac{CK}{2\pi} \sin 2\pi(t-t_s)]} \quad (3)$$

The derivative of length with respect to time in the ordinary VBGF (Eq. 1) is:

$$\frac{dL_t}{dt} = KL_{\infty} e^{-K(t-t_0)} \quad (4)$$

The ratio of slopes, R , (i.e. the instantaneous growth rate relative to the average annual value) is Eq. (3) divided by Eq. (4):

$$R = [1 + C \cos 2\pi(t - t_s)] e^{-\frac{CK}{2\pi} \sin 2\pi(t-t_s)} \quad (5)$$

On a global scale, C , the amplitude term in the seasonal VBGF, is strongly positively correlated with the difference between mean monthly summer and winter water temperatures (ΔT), with $C = 0.113\Delta T$ (Longhurst & Pauly 1987). In the Cape Rodney to Okakari Point Marine Reserve, long-term average monthly minimum and maximum sea surface temperatures (SSTs) are 14.0 and 20.6°C respectively (Evans 1992). The difference of 6.6°C is predicted to result in seasonally oscillating growth with an amplitude (C) of 0.75 (Longhurst & Pauly 1987). By means of comparison, the only empirical value of C that I could locate for the region is 0.85, for combined 1985–89 juvenile year classes of the snapper, *Pagrus auratus* (Francis 1994). For the present study, I used Francis's mean phase (t_s) of ~ 0.03 yr (theoretical birthdate of January 1) in Eq. (5). Average annual productivity values calculated using Eq. (1) were scaled for seasonal variability in growth using the

ratio in Eq. (5) to yield an estimated productivity for the survey time.

Productivity of megainvertebrates was estimated as for fishes, except that L_{∞} was estimated from the length of the largest individual collected for the length-weight relationships (L_{\max}), where $L_{\infty} = 1.0L_{\max}$ ($r^2 = 0.997$). K was estimated using the following regression equation, based on data from Table 3: $K = 0.823 \times (\text{AFDW}_{L_{\infty}})^{-0.415}$, where $\text{AFDW}_{L_{\infty}}$ is ash-free dry weight at L_{∞} (g AFDW) [$r^2 = 0.914$, correction factor of Snowdon (1991) = 1.0991].

Fishes were categorised according to their major food source as (1) herbivores, (2) predators of epifauna, (3) predators of megafauna, or (4) predators of sessile animals (from references in Jones 1988). Consumption rates of fishes that prey upon epifauna were estimated in 2 different ways: (1) by applying an assumed conversion efficiency of 10% (Pauly & Christensen 1995) to fish productivity data (from Table 7), and (2) by applying a daily consumption rate of 3.1% of fish body weight (Edgar & Shaw 1995) to fish biomass data (from Table 6). These consumption rates were then expressed as a percentage of (1) total epifaunal productivity and (2) productivity of crustaceans >1 mm sieve size (the primary food source for fish of 0.1 to 100 g wet weight; Edgar & Shaw 1995).

Seasonality. All 4 habitats were surveyed once, as described above, during October–November 1994 (austral spring). Productivity values for megafauna were calculated for the common date of October 15, which corresponded to 0.789 as a fraction of the year (to substitute for t in Eq. 5). Productivity values for epifauna were also calculated for October 15, using the Goat Island 25 yr mean SST for this date of 15.3°C (Evans 1992) in the equation of Edgar (1990) (his Eq. 1 in Table V).

Plans to survey all 4 habitats seasonally for 1 yr turned out to be logistically impractical. Instead, a single habitat, the turf flats, was resurveyed during each of the 3 seasons following spring 1994, in order to examine variability in density, biomass, and secondary productivity throughout the year. Productivity for each season was calculated based on the actual dates and SSTs at sampling.

To allow comparisons to be made with literature values for secondary productivity in other aquatic habitats, the daily production value for each of the 3 habitats measured once in spring was converted to an annual estimate using the following equation:

$$\text{AP}_h = \text{SP}_h \times 365 \times \text{AP}_t / \text{SP}_t \quad (6)$$

where AP_h = estimated annual production in habitat h , SP_h = daily production in habitat h during spring, AP_t = average annual daily production in the turf flats habitat (i.e. the average of the 4 seasonal values), and SP_t =

daily production in the turf flats habitat during spring. Separate factors were calculated for epifauna and megafauna. The same procedure was also carried out for density and biomass.

Reef-wide annual density, biomass and productivity. Estimates of average annual density, biomass and productivity were scaled to give single reef-level values according to values provided by Ayling (1978) for percent cover of subtidal rock in the marine reserve (Table 1). The 4 habitats sampled covered a total of ~71.3% of subtidal rock in the marine reserve, and it was assumed that the reef-level values for density, biomass and productivity were equivalent for fauna in habitats comprising the remaining 28.7%. This may have resulted in a slight overestimation of reef-level density, biomass and productivity if these values were negatively correlated with water depth, as none of the 4 habitats surveyed was deeper than 9 m, and the reef often extends to 15–18 m depth (Ayling 1978).

Standard errors. Standard errors presented in this paper are based on variability amongst final estimates of density, biomass and productivity calculated for each sample (or quadrat or transect). Where necessary, errors were compounded following Topping (1962). The errors are exact for the density estimates, but the errors on the biomass and productivity estimates do not incorporate variability due to (1) error in estimating animal lengths in the field, or (2) variance in relationships amongst length, weight and growth parameters.

RESULTS

Density

Epifauna comprised the overwhelming majority (>99.6%) of individual animals >0.5 mm sieve size in all 4 habitats (Table 4). Densities were positively correlated with the apparent structural complexity of the habitats, being highest in the *Carpophyllum* forest (2.0×10^5 ind. m^{-2}), and lowest in the urchin barrens (2.4×10^4 ind. m^{-2}). Grazing gastropods (*Calliostoma punctulatum*, *Cantharidus purpureus*, *Cellana stellifera*, *Cookia sulcata*, *Trochus viridis*, *Turbo smaragdus*; Creese 1988, West 1991) were the next most abundant group, reaching densities of 50 to 60 ind. m^{-2} in the *Ecklonia* forest and the urchin barrens. Densities of fish and megainvertebrates such as decapods (mostly *Jasus edwardsii* and *Plagusia chabrus*), echinoids, and neogastropods (*Buccinulum* spp., *Dicathais orbita*) were generally in the order of 0.01 to 10 ind. m^{-2} .

Epifaunal assemblages tended to be dominated numerically by gastropods and gammarid amphipods, with 1 of these 2 being the most abundant taxon on 12 of the 15 substrata sampled (Table 5). Polychaetes,

Table 4. Density (ind. m⁻²) of animals >0.5 mm sieve size in 4 subtidal rocky reef habitats in northeastern New Zealand

Taxon	<i>Carpophyllum</i> forest			<i>Ecklonia</i> forest			Urchin barrens			Turf flats		
	Mean	(1 SE)	%	Mean	(1 SE)	%	Mean	(1 SE)	%	Mean	(1 SE)	%
Fish												
Feeding on seaweeds	0.014	(0.004)	0.0000									
Feeding on epifauna	2.864	(2.497)	0.0014	4.609	(1.850)	0.0065	3.700	(0.755)	0.0151	0.080	(0.075)	0.0001
Feeding on megafauna	0.012	(0.003)	0.0000	0.007	(0.003)	0.0000	0.012	(0.000)	0.0001	0.007	(0.007)	0.0000
Feeding on sessile animals				0.002	(0.002)	0.0000	0.004	(0.001)	0.0000	0.003	(0.003)	0.0000
Spiny lobsters				0.018	(0.000)	0.0000						
Brachyuran crabs	0.12	(0.05)	0.0001	1.40	(0.97)	0.0020	0.14	(0.07)	0.0006			
Hermit crabs	1.90	(0.60)	0.0009	2.30	(0.92)	0.0032	1.60	(1.22)	0.0065	1.61	(0.56)	0.0010
Echinoids	0.40	(0.40)	0.0002	2.58	(1.60)	0.0036	4.00	(0.60)	0.0164			
Grazing gastropods												
On seafloor	2.20	(0.92)	0.0011	15.60	(1.97)	0.0219	62.00	(10.20)	0.2538	0.08	(0.00)	0.0001
On seaweeds				33.54	(6.13)	0.0472						
Suspension-feeding gastropods										0.40	(0.16)	0.0003
Neogastropods	1.70	(0.45)	0.0008	2.90	(0.48)	0.0041	7.90	(2.60)	0.0323	4.21	(1.06)	0.0026
Epifauna	203301	(31682)	99.995	71059	(8403)	99.911	24349	(5462)	99.675	159080	(13515)	99.996
Total	203310	(31682)		71122	(8403)		24428	(5462)		159086	(13515)	

Table 5. Percentage composition of epifaunal assemblages on substrata within 4 subtidal rocky reef habitats. Totals are averages calculated for each habitat, weighted by the relative densities of total epifauna on each substratum (last column). Reef-level values are the habitat averages scaled according to the relative extents of the habitats (from Table 1). Taxa are ranked in decreasing order of reef-level density. Gast. = gastropod, Gamm. = gammarid amphipod, Poly. = polychaete, Ostr. = ostracod, Tana. = tanaid, Iso. = isopod, Biv. = bivalve, Harp. = harpacticoid copepod, Nem. = nematode, Cuma. = cumacean, Ophi. = ophiuroid, Capr. = caprellid amphipod. Taxa not tabulated comprised <3% of total epifaunal individuals for any substratum

Substratum	Gast.	Gamm.	Poly.	Ostr.	Tana.	Iso.	Biv.	Harp.	Nem.	Cuma.	Ophi.	Capr.	Density (ind. m ⁻²)
<i>Carpophyllum</i> forest													
<i>C. plumosum</i> stipes	9.3	78.5	1.8		1.1	7.7	0.02	0.6	0.1		0.004	0.2	139124
<i>C. plumosum</i> holdfast	19.7	22.6	24.5	9.6	1.4	3.5	12.7	0.03	0.9	3.5	0.3	0.1	53613
Coralline turf	28.5	10.8	26.9	6.1	0.8	3.8	16.6	0.03	1.2	4.4	0.1	0.1	9563
Bare rock/coralline paint	33.1	22.8	21.7	7.2	1.2	2.4	7.1	0.6	0.9	0.6			820
Vertical rock faces	40.3	23.9	8.1	8.5	1.3	5.9	5.7			3.0	0.8	0.5	182
Total	13.0	60.3	9.1	2.9	1.2	6.4	4.2	0.4	0.3	1.1	0.1	0.2	203301
<i>Ecklonia</i> forest													
<i>Ecklonia radiata</i>	3.7	27.4	19.3	2.4	2.7	8.0	8.2	15.6	4.7	0.5	5.4	0.03	9511
Coralline turf	20.1	26.2	19.7	12.5	9.6	1.9	4.4	0.2	1.1	1.7	1.1	0.1	52329
<i>Ceramium</i> sp. (red alga)	1.7	78.6	11.1	0.1	0.9	2.1	0.1	0.04	0.1	0.04	0.04	4.2	1212
<i>Polymastia</i> sp. (sponge)		97.9	0.1			0.1	1.0	0.6		0.02	0.1		46
Sand	4.9	17.5	5.7	13.3	4.6	1.3	3.9	0.1	37.7	10.3		0.1	2014
Bare rock/coralline paint	21.1	29.3	18.4	4.5	4.1	4.6	5.5	1.3	1.9	2.9	4.6	0.2	5947
Total	17.2	27.3	19.0	10.3	7.9	2.9	4.9	2.4	2.7	1.8	1.9	0.2	71059
Urchin barrens													
Beneath <i>Evechinus chloroticus</i>						100.0							18
Bare rock/coralline paint	50.1	17.5	14.2	4.8	2.4	4.1	1.6	1.5	0.3	0.2	0.4	0.9	24331
Total	50.1	17.5	14.2	4.8	2.4	4.2	1.6	1.5	0.3	0.2	0.4	0.9	24349
Turf flats													
Coralline turf	4.0	45.3	30.9	7.8	1.9	3.2	1.5	0.3	2.8	0.9	0.3	0.3	159006
<i>Polymastia</i> sp. (sponge)	2.4	86.5	4.6		1.1	1.6			2.1	0.1			74
Total	4.0	45.3	30.9	7.8	1.9	3.2	1.5	0.3	2.8	0.9	0.3	0.3	159080
Reef-level	30.4	26.6	17.0	7.2	4.6	3.7	3.2	1.7	1.5	1.0	1.0	0.5	66058

Table 6. Biomass (g AFDW m⁻²) of animals >0.5 mm sieve size in 4 subtidal rocky reef habitats

Taxon	<i>Carpophyllum</i> forest			<i>Ecklonia</i> forest			Urchin barrens			Turf flats		
	Mean	(1 SE)	%	Mean	(1 SE)	%	Mean	(1 SE)	%	Mean	(1 SE)	%
Fish												
Feeding on seaweeds	0.67	(0.66)	2.1									
Feeding on epifauna	0.59	(0.33)	1.9	1.60	(0.51)	7.5	0.42	(0.09)	1.0	0.39	(0.39)	1.5
Feeding on megafauna	0.29	(0.10)	0.9	0.31	(0.18)	1.4	0.34	(0.05)	0.8	0.10	(0.10)	0.4
Feeding on sessile animals				0.06	(0.06)	0.3	0.16	(0.07)	0.4	0.12	(0.12)	0.5
Spiny lobsters				1.48	(0.00)	6.9						
Brachyuran crabs	0.18	(0.07)	0.6	1.02	(0.56)	4.8	0.09	(0.06)	0.2			
Hermit crabs	0.10	(0.03)	0.3	0.12	(0.05)	0.6	0.30	(0.25)	0.7	0.07	(0.03)	0.3
Echinoids	1.46	(1.46)	4.6	0.22	(0.14)	1.0	24.73	(3.98)	58.6			
Grazing gastropods												
On seafloor	1.19	(0.63)	3.7	2.59	(0.48)	12.1	11.08	(1.60)	26.3	0.39	(0.00)	1.5
On seaweeds				2.60	(0.57)	12.2						
Suspension-feeding gastropods										0.02	(0.01)	0.1
Neogastropods	0.04	(0.02)	0.1	0.06	(0.01)	0.3	0.34	(0.09)	0.8	0.07	(0.02)	0.3
Epifauna	27.19	(4.59)	85.8	11.24	(1.14)	52.8	4.71	(0.89)	11.2	25.26	(5.36)	95.6
Total	31.70	(4.92)		21.30	(1.58)		42.16	(4.39)		26.42	(5.38)	

ostracods, tanaids, isopods, and bivalves were also common across a range of substrata. Taxa that were uncommon overall, but relatively abundant on a single substratum, were harpacticoid copepods (*Ecklonia radiata* plants), and nematodes and cumaceans (sand).

Biomass

Biomasses of the different animal groups were more equitable (Table 6). Epifauna comprised 85 to 95% of total biomass in the *Carpophyllum* forest and turf flats habitats, 53% in the *Ecklonia* forest, and 11% in the urchin barrens. In the *Ecklonia* forest, the other 47% of biomass comprised mostly grazing gastropods, fish preying upon epifauna (mainly the morwong *Cheilodactylus spectabilis*), and decapods (spiny lobsters and brachyuran crabs). In the urchin barrens, most of the biomass was found in echinoids (59%) and grazing gastropods (26%). Total biomass varied relatively little across the 4 habitats (range = 21 to 42 g AFDW m⁻²), being highest on the urchin barrens.

Productivity

In the structurally complex vegetated habitats (*Carpophyllum* forest and turf flats), epifauna contributed 98 to 99% of total secondary productivity (Table 7). The epifaunal contribution was 84% in the *Ecklonia* forest, where the only other significant contributions to

productivity were made by grazing gastropods (7%) and fish preying upon epifauna (4%). Epifaunal productivity was lowest (54% of the total) in the urchin barrens, where grazing gastropods (24%), fish preying upon epifauna (10%), and echinoids (8%) made their greatest contributions to productivity in any habitat.

As with density, total productivity was positively correlated with the structural complexity of the habitat, being highest in the *Carpophyllum* forest (482 mg AFDW m⁻² d⁻¹), and lowest in the urchin barrens (117 mg AFDW m⁻² d⁻¹). In each habitat the most productive fish feeding guild was the predators of epifauna.

Epifaunal productivity was highest on finely structured vegetated substrata, such as *Carpophyllum plumosum* var. *capillifolium* stipes and coralline turf (Table 8). This was most apparent in the *Ecklonia* forest, where epifaunal productivity was higher in the coralline turf than on the more conspicuous, but flat-bladed, *Ecklonia radiata* plants themselves. Productivity of crustaceans >1 mm sieve size amounted to 50% of total epifaunal productivity in the *Carpophyllum* forest, and 15 to 19% in the other habitats (Table 8). Crustaceans >1 mm sieve size contributed the highest percentages (40 to 100%) of epifaunal production in habitats that were very sheltered (in sponges and beneath *Evechinus chloroticus*) or finely structured (*Carpophyllum plumosum* var. *capillifolium* stipes). The contribution was much lower on bare rock/coralline paint (7 to 15%) and coralline turf (19 to 24%).

The proportion of total epifaunal production consumed by fish was estimated to be less than 10% in the

Table 7. Productivity (mg AFDW m⁻² d⁻¹) of animals >0.5 mm sieve size in 4 subtidal rocky reef habitats

Taxon	<i>Carpophyllum</i> forest			<i>Ecklonia</i> forest			Urchin barrens			Turf flats		
	Mean	(1 SE)	%	Mean	(1 SE)	%	Mean	(1 SE)	%	Mean	(1 SE)	%
Fish												
Feeding on seaweeds	0.63	(0.54)	0.1									
Feeding on epifauna	2.98	(0.90)	0.6	9.02	(2.03)	4.3	11.43	(2.14)	9.7	2.98	(2.96)	0.7
Feeding on megafauna	0.58	(0.20)	0.1	0.28	(0.17)	0.1	0.39	(0.03)	0.3	0.25	(0.25)	0.1
Feeding on sessile animals				0.14	(0.14)	0.1	0.31	(0.11)	0.3	0.27	(0.27)	0.1
Spiny lobsters				0.42	(0.00)	0.2						
Brachyuran crabs	0.56	(0.23)	0.1	3.95	(2.57)	1.9	0.30	(0.15)	0.3			
Hermit crabs	1.36	(0.42)	0.3	1.54	(0.60)	0.7	1.06	(0.77)	0.9	1.03	(0.37)	0.2
Echinoids	1.15	(1.15)	0.2	2.05	(1.28)	1.0	9.43	(1.51)	8.0			
Grazing gastropods												
On seafloor	2.44	(0.90)	0.5	9.76	(1.34)	4.7	27.98	(3.76)	23.8	0.28	(0.00)	0.1
On seaweeds				5.17	(1.18)	2.5						
Suspension-feeding gastropods										0.26	(0.11)	0.1
Neogastropods	0.66	(0.16)	0.1	1.00	(0.23)	0.5	2.55	(0.65)	2.2	1.15	(0.27)	0.3
Epifauna	472.00	(76.10)	97.9	174.20	(17.70)	83.9	63.90	(11.50)	54.5	413.60	(67.10)	98.5
Total	482.35	(76.12)		207.53	(18.15)		117.35	(12.42)		419.83	(67.17)	

Table 8. Productivity (mg AFDW m⁻² d⁻¹) of epifauna on substrata within 4 subtidal rocky reef habitats. %₁ = percentage of total productivity for habitat, %₂ = percentage of productivity contributed by crustaceans >1 mm sieve size (the primary prey for small fish)

Substratum	<i>Carpophyllum</i> forest				<i>Ecklonia</i> forest				Urchin barrens				Turf flats			
	Mean	(1 SE)	% ₁	% ₂	Mean	(1 SE)	% ₁	% ₂	Mean	(1 SE)	% ₁	% ₂	Mean	(1 SE)	% ₁	% ₂
<i>Ecklonia radiata</i> (entire plant)					40.8	(5.4)	23.4	12.4								
<i>Carpophyllum plumosum</i> stipes	294.0	(69.5)	62.3	58.2												
<i>Carpophyllum plumosum</i> holdfast	156.1	(30.8)	33.1	37.9												
Coralline turf	19.4	(3.1)	4.1	23.7	104.7	(15.6)	60.1	21.2					413.4	(67.1)	100.0	19.1
<i>Ceramium</i> sp. (red alga)					2.1	(1.3)	1.2	34.9								
<i>Polymastia</i> sp. (sponge)					0.1	(0.1)	0.0	40.1					0.2	(0.1)	0.1	69.0
Beneath <i>Evechinus chloroticus</i>									0.3	(0.1)	0.5	100.0				
Sand					3.9	(0.5)	2.2	7.4								
Bare rock/coralline paint	1.9	(0.3)	0.4	14.0	22.7	(6.2)	13.0	6.6	63.6	(11.5)	99.5	14.9				
Vertical rock faces	0.5	(0.1)	0.1	15.1												
Total	472.0	(76.1)		49.8	174.2	(17.7)		17.1	63.9	(11.5)		15.4	413.6	(67.1)		19.1

Carpophyllum forest and turf flats, and 28 to 52% in the *Ecklonia* forest (Table 9). The very high upper values estimated for the consumption of total epifaunal and crustacean production on the urchin barrens were strongly influenced by the high productivity resulting from a large recruitment pulse of juvenile tripterygiids (*Forsterygion varium*) prior to censusing, and can be disregarded since it is almost certain that most of these

fish would disappear during the following few weeks (Connell & Jones 1991). The lower value of 20% is probably a much more realistic estimate of fish consumption of total epifaunal production. At the level of the entire reef, fish consumed ~26% of total epifaunal production [taken to be the average of values obtained from Methods (1) and (2) in Table 9, except for the urchin barrens, where the value obtained from

Method (2) was used, scaled for habitat extents provided by Ayling (1978)]. Crustaceans >1 mm sieve size are the primary prey of small predatory fish (Edgar & Shaw 1995), and it was estimated that all of their production was consumed in the *Ecklonia* forest and urchin barrens habitats. However, fish only consumed 8 to 13% of production of crustaceans >1 mm sieve size in the *Carpophyllum* forest, and 15 to 38% in the turf flats.

Seasonality

In the turf flats habitat at Goat Island Bay, epifauna were about 4 orders of magnitude more abundant than any other animal group throughout the entire year (Fig. 1a). Epifauna were also the major contributors to faunal biomass in all 4 seasons, always comprising at least an order of magnitude more biomass than any

Table 9. Percentage of production by total epifauna and crustaceans >1 mm sieve size consumed by fish within 4 subtidal rocky reef habitats. See 'Methods: Megafauna' for details regarding calculations

Prey class Method	<i>Carpophyl- lum</i> forest	<i>Ecklonia</i> forest	Urchin barrens	Turf flats
Total epifauna				
1	6	52	179	7
2	4	28	20	3
Crustaceans >1 mm				
1	13	303	1163	38
2	8	167	134	15

other group, with fish preying upon epifauna usually second (Fig. 1b). The pattern was consistent for productivity, with epifauna always at least 2 orders of magnitude more productive than the next group (again, usually fish preying upon epifauna) (Fig. 1c).

Scaling factors calculated from measurements of annual variability in the turf flats habitat for epifauna were 0.756 (density), 0.548 (biomass) and 0.653 (productivity). The respective values for the megafauna were 0.891, 1.155 and 0.777. Values were lower than 1 for everything except megafaunal biomass, indicating a trend for values of density, biomass and productivity measured in spring to be higher than the mean annual values. These factors were used to generate average annual estimates of density, biomass and productivity for the other 3 habitats from measurements made during spring.

Reef-wide annual density, biomass and productivity

When estimated average annual density, biomass and productivity values for each habitat were combined according to the relative habitat prevalences to yield single reef-level values, the epifaunal contribution decreased due to the high coverage of the *Ecklonia* forest and urchin barrens habitats in which (1) total faunal productivity was relatively low and (2) the epifaunal contribution to this productivity was relatively low (Table 10). Even so, epifauna still contributed ~19% of faunal biomass, and ~78% of secondary productivity. The biomass of echinoids was high (43%), but their productivity was low (3%). Grazing gastropods made substantial contributions to biomass (27%) and productivity (11%), while fish preying upon epifauna were the next most important group (4% of biomass, 5% of productivity). As described above, however, the importance of these fish may have been overestimated due to recruitment of tripterygiids to the urchin barrens prior to censusing.

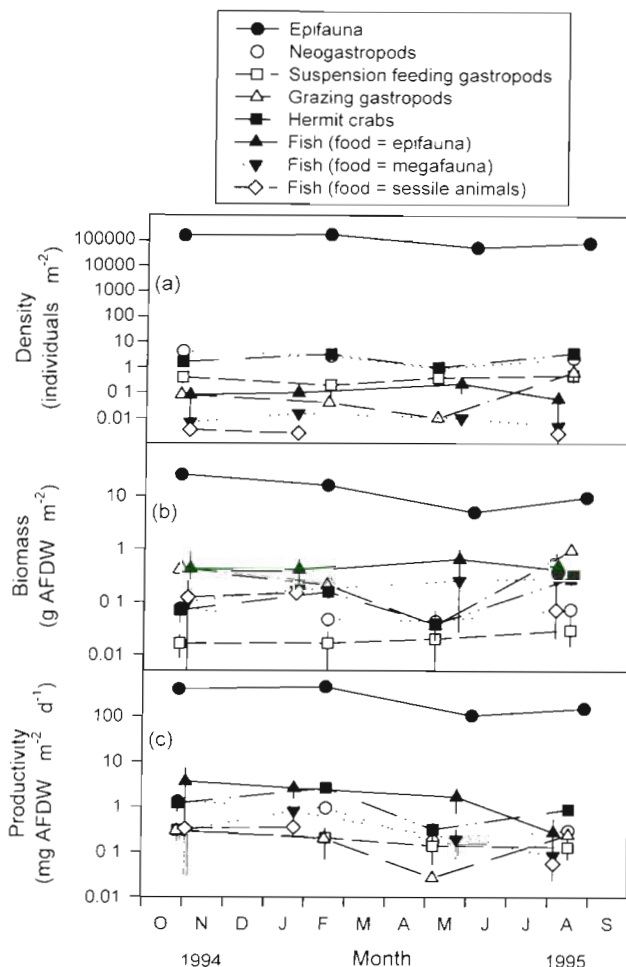


Fig. 1. Animals >0.5 mm sieve size inhabiting turf flats habitat vs time. (a) Density, (b) biomass, and (c) productivity. Bars represent 1 SE

Table 10. Estimated average annual density, biomass and productivity of animals >0.5 mm sieve size across the entire reef. See 'Methods: Seasonality' and 'Methods: Reef-wide annual density, biomass and productivity' for details regarding calculations

Taxon	Density (ind. m ⁻²)		Biomass (g AFDW m ⁻²)		Productivity (g AFDW m ⁻² yr ⁻¹)	
	Mean	%	Mean	%	Mean	%
Fish						
Feeding on seaweeds	0.00	0.00	0.05	0.18	0.01	0.02
Feeding on epifauna	3.35	0.01	1.07	3.55	2.61	5.23
Feeding on megafauna	0.01	0.00	0.35	1.18	0.10	0.20
Feeding on sessile animals	0.00	0.00	0.12	0.40	0.06	0.12
Spiny lobsters	0.01	0.00	0.71	2.37	0.05	0.10
Brachyuran crabs	0.58	0.00	0.55	1.83	0.52	1.03
Hermit crabs	1.71	0.00	0.22	0.74	0.36	0.72
Echinoids	2.56	0.01	12.80	42.52	1.44	2.89
Grazing gastropods						
On seafloor	30.28	0.06	7.01	23.28	4.70	9.41
On seaweeds	12.49	0.02	1.26	4.18	0.61	1.23
Suspension-feeding gastropods	0.03	0.00	0.00	0.00	0.01	0.01
Neogastropods	4.55	0.01	0.21	0.71	0.47	0.95
Epifauna	49961	99.89	5.74	19.07	39.02	78.08
Total	50017		30.11		49.97	

DISCUSSION

This study is the first to quantify directly the contribution of small mobile invertebrates to the flux of materials on subtidal rocky reefs. As predicted by Edgar & Moore (1986), the high densities and rapid turnover rates of epifauna make them very productive relative to other reef-dwelling animals. Their contribution to total annual secondary productivity was ~78% on the scale of the entire reef, and up to 99% in finely structured vegetated habitats. Since productivity is proportional to other metabolic rate parameters (all scale to body mass with a power of ~0.75; Peters 1983), this indicates that epifauna are the major consumers and nutrient recyclers amongst the reef-dwelling fauna, and hence deserve inclusion in trophic models such as those of Miller et al. (1971) and Newell et al. (1982).

The high productivity of the epifauna also indicates that more attention needs to be paid to their functional role, i.e. their ability to influence the distribution and abundance of other organisms. The major challenge is to find ways of experimentally manipulating epifaunal abundances under realistic conditions in the field. This has proven to be difficult due to the small size and high mobility of epifaunal individuals (e.g. Edgar & Aoki 1993). Nevertheless, it is becoming clear that epifauna are capable of significantly reducing abundances of seaweeds (Kennelly 1983, Tegner & Dayton 1987), epiphytic algae (Brawley & Fei 1987, Duffy 1990), and newly settled sessile

animals (Osman et al. 1992), and as prey items the epifauna appear to regulate populations of many reef fish species (Holbrook & Schmitt 1996, Holbrook et al. 1997).

Factors affecting epifaunal productivity

Epifaunal productivity was highest in habitats occupied by brown seaweeds and articulated corallines, and lowest in the crustose coralline-dominated urchin barrens, probably because the former provide better shelter from fish predation (Coull & Wells 1983), a larger surface from which to graze (Edgar 1991a), and a better anchorage for resisting removal by wave action (Hacker & Steneck 1990). It follows that factors influencing the relative abundances and dynamics of these habitat patches are likely to have a major impact on reef-level epifaunal productivity. Here echinoids are of great functional importance, because in spite of their low contribution to the flux of organic matter they can strongly influence abundance patterns of erect seaweeds (Lawrence 1975, Harold & Pearse 1987). This has been demonstrated on a large scale in many parts of the northeastern Pacific, where the suppression of urchin populations by reintroduced sea otters causes a predictable shift from unproductive barren grounds to dense kelp forests that support highly productive epifaunal assemblages (Estes et al. 1978, Simenstad et al. 1978). Physical agents, such as storms, and El Niño conditions that interrupt the supply of

nutrients, can also remove large seaweeds and turfing algae (Dayton 1994), having important long-term effects on epifaunal productivity that are reflected in the abundances of predatory fish (Holbrook & Schmitt 1996, Holbrook et al. 1997).

Where the above factors allow suitable habitat to exist, epifaunal productivity is often affected by variation in light intensity along gradients of depth and turbidity, via its impact on epiphytic algal food sources (Edgar 1991b, 1993). Water movement is also important, as shores exposed to strong wave action or currents can support high densities of suspension-feeding amphipods (Fenwick 1976, Edgar 1983). The effects of fish predation on epifaunal productivity have been difficult to evaluate due to epifaunal movement in and out of fish exclusion cages (Edgar & Aoki 1993). Results of studies to date have been inconsistent (Edgar & Aoki 1993), although it appears that when food is limiting to the epifauna the main effect of predatory fish is to alter the size structure of epifaunal assemblages by the selective consumption of larger individuals (Edgar 1993, Edgar & Aoki 1993). While not influencing total epifaunal productivity, this predation will lower the proportion of epifaunal productivity that is composed of individuals large enough to be consumed by fish (Edgar & Shaw 1995).

Fate of epifaunal production

Small fishes are almost certainly the major predators of epifauna on temperate reefs. In finely structured vegetated habitats, small predatory fish were the next

most productive group after the epifauna, confirming the widely perceived importance of the epifauna-fish trophic link (e.g. Edgar & Moore 1986). A high proportion of reef fishes feed on epifauna for at least the early parts of their lives (Jones 1988, Holbrook et al. 1990), and these fishes in turn support a range of larger predators (Estes et al. 1978, Simenstad et al. 1978, Russell 1983).

However, it was estimated that only ~26% of epifaunal production was consumed by fish, a value in agreement with the results of several soft-sediment studies (Edgar & Shaw 1995 and references therein). Decapods such as caridean shrimps and crabs are probably the only other potentially important predators (Howard 1984), but were rare on seaweeds in this study (pers. obs.). The intensity of fish predation was probably underestimated in the turf flats due to the undersampling of transient schools of juvenile mackerels and carangids that sometimes fed on epifauna there, but non-resident fish were not seen feeding in any of the other habitats (pers. obs.).

Epifauna contributed ~78% of secondary productivity on the reef, and ~74% of this production did not appear to be consumed, meaning that at least ~58% of total secondary productivity on the reef is apparently not utilized by higher trophic levels. What is the fate of this component? It is possible that a substantial proportion is advected from the reef when epifaunal individuals enter the water column at night as demersal zooplankton (Hobson & Chess 1976). The fate of animals transported from the reef is completely unknown in terms of their survival and likelihood of relocating suitable habitat and their importance to organisms in other

Table 11. Estimated annual productivity of animals >0.5 mm sieve size in shallow coastal habitats. Where necessary, conversion factors cited in Riddle et al. (1990) were used to derive AFDW from other measures of biomass. Habitats are ranked in decreasing order of productivity

Habitat	Locality	Depth	Productivity (g AFDW m ⁻² yr ⁻¹)	Source
Macrophyte detritus	California	Subtidal	~7000	Vetter (1995)
Mussel bed	Wadden Sea	Intertidal	468	Asmus (1987)
<i>Carpophyllum</i> forest	New Zealand	Subtidal	115	Present study
Turf flats	New Zealand	Subtidal	100	Present study
Mud flat	California	Intertidal	53–100	Nichols (1977)
Mud flat	Portugal	Intertidal	72	Sprung (1994)
Seagrass bed	Portugal	Intertidal	58	Sprung (1994)
<i>Ecklonia</i> forest	New Zealand	Subtidal	51	Present study
Sand flat	Portugal	Intertidal	34	Sprung (1994)
Urchin barrens	New Zealand	Subtidal	30	Present study
Fine sand	Wales	Subtidal	26	Warwick et al. (1978)
Sediments	Delaware	Subtidal	4–47	Maurer et al. (1992)
Coral reef lagoon sand	Great Barrier Reef	Subtidal	19	Riddle et al. (1990)
Mud flat	England	Intertidal	13	Warwick & Price (1975)
Mud	England	Subtidal	2	Buchanan & Warwick (1974)

habitats. Observations and experiments on the epifauna of *Carpophyllum plumosum* var. *capillifolium* have indicated that most epifaunal individuals and taxa did not move into the water column at night (Taylor 1998), but in other studies in northeastern New Zealand (Moltschaniwskyj 1989, White 1989) and elsewhere (Jansson & Källander 1968, Fincham 1974, Hobson & Chess 1976) the presence of numerous epifaunal individuals in the water column at night has been observed or inferred.

What sources of primary production fuel the epifauna?

Epifaunal assemblages typically comprise a diverse array of taxa that can collectively consume a wide variety of living and detrital plant material (Edgar & Moore 1986, Brawley 1992), and this ability to utilise a broad range of resources may contribute to their high productivity (e.g. Chapin et al. 1997). Since kelp forests are extremely productive and release most of their production as detritus (Mann 1973), it is tempting to follow researchers working in the eastern Pacific and conclude that kelp detritus is the major food source for reef-dwelling epifauna (Simenstad et al. 1977, 1978, Moreno & Jara 1984, Ebeling et al. 1985). However, this is not necessarily so, as evidence exists that epiphytic algae are the primary food source for epifauna in many habitats, including kelp forests (Edgar 1991a, 1993). A discussion of this issue is beyond the scope of this paper, but identifying the sources of primary production that drive epifaunal productivity is clearly important for a better understanding of rocky reef ecosystems.

Other flux studies

To enable comparison of results from the present study with figures from other coastal benthic habitats, I compiled annual productivity values from published studies that used a sieve mesh size of 0.5 mm to sample the benthos (Table 11). Productivity in the finely structured vegetated habitats (*Carpophyllum* forest and turf flats) was high, being surpassed only by an extremely productive leptostracan-dominated crustacean assemblage inhabiting localised mats of macrophyte detritus in submarine canyons off southern California (Vetter 1995) and an intertidal mussel bed in the Wadden Sea (Asmus 1987). Productivities of all habitats examined in this study were higher than values for most subtidal habitats elsewhere, which were all soft-sediment with the exception of those described by Asmus (1987) and Vetter (1995).

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