Ecology of molluscan grazers and their interactions with marine algae in north-eastern New Zealand: A review

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Abstract Molluscan grazers are known to exert an important influence on the overall structure of benthic marine communities. Published information on grazers in these communities in New Zealand is currently insufficient to propose any general models for the nature or role of herbivore–algal interactions in this country. However, a considerable amount of unpublished material exists for intertidal and shallow subtidal rocky reefs in north-eastern New Zealand. Much of the information is from unpublished theses, and this review summarises this material and discusses it in the light of published accounts from the north-eastern coast (especially the areas around Leigh, Northland), and studies from elsewhere within and outside New Zealand. While some reasonably well-supported models for subtidal grazers can now be formulated, the intertidal material is still too diffuse to allow meaningful models to be proposed. Suggestions are made as to the type of additional data that is required to complement and augment the material that already exists.

Keywords ecology; molluscs; grazers; algae; rocky reefs

INTRODUCTION

Interactions among grazing marine invertebrates and between grazers and their algal food supply are known to have a major influence on the population dynamics of the species involved and on the overall structure of marine benthic communities. Considerable attention has been focused on these interactions on rocky, intertidal shores (see reviews by Underwood 1979; Branch 1981; Lubchenco & Gaines 1981; Gaines & Lubchenco 1982; Hawkins & Hartnoll 1983), and on shallow, subtidal reefs (Lawrence 1975; Lawrence & Sammarco 1983). New Zealand has an extensive and varied coastline, much of which is dominated by rocky substrata. These reefs, both intertidally and subtidally, support a diverse fauna of grazing invertebrates and benthic algae (Dellow 1955; Morton & Miller 1973). There is, therefore, considerable scope for investigating algal–grazer interactions and their ecological implications.

Despite this, comparatively little work has been published on the dynamics of these interactions in New Zealand, or on the basic biology of even the most common and widespread species of grazers. One of the best documented examples for New Zealand comes from the work done on the sea urchin, *Evechinus chloroticus*, and its interactions with subtidal kelps and other algae. This information is reviewed elsewhere (Andrew 1988). Material on other macroinvertebrate grazers is limited to intertidal and subtidal herbivorous molluscs. The aim of this review is to summarise this diffuse material, especially as it relates to north-eastern New Zealand, and to suggest avenues for future research which might prove profitable in understanding the dynamics of algae–grazer interactions.

Early work in north-eastern New Zealand concentrated on the ecology of intertidal rocky shores. The emphasis then was on the description of patterns of distribution and abundance of the major intertidal groups (Morton & Chapman 1968; Smith 1969). Later studies included more detailed work on distribution patterns, aspects of the demography of grazing invertebrates, relationships between the grazers and their algal food supply, and interactions among co-occurring grazers. This paper looks at each of these topics in turn, drawing mainly on published and unpublished material collected by workers at the Leigh Marine Laboratory, which has

been at the centre of marine ecological work in this part of New Zealand over the last 20 years. Comparative information from elsewhere in New Zealand is included where appropriate.

BROAD-SCALE PATTERNS OF DISTRIBUTION OF MOLLUSCAN GRAZERS

Intertidal reefs

Few quantitative descriptions of species distributions over a gradient extending from the top of the shore to the sublittoral fringe have been published for rocky intertidal shores in any region of New Zealand. This contrasts with the many qualitative accounts in the literature (Oliver 1923; Cranwell & Moore 1938; Knox 1953; Dellow 1955; Batham 1956, 1958; Morton & Miller 1973). For north-eastern New Zealand, the most detailed descriptions are contained in Morton & Chapman (1968) and Morton & Miller (1973). As detailed as these descriptions are, however, they give no indication of actual densities of intertidal organisms, nor of the variability in densities occurring at various spatial scales. Rather, they give an indication of what groups of organisms one might expect to find in certain places. Following on from these purely qualitative early descriptions, two quantitative approaches were used to pursue the search for a general, all encompassing pattern for intertidal grazers.

First, the classical approach of describing the distributions of intertidal organisms on a simple vertical scale (based on Stephenson & Stephenson 1972) was extended for north-eastern New Zealand to include a horizontal component. Based on an earlier model for British shores (Ballantine 1961), the "wave exposure model" sought to describe the distribution of a species in terms of both its vertical height on a shore and its occurrence on shores of different degrees of exposure to wave action (Smith 1969). Although this model is mensurative in its formulation, the measures of numbers or weights are combined or averaged over large areas into abundance categories, and can therefore only provide relative measures of species abundances (see example in Walsby 1977).

Recent surveys of rocky shores on offshore islands in north-eastern New Zealand have used vertical transects with haphazard quadrat sampling at set intervals down the transects (see example in Creese & Ballantine 1986). These surveys not only

provided a quantitative description of the distributions of the major intertidal organisms, but they also provided a partial test of some of the hypotheses generated by the wave exposure model. This analysis has shown that many of the patterns predicted by this model do not occur on the very exposed shores of offshore islands (Creese & Ballantine, 1986). For instance, *Chiton pelliserpentis* (which reaches peak abundances on exposed mainland shores) is virtually absent, and *Nerita atramentosa* (which is generally restricted to the sheltered end of the scale on the mainland) is very abundant over much of the tidal range.

A second approach was adopted by Raffaelli (1979), who quantified the vertical distribution patterns of intertidal grazers and macroalgae on several New Zealand shores, in the vicinity of Leigh (in the north) and Otago (in the south). His analyses were based on diversity indices for the two groups. At both localities, the mean algal diversity per quadrat and the total number of algal species per quadrat increased from high shore to low shore. This pattern was consistent on all shores examined. Superimposed on this, grazer diversity (based on biomass estimates) increased from high to midshore levels, then decreased slightly at low levels on most shores. Raffaelli (1979) recognised, however, that patterns in grazer diversity were unlikely to bear a simple relationship to tidal height, and he developed a subjective "habitat diversity scale" based on scores for rugosity and patchiness of the substratum. He showed that grazer diversity increased as the habitat became more heterogeneous. Because information on individual species is not provided, however, this study did little to increase our understanding of the distribution patterns of intertidal molluscan grazers.

The shortcomings of these two broad-scale approaches highlight the need for more extensive quantitative descriptions of the distribution patterns of intertidal organisms on particular rocky shores. This is especially true when one considers that many shores in northern New Zealand are structurally far more complex than the simple sloping bedrock shores covered by these models. One common situation, for example, is that of a flat or gently sloping platform reef which may provide a wide range of different intertidal microhabitats. This situation will be considered in more detail later.

Subtidal reefs

The broad-scale distribution patterns of subtidal grazing molluscs are poorly documented. A general survey of the benthic biota at seven localities in

northern New Zealand by Choat & Schiel (1982) provided information on the abundance of 4 open rock species (*Cookia sulcata, Cellana stellifera, Trochus viridus, Cantharidus purpureus*). These species were rare at the 3 most exposed localities, but showed similar distribution patterns at the other 4 sites. Highest densities were consistently found at intermediate depths (5–10 m), which also coincided with high densities of the echinoid *Evechinus chloroticus*, and with a bottom type dominated by crustose coralline algae.

Areas of cobbles and boulders subtidally also provide a suitable habitat for molluscan grazers; haliotids, small trochids, and chitons are particularly abundant. The only broad-scale study of the distribution of these grazers was carried out by Mortimer (1985) for 11 species of chitons at three localities in Northland. This analysis showed that certain species had well-defined depth distributions while others did not (see Table 1). This work is being continued (Mortimer & Creese unpubl. data), and augmented by information on juvenile paua (Hooker 1988).

SMALL-SCALE DISTRIBUTION PATTERNS

For any particular intertidal shore, the distribution of molluscan grazers can often be adequately described by line transects sampled from the top of the shore to the sublittoral fringe (Price et al. 1980). Quadrats can be sampled contiguously, or at set distance or tidal height intervals. Because the organisms are invariably patchily distributed and often highly clumped (Underwood 1979; Lubchenco & Gaines 1981; Hawkins & Hartnoll 1983), it is necessary to do several replicate quadrats at each distance interval, or to do many replicate transects on the same shore. Although Raffaelli (1979) did sufficient samples to cover any potential within-shore variability (algae were sampled in 15–25 quadrats and grazers in 4–13 quadrats at each of 4 vertical levels at one locality in the Leigh Marine Reserve and 6 levels at another), the potentially interesting information on the distributions of individual species was lost by subsuming all the data into diversity indices.

Further transect information on the major molluscan grazers at these sites is provided by Watts (1977) and Edwards (1982), and summarised in Table 1. In addition to plotting densities of grazers against height on the shore, Watts (1977) used

pattern analysis on his transect data to describe the degree of clumping of each species of grazer. *Nerita* was always highly clumped at small scales, *Turbo* and *Melagraphia* less so, and *Cellana* and *Chiton* rarely so. The Waterfall/Pumphouse Reef area (see Ayling et al. 1981) represents one of the two main intertidal shore types within the Reserve (and in north-eastern New Zealand generally), and has been used as a study site for three investigations of algae–grazer interactions (Luckens 1974; Watts 1977; Raffaelli 1979). The reef here is narrow in horizontal extent, and is made of a hard, greywacke/conglomerate substratum which is often thrown into high relief by deep pools and channels; tidal height can change abruptly over short horizontal distances.

The second major intertidal shore type in north-eastern New Zealand consists of a soft, mudstone substratum in the form of extensive, flat, low-lying platforms, often formed into low terraces which are separated by shallow, cobble-filled gutters or depressions. In the Marine Reserve, this type of habitat is represented by Echinoderm Reef (see Ayling et al. 1981), which has been the focus for the remaining studies of intertidal algae–grazer interactions at Leigh (Walsby 1977; Edwards 1982; Jeffs 1985; Mortimer 1985; Manson 1986). It is also the site for extensive, long-term investigations (Creese & Ballantine unpubl. data).

Despite the detailed experimental analyses contained in these studies, no quantitative description of the overall pattern of distribution of molluscan grazers has yet been presented for Echinoderm Reef, although a subjective account is given in Morton & Chapman (1968), and data from a single transect with densities grouped into abundance categories are given in Burgett (1982). The reason for this probably lies in the fact that tidal height changes so gradually over the Reef that it is difficult to relate horizontal distance down the shore to tidal height. This difficulty is further compounded by the frequent, but irregular, occurrences of terraces and cobble-filled gutters. This situation is amenable to stratified random sampling as used in recent descriptions of the rocky shore biota in New South Wales, Australia (Underwood 1984). A pilot stratified sampling exercise was carried out on Echinoderm Reef in December 1982. These data give a preliminary picture of the overall situation on Echinoderm Reef as a background to some of the more detailed localised investigations considered in the remainder of this paper.

The major habitat subdivision was into cobble-filled gutters and open bedrock terraces, and these are considered separately below. Several sites of each habitat type were sampled at three, loosely defined shore levels; inner, mid, and outer (see Fig. 1). Further stratification was carried out in the bedrock areas according to 3 topographical features (see Fig. 1), and in the cobble areas according to the size of the rocks. This latter investigation was extended into the sublittoral beyond Echinoderm Reef for 3 depth categories (0–5 m, 5–10 m, 10–15 m).

Bedrock habitat

On these surfaces the five most conspicuous molluscan grazers were the limpet *Cellana radians*, the neritid *Nerita atramentosa*, the trochid *Melagraphia aethiops*, the turbinid *Turbo smaragdus*, and the chiton *Chiton pelliserpentis*, as also reported for Pumphouse Reef (Watts 1977; Edwards 1982). The small littorinid *Littorina unifasciata* was the most abundant in terms of numbers, but was very patchily distributed on the "inner" Reef and occurred in only a couple of the 135

Table 1 Distribution patterns of molluscan grazers in the Leigh Marine Reserve with respect to vertical position or to habitat type. Sites are named in accordance with Ayling et al. (1981).

Author	Site and method	Species	Highest mean density (m⁻²)	Area of greatest concentration	Comments
Watts (1977)	Pumphouse Reef; 2 transects sampled by contiguous quadrats across whole reef	*Nerita atramentosa*	142	High shore	Highly clumped
		Turbo smaragdus	62	Low shore	Partly clumped
		Cellana radians	56	All levels	Randomly dispersed
		Melagraphia aethiops	24	Mid+high levels	Partly clumped
		Chiton pelliserpentis	19	All levels	Randomly dispersed
Edwards (1982)	Pumphouse Reef; 1 transect sampled by contiguous quadrats in mid and low shore areas	*T. smaragdus*	75	Low shore	Adjacent to fucoid fringe
		C. radians	75	Mid shore	
		M. aethiops	45	Low shore	
		C. pelliserpentis	50	All levels	
Jeffs (1985)	Echinoderm Reef; 3 transects sampled by contiguous quadrats across whole shore	*Siphonaria zelandica*	200	Patches of *Ralfsia*	Not found elsewhere on the shore
Mortimer (1985)	Echinoderm Reef, West side of Goat I., Waterfall/Tabletop; 15 random quadrats at 2 sites for each locality	*Amaurochiton glaucus*	23	Mid-low shore	Rare subtidally
		Ischnochiton maorianus	35	All sites+depths	
		Onithochiton neglectus	9	All sites+depths	Often highly clumped
		Rhyssoplax spp.	10	Deep reefs	Rare intertidally
Manson (1986)	Echinoderm Reef; 5 quadrats sampled at 3 sites at 3 shore levels and 2 habitats (open rock and boulder clumps)	*A. glaucus*	52	Mid shore	Almost entirely restricted to boulder areas
Hartley (1978)	Waterfall Reef; 3 habitat types (rockflats, boulders and algal stands) sampled by random quadrats	*Cookia sulcata*	4.9	All habitats	Largest animals on boulders
		Trochus viridus	5.6	Rock flats	Absent from algal stands
		Cantharidus purpureus	14.7	Algal stands	Smallest animals on rock flats
		Cellana stellifera	3.9	Rock flats	Absent from algal stands
Keestra (1987)	Goat I. Bay; 3 habitat types (rock flats, fucoid stands, *Ecklonia* forests) sampled by random quadrats	*C. sulcata*	7.5	Fucoid algae	Large animals on rock flats
		T. viridus	6.3	*Ecklonia* forest	Smallest animals on rock flats
		C. purpureus	8.8	*Ecklonia* forest	Smallest animals on rock flats
		C. stellifera	3.6	Rock flats	Absent amongst algae

quadrats sampled. The only other molluscan grazer encountered was the pulmonate limpet *Siphonaria zelandica*, and this is considered in more detail later. The asteroid *Patiriella regularis* was also occasionally sampled in the moist, coralline turf habitat. The distribution and abundance of this species is considered in more detail by Burgett (1982). Some molluscan grazers, particularly members of the Opisthobranchia, were not encountered during the 1982 survey but are known to be seasonally very abundant (e.g., Willan 1979).

The distribution patterns of the 5 widespread grazers are shown in Fig. 1. *Nerita* and *Turbo* both show a relationship with position on the shore, *Nerita* being restricted to upper levels, and *Turbo* being more abundant closer to the sublittoral fringe; both patterns are consistent with those reported for Pumphouse Reef (Watts 1977; Edwards 1982). No obvious and consistent relationships between densities and topographical features were apparent (despite initial, subjective assessments to the contrary), although there is the suggestion that *Melagraphia* and *Turbo* are more common in "ledge/cobble" areas low on the shore (Fig. 1). Further sampling is needed to confirm this. Where *Turbo* does occur closer to the beach, it is apparently restricted to the moist coralline flat areas. The vertical distribution pattern of *Turbo* is known to be related to the size of the animals. Walsby (1977) sampled 3 areas of the Reef over 3.5 years, and showed that animals were abundant on "inner" coralline flats, but were rarely greater than 8 mm long. Many of these small snails may have been missed in the 1982 pilot survey, as subsequent sampling in this habitat has revealed consistently high densities of juvenile *Turbo*. Larger animals (up to 20 mm) were found at "mid" levels on Echinoderm Reef, and the largest animals (up to 30 mm) at the sublittoral fringe. Together with *Cellana*, *Turbo* is the most common grazer at these low levels (Fig. 1), and the effects of their grazing activities on algal distributions have been studied by Edwards (1982; see Interactions with algae, below).

Apart from a few isolated individuals, *Siphonaria* was sampled in any significant numbers at only one place during the 1982 survey. This was at one of the midshore sites in regions of raised, dry rock at the edge of a terrace (Stratum B in Fig. 1). Here the mean density from 5 quadrats was 64 per 0.25 m². These areas are frequently characterised by large patches of the encrusting brown alga *Ralfsia verrucosa* (Morton & Chapman 1968; Edwards 1982; Jeffs 1985). Jeffs (1985) sampled several

patches of *Ralfsia* and adjacent areas of bare rock, and showed that over 99% of all *Siphonaria* were associated with this alga, and all but a few *Ralfsia* patches contained *Siphonaria*. Densities in these patches often exceeded 5000 m⁻², and there is obviously a very close interrelationship between these two species which is discussed further below.

Boulder habitat

Forty randomly chosen cobbles of each of 5 size classes were sampled at each of the 3 shore levels on Echinoderm Reef as part of the 1982 survey. The results, and the corresponding data for the 3 subtidal depth categories at Goat Island Bay, are presented in Table 2. In addition to the 5 molluscan grazers commonly found on open rock surfaces (see above), a further 5 species of grazers were commonly encountered on intertidal boulders. Most numerous amongst these was the limpet *Notoacmea daedala* which appeared to be restricted to the undersides of the smaller categories of cobbles, and the chitons *Ischnochiton maorianus* and *Amaurochiton glaucus* which were abundant on all sizes of cobbles (Table 2). In some areas of Echinoderm Reef, the total density of chitons exceeded 400 m⁻² (Mortimer 1985; Creese unpubl. data). With the exception of *Chiton pelliserpentis*, all these chitons were recorded underneath the boulders; the survey was undertaken during daytime low tides. Following some preliminary findings by Creese (1983), Manson (1986) subsequently demonstrated, however, that *Amaurochiton* makes extensive forays on to the tops of cobbles and on to surrounding bedrock surfaces during night-time low tides.

It is interesting to note from this pilot survey that there is an almost complete change in the species composition between intertidal and subtidal areas (compare two parts of Table 2). For instance, the common intertidal limpet *Cellana radians* is replaced subtidally by *C. stellifera*. This is in contrast to the situation in south-eastern Australia where two common subtidal limpets are also abundant intertidally (Fletcher & Creese 1985). Similarly, the turbinid *Turbo smaragdus* is primarily an intertidal species whereas *Cookia sulcata* is solely subtidal, and the place of the intertidal trochid *Melagraphia aethiops* is taken by 2 other trochid species. This pattern is also evident for open bedrock surfaces, although no direct quantitative comparison has yet been made (further quantitative analyses of the distribution patterns of subtidal molluscan grazers are given by Hartley (1978) and Keestra (1987); see Table 1). Although intertidal
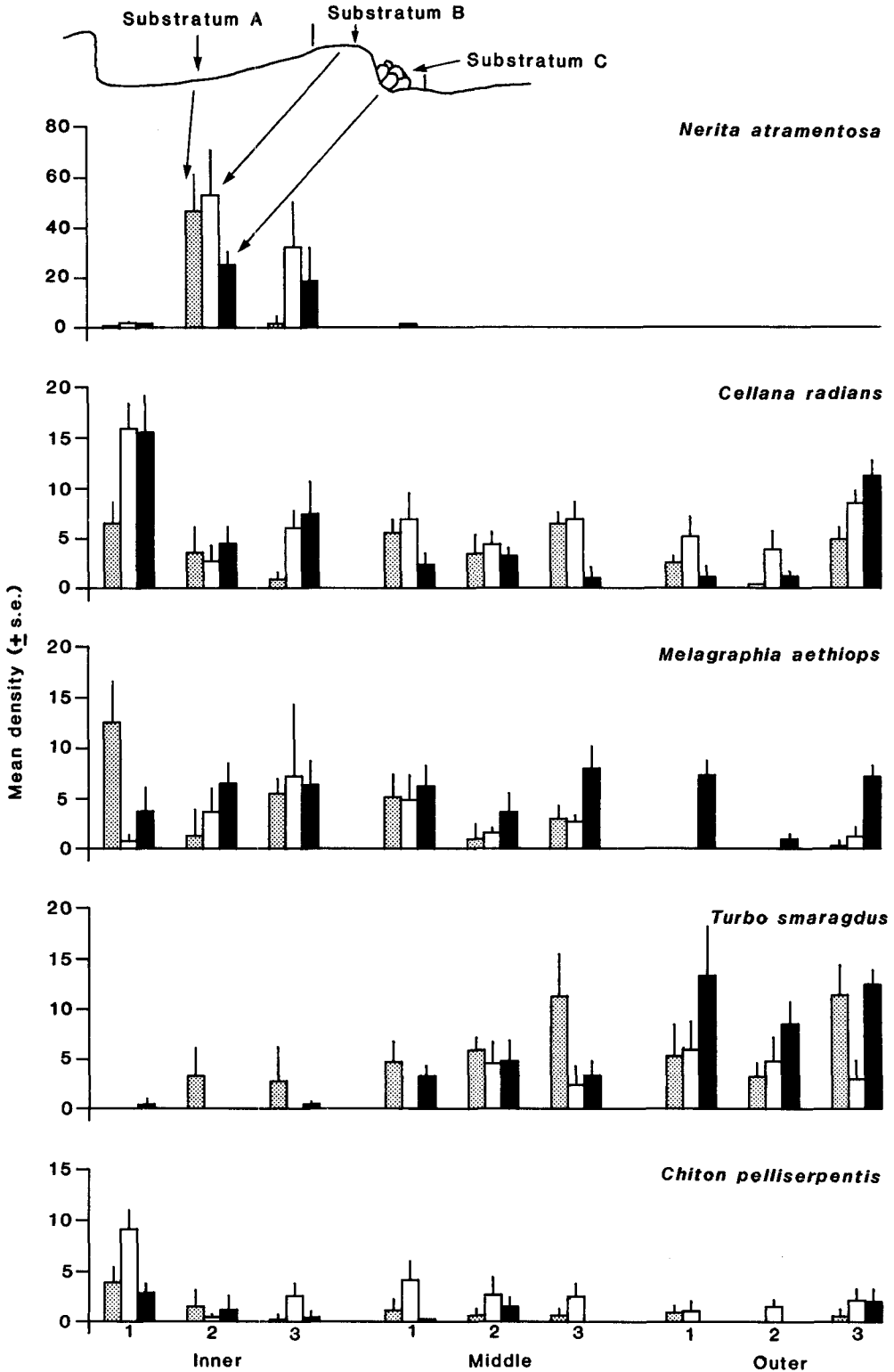
Fig. 1 (*Opposite page*) Mean densities (± s.e.) per 0.25 m² of common molluscan grazers in three habitat types on Echinoderm Reef. Three sites (labelled 1, 2, 3) were sampled at each of three levels on the shore using 5 haphazardly-thrown quadrats. The "inner" level was within 15 m of the beach which forms the landward boundary to the reef, the "outer" level was within 15 m of the fucoid fringe, and the "mid" level was approximately equidistant from, and in between, the other two levels. Substratum A is a habitat consisting of flat, low-lying rock often containing large patches of turfing or crustose coralline algae; Substratum B consists of drier, raised rock at the edge of a terrace, extending back 1.5 m and typically supporting patches of the barnacle *Chamaesipho columna*; Substratum C is the habitat immediately over the edge of a terrace and extending out for 1.0 m where small clumps of cobbles often accumulate.

grazers are occasionally encountered subtidally and vice versa, the main exception to this generalisation is found among the chitons, 2 of which in particular (*I. maorianus* and *O. neglectus*) are commonly found in both environments. Both these species appear to be permanently restricted to the undersides of boulders (Mortimer 1985; Creese unpubl. data), and hence may be unaffected by changes that occur in the transition between habitats. A profitable area of future research would be to examine, by means of reciprocal transplant experiments, possible hypotheses relating to the abrupt replacements of closely related species at the sublittoral fringe.

DEMOGRAPHY

Growth

Temporal changes in age or size structures, and growth rates of populations of only a few molluscan grazers at Leigh have been investigated. Most studies have been of a short-term nature (1–1.5 years), and have relied on polymodal size frequency distributions to provide information on changes in total densities and in the size structure of the population (Hartley 1978; Edwards 1982; Manson 1986; see Table 3). Longer-term information is available only for intertidal *T. smaragdus* (Walsby 1977). If distinct age cohorts can be reliably distinguished from the size–frequency distributions, such information can also be used to estimate the growth rates of given cohorts, and to subsequently build up a composite growth curve for the whole population (Underwood 1975; Creese 1981). Such age cohorts (representing discrete year

classes) can be distinguished for *T. smaragdus*, and Walsby (1977) showed that growth was linear over 4 years at a rate of c. 6 mm per year (a similar rate was obtained by Edwards 1982).

Walsby also showed that animals moved successively from mid-shore areas to low-shore areas (at an age of about 1.5 to 2 years) and finally into the sublittoral fringe (at an age of about 3 years), apparently as a result of the passive effects of wave action (which were related to the size of the snails) rather than by active migration. *Cellana radians* also had distinct cohorts in its size–frequency distributions (Edwards 1982), but these were apparently not year classes as several discrete cohorts of recruits could be identified within a one-year period. This was subsequently confirmed by Creese & Ballantine (1983), who showed that *C. radians* had an extended breeding season with multiple spawnings. This resulted in irregular bursts of recruitment at several times during the year. Because *C. radians* is short-lived (of the order of 1.5–2 years), however, size–frequency analysis can still be effectively used to investigate population growth rates for this species (Creese unpubl. data).

Hartley's (1978) analysis of growth in 4 subtidal gastropods showed that *Cellana stellifera* and the 2 trochid species also had initial linear growth which levelled off after the first year in a form typical of a von Bertalanffy growth curve, but that the turbinid *Cookia sulcata* had a sigmoidal growth curve. These assessments of growth were enhanced by information on the rates of growth of individually tagged animals, which gave an independent confirmation of the estimates obtained for the populations as a whole. This approach is currently being used to provide demographic information for intertidal *C. radians* and *N. atramentosa* (Creese unpubl.data) and for subtidal *Haliotis iris* (Hooker unpubl. data).

A different approach was adopted by Jeffs (1985) for investigating the growth of *S. zelandica* because size–frequency analysis did not produce discrete cohorts and because most of the limpets were smaller than 10 mm and could not be easily tagged *in situ*. Instead, he made repeated measures of the sizes of small groups of similar-sized limpets on isolated patches of *Ralfsia*. Because *Siphonaria* was known to return to specific home scars (Beckett 1969), it was reasonable to assume that the same individuals were being remeasured at each sampling time. Jeffs (1985) found that growth rates could be very high (of the order of 1.5 mm per month), but that they were also extremely variable and dependent on

Table 2 Abundances (mean numbers per rock) of molluscan grazers found on boulders in the Marine Reserve in December 1982 at intertidal sites (Echinoderm Reef) and subtidal sites (Goat Island Bay). Blank spaces indicate total absence of a grazer; * indicates that the grazer was present but at an abundance of less than 0.1 per rock. Size categories of rocks are as follows: A, 8 cm diameter; B, 8–15 cm diameter; C, 15–25 cm diameter; D, 25–40 cm diameter; E, >40 cm diameter.

Echinoderm Reef		Inner Reef					Middle Reef					Outer Reef				
		A	B	C	D	E	A	B	C	D	E	A	B	C	D	E
Chitons:	Chiton pelliserpentis		*	0.2	0.4	1.8		*	0.9	0.4	2.0			*		*
	Amaurochiton glaucus	0.1	0.7	1.4	1.5	1.3	*	0.7	1.6	3.0	3.2	0.1	0.7	1.7	1.4	1.0
	Ischnochiton maorianus	*	*	0.3	1.9	1.2	*	0.8	1.0	4.2	3.4	0.2	0.6	0.7	0.9	2.0
	Onithochiton neglectus												*	0.2	0.6	*
	Other (4 species)		*	*	0.1	*	*	*	*	*	*	*	*	0.2	0.1	0.1
Limpets:	Cellana radians	0.1	*	2.1	4.2	5.6		0.2	1.9	2.5	4.8	0.1	0.4	0.9	1.7	1.9
	Notoacmea daedala	1.5	5.3	11.7	1.4	0.9	1.5	4.5	3.2	1.4	1.5	0.3	0.4			
	Siphonaria zelandica	0.1	0.2	*	*	*		*	0.2	0.6			0.8	1.9	8.2	19.1
Snails:	Turbo smaragdus	*	0.1	*		*			*	*	0.4	0.4	1.2	1.8	2.5	4.5
	Nerita atramentosa	1.9	3.6	15.9	8.4	37.6	2.0	7.1	9.2	9.7	20.7					
	Melagraphia aethiops	0.1	0.4	*	3.8	1.5	0.3	0.7	1.9	1.9	4.6	*	0.3	1.5	1.9	1.9

Goat Island Bay		0–5 m subtidal					5–10 m subtidal					10–15 m subtidal				
		A	B	C	D	E	A	B	C	D	E	A	B	C	D	E
Chitons:	I. maorianus	0.9	3.0	2.5	5.7	5.2	0.2	1.0	4.4	1.6	2.0	*	0.2	1.0	0.7	1.2
	O. neglectus			*	0.2	0.3	0.1	0.1		0.9	2.0		*	*	0.1	0.3
	Rhyssoplax spp	*		*	0.3		*	*	0.1	0.2	0.7	*	0.3	0.7	1.0	0.9
	Others (4 species)	*	*	*	0.2	0.8	*	*	0.1	0.4	0.7		0.2	*	0.3	0.3
Limpet:	Cellana stellifera		*	*	0.2	0.6	0.1	*	1.0	1.5	3.4		0.1	0.7	2.2	3.6
Snails:	T. smaragdus	*	0.3	0.4	0.2	1.2										
	Cookia sulcata		*		*	0.4			0.4	0.8	1.5			*	*	*
	Trochus viridis				*	0.1	*		0.4	0.4	3.2	*	0.3	0.6	1.4	2.9
	Cantharidus purpureus								0.2	0.4	0.7	*	*	*	0.2	0.4
	Haliotis iris				*				0.5	0.4	0.9		*	0.2	0.7	0.8

Table 3 Demographic information on molluscan grazers in the Leigh Marine Reserve.

Species	Maximum size (mm)	Estimated longevity (year)	Size at maturity (mm)	Reproductive season	Reference
Amaurochiton glaucus	40	4–5	16	Jan–May	Manson 1986
Onithochiton neglectus	45	5–6	17	Oct–Jun	Mortimer 1985 Creese 1986
Cellana radians	42	2	20	year round	Creese & Ballantine 1983 Edwards 1982
Turbo smaragdus	40	5	15	Feb–Apr	Grange 1974 Walsby 1977 Edwards 1982
Cookia sulcata	80	8–10	20	Dec–Feb	Hartley 1978 Keestra 1987
Trochus viridis	23	3	15	Dec–Feb	Hartley 1978 Keestra 1987
Cantharidus purpureus	25	3	15	Nov–May Dec–Feb	Hartley 1978 Keestra 1987
Cellana stellifera	45	4–5	20	?	Hartley 1978

density. It was not meaningful, therefore, to consider a population growth model for *Siphonaria*.

Indeed, it is likely that growth in most molluscan grazers is highly variable, as many experimental studies have shown that growth can be greatly affected by factors such as density of conspecifics, densities of other co-occurring invertebrates, seasonal supply of food, or position on the shore (Underwood 1979; Branch 1981). For this reason it is often instructive to examine populations in more than one area or habitat, to use individually tagged animals to supplement growth information from population size distributions, and if possible to use an assessment of age that is independent of size. Unlike molluscs from higher latitudes that often have obvious annual growth marks on their shells (e.g., Picken 1980), temperate species rarely have easily identifiable growth rings. Recent uses of grinding techniques (similar to those used on fish otoliths; see review by Kingsford 1988), however, have shown the existence of microgrowth bands in the shell plates of chitons (Jones & Crisp 1985) and in the operculi of trochid and turbinid gastropods (Ekartene & Crisp 1982). Further work is needed to confirm whether these bands are laid down on a daily, tidal, or lunar basis, but once adequately validated, this technique might prove a useful tool in studying patterns of growth in some New Zealand molluscan grazers, especially among the younger members of a population.

Settlement and recruitment

The initial appearance of a new cohort in a size–frequency distribution indicates the arrival of new recruits into a population. Unfortunately, the newly-settled juveniles of most molluscs are cryptic, and rarely appear in population samples until they are 4–5 mm long, at which stage they may be several months old (Underwood 1979). The reproductive cycles of most New Zealand molluscan grazers are also very poorly known, which makes it even more difficult to predict times of settlement, let alone intensity of settlement. What information there is suggests that most species in north-eastern New Zealand breed during summer or autumn (Grange 1974, 1976; see also Table 3), with some species having extended breeding seasons and multiple spawnings (e.g., *Cellana radians*: Creese & Ballantine 1983; *Onithochiton neglectus*: Creese 1986). In these 2 particular species it is possible to predict spawning events based on a knowledge of their reproductive status and the prevailing

conditions (strong wave action in the case of *Cellana*, and the lunar cycle in the case of *Onithochiton*). Despite this detailed knowledge, attempts to obtain newly settled juveniles in the field have so far met with limited success, and no information is currently available on the microhabitats chosen by settling larvae, or the processes affecting newly-settled individuals.

INTERACTIONS WITH ALGAE

Apart from the broad-scale, usually qualitative, descriptions of distribution patterns contained in the general accounts of rocky shore ecology mentioned earlier, very little information is available on the ecology of marine algae in north-eastern New Zealand. The work of Schiel (1980) on the small-scale distribution patterns and demography of subtidal kelps is a notable exception. This material, along with other existing information on subtidal algae in the north-eastern region is reviewed elsewhere (Schiel 1988).

Rocky intertidal shores in north-eastern New Zealand usually support a rich flora of benthic algae (Morton & Miller 1973). The species of macroalgae occurring in the Hauraki Gulf, together with notes on their distribution patterns, have been thoroughly described by Dellow (1955); those occurring on remoter offshore islands are covered in Cranwell & Moore (1938). Microalgae have received only minimal attention, although a list of over 50 species of littoral diatoms found at Leigh is given by Levis (1975), along with some descriptions of their vertical and seasonal abundance patterns. Many intertidal grazers are known or suspected to feed primarily on diatoms, cyanobacteria (blue-green algae) and other microalgae (see review by Underwood 1979), but the nature of any interactions between grazers and microalgae remains largely unknown, although some cursory examinations have been made by Edwards (1982), Jeffs (1985), and Manson (1986). These largely speculative accounts are considered further below.

Macroalgal distributions

It is beyond the scope of this paper to review comprehensively the distribution patterns of inter-tidal algae. However, a few general features need to be mentioned as background for a consideration of algae–grazer interactions. The most conspicuous feature of intertidal algal distributions in north-

eastern New Zealand is the band of algae that dominates the lower levels on the shore. This band is usually characterised by fucoid algae (notably *Carpophyllum* spp.), and forms the upper edge of the distinctive fucoid zone which is characteristic of the immediate subtidal in northern New Zealand (Choat & Schiel 1982). Consequently, this region is often referred to as the "sublittoral fringe" (Walsby 1977) or the "fucoid fringe" (Edwards 1982). As noted previously, grazers are usually absent from this band, although localised aggregations of sea urchins may occur in areas with gutters, channels, or ledges (Kerrigan 1987).

Mid-intertidal areas contain a mosaic of encrusting, turfing, and foliose species, with many of the latter group being ephemeral species. Low-lying platforms such as Echinoderm Reef are often dominated by erect coralline algae which form a tight turf 1-2 cm thick. This mat forms a suitable substratum for many microalgae and filamentous or ephemeral macroalgae. *Ralfsia verrucosa* is also abundant, especially in areas of raised dry rock (see Small-scale distributions patterns, above). The fucoid alga *Hormosira banksii* is also locally abundant at mid-tidal levels, especially on shores that are relatively sheltered from strong wave action. These three algal species have formed the basis of almost all the experimental studies on intertidal algae–grazer interactions that are described in the following sections.

High-shore areas usually contain few macroalgae (as noted by the diversity indices used by Raffaelli (1979) and described above). Most species here are encrusting, filamentous, or form a wiry turf often associated with patches of barnacles (notably *Gelidium caulacantheum*), although some foliose forms may be seasonally abundant (especially *Porphyra columbina*). The molluscan grazers that inhabit these regions can be extremely numerous but are often small (e.g., *Littorina unifasciata, Risselopsis varia*, and *Notacmea* spp.). Larger species do occur here in lower numbers (notably *Nerita atramentosa, Cellana ornata*, and *Chiton pelliserpentis*), but their feeding habits on these regions of the shore have not been investigated at Leigh. The effects of grazing by both small and large species of molluscs on both macro- and microalgae at high-shore levels could prove a profitable area for further research, as studies on similar shores in Australia have indicated that grazing at these levels can have significant effects on algal ecology and vice versa (e.g., Creese 1980; Underwood 1984; Jernakoff 1985a, 1985b).

Diet and feeding behaviour of grazers

Most intertidal grazing gastropods are apparently generalist herbivores (Underwood 1979), and are not associated with any particular species of alga. The same is probably true for subtidal grazing gastropods (Choat pers. comm.) and for herbivorous chitons (Boyle 1977). Examination of the diets of these grazers typically reveals a mixture of several different species or groups of algae, often with a large amount of "unidentifiable" or "detrital" material (Zeldis & Boyden 1979; Steneck & Watling 1982). The same species of grazer may also have quite different gut contents depending on the locality or season of collection, on the size of the animals collected, and on the methods used to assess diets. It is therefore difficult to construct a general feeding model for molluscan grazers, and to address questions on dietary preferences.

One approach is to place both the grazers and the algal food into so-called "functional groups". The model developed by Steneck & Watling (1982) predicts that grazers with certain types of radulae are physically constrained to feed on only certain kinds of algae. Their analysis of 140 species contains 6 New Zealand molluscs, but their information on these species is very meagre, relying mainly on the anecdotal material given by Luckens (1974) for grazers at Leigh. A major problem with the model of Steneck & Watling (1982) is that they had already defined their molluscan groups before analysing their diets. In confronting this problem, Raffaelli (1985) used an ordination technique to analyse the gut contents of 11 New Zealand species of molluscan grazers which occurred at Leigh and Otago. His analysis showed that although some species fitted into the categories suggested by Steneck & Watling (e.g., *Nerita* had a diet similar to that proposed for typical rhipidoglossans), other species did not. (*Turbo*, another rhipidoglossan grazer, had a diet that was more similar to that of 4 species of chitons than of *Nerita*.) Raffaelli's study emphasises that, while it may be possible to identify patterns in the diets of grazers, such patterns are not necessarily related to radular morphology, but may simply be a function of the availability of algae to different molluscs because of such factors as their position on the shore (see also Hawkins & Hartnoll 1983).

Further quantitative information on the gut contents of molluscan grazers at Leigh is available for only 3 species: *Turbo, Siphonaria*, and *Amaurochiton*. Macroalgal material was a large component of the diets of all 3 species; foliose reds

and fucoids in the case of *Turbo* (Edwards 1982), coralline algae in the case of *Amaurochiton* (Manson 1986), and *Ralfsia* in the guts of *Siphonaria* (Jeffs 1985). Microalgal material was quantified only in the latter case, and the dietary significance of bacteria, diatoms, cyanobacteria, and macroalgal spores awaits further critical study. Much of this material may pass through the gut undigested, as demonstrated by Santelices & Correa (1985) and suggested for *Amaurochiton* by Manson (1986), or it may form the major part of the diet.

Most molluscan grazers may be trophic generalists, but there are several species that are known to be closely associated with and/or to feed exclusively on specific algae. Within the limpets, for example, such associations have been reported for large kelps (Branch 1975; Black 1976;) and encrusting corallines (Steneck 1982). At Leigh, only the association involving *Siphonaria* on Echinoderm Reef has received much attention, with the encrusting brown alga *Ralfsia verrucosa* providing the substratum for the snails and also forming their largest dietary component (Jeffs 1985). Most, if not all, of the fragments of *Ralfsia* occurred intact in the faeces, however, and were demonstrated in culture experiments to remain viable. Microalgal material on the other hand decreased in abundance between the foregut and the faeces, and many diatom frustules had ruptured in the faecal material. Jeffs (1985) therefore hypothesised that, despite the low proportional volume of microalgal material ingested (1%), this algal category probably provided the principal nutritional requirements. Indeed, rather than destroying the macroalga during the process of eating it, the grazer may actually enhance dispersal and the establishment of new plants as has recently been suggested for *Rhodochorton purpureum* by Breeman & Hoeksema (1987).

The situation for another New Zealand species, *Zeacumantis subcarinatus*, parallels that described above for *Siphonaria* and *Ralfsia*. This gastropod occurs predominantly on dense beds of *Ulva lactuca* in shallow pools, and has been shown to remove the outer cell layers from this macroalga (McClatchie 1979). Gut samples also contained large numbers of epiphytic microalgae, however, and again it was argued that these probably supplied most of the nutrition to the gastropod. Such examples suggest that the algae involved in close algae–grazer associations are not necessarily an important food source, even when ingested in large quantities, and care should therefore be taken before construing

such associations as "co-evolved mutualisms" (Steneck 1982).

The effects of grazers on algae

Many studies worldwide have demonstrated that molluscan grazers can have a profound influence on the distribution and abundance of algae (reviewed in Hawkins & Hartnoll 1983). The simplest demonstration of this comes when grazers are removed from large areas of substratum, or where artificial cages or fences are used to exclude grazers from smaller areas. Such procedures usually result in the growth of filamentous or foliose macroalgae in areas where they would normally be absent, suggesting that the feeding activities of the grazers are sufficient to prevent the establishment of these macroalgae (e.g., Burrows & Lodge 1950; May et al. 1970; Jernakoff 1985a, 1985b). Encrusting macroalgae are usually less affected, and many are grazer-resistant (e.g., *Hildenbrandia prototypus* (Underwood 1980), and *Gigartina papillata* (Slocum 1980)), while others may actually require grazing in order to survive (see Steneck 1982). Assemblages of microalgae may also be strongly influenced by the activities of grazers (see Castenholz 1961; Nicotri 1977). Intertidal and subtidal experiments done at Leigh are discussed below.

Large-scale removals of all gastropods on a section of Pumphouse Reef, supplemented by the total exclusion of all grazers from small areas of cleared rock, resulted in a rapid increase in ephemeral green algae and cyanobacteria, and a slower increase in the cover of crustose coralline algae (Watts 1977). Control areas did not show this pattern. Watts (1977) then sought to examine the effects of individual species of grazers by selectively excluding them from small areas of rock using a variety of artificial structures. On the basis of these experiments he showed that *Nerita* had no visible effect on macroalgal abundances, that *Cellana* removed much of the pre-existing crustose coralline and reduced the amount of ephemeral green algae and cyanobacteria that developed, and that *Turbo* completely removed *Gelidium*, *Hormosira*, and all other foliose algae but had little effect on established crusts. It is difficult to determine conclusively what differential effects these 3 grazers had because the experiments were carried out at different levels on the shore (depending on where the particular grazer was most abundant), and the precise grazing regime in each series was unknown because grazers other than the

target species theoretically had continuous access to the experimental treatments.

An improved experimental design was used by Edwards (1982) for 2 of the same species used by Watts (1977): *Cellana radians* and *Turbo smaragdus*. These 2 species were separately enclosed at fixed densities in artificial cages, and the rock surface was scraped clear of all algae before the start of the experiments. The absence of particular algae from the experimental cages compared to the controls could therefore be directly attributed to the action of the target grazer. The experiments were done at mid-tidal levels and on the low shore adjacent to the fucoid fringe. These experiments showed conclusively that encrusting algae, particularly *Ralfsia verrucosa*, developed at both levels on the shore in the presence of *Turbo* but not in the presence of *Cellana*, and that foliose red algae developed at low shore levels in cages containing *Cellana* but not in those containing *Turbo*. The combined effect of the 2 grazers was to prevent the establishment of stands of macroalgae, even at low shore levels adjacent to the fucoid zone. This evidence was used to support the hypothesis that molluscan grazers determined the upper limit of the sublittoral algal fringe, because these algae extended shoreward in the absence of grazers. It should be noted that these experiments were only carried out at one time of the year. Experiments by Jernakoff (1985b) in south-eastern Australia suggest that different results may be obtained at different times of the year.

Another New Zealand study which focused on the influence of grazers on algal distributions also showed that limpets determined the upper limit to the distribution of low-shore algae. Hay (1979) removed limpets from a shore in southern New Zealand and found that spores and sporelings of the kelp *Durvillaea antarctica* became established at higher levels on the shore. Although these died in summer, confirming that desiccation is an important factor limiting the vertical distribution of some algae, several other species of algae survived the physical environment at a level higher than that before the experiment. The studies of Hay (1979) and Edwards (1982) support, for the New Zealand situation, the findings from the extensive intertidal experiments done on shores in New South Wales, Australia, which clearly show that the shoreward extent of the characteristic sublittoral algal fringe is set by the activities of molluscan grazers (Underwood 1980; Underwood & Jernakoff 1981).

Edwards' (1982) contention that limpets and turbinids have fundamentally different effects on algal assemblages is in agreement with the predictions made by Raffaelli (1979) based on information on gut contents from randomly collected individuals, and is further supported by the findings from 2 subtidal studies done at Leigh. Both Hartley (1978) and Schiel (1980) used inclusion experiments to show that the limpet *Cellana stellifera* could neither remove nor prevent the establishment of foliose red algae, whereas the turbinid *Cookia sulcata* had a pronounced effect on these algae. *Trochus viridus*, a trochid, apparently grazed in a similar way to *Cellana* and was unable to influence the abundance of algae. Schiel (1980) was further able to demonstrate the differential effects of the 3 subtidal grazers by settling known densities of fucoid spores onto fibrolite plates and then introducing the plates into cages containing the various grazers either on their own or in combination. Feeding by *Cookia* always resulted in a significant and substantial decrease in the number of fucoid spores and in the percentage cover of ephemeral algae. The ability of *Cookia* to keep areas of substratum free from foliose macroalgae probably allows smaller grazers such as *Cellana* to live in these subtidal areas (Choat & Andrew 1986).

Edwards (1982) also used fucoid spores settled onto artificial plates (in this case the alga was *Hormosira banksii*) to substantiate her earlier finding of differential effects of grazing. The experiments clearly showed that *Turbo* removed the spores but that *Cellana* did not. Edwards suggested that this result was not due merely to the fact that *Turbo* consumed more algae or grazed the area more efficiently than *Cellana* and thus had a "greater effect", but that selective grazing was occurring at the level of the microscopic spores and sporelings. Either *Turbo* was deliberately selecting the spores, or else *Cellana* was deliberately avoiding them. There was little evidence to support this hypothesis, although in a North American study Duggins & Dethier (1985) also suggest that a common chiton may be able to selectively graze the spores of a particular alga. If it is subsequently shown that such selection does occur, the implication is that grazers could have an even more fundamental role in determining the patterns of distribution and abundance of algae than is currently supposed.

The consistently strong effect of *Cookia* on subtidal algae demonstrated by Hartley (1978) and Schiel (1980) led to the hypothesis that its presence may be necessary to support members of the other molluscan grazers, which might otherwise be displaced from their habitat by the rapidly growing

algae. This model was subsequently confirmed experimentally by Choat & Andrew (1986). The subtidal echinoid *Evechinus* is also known to feed on fucoids and foliose red algae and can consequently keep areas of the substratum clear (Ayling 1981), and may act in a similar way to *Cookia* by providing a suitable habitat for the smaller, less voracious gastropods (Hartley 1978; Schiel 1980; Choat & Andrew 1986). Such mutual relationships among co-occurring grazers can thus be the direct result of the different effects that different grazers have on the same suite of algae.

Luckens (1974), Watts (1977), and Edwards (1982) noted that *Turbo* had little effect on encrusting algae such as *Ralfsia*, but that *Cellana* could both remove existing crusts and prevent their re-establishment. Edwards (1982) also noted that in areas where *Turbo* grazed in the absence of any *Cellana*, the substratum was often covered by a homogeneous mat of *Ralfsia*. She suggested that *Turbo* may be enhancing the survival of the crust, perhaps by removing epiphytic algae which might otherwise smother the *Ralfsia*. This idea was investigated by Jeffs (1985) using the pulmonate limpet *Siphonaria zelandica* which is closely associated with *Ralfsia* on Echinoderm Reef (see above). In a series of removal experiments, Jeffs demonstrated that, in the absence of limpets, *Ralfsia* rapidly became overgrown by a mat of cyanobacteria and diatoms, and that this was followed soon afterwards by the death and sloughing off of the crusts. Although *Siphonaria* ingested large amounts of the alga (as noted earlier), its grazing activities were essential to the continued survival of *Ralfsia*. Grazing by *Turbo* may act in the same way, and hence provide another example of a grazer helping to ensure that a suitable substratum (*Ralfsia*) is locally available for another species of molluscan grazer (*Siphonaria*). Similarly, chitons (*Chiton pelliserpentis*) may, by removing turfing coralline algae, provide patches of substratum on a local scale suitable for colonisation by limpets (Creese unpubl. data).

INTERACTIONS AMONG GRAZING MOLLUSCS

Indirect interactions between co-occurring grazers may be mediated by the different feeding effects of the species involved as noted above. For example, Jeffs (1985) showed that a crust of *Ralfsia* soon developed on artificial plates raised above the substratum, whereas those placed flush with the substratum allowed access by another limpet, *Cellana radians*, and did not develop a crust. The resulting hypothesis that *Cellana* would have a detrimental effect on *Siphonaria* by preventing the establishment of its preferred habitat was subsequently demonstrated by further experiments (Jeffs 1985). As discussed above, examples of the converse effect (grazers ameliorating the conditions for other species) also exist (e.g., Choat & Andrew 1986).

Even if individual species of grazer affect the algal resource in slightly different ways, the possibility always exists that the total food resource may be inadequate to support large numbers of grazers. Such large numbers may often occur as the result of the variable levels of recruitment that are a common feature of the life histories of many molluscan species, especially those which have planktonic dispersal larvae. In these situations, competition for the limited food supply may occur. Because most grazers apparently feed indiscriminately (despite the hypotheses of selective feeding advanced by Edwards (1982) and Duggins & Dethier (1985)), and because information on their precise diets is generally incomplete, it has been very difficult to directly demonstrate that food is a limiting resource for molluscan grazers. This difficulty is compounded by the fact that the microalgal food of intertidal grazers may be replaced on a twice daily basis as the tide returns and inundates the shore. Generally, only indirect or circumstantial evidence is available to support the hypothesis that food is a limiting resource for molluscan grazers, and two such lines of evidence are given in Creese & Underwood (1982). These were that increased mortality of experimental limpets was associated with decreased growth and tissue weights, and that experimental removals of even a few animals from natural areas led to an immediate and massive growth of foliose algae. Only in a few studies of competition among intertidal gastropods in New South Wales has the food resource been quantified by using the relative concentration of chlorophyll pigments on the rock surface as a measure of food availability (Creese 1980; Underwood 1984, 1986).

Although there have been many suggested examples of competition between molluscan grazers, conclusive experimental evidence is available in only a few cases (see reviews by Underwood 1979, 1986). A convenient design for such experiments consists of using some treatments

containing a series of increasing densities of single species on their own while other treatments have combinations of the species at various densities. Factorial analyses of variance can then be used to investigate the effects of both inter- and intra-specific competition on such variables as proportional mortality, weight loss, or growth rate (Underwood 1978; Creese & Underwood 1982; Fletcher & Creese 1985).

Multifactorial experiments of the type outlined above have been used at Leigh to investigate competition amongst both intertidal and subtidal gastropods. Hartley (1978) examined intraspecific and interspecific competition among 3 subtidal gastropods on Waterfall Reef. Interspecific effects were investigated by caging 10 animals of each of *Cellana stellifera, Trochus viridus,* and *Cookia sulcata* on their own, and then comparing mortality rates and changes in weights over a 7-month interval with treatments containing combinations of two different species (5 of each per cage). No one species appeared to be competitively dominant over the others at the densities used, and, in fact, *Trochus* and *Cellana* may benefit from the presence of *Cookia* because of its ability to remove foliose algae. Intraspecific effects were examined by comparing the single species treatments with uncaged populations which were at a much lower density. Although weight loss was up to 25% higher in the caged animals, no increase in mortality occurred. In fact, mortality in both *Cookia* and *Trochus* was significantly lower than in the natural population. Hartley concluded that intraspecific competition was not of major importance to these grazers. This conclusion is not valid, however, as the main comparison was between a natural (uncaged) population and an artificial (caged) one, and there could have been many other reasons apart from competition for the observed differences. A better design would have been to include two or more intraspecific densities in the caged treatments. Such a design was used by Choat & Andrew (1986) to investigate interactions among *Cellana, Cookia,* and *Evechinus.* They were able to find no evidence of density-related mortality in any of the species, although *Cookia* and *Evechinus* both showed reduced weight at increased intraspecific densities. They also conclusively confirmed that *Cellana* did better in terms of both survival and weight gain in treatments containing *Cookia.*

Edwards (1982) used a similar design to investigate the competitive interactions between intertidal *Cellana radians* and *Turbo smaragdus* on Echinoderm Reef. Control densities of 5 animals per cage were set up; intraspecific comparisons were made with treatments containing an additional 5 or 15 animals of the same species per cage, interspecific ones with treatments containing 5 or 15 animals of the other species. The proportional mortality of *Turbo* was not affected at any density by either members of its own species or by *Cellana.* On the other hand, *Cellana* was adversely affected when more *Cellana* were added, but not when *Turbo* were added. The strong intraspecific response by *C. radians* to increased densities has subsequently been confirmed by Creese (unpubl. data), and is also a prominent feature of the population biology of *C. tramoserica* in south-eastern Australia (Underwood 1978; Creese & Underwood 1982; Fletcher & Creese 1985). Further experimental work with other species of *Cellana* might suggest why this genus is apparently so susceptible to intraspecific competition at high densities.

There is a need to follow up the hypotheses generated by these initial experiments on competition, and to investigate the consequences of any competitive interactions among grazers on the overall structure of intertidal and shallow subtidal communities. It is very likely, given the preliminary findings of Edwards (1982) and Jeffs (1985), that interactions between *Cellana* and *Turbo* will have important consequences for the small-scale distribution patterns of *Ralfsia,* and hence for other grazers such as *Siphonaria.* A similar series of interactions involving the feeding abilities of *Cellana* and *Chiton,* the interactions between them, and their effects on turfing coralline algae are currently in progress (Creese unpubl. data). Because intertidal grazers are relatively easy to manipulate in field experiments, studies of these sorts of interactions can provide valuable information on the mechanisms involved in competition and the resulting community consequences (see also Underwood 1986).

CONCLUSIONS

In the past 10 years there has been an increased awareness that invertebrate grazers can play an important, though often subtle, role in determining the structure of marine benthic communities. During this period, several comprehensive studies (mostly unpublished) have been done at Leigh. These studies have combined detailed quantitative investigations of distribution patterns at a number of

spatial scales, enumeration of short-term temporal changes in abundances and population structures, observations on the feeding biology of the species concerned, and experimental manipulations to examine the effects of grazers on their algal food supply and on each other. Extensive background information is now available for a suite of 4 common intertidal gastropods and 4 subtidal ones. Less detailed information is available for 5 common chitons. Overall, however, there is less detailed ecological information available for these molluscan species than for the grazing echinoid *Evechinus*, and models on the community effects of their grazing have not been formulated to the same extent as for the sea urchins. Clearly, then, there is much scope for further research on the ecology of molluscan grazers, and I outline below several areas where more attention is warranted.

With the exception of Walsby (1977), the demographic studies considered in this review have been less than 2 years in duration, and most have only covered a timespan of 12 months. While this information can give some indication of seasonal trends in abundances and population structures, longer-term studies are needed to document more fully year-to-year variations in recruitment and the subsequent effects of this on overall population densities. Such studies should also quantify long-term changes in the abundances of other organisms in the area, including macro- and microalgae, potential predators, and other sessile organisms such as barnacles. Grazers can have both direct and indirect effects on the distributions of barnacles (e.g., Jernakoff 1985a), but to date only Jeffs (1985) has considered the implications of this in New Zealand. Detailed ecological information is currently scarce not only for barnacles and microalgae, but also for some of the molluscan grazers themselves; virtually no data are available for such groups as acmaeid limpets and littorinids, although several species in both groups occur in large numbers in certain habitats.

To obtain better models (i.e., models with better predictive ability) of the community effects of interactions among molluscan grazers and between grazers and other components of shallow water communities, it will be necessary to conduct experiments at more than one locality. To date all intertidal work in north-eastern New Zealand has been done on either Pumphouse or Echinoderm Reefs at Leigh, and it would be very instructive to have comparable data from shores other than these. The models developed for molluscan grazers on subtidal reefs have slightly more generality because experiments have been carried out at a number of locations (Hartley 1978; Choat & Andrew 1986; Keestra 1987), although all are restricted to the area around Goat Island in the Leigh Marine Reserve. Because the effect of *Cookia* in maintaining cleared areas suitable for colonisation by smaller species has been demonstrated at each of these localities, the model concerning the role of this subtidal turbinid is considerably strengthened. Another area of experimental design that has yet to be fully explored for molluscan grazers at Leigh concerns multifactorial experiments. So far, experiments have been generally restricted to one time of the year at one place on a reef or in one type of habitat. More information can be gained by incorporating treatments such as height on the shore (or other physical variables), time of year, and presence/absence of other biological characteristics. This technique has been used to good advantage in studies of rocky shore communities in New South Wales (Underwood 1984; Jernakoff 1985b).

At present, general models of the role of molluscan grazers in structuring marine communities in north-eastern New Zealand are poorly developed, especially for intertidal communities. The quantitative information that does exist is diffuse, and it will not be possible to draw it together into a comprehensive model until further multifactorial experiments are done at a number of scales, and these are supplemented by longer-term demographic data.

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