

Ecology of rocky reef fish of north-eastern New Zealand: a review

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Abstract This review discusses the major factors producing spatial and temporal patterns in abundance and the structure of reef fish populations in north-eastern New Zealand. It also examines the potential impact of fish feeding on prey populations and habitat structure. Major biological features of the habitat, such as the distribution of macroalgae and echinoids, appear to affect fish populations at a variety of spatial scales. These spatial patterns remain coherent over time, despite temporal variation in population densities, which can be independent of habitat structure. Demographic studies have not yet resolved whether pre- or post-settlement processes are most important in structuring reef fish populations. Feeding categories, and details of diet, prey selection, and the use of microhabitats are discussed as necessary steps toward examining the impact of fish as predators. Experimental studies have not demonstrated that either carnivores or herbivores play a major role in determining the biological structure of habitats, or in modifying prey communities. A picture is emerging which suggests that the habitat has a far greater impact on fish populations than vice versa. It is stressed that the factors influencing patterns of distribution and abundance are likely to be species-specific; there is unlikely to be a general effect attributable to fish in shallow reef communities.

Keywords marine reef fish; distribution; abundance; habitat; recruitment; post-recruitment processes; trophic organisation; prey selection; predation; herbivory

INTRODUCTION

Subtidal rocky reefs in temperate waters harbour a variety of fish species which derive food and/or shelter from the reef substratum. Until ten years ago, these "reef fishes" had attracted only a little attention from marine ecologists (Clarke 1970; Stephens et al. 1970; Bray & Ebeling 1975; Russell 1975; Hobson & Chess 1976). The term was virtually synonymous with the diverse coral reef fish communities, which have been a topic of considerable interest (see reviews by Ehrlich 1975; Sale 1980, 1984; Munro & Williams 1985). The number of studies on the ecology of temperate reef fish has increased exponentially over the past decade. Although the body of information does not yet match that for their tropical counterparts, a consideration of the status of temperate reef fish ecology has been necessary for some time.

Studies on the fishes inhabiting reefs of the north-eastern coast of New Zealand have made a significant contribution to our knowledge of temperate, subtidal ecology. The aims of this review are to assemble this information, to describe the conclusions which have emerged, and to highlight areas in need of further work. The present literature comes mainly from studies carried out at the University of Auckland's Marine Research Laboratory at Leigh. The original source of much of this information can be traced to MSc and PhD theses, but these will be cited only when the data have not yet appeared in published form. In drawing this information together, the ultimate goal is to see whether any generalisations can be made for this one geographic area.

Ecological studies on the reef fishes of north-eastern New Zealand have been concerned with relationships between fish populations and benthic components of reef communities, such as kelp forests and grazing invertebrates. These interactions have been approached from two major perspectives: Many have attempted to assess the major features of the benthic habitat influencing the distribution and

abundance of fishes inhabiting shallow reef environments. A second set of questions have concerned fish feeding activities, and the impact of fishes on the structure of benthic algal and invertebrate communities on reefs. These two broad topics provide the framework for this review. However, this dichotomy is more for convenience than real. The effect of fish predation upon community structure is likely to be closely linked to their abundance patterns (Choat 1982). Likewise, any depression in the abundance of prey species can, potentially, have strong feedback effects on the abundance patterns of fish predators. This review discusses the importance of fish-benthos interactions, from the points of view of both participants.

A brief history

The first detailed study on the ecology of reef fish in New Zealand was carried out between 1969 and 1971 (Russell 1971), which included a general account of the colonisation of artificial reefs (Russell 1975), the abundance and biomass of reef fishes (Russell 1977), and their feeding habits (Russell 1983). However, most of the work followed the establishment, in 1975, of New Zealand's first marine reserve between Cape Rodney and Okakari Point, near Leigh. The baseline survey of the marine reserve, carried out by A. M. Ayling (1978), provided much information on the abundance and size-structure of reef fish populations in different, biologically defined, habitats. Data on spatial pattern and temporal change in reef fish abundances, accumulated between 1975 and 1986, have recently been published (Choat & Ayling 1987; Choat et al. in press). A study on subtidal encrusting communities, carried out between 1975 and 1976; was the first to examine the influence fishes might have on the structure of these communities (A. M. Ayling 1981). The first detailed investigation into the population dynamics and demography of a reef fish species was on the ubiquitous paketi, *Notolabrus* (= *Pseudolabrus*) *celidotus*, and was conducted between 1976 and 1981 (Jones 1980, 1981a, 1981b, 1983, 1984a, 1984b, 1984c; Jones & Thompson 1980; Thompson & Jones 1983). From then on the number of studies has proliferated. Twelve theses dealing with aspects of the population dynamics of reef fishes have been completed at the University of Auckland over the past decade, with a further five dealing with the potential effects that fish may have on prey species.

DISTRIBUTION, ABUNDANCE, AND STRUCTURE OF REEF FISH POPULATIONS

The fundamental questions in population ecology of reef fishes concern the factors limiting or inducing change in population numbers. The answers are dependent on the spatial scale at which the population is defined, and the time scale over which it is monitored. Before appropriate scales can be chosen, the variation in numbers and age/size structure in space and time need to be considered. The first stage is getting an accurate description of the changes in abundance in these two dimensions. During this phase, observations are made upon which to erect models about the processes underlying these patterns. The second phase involves establishing which processes are of major importance, by making predictions from the models, and testing these predictions. The study of temperate reef fish populations is essentially at the first stage. A great deal of information has accumulated on spatial and temporal patterns of abundance and population size-structure, but few of the mechanisms underlying these patterns have been well established. In this section I consider:

- (1) spatial patterns in population size and structure;
- (2) temporal patterns in population size and structure;
- (3) the demographic parameters (e.g., recruitment, mortality) involved in establishing these patterns; and
- (4) speculation about the ultimate factors limiting population size and structuring reef fish communities.

Spatial patterns

Patterns of density change have been considered at a number of spatial scales, ranging from different geographic locations throughout the North Island of New Zealand, down to differences in patch use within sites less than 0.01 km² in size. To avoid confusion due to the common use of different terminologies, these scales of focus have been divided into a number of categories: comparisons among different geographic "locations" (>5 km apart), comparisons among "sites" within a geographic location scale (<5 km apart) and a within-site (0.1 km² or less) scale (Table 1). The area of interest, regardless of scale, can be stratified into different types of habitat, defined on the basis of physical characteristics or dominant benthic

organisms. Comparisons among habitats, and among sites within habitats, can be made at any spatial scale. For reef fishes, this has commonly been done at a within-location scale, and to a lesser extent, within sites (for the latter the term "micro-habitats" is usually applied). Such comparisons have led to most of the insights into the factors responsible for different density patterns.

Density estimates have generally been made visually along transects of different dimensions. It is beyond the scope of this paper to assess critically the biases and sources of error often inherent in this technique (see discussions by Leum & Choat 1980; Sale & Sharp 1983; Bortone et al. 1986). Important is that the technique has been extremely useful for making quantitative comparisons of species abundances among areas and over time. The description of pattern is dependent partially upon the size of the transect employed. In the past, the choice of the dimensions has been based upon a variety of criteria, such as the size of habitat patches, the actual densities recorded, and a variety of logistic constraints. Traditional "standards", such as the 50 × 10 m transect commonly used for large reef fish, may

have some comparative value, but are likely to be less appropriate for detecting pattern in some species. Formal statistical techniques are useful for determining the transect size and number which offer the greatest possible precision, within the constraints of the time and effort available (Underwood 1981; Andrew & Mapstone 1987). These techniques have only recently been applied to temperate reef fishes (McCormick & Choat 1987), and their further use is to be encouraged.

Almost without exception, significant differences in density have been recorded at all spatial scales examined. However, it is the magnitude of the variation at each scale which is biologically important, as this knowledge determines the scale at which it will be profitable to ask questions about pattern and process. These levels of variation can be directly measured when fully hierarchical sampling programs are employed (Underwood 1981; Choat & Bellwood 1985). Such sampling designs have been used to some extent for reef fishes in New Zealand (e.g., Sylvester 1986; Choat & Ayling 1987), but not to a level where the variance present at all scales of interest has been partitioned.

Table 1 Spatial scales examined in studies on the distribution and abundance of rocky reef fishes of north-eastern New Zealand. Spatial scale: Large, among locations; Medium, among sites within locations (B, between habitats; W, within habitats); Small, within sites. For explanation of each scale see text.

Reference	Species	Spatial scale		
		Large	Medium B	W Small
Ayling 1978	Large reef fish		•	•
Choat & Ayling 1987	Large reef fish	•	•	•
Handford 1979	Blennioids		•	•
Jones 1980	<i>Notolabrus celidotus</i>	•	•	
Jones 1983	<i>N. celidotus</i>	•	•	
Jones 1984a	<i>N. celidotus</i>			•
Jones 1984b	<i>N. celidotus</i> , juveniles		•	•
Jones 1984c	<i>N. celidotus</i> , adults		•	•
Kingett & Choat 1981	<i>Chrysophrys auratus</i>		•	
Kingsford 1980	<i>Chromis dispilus</i>	•	•	
Leum & Choat 1980	<i>Cheilodactylus spectabilis</i>	•	•	
MacDiarmid 1981	<i>Scorpius violaceus</i>		•	
MacDiarmid 1981	<i>Pempheris adspersus</i>		•	
McCormick 1986	<i>Cheilodactylus spectabilis</i>	•	•	•
Meekan 1986	<i>Odax pullus</i>		•	•
Milicich 1986	<i>Parika scaber</i>		•	
Mutch 1983	<i>Parapercis colias</i>		•	•
Poynter 1980	<i>Parika scaber</i>		•	
Russell 1977	All reef fish		•	
Sylvester 1986	Large carnivores & Blennioids	•	•	•
Thompson 1979	Blennioids		•	•

Table 2 Significant correlations between reef fish abundance and habitat covariates from medium-scale studies in north-eastern New Zealand. (p, Pearson's correlation coefficient).

Species	Family	Category	Covariate	p	Reference
<i>Cheilodactylus spectabilis</i>	Cheilodactylidae	All	Topographic complexity	0.88	Leum & Choat (1980)
<i>Chromis dispilus</i>	Pomacentridae	All	Topographic complexity	0.83	Kingsford (1980)
<i>C. dispilus</i>	Pomacentridae	All	Current speed	0.73	Kingsford (1980)
<i>C. dispilus</i>	Pomacentridae	Juveniles	Topographic complexity	0.53	Kingsford (1980)
<i>Chrysophrys auratus</i>	Sparidae	Juveniles	Turf-algae cover	0.79	Kingett & Choat (1981)
<i>Forsterygion varium</i>	Tripterygiidae	Adults	Topographic complexity	0.82	Thompson (1979)
<i>Notolabrus celidotus</i>	Labridae	Juveniles	Shallow, Macroalgae cover	0.94	Jones (1984b)
<i>N. celidotus</i>	Labridae	Juveniles	Deep, Macroalgae cover	0.90	Jones (1984b)
<i>Parapercis colias</i>	Parapercidae	Adults	Topographic complexity	0.59	Jones (1984c)
<i>P. colias</i>	Parapercidae	Juveniles	Turf-algae cover	0.79	Mutch (1983)
<i>Parika scaber</i>	Monacanthidae	Adults	Macroalgae cover	-0.68	Jones (1981a)
<i>Pempheris adspersus</i>	Pempheridae	Adults	Sessile-invertebrate cover	0.86	Jones unpubl. data
<i>Scorpius violaceus</i>	Kyphosidae	All	Topographic complexity	0.89	MacDiarmid (1981)
		Juveniles	Topographic complexity	0.81	MacDiarmid (1981)

PATTERNS AMONG LOCATIONS: Not surprisingly, there are substantial changes in species composition and abundance of reef fish faunas on a broad geographic scale encompassing the North Island of New Zealand, and associated offshore islands to the north (Choat & Ayling 1987). Factors which have produced and currently maintain these biogeographic patterns are unknown. Choat and Ayling note the distinct differences among offshore islands in faunal composition, and among different locations along the mainland. When grouped in terms of feeding categories, variation in densities at this scale appeared to relate to habitat, with small wrasses, regardless of species, dominating areas of high algal cover. Larger carnivores were more abundant in areas characterised by coralline algal flats grazed by urchins. Distinct island and mainland fish communities have been linked to differences in habitat-structure in a northern temperate region (Ebeling et al. 1980a, 1980b).

Interestingly, those studies comparing abundances of individual species among different geographic locations, and among different sites between and within habitats, have found a similar range of mean densities at both scales (Jones 1984c; Choat & Ayling 1987). For example, adults of the wrasse *N. celidotus* exhibit the same range of densities, when sites within the marine reserve at Leigh are compared, as they do for comparisons among locations sampled throughout the North Island (Jones 1984c). Since marked changes in density occur over a relatively small spatial scale, it is an important (and logistically feasible) scale upon which to focus questions about patterns of abundance and their causes.

PATTERNS WITHIN LOCATIONS: Most descriptions of spatial pattern in density have worked at an intermediate or "within-location" scale. Densities have been compared among randomly chosen sites (0.5–5km apart). Alternatively, locations have been stratified in terms of habitats, and densities have been compared both among habitat types, and among sites within habitats (Table 1). Significant differences among habitats and sites are the rule, rather than the exception. A. M. Ayling (1978) described the patterns of abundance and species composition characteristic of seven different habitats in the marine reserve at Leigh. Species-specific patterns of abundance at this scale have been correlated with a variety of physical and biological variables (Table 2). Biological factors, such as the amount of macroalgae versus turf-algae,

and physical factors such as the degree of topographic complexity, appear to have important consequences for fish populations and the structure of local communities. Although cause-effect links between these variables have not been established at this scale, they may be useful as predictors of relative abundance. Causation is probably a far more complex problem than these simple correlations would imply.

The relationship between fish faunas and the disjunct distributions of kelp, coralline-algal turf flats, and areas grazed by urchins, is clearly evident on this medium scale. The densities of small wrasses, such as *N. celidotus*, are positively related to the quantity of macroalgae (Jones 1984b; Choat & Ayling 1987), whereas larger carnivores such as *Chrysophrys auratus*, *Parapercis colias*, and others are more common in turf areas (Jones 1981a; Kingett & Choat 1981; Mutch 1983; Choat & Ayling 1987).

There is considerable evidence that topographic complexity, or the amount of relief, plays another fundamental role. Not only do the densities of a number of individual species correlate with this variable (Table 2), the species richness and total densities of groups like tripterygiid blennies (Thompson 1979) and planktivorous fishes (Kingsford 1980) are also related in the same way. Topographic complexity may partially reflect the type of rock substratum. Meekan (1986) found that the herbivorous fishes *Odax pullus* and *Girella tricuspidata* were more abundant on the dissected greywacke reef areas, than on the flatter sandstone reefs.

PATTERNS WITHIN SITES: The distribution of individuals within sites at any time appears to be non-random and related to a host of ecological and behavioural factors, which probably interact in a complex way (Jones 1984a; McCormick 1986). Behavioural factors can include intraspecific association or aggression (Leum & Choat 1980; Kingett & Choat 1981; Jones 1983, 1984a; Mutch 1983), interspecific association or aggression (Mutch 1983; Thompson & Jones 1983; Jones 1984a), and spawning-site choice (Thompson 1979, 1986; Jones 1981b).

Within-site variability is demonstrably due to the effect of micro-habitat on the use of space. All the experiments which have linked densities to features of the habitat have been done at this scale. Jones (1984b) showed that kelp removal caused a decrease in the densities of juvenile *N. celidotus*, and

kelp addition (via urchin removal) caused an increase, presumably owing to an effect on local recruitment patterns. Choat & Ayling (1987) showed that patch use by larger carnivores, including *C. auratus*, decreased when kelp forests became established following urchin removal. Kingett & Choat (1981) showed by experimental clearances, that coralline algal turf had a direct effect on patch use by *C. auratus*, activity being reduced when turf cover was low. These studies provide clear evidence that these ecological factors affect the relative use of space at a within-site scale. Extrapolations of these effects to explain patterns among locations or among habitats within locations should be made with caution.

POPULATION STRUCTURE: Knowledge of spatial and temporal pattern in age structure is crucial to an understanding of the mechanisms causing change in population size, since processes may not uniformly affect all age classes (Jones 1987). Also, constancy of overall abundances may mask an underlying instability in the age composition. Unfortunately, attempts to compare age distributions at different locations have been made only for one species (Jones 1980, 1981a). Due to difficulties in obtaining unbiased estimates of age structure, size-frequency distributions are commonly presented as an alternative description of the structure of populations. For many questions these may actually be more appropriate, since life history stages in fishes (such as entry to adult populations) and the ecological processes (such as prey selection) are often more dependent upon size than age.

Differences in the size-frequency distributions have been detected at all spatial scales examined. Choat & Ayling (1987) note differences in the size structure of populations occupying macroalgal and urchin-grazed habitats, among locations, among local sites, and among patches within sites. Several workers have recorded habitat and depth-related patterns in size-distributions, larger fish often being found in deeper water (Leum & Choat 1980; Jones 1981b; MacDiarmid 1981; McCormick 1986; Meekan 1986). These trends could have important implications with regard to spatial pattern in breeding population size, and the impact of fish predation.

Temporal patterns

At present most of the data on temporal variability in population numbers spans the average length of

MSC or PhD studies—which is too short, relative to the life spans of most fish species, to get an appropriate measure of population stability. Ecological studies on other temperate reef and coral reef systems have suffered from similar constraints, with studies extending greater than 3–4 years the exception rather than the rule (Sale 1984; Ebeling et al. 1980b; but see 12-year study by Stephens et al. (1986) in California).

The single exception, for north-eastern New Zealand, was the 12-year survey of reef fish densities made at Nursery Cove, Poor Knights Islands, between 1975 and 1986 (Choat et al. in press). All species exhibited substantial temporal changes in density over this period, but some more than others. Species with a subtropical distribution declined from moderate numbers in 1974 to near local extinction in 1979, with one labrid species, *Suezichthys aylingi*, exhibiting a 15-fold fluctuation in numbers. Labrids which have southern distributions, including *Notolabrus fucicola* and *N. celidotus*, showed much less variation in numbers. The magnitude of temporal change could be related to sea temperatures, with storm-induced disturbance also paying a role (also see Ebeling et al. 1985).

Those studies which have combined a description of spatial and temporal pattern over a number of years, have shown that temporal variation is relatively small and spatial patterns remain consistent over time. For example, Jones (1984c) estimated the abundance of *N. celidotus* at 10 sites (between and within habitats) in the Leigh Marine Reserve, over a five-year period, and found that the ranking of locations in terms of abundance remained unchanged, despite measurable changes in abundance. The same appears to apply for this species at the Poor Knights Islands (Choat et al. in press), and is consistent with results for other reef fishes in north-eastern New Zealand (Thompson 1979; Leum & Choat 1980; MacDiarmid 1981; Mutch 1983; McCormick 1986) and other temperate areas (e.g., Ebeling et al. 1980b).

Within-year sampling has shown that some species, such as *Chrysochrysis auratus*, exhibit marked seasonal changes in abundance (Kingett & Choat 1981). The spatial patterns established during the summer peak in abundance, however, are consistent among years.

Demographic parameters

The distribution and abundance of a reef fish species potentially reflects survival through all life stages: egg, larval, juvenile, and adult. At present, opinions

are divided as to the relative importance of events occurring during pre-settlement and reef-associated phases. Early models considered only those processes affecting settled juveniles and adults (see Sale 1980). It was assumed that events happening during the early pelagic phase, which could affect numbers settling (e.g., mortality, development, movement) were unimportant, since patterns established at the time of settlement were modified by interactions among juveniles and adults. Recent studies on coral reefs have suggested that the distribution and abundance of many species merely reflect variation in numbers setting (e.g., Doherty 1983; Victor 1986). The relative importance of the processes occurring in the two phases has yet to be resolved for any species (Jones 1987). Certainly, the parameters responsible for spatial pattern may be totally different from those bringing about temporal change. In this section I discuss the information that is available on recruitment and potentially important post-recruitment processes such as mortality, maturation, and movement. Kingsford (1988) has reviewed the information available on larval processes.

RECRUITMENT: The potential importance of recruitment has been a topic of great interest in rocky reef fish studies. All reef fishes in north-eastern New Zealand recruit seasonally, most species during the months of spring and summer (Thompson 1981; Ayling & Cox 1982). Actual numbers settling have proved difficult to assess, so the term "recruitment" usually refers to estimates of the densities of recently settled juveniles. Recruitment to the reef environment will only reflect numbers which have settled, if the latter is not modified by immediate post-settlement processes (Connell 1985). Milicich (1986) has come the closest to examining settlement patterns in a temperate reef fish. Input of pre-settled *Parika scaber* into the reef system were monitored every two days, by sampling kelp plants suspended on ropes near the surface waters. Pre-settled juveniles of many species are attracted to drift-algal material (see Kingsford 1988). Patterns of recruitment to kelp plants attached to the reef were also monitored. The temporal patterns of recruitment partially reflected changes in the availability of potential settlers.

Recruitment appears to be highly variable both spatially (within and among locations) and temporarily (within and among years) for most species (Kingsford 1980; Poynter 1980; MacDiarmid 1981; Mutch 1983; Jones 1984b; but

see Thompson 1979). This generalisation may apply equally well to other temperate locations (Cowan 1985; Stephens et al. 1986) and to coral reefs (Sale 1984; Munro & Williams 1985). Such variation probably makes a major contribution to changes in the abundance and composition of reef fish faunas in north-eastern New Zealand, between areas and over time (Jones 1984b; Choat et al. in press). Where spatial and temporal patterns in recruitment have been considered together, differences among areas have been greater than differences among times (Jones 1984b). The magnitude and direction of change appears to be consistent over a number of sites within a location. Hence, certain sites receive consistently higher recruitment than others.

The causes of spatial variation in recruitment probably differ from those bringing about temporal change. Spatial variation in recruitment has been shown to relate to habitat, but the relative importance of habitat selection, before or after settlement, or early differential survival is not known (Jones 1984b). Temporal variation in recruitment, within and between seasons, probably relates to a variety of factors including spawning patterns, processes influencing larval survival and development, processes transporting fully developed larvae back to the reef, and long-term changes in habitat structure (Kingsford 1980; Jones 1984b; Milicich 1986; Choat & Ayling 1987).

POST-RECRUITMENT EVENTS: Obtaining reliable information on post-recruitment processes which may affect adult population size and age/size structure has high priority (Sale et al. 1985). Spatial patterns in recruitment are positively correlated with adult density patterns in some species, but certainly not in all. No obvious temporal relationships between interannual variation in recruitment and subsequent changes in adult numbers have been recorded (e.g., Jones 1984b, 1984c). However, with the exception of Choat et al. (in press), the period encompassed by most studies would probably be too short to detect such patterns.

Variation in adult densities may be affected by changes in post-recruitment mortality rates, maturation times, and systematic movements, none of which have received a great deal of attention in reef fish studies (but see Doherty 1983; Jones 1984c, 1987; Eckert 1987). Differential juvenile mortality appears to have a substantial effect on adult distributions in the blenny *Forsterygion varium* in north-eastern New Zealand (Thompson 1979). This is one of the few species in which juveniles tend to

recruit fairly evenly across a variety of habitat types. However, survival appears to be much higher at sites with greatest topographic complexity, which closely correlates with adult numbers. These patterns are unlikely to be explained by movement. Behavioural studies on *F. varium* show juveniles to be extremely site-attached; they will in fact return to their home ranges when displaced enormous distances (Thompson 1979, 1983).

Other workers in this area have stressed the potential importance of post-recruitment mortality and growth (Jones 1984c; Milicich 1986). Jones (1984c) showed that although spatial patterns in adult density in *N. celidotus* were correlated with recruitment, the relationship was not linear. Both density-dependent growth and mortality appear to restrict input to the adult population at high recruitment levels. Density-dependent growth is important, because it means that the time taken to reach maturity is prolonged with increasing densities (Jones 1984c, 1987). There is some evidence of social control of maturation in female *N. celidotus* at high densities (Jones & Thompson 1980). Jones (1984c) argued that the relative importance of recruitment and post-recruitment events, shifted in favour of the latter, at sites which consistently exhibited high recruitment levels.

The role of movement obviously becomes increasingly important in determining pattern at smaller spatial and temporal scales. It is clearly one of the primary factors operating at a within-site scale (see previous section). Local movements on a diel or tidal basis are common, and known to be associated with breeding, foraging, and resting activities (Bray 1981; Jones 1981b; McCormick 1986; Meekan 1986). It may also be implicated in many of the patterns in abundance and size-frequency evident at a broader scale. Some species show a tendency to recruit into shallow water, and appear to systematically shift into deeper water as they grow (e.g., *Cheilodactylus spectabilis*: Leum & Choat 1980; McCormick 1986). The summer influx of 0+ and 1+ year age classes of *C. auratus* into the reef system would appear to be the result of fairly large-scale movements (Kingett & Choat 1981). Reef populations of the parore, *G. tricuspidata*, may be replenished by migration from sheltered harbour reefs, where they appear to settle in large numbers.

Limiting processes

The question of what ultimately limits population size in the reef fishes of New Zealand has yet to be answered. A variety of processes are likely to be

operating before, during, and after recruitment; their relative importance within any one species is likely to change, as spatial and temporal scales are altered. There is no reason to expect generalisations among species, since each exhibits distinct patterns of ecology and behaviour, both during larval (see Kingsford 1988) and benthic phases of the life history. The multitude of correlations between abundance and habitat variables, such as the presence of kelp and turf, may offer clues as to important processes, but they are just as revealing as attempts to find simple solutions. The small-scale experiments linking distributions directly to these variables (Kingett & Choat 1981; Jones 1984b; Choat & Ayling 1987) clearly establish their importance at one level, but raise more questions than they answer. Do these factors determine larger-scale patterns of distribution and abundance? Are these habitat associations based on the availability of preferred food or shelter, or a complex interaction between the two? How important are habitat selection by larvae, post-settlement survival, or movement, in establishing these larger-scale patterns?

The potential roles of competition and predation, in relation to these population patterns and habitat associations, have not been fully considered. Thompson (1979) suggested that the site-specific mortality patterns in *F. varium* may be due to differential predation pressure in habitats offering less shelter. Jones (1984a, 1984b) could find no evidence of intra-specific competition between adults and small juveniles in *N. celidotus*, but presented one interesting scenario to explain density-dependent growth and mortality. He suggested that juveniles were restricted to kelp heads as a shelter site from predators, and, as a result, were subject to intra-cohort competition for food. These arguments are mere speculation, but serve to remind how complex the relationships may be between competition for resources and the avoidance of predators.

The diet of *N. celidotus* of intermediate sizes overlaps considerably with that of the blennioid fish *F. varium*, which behaves aggressively toward the wrasse (Thompson & Jones 1983). There is strong evidence from removal experiments that the two species compete, but only while the wrasse passes through a restricted size range. There is no suggestion that this interaction affects patterns of distribution and abundance. Large-scale effects of interspecific interactions have been recorded in some Californian reefs (Hixon 1980; Larson 1980), but not in New Zealand.

Sorting out the relative importance of processes occurring during pelagic and reef-associated phases will require comprehensive studies, which focus on both portions of the life cycle at the same time. We need to monitor the fate of successive cohorts running the gauntlet of the pelagic environment, managing to settle in the reef habitat, and surviving to breeding age (e.g., Stephens et al. 1986). Experiments testing the importance of different factors at each stage must not only establish that a process is operating, but must establish the degree to which it contributes to the observed patterns in space and time (Weinberg et al. 1986).

FISH FEEDING AND THE STRUCTURE OF REEF COMMUNITIES

A growing generalisation that fish feeding has a major impact on prey populations and the structure of communities in temperate waters was challenged by Choat (1982). He stressed the need for more fundamental information on predator-prey interactions and urged a cautious interpretation of experiments carried out without this knowledge. The potential impact of a fish species on benthic community structure cannot be assessed without basic information on its diet, use of microhabitats, and feeding behaviour. These may vary between areas and over time, in response to changes in the distribution and abundance of prey species. An individual may contribute to different effects with time, as it undergoes ontogenetic changes in diet, and in its choice of microhabitats. The impact will be dependent on how much fish predation contributes to the mortality in prey populations, and can be assessed, unequivocally, only by the experimental manipulation of fish feeding pressure over appropriate spatial and temporal scales. The necessary dietary information on fish feeding over rocky reefs in north-eastern New Zealand is accumulating, and is summarised here, along with a discussion of the preliminary experiments designed to test the effects of fish predation.

Trophic organisation and diets

When considering broad trophic categories, the reef fishes of north-eastern New Zealand are primarily carnivorous. Of 44 "reef" species examined by Russell (1983), 82% were carnivores, 11% were herbivores and 7% were omnivores (Table 3). These proportions appear to be broadly similar in other temperate reef communities (Hobson 1982), and in some coral reef communities, although herbivores

Table 3 Trophic organisation of the reef fish community around Goat Island, north-eastern New Zealand. Diet information from Russell (1983); abundance information from Russell (1977) includes % of total abundance and total biomass. NI = not included in Russell's (1977) survey.

Species	Family	% Abundance	% Biomass
CARNIVORES		93.1	57.5
Benthic Feeders:		15.4	39.9
<i>Myliobatus tenuicaudatus</i> (Hector)	Myliobatidae	>0.1	>0.1
<i>Gymnothorax prasinus</i> (Richardson)	Muraenidae	0.2	4.6
<i>Conger wilsoni</i> (Bloch & Schneider)	Congridae	>0.1	3.9
<i>Dellichthys morelandi</i> Briggs	Gobiesocidae	NI	NI
<i>Trachelochismus melobesia</i> Phillips	Gobiesocidae	NI	NI
<i>Lotella rhacinus</i> (Bloch & Schneider)	Moridae	>0.1	>0.1
<i>Pseudophycis breviuscula</i> (Richardson)	Moridae	>0.1	>0.1
<i>Zeus faber</i> Linnaeus	Zeidae	>0.1	1.1
<i>Scorpaena cardinalis</i> Richardson	Scorpaenidae	1.4	0.5
<i>Ellerkeldia huntii</i> (Hector)	Serranidae	0.2	0.2
<i>Chrysophrys auratus</i> (Bloch & Schneider)	Sparidae	0.6	1.1
<i>Upeneichthys lineatus</i> (Bloch & Schneider)	Mullidae	1.7	2.3
<i>Paristiopercus labiosus</i> (Günther)	Pentaceroptidae	>0.1	>0.1
<i>Chironemus marmoratus</i> Günther	Chironemidae	4.2	7.4
<i>Cheilodactylus spectabilis</i> Hutton	Cheilodactylidae	0.6	6.6
<i>Nemadactylus douglasii</i> (Hector)	Cheilodactylidae	>0.1	3.4
<i>Latridopsis ciliaris</i> (Bloch & Schneider)	Latridae	>0.1	>0.1
<i>Coris sandageri</i> (Hector)	Labridae	>0.1	0.8
<i>Notolabrus celidotus</i> (Bloch & Schneider)	Labridae	4.0	5.3
<i>N. fucicola</i> (Richardson)	Labridae	1.2	4.5
<i>Pseudolabrus miles</i> (Bloch & Schneider)	Labridae	0.3	0.7
<i>Parapercis colias</i> (Bloch & Schneider)	Mugiloididae	0.8	1.8
<i>Ruanoho whero</i> Hardy	Tripterygiidae	NI	NI
<i>Bellapiscus medius</i> (Günther)	Tripterygiidae	NI	NI
<i>Notoclinops segmentatus</i> (McCulloch & Phillips)	Tripterygiidae	NI	NI
<i>Forsterygion capito</i> (Jenyns)	Tripterygiidae	NI	NI
<i>F. varium</i> (Bloch & Schneider)	Tripterygiidae	NI	NI
<i>Forsterygion</i> sp. (see sp.b, Thompson 1981)	Tripterygiidae	NI	NI
<i>Notoclinops yaldwyni</i> Hardy	Tripterygiidae	NI	NI
Open-water feeders:		77.7	17.6
<i>Optivus elongatus</i> (Günther)	Berycidae	4.5	0.4
<i>Caesioperca lepidoptera</i> (Bloch & Schneider)	Serranidae	0.4	0.3
<i>Pseudocaranx dentex</i> (Bloch & Schneider)	Carangidae	2.8	3.3
<i>Pempheris adspersus</i> Griffin	Pempheridae	20.5	1.8
<i>Chromis dispilus</i> Griffin	Pomacentridae	1.3	0.5
<i>Obliquichthys maryannae</i> Hardy	Tripterygiidae	NI	NI
<i>Scorpius lineolatus</i> Richardson	Kyphosidae	51.2	11.2
HERBIVORES		4.9	38.0
<i>Girella tricuspidata</i> (Quoy & Gaimard)	Kyphosidae	4.7	36.0
<i>Kyphosus sydneyanus</i> (Günther)	Kyphosidae	>0.1	>0.1
<i>Parma alboscapularis</i> Allen & Hoes	Pomacentridae	>0.1	>0.1
<i>Aplodactylus arctidens</i> Richardson	Aplodactylidae	0.1	1.8
<i>Odax pullus</i> (Bloch & Schneider)	Odacidae	>0.1	>0.1
OMNIVORES		1.8	3.4
<i>Parablennius laticlavius</i> (Griffin)	Blenniidae	NI	NI
<i>Parika scaber</i> (Forster)	Monacanthidae	1.8	3.4
<i>Scorpius violaceus</i> (Hutton)	Kyphosidae	NI	NI

reach 20–30% at some tropical locations (Goldman & Talbot 1976; Hobson 1982; Williams & Hatcher 1983).

Russell (1983) divided carnivores into two broad categories. The majority of the species (81%) are the "benthic feeders", which primarily feed on mobile invertebrates. The group is represented by relatively large families, such as labrids and tripterygiids, and numerous species, including red moki, *C. spectabilis*, the goatfish *Upeneichthys lineatus* and the commercially important snapper *C. auratus* (Table 3). The most important prey categories are amphipods, with crabs, gastropods, errant polychaetes, and small bivalves utilised heavily (Russell 1983). Several species include small reef fish in their diets, but only one, *Zeus faber*, is totally piscivorous.

The other group of carnivores are "open-water feeders", which include fish that shelter among reefs, but feed in the water column on zooplankton (Table 3). Although benthic feeders predominate in terms of number of species, Russell's (1977) censuses at Goat Island showed that open-water feeders make up 78% of the total number of individuals recorded. However, these censuses did not include the numerous small tripterygiid blennies and gobiosocids, which are largely benthic feeders. The most abundant open-water feeders are the sweep *Scorpius lineolatus* and the bigeye *Pempheris adspersus*. The numerical dominance of open-water feeders over large carnivores is reversed when estimates of biomass are considered (Russell 1977). Benthic carnivores account for 40% of the total reef fish biomass, while open-water feeders make up 18% (Table 3).

The herbivorous fish of temperate reefs are primarily "browsers", feeding selectively on foliose macroalgae. This contrasts with tropical coral reefs where the predominant herbivorous families, such as scarids and acanthurids, are "grazers", feeding non-selectively on microalgae. In north-eastern New Zealand, herbivorous fish, the most common of these being the parore, *G. tricuspidata*, primarily consume red or green algae. The only exception is the odacid, *O. pullus*, in which adults feed exclusively on large brown algae. Numerically, herbivores made up only 5% of the reef fish recorded by Russell (1977), but this figure expanded to 38% of the total reef fish biomass (Table 3).

Inter- and intraspecific differences in diet

More recent detailed studies on the diets of individual species suggest that the above categorisation

may be an oversimplification, which neglects the considerable interspecific differences, and ontogenetic, spatial, and temporal variation in prey consumption within a species. Russell's (1983) paper points to a high degree of partitioning of food resources, at least among adults of most species. The level of partitioning may be inflated, since his specimens came from a variety of locations and habitat types. However, studies on ecologically similar species collected from within the same habitat types have also revealed significant differences among species in prey composition (Thompson 1979; MacDiarmid 1981; Sylvester 1986).

What is not apparent from Russell's (1983) general dietary study is that juveniles and adults have almost totally different diets in 11 of the 13 species which have been examined in detail (Table 4). Not only do the relative proportions of different prey categories change as fish grow, but the mean sizes of prey types also increase (MacDiarmid 1981; Thompson & Jones 1983; Jones 1984a). Even in species in which the dominant prey types do not change with growth, there are subtle differences in prey sizes and proportions (Clements 1985; McCormick 1986). Thus, a species may have an impact on a much wider range of prey categories and sizes than would be evident from Russell's (1983) study.

When juveniles are considered, the importance of gammarid amphipods as a food source is startling (Table 4). Nearly all benthic carnivores, and even some herbivores (e.g., *O. pullus*: Clements 1985) grow through a phase when a large proportion of their diet consists of these small crustaceans. Some benthic carnivores, such as *C. spectabilis* and *U. lineatus*, which appear to be relatively non-selective in their feeding, continue to consume amphipods throughout their lives. In general, adult fish appear to feed on a much wider range of prey categories, and this is evident both within and among species.

In considering the importance of predator-prey interactions, both spatial and temporal variation in diets may be extremely important. In the few instances that spatial variation has been considered for temperate reef fish, substantial differences among geographic locations have been found (Cowan 1986). In New Zealand, juvenile *N. celidotus* have been shown to feed almost exclusively on benthic substrata at the Leigh Marine Reserve, but feed on pelagic zooplankton at a high-density site on Takatu Peninsula (Jones 1983, 1984a). Kingsford (1980) found that *Chromis*

dispilus, at the Poor Knights Islands, consume much larger quantities of euphausiids and copepods than they do near Leigh, on the mainland. Local-scale differences among habitats have been recorded by Sylvester (1986). He found that the diets of some species (e.g., *N. celidotus* and *P. colias*) differed markedly between shallow turf flats and deep reefs, while others (e.g., *U. lineatus*, *C. auratus*, and most blennioids) did not. Differences among locations within habitats may also be important, but these have rarely been considered.

Temporal variation in diet can also be pronounced. Several species, such as *P. scaber*, *N. celidotus* (Jones unpubl. data), and *Pseudocaranx dentex* (Russell 1983) are known to switch between benthic feeding and open-water feeding at irregular intervals. Juvenile *P. adspersus* feed diurnally on small copepods near the substratum, but adults feed on zooplankton in the water column at night (MacDiarmid 1981). On a larger time scale, there appear to be seasonal changes in the diets of most

benthic carnivores (Thompson 1979), open water feeders (Kingsford 1980; MacDiarmid 1981), and herbivores (Clements 1985), which have been examined.

Foraging patterns within habitats

Broad-scale and among-habitat differences in the effects of fishes may reflect changes in fish density. Within-habitat variation may reflect preferences for foraging in certain microhabitats. Microhabitats are considered to be physically, or biologically, distinguishable feeding substrata, which occur on a spatial scale such that individuals may encounter the entire range present at a site within their normal home range. As with diet, detailed knowledge of feeding substrata is essential when examining the role of fish predation, since fish feeding will be patchy at a within-site scale.

There appears to be a high degree of partitioning of microhabitats among co-occurring species in temperate waters (e.g., Bray & Ebeling 1975;

Table 4 Dominant prey categories taken by juveniles (<100 mm SL) and adults of several reef fishes.

Species	Juveniles	Adults	Reference
<i>Aplodactylus arctidens</i>	red algae	red algae	Clements (1985)
<i>Cheilodactylus spectabilis</i>	amphipods	amphipods	Leum & Choat (1980); McCormick (1986)
<i>Chromis dispilus</i>	copepods	appendicularia fish eggs copepods	Kingsford (1980)
<i>Chrysophrys auratus</i>	amphipods	crabs urchins	Choat & Kingett (1982); Russell (1983)
<i>Fosterygion varium</i>	amphipods gastropods	hermit crabs crabs	Thompson (1979)
<i>Notolabrus celidotus</i>	amphipods	gastropods molluscs crabs	Jones (1984a)
<i>N. fucicola</i>	amphipods	crabs hermit crabs molluscs	Jones, unpublished
<i>Odax pullus</i>	red algae	brown algae	Clements (1985)
<i>Parapercis colias</i>	amphipods	fish urchins molluscs	Mutch (1983)
<i>Parika scaber</i>	amphipods	sponges ascidians red algae	Poynter (1980); Russell (1983)
<i>Pempheris adspersus</i>	copepods	amphipods polychaetes	MacDiarmid (1981)
<i>Scorpius violaceus</i>	copepods	appendicularia fish eggs red algae	MacDiarmid (1981)
<i>Upeneichthys lineatus</i>	amphipods	crabs amphipods	Choat & Kingett (1982); Russell (1983)

Ebeling & Laur 1986). Sylvester (1986) studied two groups of fishes, large carnivores and blennioids, which feed over open rocky areas. He found significant differences among species in the use of microhabitats within both of these groups. A comparison of two habitats, rock flats and deep broken rock, indicated that large carnivores differed in their use of microhabitats between the two habitats. However, it is not certain whether this is due to changes in microhabitat preference or microhabitat availability.

Foraging preferences within a species often change as individuals grow larger, both in north-eastern New Zealand (Poynter 1980; Mutch 1983; Jones 1984a; McCormick 1986; Sylvester 1986) and other temperate regions (Holbrook & Schmitt 1984; Schmitt & Holbrook 1984). For example, *N. celidotus* and *P. scaber* switch from feeding on amphipods in the macroalgal canopy when small, to feeding on a range of invertebrates from rocky substrata as adults (Poynter 1980; Jones 1984a). Jones established that both adults and juveniles were feeding non-randomly with respect to the proportional cover of these microhabitats. Adult *P. celidotus* avoided foraging on rock surfaces beneath the algal canopy where prey numbers were low. Other species, such as the generalist carnivore *Cheilodactylus spectabilis*, primarily forage among turf algae throughout their lives, although there is greater emphasis on foraging in crevices on ophiuroids as they grow larger (McCormick 1986). Planktivores can also exhibit changes in foraging location with size, with larger fish tending to forage higher in the water column (Kingsford 1980).

Prey abundance, availability, and selection

A description of spatial and temporal pattern in prey abundance, within appropriate microhabitats, is critical to interpreting experiments and assessing the importance of fish predation. The above patterns in diet and foraging may reflect changes in prey abundance, prey availability, and/or prey selection. Prey abundance does not equate directly with availability in most circumstances, since the latter can be affected by a variety of factors other than abundance, such as prey mobility, visibility, and behaviour (Main 1985). However, the relative availabilities of different prey types is difficult to quantify. Diet and prey abundance measures can be compared to obtain the degree of "apparent" prey selection, which can indicate the prey species most likely to be affected by predation.

There have been a few attempts to quantify prey abundance and examine apparent feeding selectivity in benthic carnivores. Jones measured differences in the abundance of prey items taken by both juveniles and adult *N. celidotus*, both among microhabitats (Jones 1984a) and habitats (Jones 1984b, 1984c). Juveniles, restricted to foraging within macroalgae, take microcrustaceans in proportion to their abundance. Adult wrasses are much more selective. This pattern of greater apparent feeding selectivity in adults is also true for *P. colias* (Mutch 1983) and *C. spectabilis* (McCormick 1986), although the role of availability needs to be established. Cheilodactylids have been described as essentially "functional grazers", taking benthic organisms non-selectively (Choat 1982). However, McCormick's study on *C. spectabilis* shows that adults consume prey in proportions which differ from those present in turf, suggesting some degree of selectivity. Sylvester (1986) is the only study which has distinguished among amphipod species when comparing diets and prey abundance. He found no evidence that either large carnivores, such as *C. spectabilis* and *U. lineatus*, or blennioids, were consuming some amphipods in preference to others. The most abundant species present in the turf, such as *Gammaropsis typica*, *Podocerus karu*, and *Ischyocerus longimanus*, were consumed in proportion to their abundance.

Prey selection has also been examined in planktivorous fishes (Kingsford 1980; MacDiarmid 1981). The large degree of temporal variation in the diets of planktivores reflects changes in the composition of the zooplankton. Planktivores appear to be very selective, but a category being selected at one time may be rejected at another. For example, *Scorpius violaceus* and *Chromis dispilus* select appendicularia during the winter months, but in spring-early summer, these are rejected in favour of fish eggs which are present at this time (Kingsford 1980; MacDiarmid 1981).

The impact of carnivores

The large biomass and variety of benthic feeding carnivorous fish has led to suggestions that they will have a major influence on the structure and dynamics of benthic invertebrate communities (Bakus 1969; Russell 1983). They may have effects directly attributable to prey consumption, or mechanical disturbance of the habitat when feeding. As an example of the latter, Battershill (1987) suggested that silt-sorting by the goatfish, *U. lineatus*, may influence the recruitment of sponges

in some areas. Nocturnal planktivores, such as *P. adspersus*, which feed on demersal zooplankton, may also produce a feeding-effect on benthic communities. Diurnally feeding planktivores may locally deplete the abundance of zooplankton being transported above reefs (Kingsford & MacDiarmid unpubl. data) and there is a suggestion that this can affect the recruitment of some benthic organisms (Gaines & Roughgarden 1987). Aggregations of open-water feeders in temperate waters may also have positive effects through defecation and ammonium excretion, which can enrich the habitat, promoting the growth of benthic organisms (Bray et al. 1981, 1986).

Studies on the role of carnivorous fish as predators in north-eastern New Zealand can be divided into those examining effects on sessile encrusting organisms, large mobile grazers (e.g., echinoids), and microcrustaceans.

Parika scaber is the only fish in north-eastern New Zealand known to consume encrusting invertebrates, such as sponges and ascidians (Russell 1983). The data available suggest that it may have a localised effect on the cover of some preferred species, but is probably not of general importance as a structuring force in these communities. A. M. Ayling (1981) tested their effect by conducting an exclusion experiment at two locations supporting low and high densities of *P. scaber* in the Leigh Marine Reserve. The exclusion treatments were simple, but ingenious, consisting of a horizontal shield close to the substratum. Fish could swim underneath, but could not orientate vertically to feed. The exclusion had a substantial effect on the cover of a number of preferred sponges, ascidians, and polyzoans at the high-density location, but not at the other. *P. scaber* only appear to reach those high densities in deep reef habitats, which make up a relatively small proportion of the total reef area. Further experiments at other sites in the Leigh Marine Reserve have found no effects of predation by *P. scaber* on sponges or ascidians (A. L. Ayling 1978; Stocker 1984), but localised effects of monacanthid fishes have been detected in temperate Australian waters (Russ 1980; Keough 1984).

Choat & Ayling's (1987) comparison of fish distribution with habitat types was conceived to examine the potential for fish to structure benthic habitats through effects on large invertebrate grazers, such as the echinoid *Evechinus chloroticus*. As a general pattern, urchins and associated grazing gastropods appear to dominate subtidal reefs at an intermediate depth range, producing relatively

stable coralline crust/turf belts (Choat & Schiel 1982; Schiel 1988). Large fish preying on these grazers preferentially forage over the urchin-grazed/turf habitats, rather than within those dominated by macroalgae. Hence, their feeding would not be responsible for maintaining the integrity of kelp forests by removing algal grazers.

It is possible that heavy predation in urchin-grazed areas eventually leads to the establishment of kelp forests. Andrew & Choat (1982) excluded predatory fish from plots in a heavily urchin-grazed area to test what impact fish were having on urchin numbers. While fish did reduce the densities of crevice-bound juveniles, enough survived to an adult size to maintain kelp free areas. Thus, while fish may be having an effect on certain size classes of important grazers, it may not follow that they are indirectly responsible for general patterns in habitat structure (see also Andrew 1988). At other temperate locations, fishes may assume greater importance as predators on sea urchins (Cowan 1983).

Since amphipods are the most important food source consumed by benthic carnivores, an effect of fish predation upon them has been considered likely, and to have important consequences. Many amphipods and other microcrustaceans are grazers, and are thought to play an important role in affecting macroalgae and seagrass communities in the Northern Hemisphere (Bernstein & Jung 1979; Zimmerman et al. 1979; Brawley & Adey 1981; Norton & Benson 1983). Indeed there is a general, although largely unsubstantiated, opinion that fish regulate the abundances of microcrustaceans associated with vegetated habitats (see Choat 1982).

There is no strong support for the latter view from studies carried out in north-eastern New Zealand, although it remains to be unequivocally tested. Gammarid amphipods are a conspicuous component of the fauna associated with coralline turf and macroalgae (Jones 1981a, 1984a, 1984b; Choat & Kingett 1982; Sylvester 1986). A summer peak in abundance coincides with the recruitment of most reef fishes, which rely heavily on amphipods as a food source at this time. Choat & Kingett (1982) excluded fish from foraging over 2 m² plots of turf in an area frequented by *U. lineatus* and juvenile *C. auratus*. This 8-month study did not demonstrate an effect of fish predation on amphipods, ostracods, or polychaetes at this scale. However, given the likely mobility of amphipods, which may emerge into the plankton at night (MacDiarmid 1981), any effect of predation may only be measurable over a

considerably broader scale. If there really is no effect of predation, it may be because coralline turf is such a good refuge for amphipods that fish are exploiting only an insignificant proportion of the prey present. The role of turf as a refuge from fish predation has been examined elsewhere in New Zealand (Coull & Wells 1983).

Jones (1981a) is the only study to examine the potential impact of small labrids on the microcrustacean fauna associated with macroalgae. Fish were excluded by placing mesh bags over individual plants. Although this caused a massive increase in gammarid numbers, the predation effect could not be distinguished from an effect of the bags themselves. A preliminary examination of an area denuded of wrasses suggested that, with appropriate replication, such clearance techniques would be much more effective to examine fish impact.

The general picture emerging is not one of a strong influence of fish on invertebrate communities or habitat-structure—although species-specific, localised effects clearly occur. Most of the experiments carried out to date have been done without reference to the distribution, dynamics, and mobility of the prey species. They have been carried out on a small scale, at only one site, and over unjustified time periods. Most have serious design flaws, such as “pseudo-replication” (Jones 1981a; Andrew & Choat 1982) and may confound real predator effects with cage artefacts (Jones 1981a).

In future, greater consideration must be given to determining the appropriate scale at which to examine the effects of predation, based on the distribution and mobility of the prey. The appropriate temporal scale will depend on the life history and dynamics of prey species, which is a necessary background for determining the importance of predator effects, relative to other processes. When cages are necessary, considerable imagination must go into the design and deployment of cages and cage controls, and collecting direct information of the relative use of cage control and open control treatments. Fish removal techniques, which have been used in the past to answer other questions (e.g., Thompson & Jones 1983; Jones 1984b, 1984c) represent a real alternative when looking at larger-scale effects. We can only expect generalisations to emerge by repeating experiments at other places and times (Underwood 1983).

The impact of herbivores

Numerous experiments designed to exclude herbivorous fish have shown a substantial impact of fish grazing on tropical reefs (see reviews by Ogden & Lobel 1978; Hixon 1983). These results have been

stated to contrast to temperate reefs, where herbivorous fishes were considered to be rare and unimportant (Ogden & Lobel 1978). While true grazing herbivores, such as scarids and acanthurids, do not penetrate temperate systems, it has been pointed out that browsing herbivorous fish are common on temperate reefs and must therefore be considered as potentially important (Choat 1982). Although herbivores, in north-eastern New Zealand, comprise only a small proportion of the overall number of reef fish, they make up a substantial proportion of the biomass (Russell 1977: table 2). In view of this, Russell (1983) argued that the importance of fish herbivory has been largely underestimated. He stated, “it seems likely that the zone of short algal turf in shallow water on rocky reefs in north-eastern New Zealand is at least partially maintained by the activities of grazing fishes”.

Subsequent work on *O. pullus*, the only herbivore consuming large brown algae, has not supported this contention. Meekan (1986) examined the distribution of *O. pullus* and surveyed plants in high-density areas for the characteristic circular bite marks in the laminae. His quantitative description of this record of feeding showed that damage was very patchy and not extensive enough to have a major impact on kelp distribution. Herbivore exclusion experiments designed to test directly the impact of herbivores have proved difficult to deploy in the shallow surgy conditions of rocky reefs in north-eastern New Zealand (Schiel 1980). The potential roles played by browsers on red and green algae, such as the common *G. tricuspidata*, remain to be examined.

CONCLUSIONS

In asking precise questions about the ecology of rocky reef fish in north-eastern New Zealand, the compiled information provides some answers, and highlights issues yet to be resolved. Much is known about patterns of their distribution and abundance, but little about the underlying causes of these patterns. Much is known about their diets and foraging patterns, but further work is required to unequivocally establish the role fish predation plays in structuring the rocky reef system. While the “big” questions remain unanswered, there is a sound basis for establishing the appropriate techniques to solve these ecological problems.

Some tentative conclusions are emerging about the interactions between fish and their habitat. Choat

& Ayling (1987) have suggested "the biological structure of shallow reef habitats, especially the presence of algae, may determine the character of the predatory fish fauna, not vice versa". This model is largely supported here. However, it is clear that experiments testing the effect of the habitat on the fish, and vice versa, need to be repeated on larger spatial and temporal scales.

Spatial and temporal pattern in reef fish populations are likely to be caused by totally different sets of processes, which differ in their importance as scales of focus are expanded. These processes involve both pelagic and reef-associated phases of the life history, and their relative importance will only be distinguished by long-term studies, which monitor what happens to successive cohorts as they pass through each life history stage.

Studies on the ecology of temperate reef fishes have differed in approach from the early coral reef fish literature, in which questions were asked about abundance and structure in the context of large assemblages, and about the effects of fish "guilds" on prey communities (Ogden & Lobel 1978; Sale 1980). Temperate-climate workers have emphasised ontogenetic and species-specific differences in reef fish ecology. These differences will be an integral part of any general ecological models which develop for shallow reef environments.

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