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R G Cole

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## TROPHIC RELATIONSHIPS BETWEEN FISHES AND BENTHIC ORGANISMS ON NORTHEASTERN NEW ZEALAND REEFS

R.G. COLE

National Institute of Water and Atmospheric Research Ltd, PO Box 893, Nelson, New Zealand  
r.cole@niwa.cri.nz

EXPERIMENTAL ARTIFACTS  
FISH FEEDING  
GEOGRAPHIC CONSISTENCY  
HABITAT STRUCTURE  
NORTHEASTERN NEW ZEALAND

**ABSTRACT.** – The influence of fish feeding on New Zealand reefs is reviewed. Assemblages of seaweeds, grazers and fishes vary over latitudinal gradients and along gradients of wave exposure, and patterns in northeastern New Zealand may be distinct from those elsewhere in the North Island, and the remainder of New Zealand. There is little evidence of broadscale effects of feeding by fishes on seaweeds. At one marine reserve site, predation by fishes and / or spiny lobsters may limit the abundances of sea urchins. Further experimentation is needed to clarify the geographic consistency of predatory effects of fishes throughout New Zealand. Small mobile invertebrates which occupy seaweeds are thought to be important prey of young fishes, and perhaps to be major contributors to secondary productivity. The presence of seaweeds and harvesting by humans are thought to be major influences on the fish fauna of reefs. The conflicting requirements of replication and realism in experiments concerning the trophic impact of fishes is noted.

ARTEFACTS DUS A L'EXPERIMENTA-  
TION  
NUTRITION DES POISSONS  
COHERENCE GEOGRAPHIQUE  
STRUCTURE DE L'HABITAT  
NOUVELLE ZELANDE DU NORD-EST

**RÉSUMÉ.** – L'influence de la nutrition des Poissons sur les récifs de Nouvelle-Zélande est passée en revue. Les communautés des herbiers, des brouteurs et des Poissons varient selon des gradients latitudinaux et des gradients d'exposition aux vagues, et les distributions au nord-est de la Nouvelle-Zélande peuvent être différentes de celles de l'île du Nord et du reste de la Nouvelle-Zélande. Il y a peu de preuves concernant les effets à large échelle de la nutrition des Poissons sur l'herbier. En un point donné d'une réserve marine, la prédation par les Poissons et /ou par les Langoustes peut limiter l'abondance des Oursins. Des expériences sont encore nécessaires pour clarifier la cohérence géographique des effets de la prédation par les Poissons dans toute la Nouvelle-Zélande. Il semble que de petits invertébrés mobiles qui vivent dans les herbiers sont des proies importantes pour les jeunes Poissons, et qu'ils contribuent peut-être majoritairement à la production secondaire. La présence des herbiers et la pêche semblent influencer principalement la faune des Poissons des récifs. Le besoin d'une expérimentation répétée mais réaliste au sujet de l'impact de la nutrition des Poissons est mis en évidence.

### INTRODUCTION

Fishes are large, mobile organisms, which generally require large amounts of energy to support their existence. The high mobilities of fishes means that the spatial extent of their foraging can be great, while their size means that they are capable of consuming relatively large organisms. As fishes are also frequently abundant, their impact on benthic organisms is potentially large. Their sensory capabilities are well-developed, and they can capture highly mobile prey. It is in this context that I review recent studies regarding fishes and their prey in northeastern New Zealand. Of necessity, I consider other components of reef assemblages where they are relevant, but the

primary intention is to review the evidence for trophic impacts of fishes, and to also consider the impact of habitat morphology on fish activity.

Reefs on wave exposed coasts in northeastern New Zealand have been relatively thoroughly investigated (reviews of Andrew 1988, Creese 1988, Jones 1988, Schiel 1988). Much of this work has been carried out at Goat Island, which is in the Cape Rodney to Okakari Point Marine Reserve near Leigh (Fig. 1). The main habitat formers (*sensu* Jones & Andrew 1993) are fucalean and laminarian seaweeds, whose distributions the echinometrid sea urchin *Evechinus chloroticus* may alter (Andrew & Choat 1982). The behaviours and abundances of some fishes are in turn affected by seaweeds (Jones 1984a, Choat & Ayling 1987, Syms & Jones 1999).



Although seaweed – echinoid – fish interactions are relatively well-known, and reviews have drawn together summaries for many geographic regions (e.g. Chapman & Johnson 1990, Foster 1990, Santelices 1990, Schiel 1990, Underwood & Kennelly 1990), more recent observations from northeastern New Zealand reefs (Cole & Keuskamp 1998, Babcock *et al.* in press, Willis *et al.* ms). provide a rather different outlook from the 1988 reviews (see above). One focus here is to identify the geographic range over which extrapolation from experimental studies should be confined.

### Biogeographic patterns

Schiel (1990) noted that as more sites were visited, the number of similarities and generalisations decreased. His work (Schiel 1990, Schiel *et al.* 1995) has greatly increased the knowledge of more southern areas of New Zealand. On the west coast of Northland (Brook unpubl), and near Raglan/Kawhia (Cole pers obs) (see Fig. 1 for localities), reefal assemblages are quite different from those in northeastern New Zealand, with limited numbers of brown seaweeds except in the sublittoral fringe, and turfing red seaweeds, mussels, ascidians and sponges dominating the substratum. While the Coromandel coast in the early 1990s had a broadly similar appearance to the site described in the late 1970s by Choat and Schiel (1982), observations near Tauranga, Gisborne, and New Plymouth (Cole, pers obs) suggest that those areas too are quite different from those further north. One interesting observation in northeastern New Zealand is the absence of the dominant laminarian *Ecklonia radiata* on some very exposed and isolated pinnacles (Brook unpubl, Cole unpubl). Within the Marlborough Sounds, particularly Queen Charlotte Sound (Fig. 1), macrophytes other than *Carpophyllum flexuosum* and *C. maschalocarpum* are relatively rare, though the introduced seaweed *Undaria pinnatifida* occurs in shallow areas subject to wave disturbance. On the coasts of Abel Tasman National Park, large seaweeds are also rare, and grazers dominate (Davidson & Chadderton 1994). Curiously, given the intervening distance without mid-depth barrens, a pattern of mid-depth barrens bordered above and below by macroalgal stands, as found in northeastern New Zealand, has been described for Dusky Sound, Fiordland (Villouta *et al.* ms), though other Fiordland sites may differ (Schiel 1990).

### Patterns along gradients of wave exposure

Observations by Brook & Carlin (1992) in Northland, and others elsewhere (Grace 1983, Cole & Taylor unpubl, Cole pers obs) suggest that

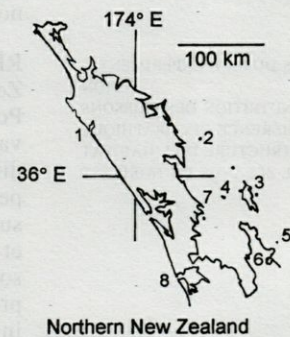
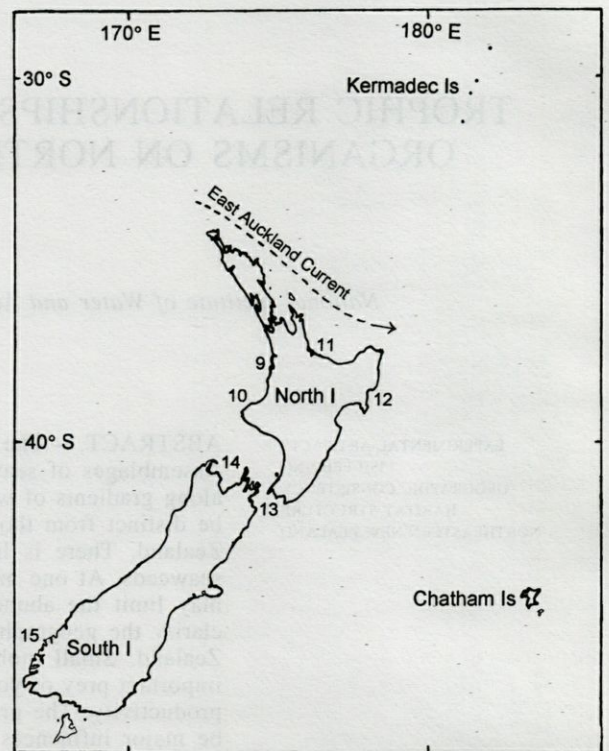


Fig. 1. – Map of New Zealand, showing localities mentioned in text, and influence of East Auckland Current. 1: Hokianga Harbour; 2: Poor Knights Is.; 3: Great Barrier/Rakitu Is.; 4: Little Barrier I.; 5: Mercury Is.; 6: Coromandel Peninsula; 7: Leigh; 8: Manukau Harbour; 9: Raglan/Kawhia; 10: New Plymouth; 11: Tauranga; 12: Gisborne; 13: Queen Charlotte Sound; 14: Abel Tasman National Park; 15: Fiordland. Kermadec Islands are approximately 800 km northeast of Auckland - see Cole *et al.* 1992 for map.

the vertical extent and lower depth limits of urchin barrens tend to decrease in shelter from wave action (Grace 1983). For example barrens habitat occurs on the western shores of Great Barrier Island, but not of southwestern Little Barrier Island, which has a shorter wave fetch from the southwest (Cole pers obs). Generally there is an increase in the abundance of *Carpophyllum flexuosum* and a decrease in the prevalence of *Ecklonia radiata*, as more sheltered areas are



encountered. This decrease of *Ecklonia* in shelter may be owing to several mechanisms: wave action limiting the effectiveness of grazing by sea urchins in shallow water (e.g. Himmelmann 1980), decreased survival of recruit or juvenile sea urchins in more sheltered water (Andrew & Choat 1985), wave-induced modifications to the morphology of *C. flexuosum* (Cole *et al.* unpubl data), and differential susceptibility of *C. flexuosum* and *Ecklonia* to a mass mortality agent (Cole & Babcock 1996).

### Descriptions of the fish fauna

Choat & Ayling (1987) described reef fish populations from a wide geographic range of sites in the North Island of New Zealand, although the emphasis was on those in northeastern areas. Francis (1996) drew on a large database of qualitative observations to divide the reef fish fauna of New Zealand (*a priori* separated into 16 regions) into eight geographic regions, on the basis of seven species distributional groups. Meekan & Choat (1997) documented differences in the abundances of herbivorous fish faunas on New Zealand, Australian, and Caribbean reefs, noting differences between mainland and offshore island faunas in northeastern New Zealand (see also Jones 1984, Choat & Ayling 1987). Subtropical currents are thought to be responsible for those patterns. Herbivorous fishes are clearly more speciose in the north, but may be abundant in some southern areas (Meekan & Choat 1997). Comparisons of this nature are difficult because of differing sample unit sizes among studies. Population size structures of fishes may differ between offshore islands and mainland coasts (Choat & Ayling 1987, Meekan & Choat 1997), and reserve and non-reserve areas (e.g. Cole *et al.* 1990, Davidson 1995, Cole & Keuskamp 1998).

### Effects of herbivorous fishes on seaweeds

The true character of the diets of nominally herbivorous fishes has only recently been determined (Clements & Choat 1997), with the most abundant "herbivore" on northeastern New Zealand coasts, *Girella tricuspidata*, being found to have a proportion of animal material in its diet. Silver drummer *Kyphosus sydneyanus*, and butterflyfish *Odax pullus* have been verified as true herbivores (Clements & Choat 1997). Meekan's (1986) study suggested that feeding by butterflyfish *O. pullus* (Odacidae) was too patchy in time and space to control the distribution of *Ecklonia* (*cf.* the related *O. cyanomelas* in New South Wales, Australia - Andrew & Jones 1990). At north-

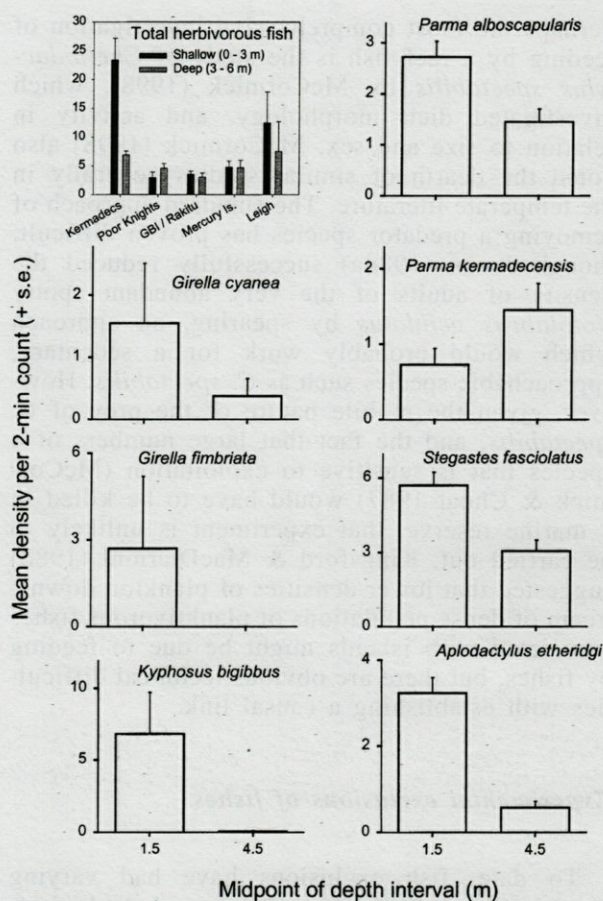


Fig. 2. - Densities of herbivorous fishes. Top left inset: Mean density (+ s.e.) of total herbivorous fishes at 5 localities in northeastern New Zealand. Data are from 2-min timed counts in 2 depth strata (0-3 m, 3-6 m). Location of sampling sites in Fig. 1. Remainder of plots: mean density (+ s.e.) of herbivorous fishes in 2-min timed counts in 2 depth strata at 3 sites at Kermadec Islands. Data derive from 3 sites sampled in May/ June 1992, with each site sampled 2 or 3 times over a 24 hr period.

eastern New Zealand offshore islands the territorial pomacentrid *Parma alboscappularis* may maintain small clearances as nest sites, presumably modifying the flora locally (Jones, Schiel, Creese unpubl). At the distant Kermadec Islands more species occur, with a kyphosid, a girellid, and several pomacentrids being abundant (Cole *et al.* 1992, Cole unpubl - Fig. 2), but there are few data to assess the likely effects of feeding by those fishes. There are also few quantitative data concerning the abundances of seaweeds at the Kermadec Islands (Schiel *et al.* 1986).

### Feeding by carnivorous fishes

Jones (1988) reviewed numerous studies of feeding by New Zealand carnivorous reef fishes.



Perhaps the most comprehensive investigation of feeding by a reef fish is the study of *Cheilodactylus spectabilis* by McCormick (1998), which investigated diet, morphology, and activity in relation to size and sex. McCormick (1998) also noted the dearth of similar studies generally in the temperate literature. The standard approach of removing a predator species has proven difficult, though Jones (1984a) successfully reduced the density of adults of the very abundant spotty *Notolabrus celidotus* by spearing, an approach which would probably work for a sedentary, approachable species such as *C. spectabilis*. However, given the mobile nature of the prey of *C. spectabilis*, and the fact that large numbers of a species that is sensitive to exploitation (McCormick & Choat 1987) would have to be killed in a marine reserve, that experiment is unlikely to be carried out. Kingsford & MacDiarmid (1988) suggested that lower densities of plankton downstream of dense populations of planktivorous fishes associated with islands might be due to feeding by fishes, but there are obvious technical difficulties with establishing a causal link.

#### *Experimental exclusions of fishes*

To date, fish exclusions have had varying results. Choat & Kingett (1982) and Andrew & Choat (1982) excluded fish from 2 m<sup>2</sup> areas of coralline flats, while Ayling (1981) prevented a monacanthid fish from feeding in 0.0625 m<sup>2</sup> areas at two sites. Choat & Kingett (1982) failed to detect any effect of excluding fish, though Jones (1988) suggested that this related to the mobility of the prey taxa. Ayling (1981) detected an effect at the site where the target fish species was abundant but not at another where it was not. Stocker (1986) showed that large benthic carnivorous fishes were unlikely to influence the abundance of the ascidian *Pseudodistoma novaezelandiae*, though small blennioids which sheltered within cages were suggested as a cause of a caging effect. Andrew & Choat (1982) suggested that the effect of fish predation on the echinoid *Evechinus chloroticus* which they detected was not important at the habitat level, as enough echinoids survived to maintain the habitat.

Experiments in which predators have been excluded require careful interpretation regarding possible caging effects (e.g. Kennelly 1983, Stocker 1986, Connell 1997). Jones (1981) encountered difficulties with differentiating caging effects from the effects of spotties feeding on epifaunal crustaceans of seaweeds. Taylor (1991) attempted to exclude fish from individual kelp heads in a design that included partial exclusions, but similar difficulties with epifaunal movement were encountered as in other systems (e.g. Edgar

& Aoki 1993). Approaches such as tethering (Danilowicz & Sale 1999), and video monitoring of reefs (Hixon & Carr 1997) have been used in studies of predation by fishes elsewhere, and to clearly separate handling artifacts from those of predation will require careful use of such techniques. Artifacts of experimentally investigating predation by fishes require further investigation on New Zealand reefs. Taylor (1998b) found that large proportions of the epifauna of a seaweed moved at night, so that any experimentally-induced increase in epifaunal abundance that might arise would likely dissipate across treatment area borders on a diel basis. The most successful experiments concerning predation have used isolated patch reefs (e.g. Hixon & Carr 1997). In coral reef lagoons such an environment may be natural, but isolated *Atrina zelandica* shells in soft sediments are one of the few parallels in temperate subtidal New Zealand of which I am aware.

Cole & Keuskamp (1998) assumed that fish predation was responsible for the greater rate of loss of experimentally transplanted *E. chloroticus* at reserve than at non-reserve sites, but without independent verification. They also presented a 10-year time-series of density of *Evechinus* at the same site as Andrew and Choat's (1982) study (which itself contained a series for 8 years), in which mean density of free-roaming adults declined from about 4 m<sup>-2</sup> to about 1 m<sup>-2</sup>. Differences in population size structure and crevice occupancy of the sea urchin between reserve and nearby coast consistent with a fish predation effect were evident 5 years earlier than Cole and Keuskamp's investigation (Fig. 3). Spiny lobsters (*Jasus edwardsii*) are usually the only potentially important invertebrate predators of echinoids in north-eastern New Zealand, as starfish are seldom abundant. Andrew & MacDiarmid (1991) concluded that there existed little evidence of an important effect of feeding by *Jasus* on the abundance of *Evechinus*. An experiment separating the effects of crustacean and piscine predators of echinoids remains to be carried out, though it should be technically possible (MacDiarmid pers comm).

The geographic consistency of marine reserve effects on large carnivores and subsequent trophic cascades is uncertain, and obviously influenced by the suite of predators present. Recent investigations suggest that blue cod are considerably larger, and perhaps more abundant, in the Long Island - Kokomohua Marine Reserve than on nearby non-reserve reefs (Davidson 1997, Davidson, Villouta, Cole unpubl data). Surveys of epibenthic gastropods (Gregory unpubl data) and triplefin fishes (Fig. 4) inside and outside the reserve, produced several patterns consistent with predation effects. A predator exclusion caging experiment over reefs is currently at the pilot study stage, but bioturbation, presumably by fish,



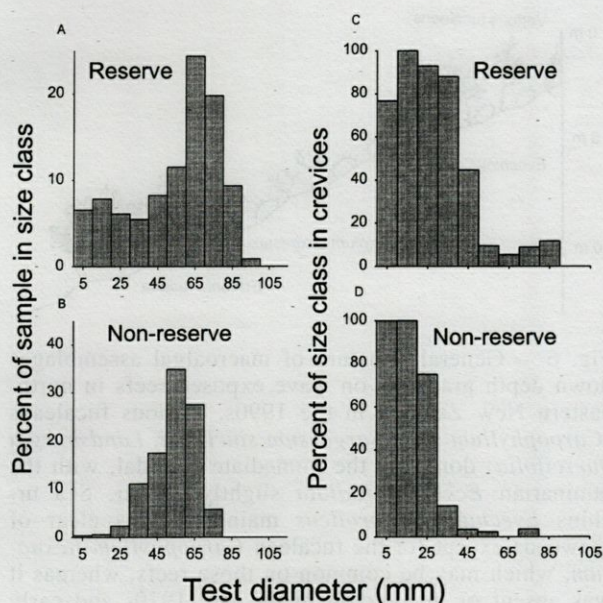


Fig. 3. – A, B: Population size structure of the sea urchin *Evechinus chloroticus* in coralline flats habitat at Cape Rodney to Okakari Point Marine Reserve (A:  $n = 460$  *Evechinus*) and the adjacent Leigh coast (B:  $n = 505$ ) in 1992. Data derive from 1 m<sup>2</sup> quadrat samples taken at 5 sites within each protection category (i.e. marine reserve and non-marine reserve). C, D: Percent of *E. chloroticus* size class occupying crevices at C: reserve, and D: non-reserve localities. Sampling as for population size structure above.

is also prominent in sandy areas adjacent to reefs. However, in another South Island marine reserve, Tonga Island (Fig. 1), clear effects on the abundances of fishes have been slower to emerge (Davidson unpubl data, Cole pers obs), although clear effects on the abundance of spiny lobsters have been documented (Davidson, Villouta & Cole unpubl data). The Long Island – Kokomohua Marine Reserve and Tonga Island Marine Reserve also afford opportunities to examine fish behaviour in an environment where the fish are neither strongly diver-negative nor strongly diver-positive (pers obs).

#### The role of small mobile invertebrates

The review of Jones (1988) documented the importance of small mobile invertebrates to the diets of juvenile fishes, finding that juveniles of almost all New Zealand benthic carnivorous fishes eat gammarid amphipods. Taylor (1998a) further showed that small mobile invertebrates which occupy seaweeds also contribute most of reefal secondary productivity (animals > 0.5 mm sieve mesh size). Recent evidence that seaweed habitats dominate the Cape Rodney to Okakari Point Marine Reserve is consistent with higher second-

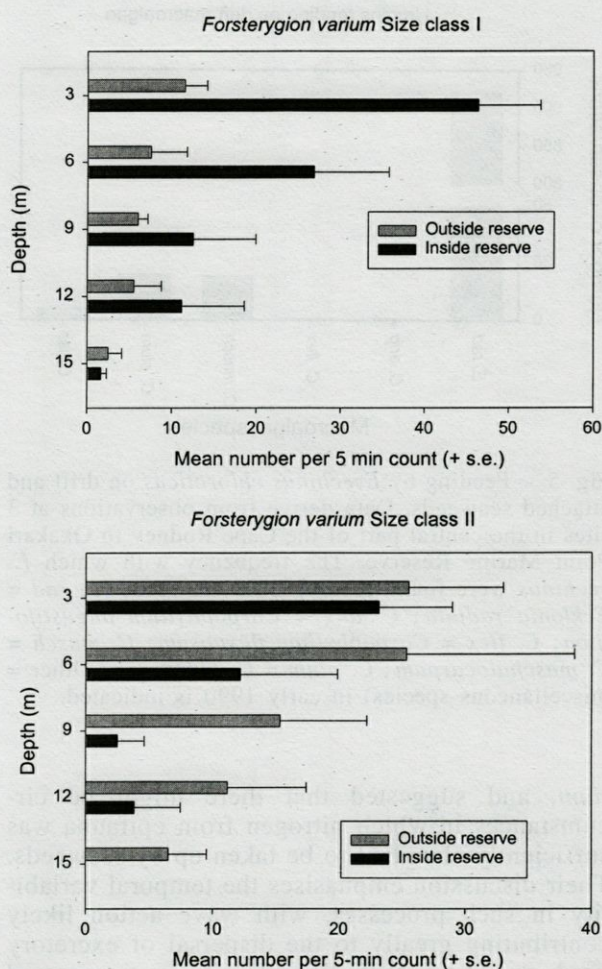


Fig. 4. – *Forsterygion varium*. Abundances of 2 size classes of *F. varium* in depth-stratified 5 min counts at 6 sites in Long Island - Kokomohua Marine Reserve and 6 sites on nearby coasts in Queen Charlotte Sound. Size class 1 represents the previous spring's recruits, while size class 2 comprises larger (presumably older) individuals. Sampling was done in March 1999, at sites where the habitat comprised boulder banks.

dary productivity in marine reserve areas than on the adjacent, harvested coast (Babcock *et al.* in press), a comparison which has been made in few other areas. However, the loss of virtually all of the kelp forest deeper than 10 m during kelp dieback in 1992/93 (Cole & Babcock 1996) did not lead to profound changes to the fish fauna (Cole pers obs). Though unquantified, this suggests that deeper kelp forests at least may not have as great an effect on piscine activity as some have interpreted (e.g. Holbrook *et al.* 1990).

Other investigations have probed the contribution that epifaunal organisms might make to seaweed growth. Taylor & Rees (1998) investigated the contribution of excretion from such epifaunal communities to the nitrogen budget of the fucalcan *Carpophyllum plumosum* var. *capillifo-*



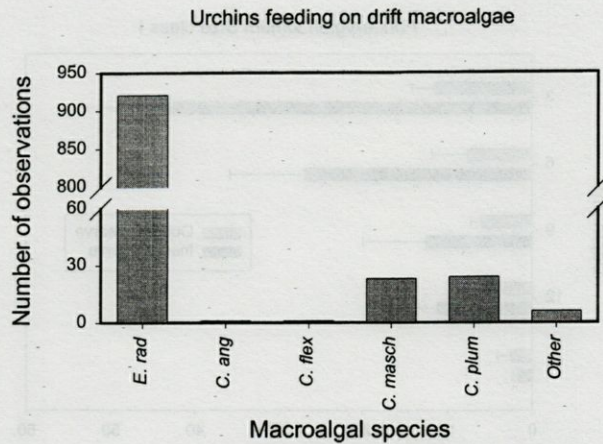


Fig. 5. – Feeding by *Evechinus chloroticus* on drift and attached seaweeds. Data derive from observations at 3 sites in the central part of the Cape Rodney to Okakari Point Marine Reserve. The frequency with which *Evechinus* were found feeding on 5 seaweeds (*E. rad* = *Ecklonia radiata*; *C. ang* = *Carpophyllum angustifolium*; *C. flex* = *Carpophyllum flexuosum*; *C. masch* = *C. maschalocarpum*; *C. plum* = *C. plumosum*; Other = miscellaneous species) in early 1990 is indicated.

*lium*, and suggested that there might be circumstances in which nitrogen from epifauna was sufficiently abundant to be taken up by seaweeds. Their discussion emphasises the temporal variability in such processes, with wave action likely contributing greatly to the dispersal of excretory products. The contribution of epifauna to seaweed nutrition may be less important, however, than their role as consumers of epiphytes. Gastropods occupy seaweeds (Andrew & MacDiarmid 1991), are highly mobile, and could also potentially contribute to seaweed nutrition (Norton 1992). They are also more readily manipulated than other epifaunal organisms, and though labour intensive, manipulations of density of gastropods to investigate effects on the host plant might be practical.

#### Habitat structure, seaweeds, epifauna, sea urchins, and fishes

Taylor & Cole (1994), and Taylor (1998c) documented the fauna of seaweeds in greater detail, suggesting that phytal architectures were important in determining the abundance and composition of the epifauna. While secondary productivity may be strongly driven by such physical structuring locally (Taylor 1998a), food webs on coralline-dominated areas may be enhanced by kelp debris from other habitats. In northeastern New Zealand the dominant component of drift seaweeds on subtidal reefs and shores is entire individuals and fragments of the laminarian *Ecklonia radiata* (Fig. 5). As in regions of South Africa

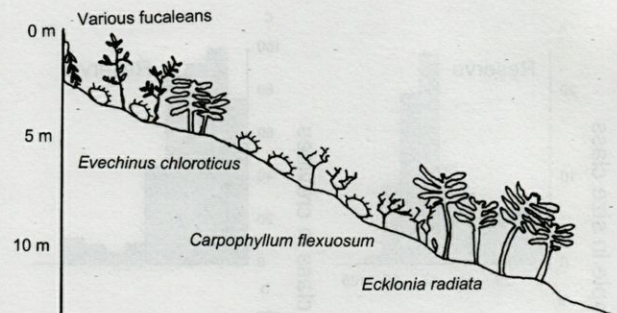


Fig. 6. – General structure of macroalgal assemblages down depth gradients on wave exposed reefs in north-eastern New Zealand in the 1990s. Various fucaleans (*Carpophyllum* spp., *Sargassum sinclairii*, *Landsburgia quercifolia*) dominate the immediate subtidal, with the laminarian *Ecklonia radiata* slightly deeper. Sea urchins *Evechinus chloroticus* maintain areas clear of seaweeds except for the fucal *Carpophyllum flexuosum*, which may be common on those reefs, whereas it was absent or uncommon in the late 1970s and early 1980s (Schiel 1988). *Evechinus* grazes among *C. flexuosum* stipes to depths of 8–10 m, where monospecific stands of *E. radiata* commence.

(Bustamante *et al.* 1995) and California (Harrold & Reed 1985) the dominant laminarian of north-eastern New Zealand reefs appears to export primary production beyond the borders of its stands. The New Zealand fucaleans are less widespread within reefs (e.g. Schiel 1988), their pneumatocysts may convey them out of the benthic subtidal when dislodged (Kingsford & Choat 1985, Kingsford 1992), and some species at least appear able to withstand considerable wave shock (e.g. Fig. 1 of Schiel 1988). The input of drift seaweed may modify the behaviour of sea urchins (Dean *et al.* 1984, Harrold & Reed 1985), thus contributing to the stability of habitats, and ultimately influencing fish presence and feeding rates (e.g. Choat & Ayling 1987). The greater prevalence of turfing corallines on flat sandstone reefs than on greywacke reefs near Goat Island (e.g. Ayling 1978, Ayling *et al.* 1981) is consistent with reduced grazing by *Evechinus*. It may be that the more rapid alteration of coralline flats to kelp forest in the western reserve (Babcock *et al.* in press, Cole pers obs) is due to greater delivery of drift from kelp forests onto coralline flats because of the shallower reef slope. Provision of seaweed food reduces movement of sea urchins (e.g. Harrold & Reed 1985), and agitation of sea urchins by kelp (real and artificial) may discourage entry of sea urchins into kelp stands (Vasquez & McPeak 1998).

Although not prevalent in early descriptions of the reefs of exposed coasts (Ayling 1974, Ayling *et al.* 1981, Choat & Schiel 1982), *Carpophyllum flexuosum* is currently moderately abundant on



Table I. – Number of visits of fishes in stands of *Carpophyllum flexuosum* and on adjacent coralline flats at Waterfall Reef. Data derive from 15-min observations ( $n = 18$ ) of 2 m  $\times$  2 m area,  $\times$  0.5 m high areas haphazardly demarcated in coralline flats and *C. flexuosum* between May and August 1991. Observations are of unmanipulated natural habitat.

Fish species	Visits to <i>C. flexuosum</i>	Visits to coralline flats
<i>Pagrus auratus</i>	69	111
<i>Parapercis colias</i>	28	81
<i>Parika scaber</i>	14	18
<i>Notolabrus celidotus</i>	62	71
<i>Notolabrus fucicola</i>	0	1
<i>Cheilodactylus spectabilis</i>	1	3
<i>Upeneichthys lineatus</i>	0	22

wave-exposed coasts in northeastern New Zealand, particularly near kelp forest borders (Fig. 6). That range expansion of *C. flexuosum* onto wave-exposed reefs had the potential to dramatically alter the nature of subtidal reefs. *C. flexuosum* is capable of forming dense stands, and reaching a large size (e.g. stipe lengths  $> 1.5$  m). However, *C. flexuosum* remains generally uncommon deeper than 10 m on wave-exposed coasts in northeastern New Zealand, despite a canopy of *Ecklonia* having been absent from some of those areas for much of 1993 (e.g. Cole & Babcock 1996). The reproductive characteristics and rapid growth of *Ecklonia*, combined with the patchy recruitment and wave-limited canopies of *C. flexuosum*, appear to limit colonisation. However, it is possible that repeated mortalities of *Ecklonia* could present the opportunity for colonisation of reefs below  $\sim 10$  m by *C. flexuosum*, and if it were able to form canopies there, it might competitively exclude *Ecklonia*. The potential effects on epifauna and fishes is unknown, though the laminarian is known to have a slightly different epifauna from the fucalcan (Taylor & Cole 1994).

The available evidence concerning the influence of macroalgal canopies on fishes mainly concerns the activity of small individuals in summer. Small spotties recruit to kelp canopies (Jones 1984a), and 0<sup>+</sup>-2<sup>+</sup> snapper and other fishes feed on coralline flats in summer (Kingett & Choat 1981, Choat & Ayling 1987). Such effects are mainly seasonal, though comparisons at other times of the year have suggested differences between habitats for some fishes (Table I). At the scale of km, the high densities of large carnivorous fishes in the kelp-dominated reserve (Babcock *et al.* in press, Willis *et al.* ms) are not consistent with expectations from early studies,

which suggested an association of those fishes with urchin-dominated habitats (Kingett & Choat 1981, Choat & Ayling 1987). However, Kingett & Choat (1981) emphasised the seasonal occurrence of small snapper on coralline flats, and most of Choat & Ayling's (1987) sampling was also done in summer.

### Predation by fishes in other systems

The other major site of investigation for the influence of predation by fishes has been the Manukau Harbour, where myliobatid rays feed on intertidal sand flats at high tide (Thrush *et al.* 1991, Thrush *et al.* 1994). The rays may influence the fauna of intertidal sandflats there seasonally, though again, the mobility of prey organisms and the high energy environment ensure that patterns at the scale of individual feeding scars are rapidly obscured (Thrush *et al.* 1991). A subsequent study there suggested that both rays and birds might have effects on infauna (Thrush *et al.* 1994), though interpretation of their relative importance was difficult because the rays were only present seasonally, whereas the birds were present year-round. Their conclusion that careful consideration needs to be given to the spatial and temporal context of an experiment (Thrush *et al.* 1994: p. 221) has been amplified in investigations of predation elsewhere (e.g. Hixon & Beets 1993, Hixon & Carr 1997). Mobility of prey has necessitated careful choice of scale and method of exclusion, and a knowledge of the behaviour of the prey.

### Historical patterns

Recent reviews have emphasised that the predatory fauna of reefs may have been considerably modified by humans, over a timescale of centuries for large mammals such as sea otters, and probably a timescale of decades for most fishes (e.g. Witman & Sebens 1992, Jackson 1997, Dayton *et al.* 1998). Archaeological analyses suggest that New Zealand Maori are unlikely to have had important effects on the marine fish species they exploited in pre-European times (e.g. Leach *et al.* 1997). A resident at Goat Island in the 1930s described going down to the shore with a garden fork to get crayfish for lunch, by wading (Matheson pers comm), and anecdotal evidence from personal acquaintances suggests that as recently as the 1960s the nearshore fish fauna in northeast New Zealand may have been considerably more abundant. Whether high abundances of carnivores might have had flow-on effects on the benthic fauna and flora remains conjecture, though the earliest descriptions of macroalgal assemblages at Goat Island (Bergquist 1960) bear little resemblance to subsequent descriptions. Such temporal



Table II. – Published studies which include subtidal experiments concerning fishes and invertebrates, which were carried out in northeastern New Zealand. MR indicates experiments done in the Cape Rodney to Okakari Point Marine Reserve, NMR indicates experiments done outside the marine reserve, CMR indicates experiments done in the central marine reserve (between Knot Rock and Waterfall Reef - see Cole 1994 for sites), BMR indicates experiments done within the marine reserve but outside the core area. x indicates experiment done in this area, – indicates no experiment done in this area.

Study	MR	NMR	CMR	BMR
Andrew 1986	x	-	x	-
Andrew & Choat 1982	x	-	x	-
Andrew & Choat 1985	x	-	x	x
Andrew & MacDiarmid 1991	x	-	x	x
Andrew & Stocker 1986	x	-	x	-
Ayling 1981	x	-	x	-
Choat & Andrew 1986	x	-	x	-
Choat & Ayling 1987	x	-	x	-
Choat & Kingett 1982	x	-	x	-
Cole & Keuskamp 1998	x	x	x	x
Connell & Jones 1991	x	-	x	-
Jones 1981	x	-	x	-
Jones 1984a	x	x	x	-
Jones 1984b	x	-	x	-
Jones & Thompson 1980	x	-	-	x
Kingett & Choat 1981	x	-	x	-
Schiel 1982	x	-	x	-
Stocker 1986	x	-	x	-
Stocker & Bergquist 1986	x	-	x	-
Stocker & Bergquist 1987	x	-	x	-
Syms & Jones 1999	x	-	x	-
Thompson & Jones 1983	x	-	x	-

fluctuations are distinct from events such as the decline in abundance of subtropical labrids through time at the Poor Knights Islands (Choat *et al.* 1988), which appears to mainly be controlled by larval supply, and longer-term alterations to the range of *Macrocystis pyrifera* which also appear to be linked to oceanographic events (Hay 1990). No-harvest marine reserves offer the opportunity to assess the capacity of existing populations to respond to cessation of harvesting, though a “global” effect of larval supply (fewer larvae settling due to fewer eggs being spawned) is unable to be addressed.

#### Geographic extrapolation

Of the 22 published subtidal experimental manipulations in northeastern New Zealand, almost all were done within one area of about 1 km

longshore extent within the Cape Rodney to Okakari Point Marine Reserve (Table II). Numerous studies (Cole *et al.* 1990, Cole 1994, Cole & Keuskamp 1998, Babcock *et al.* in press) showed that that area is now quite different from most of the rest of (a) the Cape Rodney to Okakari Point Marine Reserve, and (b) the remainder of the coast. It is visited by large numbers of people, some of whom feed either food they have brought with them, or benthic organisms found within the reserve, to fish. The *Modiolus* beds noted in Andrew & Stocker (1986) were no longer present in the late 1980s, possibly due to divers breaking up the mussels to attract fish (pers obs). The decline of the abundance of the sea urchin *Evechinus* in some areas of the marine reserve (e.g. Cole & Keuskamp 1998) may have also been accelerated by such activities (pers obs). Numerous commentaries have noted the advantages of conducting research in marine reserves (Ballantine 1991, Creese & Jeffs 1993), and clearly if the goal is to understand natural systems, research in such areas is essential. However, extrapolating the results of some research from marine reserves to other areas may be misleading, and the results of experiments in marine reserves need not necessarily apply to the wider coast. Comparisons of experiments conducted inside and outside marine reserves will be instrumental in revealing the type of impact human harvesting is having on reef systems.

#### Scales of natural disturbance : replication vs realism

An appreciation of the importance of scale for interpreting the results of experiments has developed in recent years (e.g. Dayton & Tegner 1984, Thrush *et al.* 1996). One experiment examining the effects of different scales of macroalgal clearance has been carried out in northeastern New Zealand (Syms & Jones 1999, Cole unpubl), along with another examining the response of different sized defaunations of triplefins (Syms & Jones 1999). Like similar studies (e.g. Thrush *et al.* 1996) those experiments addressed a relatively small range of spatial scales (in the case of Syms & Jones 1999 and Cole unpubl, 4 m<sup>2</sup> – 100 m<sup>2</sup>). The scale of the experimental macroalgal clearances were greatly exceeded by the scale of subsequent natural macroalgal mortalities (e.g. Cole & Babcock 1996). Generally there are practical constraints on the size of area that can be manipulated with replication. For researchers whose results may lead to management decisions, the possibility that their experiments are carried out at scales that render their results irrelevant to managers must be a concern. The alternative is to carry out very large unreplicated studies, and sacrifice replication to realism (e.g. Pridmore *et*



al. 1991, Thrush *et al.* 1995). Personally I favour realism, but there are other approaches to addressing such difficulties (Thrush *et al.* 1997a). Unfortunately such large studies are expensive, and the best example I am aware of was carried out (with replicate sites) at the level of the fishery (Schiel 1993). Anticipating scale-dependent effects and making predictions at scales which are relevant to management will become more manageable as our understanding of reefal systems develops further (Thrush *et al.* 1997b).

As noted above, humans have very efficiently modified the abundances and population size structures of reef fishes at very large scales. It might therefore be expected that fish exclusions in marine reserves would produce dramatic effects on the abundance and population structure of their prey. To date most of the experimental exclusions have been small (e.g. 2 m<sup>2</sup> – Andrew and Choat 1982, Choat & Kingett 1982), and it is at these scales that experimental artifacts are most likely to emerge rapidly. As marine reserves are established in areas with wave climates that permit larger cages to be deployed, more sophisticated methods of assessing artifacts develop, and an appreciation of the difficulties of scaling experimental results accrues, better evidence will be gathered regarding the influence of humans.

## CONCLUSIONS

Studies of the impacts of fish-feeding on reefs in New Zealand have mainly been done in one small area of northeastern New Zealand where both fishes and spiny lobsters are abundant. Much of the rest of New Zealand has a quite different fauna and flora. There is little evidence that herbivorous fishes influence seaweeds in northeastern New Zealand. There is clear evidence that predation at one well-studied site is responsible for patterns of sea urchin size structure, and perhaps the distribution of habitats, but it is not clear whether fish or lobsters are the predators. The location of most reefal investigations to date is a marine reserve, and marine reserves will continue to be a focus for investigations of fish feeding. However, a greater emphasis on geographical consistency of effects, and comparisons of experiments carried out in reserves with those done outside reserves will afford a greater understanding of the influence of the feeding of fishes on benthic organisms.

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