# Interrelations between planktivorous reef fish and zooplankton in temperate waters

## M. J. Kingsford*, A. B. MacDiarmid**

University of Auckland, Department of Zoology, Marine Laboratory, R. D. Leigh, New Zealand

ABSTRACT: Interrelations between zooplanktivorous fish and zooplankton were examined at the Poor Knights Islands 20 km off the east coast of Northland, New Zealand from 1980 to 1983. The pomacentrid *Chromis dispilus* was the most abundant planktivore at all locations; high densities of other planktivores were also found. The rankings of these species varied considerably among locations. These differences may have been due in part to *Caprodon longimanus* (Serranidae), *Scorpis violaceus* (Kyphosidae), and *Decapterus koheru* (Carangidae) making forays for food away from the immediate vicinity of rocky reefs. The hypothesis that fish have a localised effect on zooplankton was investigated in detail within a small reef area ($\sim 2500$ m$^2$) on 7 separate occasions. Distribution patterns of planktivorous fish changed according to current direction. Fish were always most abundant on the incurrent side of the reef and within an archway during the day. Large differences in densities of zooplankton were detected along a 200 m transect where samples were taken upcurrent, within, and downcurrent of the archway during the day. Lowest zooplankton densities were usually found in the archway where planktivorous fish were abundant. At night when fish were absent from the water column, there was a trend for highest abundances of plankton within the arch, relative to upcurrent and downcurrent sites. A similar 200 m transect parallel to the arch, but 1 km offshore where planktivorous fish were absent, showed no significant differences in density of plankton along its length during the day or night. Zooplankters that showed greatest reductions in density in the vicinity of feeding fish were most abundant in the guts of *C. dispilus* sampled from the arch. Estimates of removal rates of zooplankters by fish based on concurrent estimates of fish densities, plankton, feeding rates, diet of fish and current speeds suggest that fish were capable of causing the measured reductions in zooplankton concentrations through the archway. The diets of *C. dispilus* changed among sampling occasions and corresponded partly to changes in the composition of zooplankton captured in nets. Accordingly, any effect that fish have on zooplankton may change between times. Ecological consequences of predation by fish are discussed in terms of zooplankton communities, fish, and rocky reef environments.

## INTRODUCTION

The impact of planktivorous fish on zooplankton has been well documented in freshwater lakes (reviews in O'Brien 1979, Lazzaro 1987). Studies suggest that fish predation may influence species composition, size frequency, morphology, and life histories of zooplankton, as well as the evolution of vertical migration (Brook & Dodson 1965, Zaret & Kerfoot 1975, Kerfoot 1980, Lynch 1980, Gliwicz 1986). Furthermore, by structuring populations of herbivorous zooplankters fish may indirectly cause changes in the mean body size and density of phytoplankton (Vanni 1986). The removal of zooplankters may also transform benthic habitats by increasing detrital loadings previously reduced by these filter feeders. Lazzaro (1987) concluded 'in addition to competition for food and nutrient limitation, predation is generally recognized as an important driving force structuring communities in freshwater systems'.

In contrast to small lakes, marine reef environments have a major input of zooplankton from oceanic currents. Although qualitative (Ebeling & Bray 1976, Hobson & Chess 1976, 1978) and some quantitative studies (Ebeling et al. 1980, Williams & Hatcher 1983, Larson & DeMartini 1984) indicate that large numbers of planktivorous fish are associated with reefs, the interrelations between these fish and their zooplankton prey have received little attention.

Present addresses:
* Zoology Department AO8, School of Biological Sciences, University of Sydney, NSW 2006, Australia
** Fisheries Research Centre, Greta Point, PO Box 297, Wellington, New Zealand

Recent studies indicate a number of potential relations between reef fish, plankton, and reef. Supply of zooplankton may influence the growth and patterns of distribution of reef fish (Bray 1981, Jones 1986). Fish in turn may affect densities and composition of zooplankton passing over reefs (Coates 1980, Bray 1981, Hamner et al. in press), as well as the input of nutrients to reefs (Bray et al. 1981, Bailey & Robertson 1982, Robertson 1982, Bray et al. 1986). Further, Gaines & Roughgarden (1987) suggested that planktivorous reef fish may influence the recruitment patterns of intertidal barnacles by consuming large numbers of incoming cyprid larvae. The relationship emphasized is the localised effect these fish have on the zooplankton, rather than the converse (e.g. Ogawa & Nakahara 1979). The implications from these investigations are that diurnal planktivorous reef fish are an important component of a reef fauna and act in ways analogous to planktivorous fish in freshwater environments. Accordingly, they warrant further attention.

The aim of this study was to describe interrelations between abundances of zooplankton and feeding activity of planktivorous reef fish at a group of islands off the northeastern coast of New Zealand. The supply of zooplankton to areas of reef is notoriously variable over short periods of time due to complex hydrological factors (Hamner & Hauri 1977, 1981). Without information on currents it is impossible to assess whether plankton and fish sampled at different sites are interrelated. In many studies, plankton have been sampled on different days to the fish (for data on diet), making it difficult to draw conclusions concerning relationships between the two (e.g. Gaines & Roughgarden 1987). Accordingly, our assessment of the relation between fish and zooplankton incorporates concurrent measures of fish abundance, feeding activity, and diet as well as densities of plankton, current direction, and speed. Emphasis was placed on examining these variables repeatedly within a small area of reef (2500 m$^2$) over short periods of time. An important component of the study was that sampling programmes were designed to differentiate the effect of location on densities of zooplankton from the effect due to fish.

## MATERIALS AND METHODS

**Study area.** Planktivorous fish and their prey were examined at the Poor Knights Islands off the northeastern coast of New Zealand (Fig. 1). Seven visits of 3 to 5 d were made to the islands between February 1980 and May 1983. The islands usually are exposed to the East Auckland current which flows in a SE direction (Denham et al. 1984). Superimposed on this there is a strong N–S current which reverses direction depending
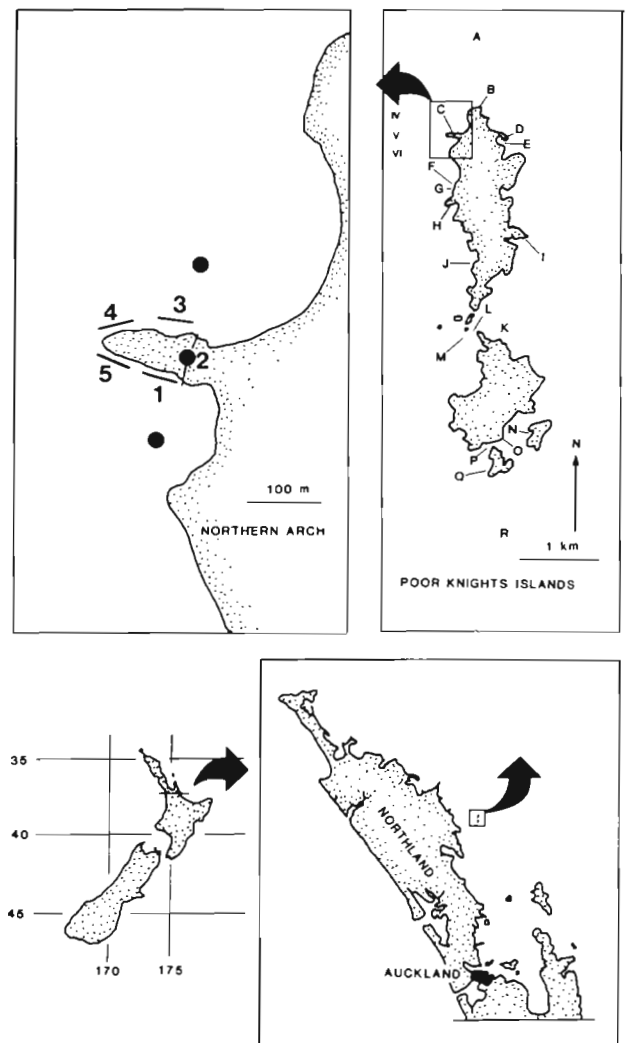


Fig. 1. New Zealand (lower left), location of Poor Knights Islands off the coast of Northland, position of sampling stations around the islands, and details of 'Northern Arch' study site with fish count areas (numbered bars) as well as approximate positions of plankton sampling stations (Stns I, II, III; solid circles). Three other stations (IV, V, VI) were spaced equidistant and parallel to these, 1 km to the west

on the state of the tide (see 'Results'). These currents carry zooplankton past the islands providing a potential source of food for the resident population of reef fish.

**Project 1: Densities of planktivorous reef fish and zooplankton around the Poor Knights Islands.** The aims of this project were 3-fold: (1) to describe the abundances of fish around the islands; (2) to compare the densities of zooplankton in areas where fish were abundant with areas where they were absent; (3) to carry out a preliminary investigation of the diets of fish (for fish fauna see 'Results').

Fish were counted visually using SCUBA in 5 replicate transects at 18 stations around the Poor Knights

and at stations 800 m to the north and south of the group (Fig. 1). Planktivore densities were expressed as number per unit volume of seawater (9000 m$^3$). Fish often fed around steep drop offs exceeding 50 m in water depth. Measures of area would have given an inappropriate picture of the distribution of these fish in a 3-dimensional environment. Transects measured 25 m long, 12 m wide and had a maximum depth of 30 m. A tape marked the length of transects. The islands are exposed to winds from all directions, thus the completion of counts at all stations took 2 yr. Temporal variability in fish abundances is addressed later in this paper. Fish were identified according to Paulin & Stewart (1985).

Zooplankton was sampled using vertical hauls with a conical plankton net of 0.28 mm mesh and a mouth diameter of 0.8 m. Mesh size was chosen on the basis of information we had on the size of prey captured from fish caught at Leigh on the coast (M.J.K. & A.B.McD. unpubl.). Zooplankton samples were preserved in 10 % formalin and 3 subsamples were analysed from each. The number of organisms was recorded and identifications were made to the generic level where possible.

Zooplankton was sampled at Stns A, H, J, L, Q, and R (Fig. 1) between 14:00 and 16:00 h (5 Feb 1980). At each site 30 m vertical hauls were made. Three replicate hauls were made at Stns A and L, but at other stations single hauls were made to expedite the complete sampling project in as short a time as possible, so minimizing variation due to time of day and state of tide. Currents flowed from north to south during sampling.

A total of 40 specimens of 5 species of fish (n in 'Results') were speared for gut analyses at site J (5 Feb 1980). Gut contents were preserved immediately after collection in 10 % formalin. Number and percentage representation of prey (using the grid method; Jones 1968) were recorded. In some cases the size-frequency distributions of prey was recorded in each fish.

**Project 2: Local distribution patterns of fish and zooplankton around a subtidal archway.** The results of Project 1 suggest that zooplankton densities were lowest where fish were abundant. A more detailed study was carried out at a small area of reef at Stn C. To test the hypothesis that fish affect abundances of zooplankton, densities of plankton were measured in an area where planktivorous fish were feeding during the day, but were absent from the water column at night. Densities of zooplankton were quantified along a 200 m transect where samples were taken upcurrent (Stn I), within (Stn II)), and downcurrent (Stn III) of an aggregation of feeding fish over a 30 h period. The predictable location of fish in a large subtidal archway (Northern Arch) allowed this procedure. The arch was approximately 4 to 5 m wide at the surface and

widened with depth to 10 to 15 m at the bottom ($\sim$ 30 m deep).

Densities of fish, plankton abundances, speed and direction of current, and feeding rates of fish were measured over a 2 h period on 5 occasions; 3 times during the day and twice at night (8 to 9 Oct 1982). The procedure we followed during the day was to drop a drogue to indicate the direction of current in the archway. One of us took 5 replicate measurements of current speed whilst SCUBA diving in the arch by timing the passage of particles past a 0.5 m$^2$ quadrat; fish counts were then commenced. Densities of fish were measured in 5 areas around the arch (Fig. 1). Within each area fish were counted in five 10 × 10 m transects to a depth of 20 m and were expressed as number per 2000 m$^3$. Another diver travelled 80 to 100 m to the upcurrent side of the arch and released 10 drogues, spaced 10 m apart. Fins of the drogues hung to 1 m depth. Three replicate vertical plankton hauls, 20 m depth to the surface were taken 100 m upcurrent, within, and 100 m downcurrent of the arch. Movements of the drogues were plotted on a map during this period. Position was calculated from compass bearings or estimated distances from rock faces. Once zooplankton was sampled the second diver recorded bite rates of 10 to 15 *Chromis dispilus* in the archway. *C. dispilus* were easily the most abundant planktivores and the only fish that allowed us to measure bite rates on all occasions. The action of feeding is well defined, and feeding rates were calculated as number of bites per minute. It was assumed that each bite captured a single item of food. Toward the end of each day, 21 to 22 *C. dispilus* were speared for analyses of their gut contents. Removal rates of zooplankton (see sampling of fish and zooplankton) were calculated for the 2 sampling occasions completed just before the fish were speared. Densities of fish used, D, in the calculation of rate of removal were those in the archway only (Area 2, Fig. 1). At night the full procedure was followed except that the numbers of fish and the current direction were measured only in the archway.

Removal rates of single prey categories from the water column were calculated using the formula below. Mean densities of fish and zooplankton were expressed as number per 2000 m$^3$.

$$T_X = \frac{a_X - b_X}{(D)\ (B)\ (N_X)/100} \quad (1)$$

where T = time required to reduce the abundance of a plankter category found upcurrent, to the densities found behind an aggregation of feeding fish; $a_X$ = mean density of prey category X upcurrent of fish; $b_X$ = mean density of prey category X behind an aggregation of feeding fish; D = mean density of the most abundant planktivore *Chromis dispilus*; B = mean bite

rate of *C. dispilus* measured concurrently with plankton densities in the area; $N_X$ = numerical percentage of prey category X in the diet of *C. dispilus*. The information obtained was used to assess whether patterns of zooplankton distribution could be attributed to fish.

Further sampling was carried out on 28 to 29 May 1983 along 2 transects. Each transect was 200 m long, with 3 sampling positions spaced at 100 m intervals. One transect went through Northern Arch (as described above), the other was parallel, but 1 km to the west of the arch (Stns IV, V and VI; Fig. 1). These transects were sampled on 2 occasions, when planktivores were feeding during the day and when planktivores were absent from the water column at night. We hypothesized that zooplankton travelling in a unidirectional current would exhibit no changes in density along the transect west of the arch. At Northern Arch, however, a reduction in densities of zooplankton was expected where the fish fed in the archway during the day. In addition to our major aim (see above) we wanted to: (1) compare abundances of zooplankton near to and away from the islands for a comparison with patterns we found in Project 1, and (2) compare densities of zooplankton and fish around the arch to those found in October 1982. It was possible that a different assemblage of zooplankton could alter the feeding behaviour of fish and any impact they had on composition of zooplankton downcurrent. Sampling procedure was the same as in the first part of this project, except that fish were counted in an additional area around the arch, between Areas 4 and 1 (Fig. 1).

## RESULTS

### Project 1: Densities of planktivorous reef fish and zooplankton around the Poor Knights Islands

Planktivorous reef fish were absent from the 2 offshore Stns A and R (Fig. 1). However, densities were high at all locations around the islands (Table 1). Of the 11 species occurring in the top 30 m of the water column, *Chromis dispilus* was most abundant at all island stations with a mean density of 1125 ± 181 (SE) per 9000 m³ The larger planktivores *Scorpis violaceus*, *Caprodon longimanus*, and *Decapterus koheru* occurred in lower and more variable densities, ranging from 436 to 0 per 9000 m³ among stations. Consistently low densities of *Caesioperca lepidoptera*, *Pseudocaranx dentex*, and *Scorpis aequipinnis* were found near the islands. The remaining 4 species occurred in low densities at a total of only 1 to 3 stations (Table 1). With the exception of *C. dispilus* the rank abundance of fish varied among locations (Table 1). This pattern was most conspicuous for *C. longimanus*, *S. violaceus*, and

*D. koheru*. The large standard errors for all abundant species reflected their patchy distributions. Fish generally aggregated in large feeding schools, often comprised of several species.

There were substantial differences among fish species in the prey types dominant in their diets (Table 2). Calanoid copepods were taken in large numbers by juvenile and adult *Chromis dispilus*. Adults, however, consumed a larger proportion of appendicularians, mainly *Oikopleura* spp. Both *Decapterus koheru* and *Scorpis violaceus* took large numbers of macrocrustaceans, especially euphausiids. *S. violaceus* fed also upon gelatinous zooplankton, predominantly siphonophores. *Caprodon longimanus* and *Caesioperca lepidoptera* fed almost exclusively on doliolids at the time of sampling. With the exception of juvenile *C. dispilus*, 75 to 98 % of the diet of planktivores was composed of large sized food items over 1.5 mm in total length.

The densities of zooplankton sampled upcurrent of the group (Stn A) were consistently higher than those near the islands (Fig. 2). All major groups exhibited lowest densities at island stations. The pattern was weak for copepod densities which were again high, 800 m south of the islands (Stn R). Appendicularians and non-copepod groups remained at low levels south of the islands. Aggregations of pelagic planktivores were not observed away from the islands at this time (Stns A and R).
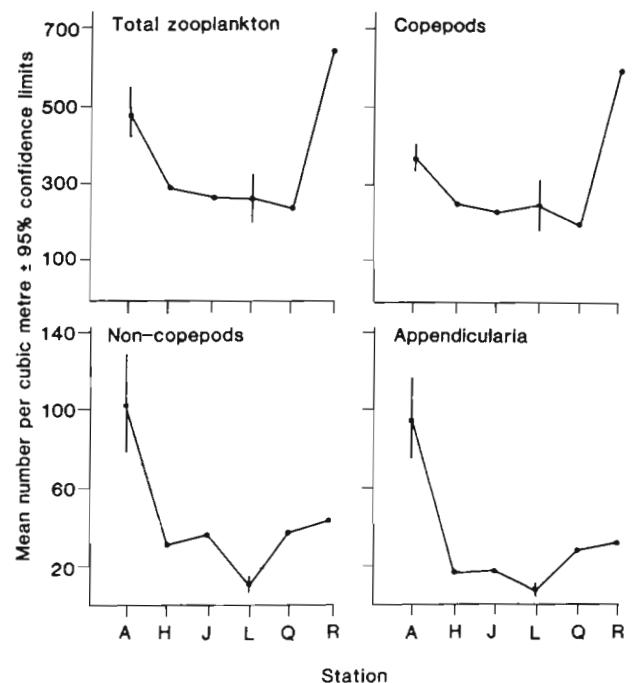


Fig. 2. Abundance of zooplankton near to and off-shore from the Poor Knights Islands between 14:00 and 16:30 h on 5 Feb 1980. Positions of stations shown in Fig. 1. Replicated hauls (*n* = 3) taken at Stns A and L only

Table 1. Densities of 11 species of planktivorous reef fish at stations around the Poor Knights Islands (mean number ± SE per 9000 m$^3$). Stations were ordered north to south according to Fig. 1 (B–Q). The year each station was sampled and the depth of water column are also shown

| Species | | B | C | D | E | F | G | H | I | J | K | L | M | N | O | P | Q |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Chromis dispilus* | X̄ | 766 | 2234 | 410 | 209 | 579 | 446 | 1213 | 570 | 1730 | 1171 | 1695 | 586 | 747 | 1499 | 1375 | 2781 |
| | SE | 410 | 675 | 154 | 96 | 235 | 123 | 610 | 304 | 639 | 310 | 886 | 236 | 193 | 576 | 865 | 360 |
| *Chromis hypsilepis* | X̄ | 0 | 0 | 0 | 0 | 0.4 | 0 | 0 | 0 | 0 | 0 | 0.5 | 0 | 0 | 0 | 0 | 0 |
| | SE | | | | | 0.4 | | | | | | 0.5 | | | | | |
| *Caprodon longimanus* | X̄ | 422 | 342 | 0.5 | 44 | 3.6 | 1.8 | 6.9 | 93 | 5.1 | 0 | 0.3 | 0 | 0 | 14 | 0 | 5.1 |
| | SE | 169 | 155 | 0.5 | 25 | 1.8 | 1.8 | 3.3 | 78 | 2.8 | | 0.3 | | | 7.0 | | 2.6 |
| *Scorpis violaceus* | X̄ | 270 | 429 | 81 | 0.4 | 29 | 22 | 11.7 | 21 | 0.8 | 436 | 12 | 4.7 | 0.2 | 0 | 99 | 0.6 |
| | SE | 270 | 410 | 41 | 0.4 | 14 | 14 | 11.7 | 19 | 0.5 | 149 | 9.1 | 3.5 | 0.2 | | 99 | 0.4 |
| *Scorpis aequipinnis* | X̄ | 2 | 0.5 | 1.1 | 0 | 0 | 1.4 | 0.5 | 0 | 0.6 | 0.5 | 0 | 3.2 | 1.1 | 3.6 | 0 | 0.6 |
| | SE | 0.7 | 0.2 | 1.1 | | | 1.4 | 0.5 | | 0.4 | 0.5 | | 1.5 | 1.8 | 2.2 | | 0.3 |
| *Decapterus koheru* | X̄ | 7 | 0.2 | 130 | 2 | 5 | 7.2 | 37 | 11 | 8.1 | 0 | 167 | 20 | 194 | 0.2 | 80 | 0.4 |
| | SE | 7 | 0.2 | 107 | 2 | 5 | 7.2 | 18 | 10 | 8.1 | | 162 | 15 | 33 | 0.2 | 79 | 0.4 |
| *Trachurus novaezelandiae* | X̄ | 0 | 0 | 0.5 | 0 | 6.3 | 0 | 0 | 0 | 0 | 5.4 | 0 | 0 | 0 | 0 | 0 | 0 |
| | SE | | | 0.5 | | 6.3 | | | | | 5.4 | | | | | | |
| *Pseudocaranx dentex* | X̄ | 72 | 0.3 | 0.5 | 0 | 3.6 | 1 | 3.6 | 0 | 0.6 | 0 | 0 | 0.5 | 0.2 | 0.4 | 1.4 | 5.8 |
| | SE | 72 | 0.3 | 0.5 | | 3.6 | 1 | 2.3 | | 0.6 | | | 0.5 | 0.2 | 0.3 | 1.1 | 2.2 |
| *Caesioperca lepidoptera* | X̄ | 0 | 7.0 | 0 | 0.2 | 0.2 | 2.7 | 5.4 | 0.4 | 4 | 0 | 0 | 0 | 0 | 8.1 | 0 | 0 |
| | SE | | 2.5 | | 0.2 | 0.2 | 2.2 | 4.9 | 0.4 | 1.8 | | | | | 5.7 | | |
| *Labracoglossa nitida* | X̄ | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 5.4 | 0 | 0 | 0 | 0 | 0 | 0 |
| | SE | | | | | | | | | | 5.4 | | | | | | |
| *Scomber australasicus* | X̄ | 0 | 0 | 0 | 0 | 0 | 0.9 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | SE | | | | | | 0.9 | | | | | | | | | | |
| Total | X̄ | 1539 | 3013 | 724 | 256 | 627 | 483 | 1278 | 695 | 1749 | 1618 | 1875 | 614 | 942 | 1525 | 1555 | 2794 |
| | SE | 861 | 944 | 180 | 114 | 234 | 158 | 536 | 392 | 637 | 352 | 1045 | 230 | 212 | 304 | 899 | 318 |
| Year | | 82 | 80 | 82 | 82 | 82 | 82 | 80 | 82 | 80 | 82 | 82 | 82 | 82 | 80 | 82 | 80 |
| Depth (m) | | 30+ | 30+ | 10 | 25 | 25 | 12 | 30 | 30+ | 30+ | 10 | 20 | 10 | 25 | 30 | 15 | 30+ |

Table 2. Diet of planktivorous fish at the Poor Knights Islands. Dietary composition expressed as mean number numerical percentage, and mean percentage representation. Sample size and mean standard length (SL ± SE) are shown for each species. Also included is the composition of zooplankton at Stn J on the same day. Categories of prey: Gelat-zoo, gelatinous zooplankton; macro-crust, macro-crustaceans; misc., miscellaneous

| Species | Calanoid copepods | Other copepods | Oikopleura | Doliolids | Gelat-zoo | Macrocrust | Misc. |
|---|---|---|---|---|---|---|---|
| *C. dispilus* (juvenile) SL = 80 ± 6.04 mm    *n* = 6 | | | | | | | |
| Mean number | 1036 | 10 | 60 | 5 | — | 4.1 | 2.46 |
| Numerical % | 92.5 | 1 | 5.4 | 0.5 | — | 0.4 | 0.2 |
| Mean % representation | 77 | 2 | 19 | 0.8 | — | 1 | 0.2 |
| *C. dispilus* (adult) SL = 141 ± 3.83 mm    *n* = 14 | | | | | | | |
| Mean number | 288 | 11 | 196 | 8 | 0.2 | 8 | 59 |
| Numerical % | 49.2 | 2 | 34 | 1.4 | 0.3 | 1.4 | 10 |
| Mean % representation | 42 | 1 | 41 | 2 | 1 | 5 | 8 |
| *C. lepidoptera* SL = 154 ± 9.04 mm    *n* = 5 | | | | | | | |
| Mean number | 37 | 3 | 11 | 147 | — | 8 | — |
| Numerical % | 18 | 1.5 | 5.5 | 71 | — | 4 | — |
| Mean % representation | 5 | 1 | 1 | 90 | — | 3 | — |
| *D. koheru* SL = 204 ± 23.89 mm    *n* = 5 | | | | | | | |
| Mean number | 3 | 2 | — | — | — | 112 | — |
| Numerical % | 2.3 | 1.7 | — | — | — | 96 | — |
| Mean % representation | 1 | 1 | — | — | — | 98 | — |
| *S. violaceus* SL = 170 ± 17.35    *n* = 9 | | | | | | | |
| Mean number | 2.4 | — | — | — | 14 | 83 | 1 |
| Numerical % | 2 | — | — | — | 14 | 83 | 1 |
| Mean % representation | 1 | — | — | — | 31 | 47 | 21 |
| *C. longimanus* SL = 238 ± 12.50    *n* = 7 | | | | | | | |
| Mean number | — | 43 | 0.2 | 1065 | 0.6 | 3 | 7 |
| Numerical % | — | 4 | 0.02 | 95 | 0.05 | 0.3 | 0.6 |
| Mean % representation | — | 1 | 0.7 | 97 | 0.2 | 1 | 0.1 |
| Plankton Stn J.    Numerical % | 83 | 4 | 6.5 | 4 | 1 | 1 | 0.5 |

Categories of zooplankton eaten by fishes were found in lowest densities at stations near the islands. Furthermore, 35 % of the zooplankton captured at Stn A measured over 1.5 mm, while 10 % or less of the zooplankton captured at stations near the islands were of this size.

## Project 2: Distribution patterns of fish and zooplankton around a subtidal archway

### Densities of fish

*Chromis dispilus* were the most abundant planktivores on each of the 4 occasions that fish were counted at Northern Arch during the day (Table 3). With the exception of Time 4, densities of *C. dispilus* were an order of magnitude higher than those of other species. *C. dispilus* and rarer species such as *Scorpis aequipinnis* showed little variation in densities among times. In contrast, the densities of *Caprodon longimanus*, *Scorpis violaceus*, and *Decapterus koheru* varied considerably. For example, between consecutive days, the abundance of *C. longimanus* fluctuated between 41 and 0.5 per 2000 m³. Casual observations suggest that these species often formed aggregations which fed away from the immediate vicinity of the reef and out of the area where fish were counted. For example, a large feeding aggregation of *S. violaceus* was observed 100 m down current of the arch in May 1983. Fluctuations in abundances of these species within the study area, therefore, may reflect these excursions.

The distribution patterns of planktivorous fish changed according to direction of the current (Fig. 3, cf. Fig. 1, position of fish counts). Fish were always most

Table 3. Abundance of planktivorous fish around Northern Arch, Poor Knights Islands on 4 occasions. Mean number per 2000 m$^3$ ± SE. Time 1: 8 Oct 1982, 15:00 h, $n = 20$. Time 2: 9 Oct 1982, 09:00 h, $n = 20$. Time 3: 9 Oct 1982, 15:00 h, $n = 20$. Time 4: 28 May 1983, 12:00 h, $n = 25$. ($n$ = no. of transects)

| Species | Time 1 | Time 2 | Time 3 | Time 4 |
|---|---|---|---|---|
| Chromis dispilus | 173 ± 51 | 186 ± 46 | 180 ± 89 | 214 ± 80 |
| Caprodon longimanus | 41 ± 22 | 0.5 ± 0.2 | 19 ± 9.2 | 25 ± 8 |
| Scorpis violaceus | 38 ± 24 | 11 ± 3.4 | 28 ± 19 | 126 ± 100 |
| Scorpis aequipinnis | 0 | 0.6 + 0.2 | 0.05 ± 0.05 | 2.4 ± 2.0 |
| Pseudocaranx dentex | 0 | 0 | 0.05 ± 0.05 | 0 |
| Decapterus koheru | 2 ± 2 | 0.5 ± 0.5 | 1.5 ± 1.5 | 70 ± 41 |
| Caesioperca lepidoptera | 0.3 ± 0.2 | 0 | 0 | 0 |
| Labracoglosa nitida | 0 | 0.05 ± 0.05 | 0 | 1.4 ± 1 |
| Total no. of fish | 254 ± 78 | 199 ± 47 | 229 ± 99 | 439 ± 162 |

abundant on the incurrent side of the archway or in the arch itself (Fig. 3 A, D). When currents changed direction during the study period (Fig. 3 B, C) fish were observed to move through the arch or around the western point to the incurrent side. *Chromis dispilus* smaller than 80 to 100 mm (SL) did not carry out these movements. Nocturnal and diurnal planktivores were absent from the arch at night. At dusk long horizontal columns of non-feeding *C. dispilus* were observed moving away from the arch. Columns of these fish were followed until it was too dark to see or time and depth constraints on divers prevented further observation. Individual fish broke off from the column and sought shelter, while many fish moved in excess of 0.6 km along the reef in a southerly direction.

## Densities of zooplankton

Large differences in total densities of zooplankton were detected among samples taken upcurrent, within, and downcurrent of the archway during the day in October 1982 (Fig. 4). Lowest densities of zooplankton always occurred in the archway where high densities of planktivorous reef fish were found. For example, on 8 October mean values of 1100 zooplankters m$^{-3}$ were captured upcurrent, while only 480 m$^{-3}$ were found in the arch. At night when fish were absent from the water column, there was a trend for highest abundances of plankton within the arch. On the night of 8 October, mean zooplankton density within the arch was 760 m$^{-3}$, while lower values were found upcurrent (580) and downcurrent (435). Data from 2 day and 2 night times of sampling (data from 09:00 h excluded using random numbers) were tested using a 4-factor partially hierarchical analysis-of-variance (Table 4A). No differences were found in the densities of zooplankton between day and night (Factor Light). Furthermore, no gross differences were found between incurrent,

within, and downcurrent stations when all sampling times were considered (Factor Position). This was due to a combination of the following: (1) densities of zooplankton within the study area varied between times (Factor Time); (2) the ranking of upcurrent, archway, and downcurrent stations changed depending on whether it was day or night. There was a significant interaction also between current and time. This indicated that different patterns of abundance were measured between stations at different times. This is shown by the results of SNK tests. During the day, total densities of plankton ranked downcurrent = upcurrent > within arch = downcurrent at Time 1 and upcurrent > downcurrent > within arch at Time 2, while during the night no significant differences were detected among stations (SNK df = 24, $p < 0.05$). There was, however, a trend for highest abundances within the arch at night.

The lowest densities of all major categories of zooplankton were measured in the arch during the day (Table 5). These groups included: calanoid copepods (e.g. species of *Clausocalanus*, *Nannocalanus*); other copepods (e.g. species of *Oncaea*); appendicularians; gelatinous zooplankton; macrocrustaceans (especially calytopis and furcilia stages of *Nyctiphanes australis*); and miscellaneous groups (e.g. fish eggs and other meroplankton). These zooplankters were found also in the plankton at night. Although some mysids and gammarid amphipods were captured at night only, their combined densities never exceeded 2 m$^{-3}$ of the totals.

When total abundances of zooplankton were compared at stations along 200 m transects through the archway (Stns I to III) and 1 km away from the arch (Stns IV to VI) in May 1983 a pattern different to that measured in October 1982 was found (Fig. 5). Amongst the 3 island stations highest abundances of zooplankton were found within the archway during both the day (when fish were feeding) and night. In contrast, among Stns IV, V, and VI where planktivorous fish were
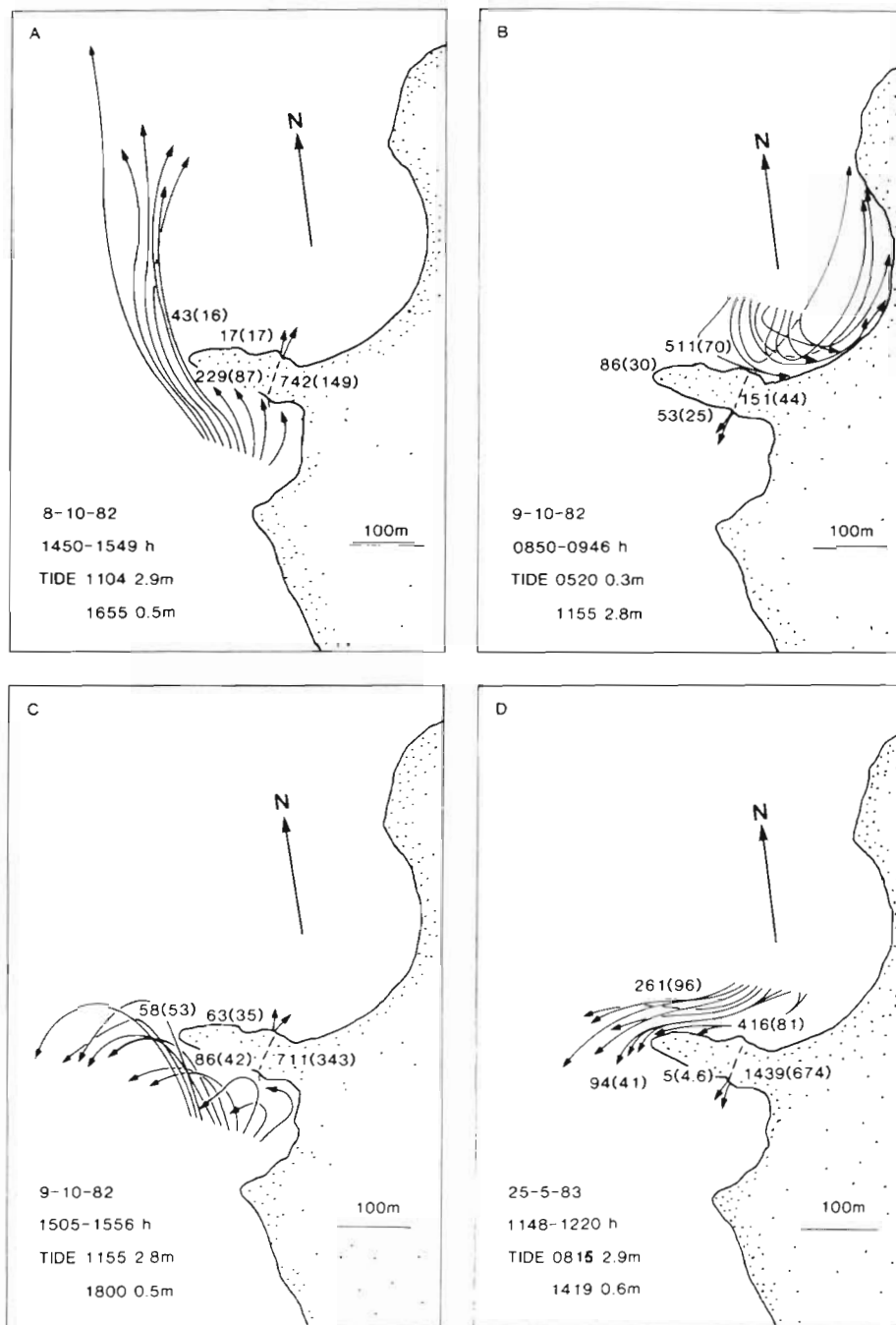
Fig. 3. Total densities of planktivorous fish (mean number per 2000 m³ ± SE) and tracks of drogues around 'Northern Arch', Poor Knights Islands on 4 different occasions (A to D). Times of sampling, and tidal height at Tutukaka Harbour on the mainland opposite the Poor Knights Islands also given

always absent, no differences in density of zooplankton were detected during day or night. These data therefore suggest that zooplankton may accumulate in the presence of an archway.

A 4-factor partially hierarchical analysis-of-variance was used to test data shown in Fig. 5. Highest densities were found during the night (Factor Light, Table 4B). This was true both at the arch and 1 km away from the arch. It may have been due to reduced avoidance of nets by zooplankters; larger numbers rising to the

upper 20 m of the water column at night; the intrusion of a different watermass; or a combination of the above. Significantly higher densities of zooplankton occurred 1 km away from shore where zooplanktivorous fish were absent (Factor Shore). The Factor Position was significant (Table 4B). The peaks in abundance of zooplankton within the archway contributed to this pattern.

Particular groups of zooplankton reflected this overall pattern while others did not. Groups such as
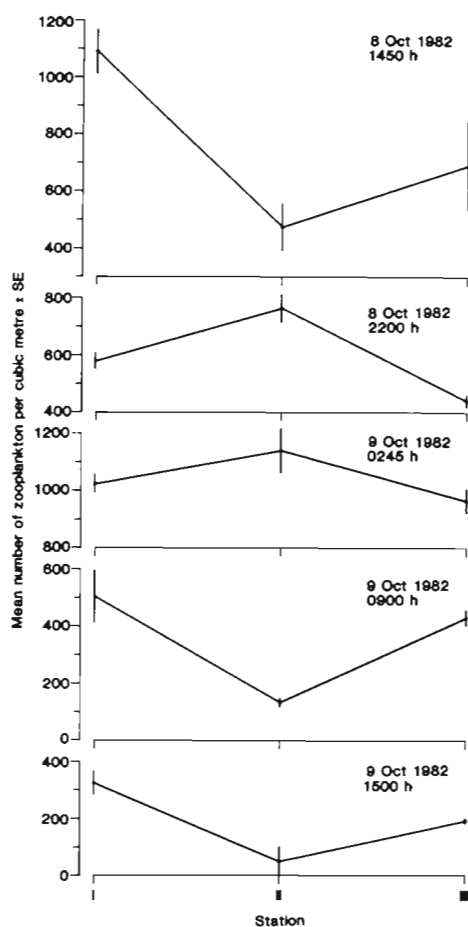
Fig. 4. Densities of total zooplankton in water column at stations upcurrent, within and downcurrent of 'Northern Arch', Poor Knights Islands on 5 occasions. Date and time of sampling shown. $n = 3$ hauls

calanoid copepods, other copepods, and macrocrustaceans had highest abundances in the archway (Stn II) during day and night. In contrast, appendicularians, gelatinous zooplankton, and miscellaneous groups (especially chaetognaths) were found in lowest densities in the arch and sometimes down current of the arch during the day. At night the densities of these groups varied little between stations. With the exception of gelatinous zooplankters, little variation in the density of any group was found among stations 1 km offshore both day and night.

## Diet of Chromis dispilus

Analysis of the diet of Chromis dispilus indicated that large numbers of zooplankters were consumed in both October (1982) and May (1983) samples (Table 6). On 8 and 9 October calanoid copepods accounted for the highest percentage representation in the diet (61 to 68 %). Calanoids also were most abundant numerically. Other copepods (especially cyclopoids), appendicularians, and macrocrustaceans made up 5 to 20 % of the prey identified. In contrast in May, appendicularians ranked as the most important type of prey, both in number and proportional representation. In addition, 20 % of the prey in the diet were represented by miscellaneous zooplankters; mainly chaetognaths. Although large numbers of copepods were consumed also, they comprised a lower proportion of the diet than in October. Interestingly, a large number of fish larvae were found in the diet ($28 \pm 5.6$ fish$^{-1}$), although the proportional representation of this group was low ($3.3 \pm 0.6$).

The numerical percentages of the prey taken by Chromis dispilus were compared with those of zooplankton sampled upcurrent of the fish and within the archway (Fig. 6). Samples taken in October at 2 times indicated that although prey were taken in broadly similar proportions to that represented in the plankton, there were some differences. 'Other copepods' and appendicularians were found in higher proportions in the diet than in the zooplankton, while gelatinous zooplankton were poorly represented in the diet. The composition of the zooplankton at stations upcurrent and within the arch resembled each other closely in October. Macrocrustaceans were an exception, comprising a lower proportion of zooplankton in the arch where fish were feeding than at the upcurrent station.

The composition of groups in the plankton and in the diet of fish was different in May from that of October. Although calanoid copepods were consumed by fish, it was in a lower proportion to that found upcurrent in the plankton. Furthermore, the proportional representation of calanoids in the plankton increased by 24 % in the arch where fish were feeding. This suggested that other components of the plankton were reduced. The representation of appendicularians and miscellaneous groups (mainly chaetognaths) was higher in the diet of Chromis dispilus than in zooplankton upcurrent. These groups showed marked drops in the archway.

## Feeding rates of Chromis dispilus and removal rates of zooplankton

Chromis dispilus consumed zooplankters at an average rate of $34 \pm 4$ (SE) bites min$^{-1}$ ($n = 52$ fish) during the study; with individual fish varying between 6 and 57 bites min$^{-1}$. Mean feeding rates on the 4 times that plankton and fish were sampled ranged from 22 to 40 bites min$^{-1}$ ($n = 10$ to 15 fish). Using information on densities of plankton, abundance of C. dispilus, feeding frequencies, and composition of the diet, it was possible to calculate the time required, for this species

Table 4. Analysis of variance for total zooplankton densities captured day and night (Factor Light) at upcurrent, within arch, and downcurrent stations (Factor Position). Factor Time in (A) = 2 times within each treatment of light. Factor Shore in (B) = stations around the arch and 1 km from the arch. Cochrans' tests were used for testing homogeneity of data (A & B 36 variances, 2df). Transformation was used if Cochrans' test was significant for raw data; transformed data were then tested. Light, position, and shore were treated as fixed factors, and time and hauls as random factors. NS = $p > 0.05$; df: degrees of freedom for $F$-test; MS: mean squares; $F$: $F$-ratio; $p$: probability

| Source | df | MS | F | p |
|---|---|---|---|---|
| **(A)** October 1982; Cochrans' C = 0.2223, NS Transformation $\log_e (x + 1)$ | | | | |
| Light | 1,2 | 21.721 | 1.22 | NS |
| Position | 2,4 | 2.566 | 2.54 | NS |
| L × P | 2,4 | 5.738 | 5.68 | NS |
| Time (L) | 2,24 | 17.825 | 128.98 | 0.001 |
| P × T (L) | 4,24 | 1.01 | 7.32 | 0.005 |
| Hauls (P × T (L)) | 24,72 | 0.138 | 6.12 | 0.001 |
| Residual | 72 | 0.023 | | |
| **(B)** May 1983; Cochrans' C = 0.1441, NS Transformation NIL | | | | |
| Light | 1,24 | 557139.27 | 15.67 | 0.001 |
| Shore | 1,24 | 920932.58 | 25.90 | 0.001 |
| Position | 2,24 | 183409.48 | 5.16 | 0.05 |
| L × S | 1,24 | 3828.31 | 0.11 | NS |
| L × P | 2,24 | 12272.50 | 0.34 | NS |
| S × P | 2,24 | 81996.16 | 2.30 | NS |
| L × S × P | 2,24 | 5792.63 | 0.16 | NS |
| Hauls (LSP) | 24,72 | 35544.21 | 10.10 | 0.001 |
| Residual | 72 | 3517.86 | | |

alone, to reduce densities of zooplankton found at the upcurrent station to those found in the archway (Table 7). With the exception of gelatinous zooplankton, which was never an important component of the diet of *C. dispilus*, the times varied between 6 min and 2 h. 'Other copepods' and appendicularians were the 2 prey types for which the estimated rate of removal was sufficient to reduce numbers to the degree observed (Fig. 4) in the time available.

## DISCUSSION

### Distribution and movements of planktivorous reef fish

High densities of planktivoirous reef fish were found at the Poor Knights Islands. The pomacentrid *Chromis dispilus* was the most abundant species accounting for 85 % of all reef planktivores sampled. *C. dispilus* ranked first in abundance at Northern Arch on the 4 occasions when counts were made. Large planktivores – *Caprodon longimanus*, *Scorpis violaceus*, and *Decapterus koheru* – were found also in high densities at the islands. Their abundances, however, varied considerably among sampling locations and times. This was attributed to the movement of fish away from the immediate vicinity of the reef. Our casual observations are supported by sightings of large aggregations of *S. violaceus*, *D. koheru*, and *Pseudocaranx dentex* near

islands off northern New Zealand during aerial surveys of pelagic fish (Clement 1978). Any samples of zooplankton taken near the islands, therefore, could have been subjected to some predation by fish. In February 1980 and May 1983, however, when zooplankton were sampled at distances greater than 800 m from the islands no aggregations of pelagic planktivorous fish were observed. Accordingly, this plankton was probably subjected to little predation by fish until it reached the reefs surrounding the islands.

The local distribution of planktivorous fish changed according to the direction of currents. Other investigations have found also highest densities of planktivores on the incurrent sides of reefs feeding on 'uncropped' zooplankton (e.g. Hobson & Chess 1978, Bray 1981). Investigations on site-attached fish (e.g. Stevenson 1972, de Boer 1978) emphasized also the importance of the velocity of tidal currents to feeding rates of pomacentrids. Fish at the Poor Knights Islands could move in response to changes in the supply of plankton. The exception to this would be male *Chromis dispilus* which guard nests during the breeding season (Kingsford 1985) and juvenile planktivores which are site attached (Kingsford & MacDiarmid unpubl.).

Fish were absent from Northern Arch during the night. Observations of hundreds of *Chromis dispilus* moving in horizontal columns away from the arch suggested that unidirectional movements of over 0.6 km were common at dawn and dusk. Further work is

Table 5. Densities of 6 zooplankton categories in the water column at stations upcurrent, within, and downcurrent of 'Northern Arch', Poor Knights Islands on 5 occasions; given in chronological order: Day 1 = 8 Oct 1982, 14:50 h; Night 1 = 8 Oct 1982, 22:00 h; Night 2 = 9 Oct 1982, 02:45 h; Day 2 = 9 Oct 1982, 09:00 h; Day 3 = 9 Oct 1982, 15:00 h. Data are means (SE)

| Category of zooplankton | Time | Upcurrent | Within | Downcurrent |
|---|---|---|---|---|
| Calanoids | Day 1 | 779 (59) | 393 (67) | 449 (109) |
| | Night 1 | 357 (14) | 453 (38) | 293 (13) |
| | Night 2 | 698 (4.3) | 712 (98) | 543 (25) |
| | Day 2 | 292 (59) | 99 (8) | 282 (20) |
| | Day 3 | 172 (14) | 32 (5) | 110 (1.5) |
| Other copepods | Day 1 | 14 (0.5) | 10 (3) | 17 (2) |
| | Night 1 | 28 (10) | 16 (3) | 11 (2) |
| | Night 2 | 32 (4.7) | 46 (11) | 24 (3.5) |
| | Day 2 | 27 (2) | 16 (6) | 30 (5) |
| | Day 3 | 45 (9) | 5 (0.4) | 21 (1.2) |
| Appendicularians | Day 1 | 12 (0.6) | 5 (1) | 8 (0.4) |
| | Night 1 | 31 (6) | 26 (5) | 37 (3.1) |
| | Night 2 | 87 (9) | 80 (7.2) | 56 (2) |
| | Day 2 | 24 (1) | 5 (0.2) | 16 (1.2) |
| | Day 3 | 12 (1.7) | 1 (0) | 6.5 (2.1) |
| Gelatinous zooplankton | Day 1 | 47 (4) | 22 (6) | 44 (2) |
| | Night 1 | 38 (7) | 26 (10) | 27 (4) |
| | Night 2 | 66 (19) | 77 (16) | 54 (13) |
| | Day 2 | 66 (4.7) | 9 (2.6) | 20 (1) |
| | Day 3 | 56 (12) | 4.5 (0.2) | 34 (3.8) |
| Macrocrustaceans | Day 1 | 227 (22) | 41 (10) | 122 (27) |
| | Night 1 | 72 (22) | 184 (17) | 46 (6.3) |
| | Night 2 | 139 (11) | 195 (38) | 239 (42) |
| | Day 2 | 94 (3) | 7 (0.2) | 66 (16) |
| | Day 3 | 29 (8) | 3.3 (1) | 17 (6) |
| Miscellaneous | Day 1 | 11 (1.7) | 1.9 (0.7) | 3.5 (1.3) |
| | Night 1 | 35 (1.5) | 51 (5) | 22 (3.4) |
| | Night 2 | 20 (3.4) | 18 (2.2) | 14 (0.8) |
| | Day 2 | 4.3 (1.4) | 0.9 (0.2) | 9.3 (5) |
| | Day 3 | 10 (3.2) | 2.6 (1.7) | 7.3 (1.8) |

required to properly document these movements, but it seems probable that many adult fish feed far from their nocturnal shelter sites. Similar movements have been described for *C. punctipinnis* (Bray et al. 1981) and nocturnal planktivores such as *Pempheris schomboughi* (Gladfelter 1979).

## Interrelations between fish and zooplankton

In the preliminary study around the Poor Knights Islands, zooplankton occurred in higher densities offshore of the islands than at sites near the islands where fish were abundant. Selective feeding by 'slurping' individual plankters was the feeding mode used by all fishes in this study (= particulate feeder *sensu* Lazzaro 1987). The types and series of prey items that were eaten by planktivorous fish were found in low densities nearshore. This suggested a possible cause and effect relationship. However, alternative explanations of

these patterns were that different watermasses were encountered, or the patterns were found by chance. More intensive sampling of fish and plankton and better knowledge of hydrology were required to differentiate between these explanations.

The nature of the relationship between fish and zooplankton was examined in detail at Northern Arch. It was impossible to exclude planktivorous fish experimentally from the study area to quantify their impact on zooplankton. Accordingly, our assessment was carried out by making spatial and temporal comparisons of the distribution and abundance of zooplankton and fish. In October 1982 the densities of zooplankton upcurrent of feeding fish were always higher than in the arch where fish were consuming zooplankters at a high feeding rate. At night when fish were absent from the water column there was a trend for highest abundances of zooplankters in the arch. Our interpretation of this was that fish and not the physical presence of the archway were responsible for the low densities of zoo-
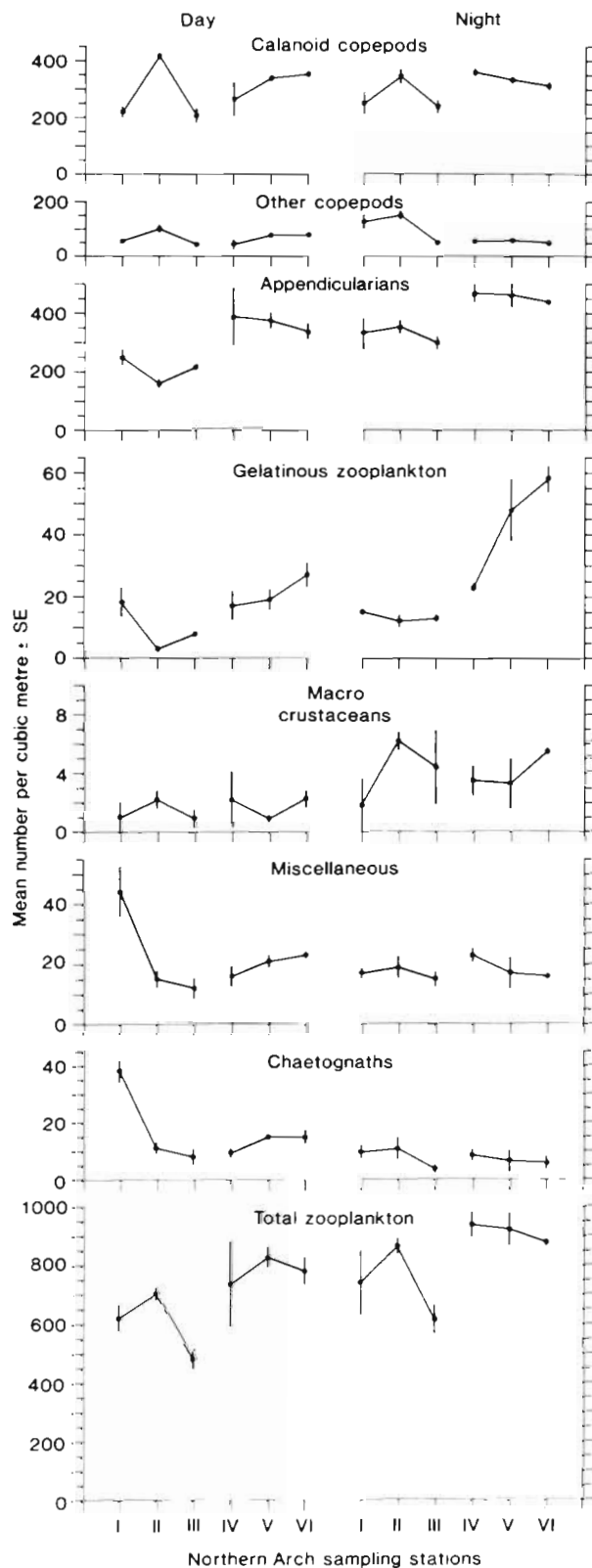
Fig. 5. Densities of total zooplankton and 7 major categories around 'Northern Arch' (Stns I, II & III) and 1 km west (Stns IV, V & VI) during day (12:00 h) and night (01:00 h) on 28 May 1983. n = 3 hauls

plankters found in the arch during the day. We do not know if shadow in the arch affected zooplankter densities. The accumulation of zooplankton in the arch at night suggested that fish fed in the arch during the day, not just because of the current, but also because feeding conditions were enhanced through the concentration of plankton. It could be argued that higher densities of plankton within the arch at night were due to the vertical migration of demersal zooplankters (Alldredge & King 1977). We consider this unlikely as few demersal zooplankters (including copepods) rise more than 2 m from the substratum at night (Alldredge & King 1985). Moreover, gammarid amphipods and mysids often move into the water column at night, but only a few individuals of these were found in the zooplankton.

A very different pattern was observed in May (1983). Total densities of zooplankton were high in the arch during the day when compared to samples taken upcurrent and downcurrent. Some groups of zooplankters, however, did show large reductions in abundance in the arch where fish fed. Comparisons of the diets of fish with the composition of the plankton captured in nets indicated that appendicularians and chaetognaths were selected and consumed actively by fish. These prey types were found in low densities through the archway during the day, while at night abundances were similar to those upcurrent. Gelatinous zooplankters exhibited lowest densities through the arch during the day also. Although *Chromis dispilus* consumed few of this prey category at this time, large numbers of other planktivores (e.g. *Scorpis violaceus* and *Caprodon longimanus*) were observed feeding in the arch and downcurrent of the arch at the time. Each of these species has been found to consume large quantities of gelatinous zooplankton (Table 2).

The contrasting patterns found in October and May indicate that the feeding behaviour of fish may change according to the composition of the plankton. In turn, the effect that fish have on the abundance of a particular group of zooplankters will vary depending on the presence of co-occurring groups.

Switching from selective to non-selective modes of feeding has been documented for planktivores in freshwater lakes (Janssen 1980). There is general agreement that prey taken by fish will vary according to a complex interaction of factors such as density of plankton, size of prey, ability of zooplankters to escape, intensity of light, and perception of the fish (O'Brien 1979, Drenner & McComas 1980, Janssen 1980, Gardner 1981, Wright & O'Brien 1984, Lazzaro 1987). Accordingly, studies on selectivity of prey by fish must be carried out at a number of times when the composition of the plankton differs.

Further support for our conclusion that fish were

Table 6. Diet of *Chromis dispilus* captured at Northern Arch, Poor Knights Islands on 8 Oct 1982 (*n* = 16), 9 Oct 1982 (*n* = 22) and 28 May 1983 (*n* = 22). Mean values and standard errors given for numerical percentage (Num. %), percentage representation (% Rep.), and number (No.) of prey items. Standard lengths of *C. dispilus* ranged from 112 to 150 mm, mean = 129 ± 2 (SE)

| Prey type | 8 Oct 1982 | | | 9 Oct 1982 | | | 28 May 1983 | | |
|---|---|---|---|---|---|---|---|---|---|
| | Num. % | % Rep. | No. | Num. % | % Rep. | No. | Num. % | % Rep. | No. |
| Calanoid copepods | 67 ± 4.0 | 68 ± 4.7 | 71 ± 31 | 52 ± 4.7 | 61 ± 5.8 | 112 ± 34 | 23 ± 1.9 | 19 ± 1.7 | 711 ± 67 |
| Other copepods | 7.6 ± 2.7 | 6.4 ± 2.2 | 11 ± 5.8 | 28 ± 5.5 | 21 ± 5.8 | 29 ± 8.4 | 16 ± 1.8 | 22 ± 2.5 | 455 ± 69 |
| Appendicularians | 7.3 ± 3.5 | 7.0 ± 3.5 | 1.8 ± 1.2 | 5.9 ± 1.6 | 5.0 ± 1.5 | 13 ± 5.3 | 52 ± 2.6 | 38 ± 2.9 | 1322 ± 120 |
| Gelat. zooplankton | 0 | 0 | 0 | 0.2 ± 0.2 | 0.2 ± 0.2 | 0.1 ± 0.07 | 0.9 ± 0.2 | 0.8 ± 0.4 | 28 ± 5.9 |
| Macrocrustaceans | 16 ± 2.7 | 15 ± 2.8 | 11 ± 4.6 | 12 ± 3.4 | 12 ± 3.5 | 17 ± 6.5 | 0.8 ± 0.2 | 1.2 ± 0.2 | 24 ± 6.4 |
| Miscellaneous | 2.0 ± 1.1 | 4.1 ± 3.1 | 2.9 ± 1.7 | 1.5 ± 0.4 | 0.7 ± 0.3 | 2.2 ± 0.8 | 7.4 ± 1.4 | 20 ± 3.6 | 212 ± 43 |
| Total | – | – | 98 ± 43 | -- | – | 173 ± 43 | – | – | 2752 ± 205 |
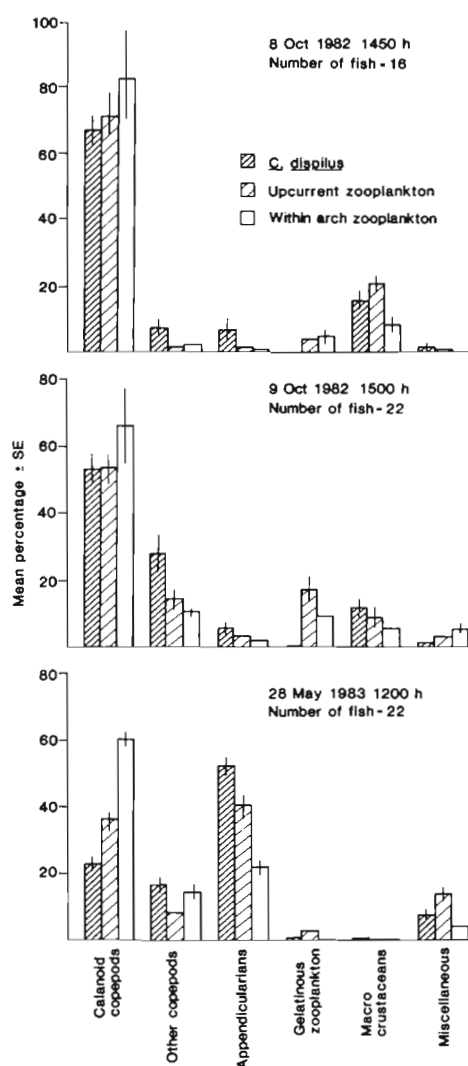


Fig. 6. Comparison of the diet of *Chromis dispilus* at 'Northern Arch' with composition of zooplankton upcurrent of and within the archway on 3 occasions. Data are mean numerical percentages ± SE

Table 7. Time (min) required for feeding aggregations of *Chromis dispilus* to reduce zooplankton densities found at the upcurrent station to those found within the archway. See 'Methods' for formula used. Where a prey type was completely absent from the diet no calculation was made. Current speeds within the archway and time for a body of water to travel 100 m are also given. Sample sizes for bite rates: 8 Oct, *n* = 12 fish, 9 Oct, *n* = 15 fish

| Zooplankton category | 8 Oct 1982 | 9 Oct 1982 |
|---|---|---|
| Calanoid copepods | 63 | 44 |
| Other copepods | 6 | 23 |
| Appendicularians | 10 | 30 |
| Gelatinous zooplankton | – | 429 |
| Macrocrustaceans | 140 | 34 |
| Miscellaneous | 37 | 75 |
| Total zooplankton | 93 | 46 |
| Mean no. of bites min$^{-1}$ | 40 | 22 |
| Current speed (cm s$^{-1}$) | 15 | 5 |
| Minutes to travel 100 m | 11 | 33 |

responsible for changes in density of some categories of zooplankton was provided by high estimates of removal rates. These removal rates are only suggestive, however, as there was no estimate of error for the combined variances of 5 measures within the formula and current speed. The formula uses average densities of fish, zooplankton, and average feeding rates. Variation in the feeding behaviour of fish, differential digestion, vertical distribution of zooplankton, and the use of nets to estimate the available prey question the accuracy of the estimates (Stevenson 1972, Gerber & Marshall 1974, Janssen 1980, Lazzaro 1987). Nevertheless, the formula was conservative in that feeding activity of *Chromis dispilus* only was considered. High densities of other feeding fish were often present in the study area which were also feeding at high rates (e.g. *Scorpis violaceus* 16 ± 1 SE bites min$^{-1}$; *n* = 5 fish, May).

The results usefully indicate that large numbers of

planktivorous fishes feeding at a constant rate are capable of causing marked changes in plankter density and composition. Bray (1981) also attributed localized reductions in density of zooplankton during the day to feeding by fish. In Bray's study, however, it was not clear whether the presence of *Macrocystis* forest influenced the distribution of plankton over a reef independently of the presence of fish.

Reduction in plankton density over coral reefs has been attributed to corals over horizontal structures (Glynn 1973, Johannes & Gerber 1974) and fish on vertical drop offs (Hobson & Chess 1978, Hamner et al. in press). In this study the effect of sessile feeders on plankton (e.g. anemones) was considered to be minimal. Sessile planktivores were restricted to vertical faces at the Poor Knights Islands.

## Ecological consequences of predation by fish

Planktivorous reef fish may affect localised distribution of zooplankton, but this is unlikely to influence gross peaks and troughs in abundance of plankton, on broader temporal (e.g. seasonal) or spatial (e.g. 10 to 100 km) scale. Predation by these fishes, therefore is unlikely to affect major processes in marine plankton communities, but conceivably could influence behaviour, morphology, and production of zooplankters associated with a reef (Alldredge & King 1977). We, however, had no information on the presence or abundance of these resident zooplankters at the Poor Knights Islands.

Planktivorous reef fish clearly have the potential to influence the abundance of larval forms leaving a reef or approaching to settle (Johannes 1978, Wallace et al. 1986, Gaines & Roughgarden 1987, Westneat in press). Although not an important component of the diet of these fishes in our study, meroplankton, including pre-settlement fish and barnacle cyprids, were preyed upon by *Chromis dispilus*. This predation may influence settlement patterns of fish and invertebrates. Nevertheless, the presence of larval forms in the vicinity of a reef does not necessarily mean that they will be consumed. The intensity of predation by fish on meroplankton may vary according to light-dark cycle, current strength, composition of zooplankton and, abundance of fish (Kingsford unpubl.). Finally, the type of prey fed on by fish should also vary according to the size and species composition of fish present.

Predation on plankton by fish may be of considerable importance to the reef environment. All types of prey consumed by fish were also captured in nets away from the island, and 99 % of the diet of fish was holoplankton. It is likely that the feeding activity of fish imports a considerable amount of energy to the Poor Knights

system. Faecal matter may provide an input of nutrients to the reef (e.g. Bray et al. 1981, Robertson 1982). Furthermore, the high biomass of planktivorous fish helps support a large population of piscivores at the islands (e.g. scorpaenids, serranids, and mueranids, own unpubl. obs.).

In conclusion, planktivorous fish were found in highest numbers on the incurrent side of a reef where there was an input of zooplankton. The feeding activity of fish was capable of causing localised reductions in the abundance of zooplankton. Rate of feeding and diet of fish, as well as density and composition of plankton changed between times. These findings emphasize the importance of making concurrent measures of these factors if the interrelations between fish and plankton are to be interpreted properly. Our study concurs with work in *Macrocystis* forests of the northern hemisphere which has shown that planktivorous reef fish appear to deplete plankton supplies on a local scale (e.g. Bray 1981, Gaines & Roughgarden 1987). This emphasizes the importance of food in influencing distribution patterns and growth of planktivorous fish. This is especially applicable to site-attached and territorial planktivores (Stevenson 1972, de Boer 1978, Jones 1986). Subsequent research should clarify whether there are density-dependent processes operating, within aggregations of planktivores, that are related to feeding behaviour.

## LITERATURE CITED

Alldredge, A. L., King, J. M. (1977). Distribution, abundance and substrate of demersal reef zooplankton at Lizard Is. Lagoon, Great Barrier Reef. Mar Biol. 41: 317–333

Alldredge, A. L., King, J M. (1985). The distance demersal zooplankton migrate above the benthos: implications for predation. Mar. Biol. 84: 253–260

Bailey, T G., Robertson, D. R. (1982). Organic and caloric levels of fish feces relative to its consumption by co-prophagous reef fishes. Mar Biol. 69: 45–50

Bray, R. N. (1981). Influence of water currents and zooplankton densities on daily foraging movements of blacksmith, *Chromis punctipinnis*, a planktivorous reef fish. Fish. Bull. U.S. 78: 829–841

Bray, R. N., Miller, A. C., Geesey, G. G. (1981). The fish connection: a trophic link between planktonic and rocky reef communities. Science 214: 204–205

Bray, R. N., Purcell, L. J., Miller, A. C. (1986). Ammonium excretion in a temperate-reef community by a planktivorous fish, *Chromis punctipinnis* (Pomacentridae), and potential uptake by young giant kelp, *Macrocystis pyrifera* (Laminariales). Mar. Biol. 90: 327–334

Brook, J. L., Dodson, S. I. (1965). Predation, body size and composition of plankton. Science 150: 28–35

Clement, I. T (1978). School fish sightings around New Zealand, 1976–1977. N. Z. Fish. Res. Div. Occas. Publ. No. 15

Coates, D. (1980). Prey size intake in humbug damselfish *Dascyllus aruanus* (Pisces Pomacentridae) living within social groups. J. Anim. Ecol. 49: 335–340

de Boer, B. A. (1978). Factors influencing the distribution of damselfish (*Chromis cyanea* Poey), Pomacentridae, on a reef at Curaçao, Netherlands Antilles. Bull. mar Sci. 28: 550–565

Denham, R. N., Bannister, R. W., Guthrie, K. M., Crook, F. G. (1984). Surveys of the East Auckland and East Cape Currents. Aust. J. mar. Freshwat. Res. 35: 491–504

Drenner, R. W., McComas, S. R. (1980). The roles of zooplankter escape ability and fish size selectivity in the selective feeding and impact of planktivorous fish. In: Kerfoot, W. C. (ed.). Evolution and ecology of zooplankton communities. Univ. Press New England, Hanover, p. 587–593

Ebeling, A. W., Bray, R. N. (1976). Day versus night activity of reef fishes in a kelp forest off Santa Barbara, California. Fish. Bull. U.S. 74: 703–717

Ebeling, A. W., Larson, R. J., Alevizon, W S., Bray, R. N. (1980). Annual variability of reef-fish assemblages in kelp forests off Santa Barbara, California, Fish. Bull. U.S. 78: 361–377

Gaines, S. D., Roughgarden, J. (1987). Fish in offshore kelp forests affect recruitment to intertidal barnacle populations. Science 235: 479–481

Gardner, M. B. (1981). Mechanisms of size selectivity by planktivorous fish. a test of hypotheses. Ecology 62: 571–578

Gerber, R. P., Marshall, N. (1974). Reef pseudoplankton in lagoon trophic systems. Proc. 2nd Int. Coral Reef Symp. 1: 105–107

Gladfelter, W B. (1979). Twilight migrations and foraging activities of the copper sweeper *Pempheris schomburgki* (Teleostei: Pempheridae). Mar Biol. 50: 109–119

Gliwicz, M. Z. (1986). Predation and evolution of vertical migration in zooplankton. Nature, Lond. 320: 746–748

Glynn, P. W. (1973). Ecology of a Caribbean coral reef. The *Porites* reef-flat biotope: part 2. Plankton community with evidence for depletion. Mar. Biol. 22: 1–21

Hamner, W. M., Hauri, I. R. (1977). Fine scale surface currents in the Whitsunday Islands, Queensland, Australia: effect of tide and topography. Aust. J. mar. Freshwat. Res. 28: 333–359

Hamner, W M., Hauri, I. R. (1981). Effects of island mass: water flow and plankton around a reef in the Great Barrier Reef lagoon, Australia. Limnol. Oceanogr 26: 1084–1102

Hamner, W. M., Jones, M. S., Carleton, J. H., Hauri, I. R., Williams, D. McB. (in press). Zooplankton, planktivorous fish, and water currents on the windward reef face: Great Barrier Reef, Australia. Bull. mar. Sci.

Hobson, E. S., Chess, J. R. (1976). Trophic interactions among fishes and zooplankters near shore at Santa Catalina Island, California. Fish. Bull. U.S. 74: 567–598

Hobson, E. S., Chess, J. R. (1978). Trophic interactions among fishes and plankton in Enewetak Atoll, Marshall Islands. Fish. Bull. U.S. 76: 133–153

Janssen, J. (1980). Alewives *(Alosa pseudopharenous)* and ciscoes *(Coregonurus artedii)* as selective and non-selective planktivores. In: Kerfoot, W. C. (ed.) Evolution and ecology of zooplankton communities. Univ. Press of New England, Hanover, p. 580–586

Johannes, R. E. (1978). Reproductive strategies of coastal marine fishes in the tropics. Environ. Biol. Fish. 3: 65–84

Johannes, R. E., Gerber, R. (1974). Import and export of net plankton by an Enewetak coral reef community. Proc. 2nd Int. Symp. Coral Reef 1 97–104

Jones, G. P. (1986). Food availability affects growth in a coral reef fish. Oecologia (Berl.) 70: 136–139

Jones, R. S. (1968). A suggested method for quantifying gut contents in hervivorous fishes. Micronesia 4: 369–371

Kerfoot, W C. (1980). Evolution and ecology of zooplankton communities. Univ. Press New England, Hanover

Kingsford, M. J. (1985). The demersal eggs and planktonic larvae of *Chromis dispilus* (Teleostei: Pomacentridae) in north-eastern New Zealand coastal waters. N.Z. Jl mar. Freshwat. Res. 19: 429–438

Larson, R. J., De Martini, E. E. (1984). Abundance and vertical distibution of fishes in a cobble-bottom kelp forest off San Onofre, California Fish. Bull. U.S. 82: 37–53

Lazzaro. X. (1987). A review of planktivorous fishes: their evolution, feeding behaviours, selectivities, and impacts. Hydrobiologia 146: 97–167

Lynch, M. (1980). The evolution of cladoceran life histories. Q. Rev. Biol. 55: 23–42

O'Brien, W. J. (1979). The predator-prey interaction of planktivorous fish and zooplankton. Am. Sci. 67: 572–581

Ogawa, Y., Nakahara, T. (1979). Interrelationships between pelagic fishes and plankton in the coastal fishing ground of the southwestern Japan Sea. Mar. Ecol. Prog. Ser 1: 115–122

Paulin, C. D., Stewart, A. L. (1985), A list of New Zealand teleost fishes held in the National Museum of New Zealand. Nat. Mus. N. Z. Misc. Ser 12

Robertson, D. R. (1982). Fish feces as food on a Pacific coral reef. Mar. Ecol. Prog. Ser 7· 253–265

Stevenson, Jr., R. A. (1972). Regulation of feeding behavior of the bicolor damselfish (*Eupomacentrus particus* Poey) by environmental factors. In: Winn, H. G. (ed.) Behavior of marine animals. 2: Vertebrates. Plenum, New York, p. 278–302

Vanni, M. J. (1986). Fish predation and zooplankton demography: indirect effects. Ecology 67: 337–354

Wallace, C. C., Babcock, R. C., Harrison, P. L., Oliver, J. K., Willis, B. L. (1986). Sex on the reef: mass spawning of corals. Oceanus 29: 38–42

Westneat, M. W. (in press). Predation on coral spawn by planktivorous fish. Coral reefs

Williams, D. McB., Hatcher, A. I. (1983). Structure of fish communities on outer slopes of inshore, mid-shelf and outer shelf reefs of the Great Barrier Reef. Mar. Ecol. Ser. 10: 239–250

Wright, D. J, O'Brien, W. J. (1984). The development and field test of a tactical model of the planktivorous feeding of white crappie *(Pomaxias annularis)*. Ecol. Monogr. 54: 65–98

Zaret, T. M., Kerfoot, W. C. (1975). Fish predation on *Bosmina longirostris*: body-size selection versus visibility selection. Ecology 56: 232–237