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Latitudinal variation in abundance of herbivorous fishes: a comparison of temperate and tropical reefs

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Abstract The aim of the study was to provide comparable estimates of abundance of herbivorous reef fishes at temperate and tropical localities using a standardized methodology. Faunas of herbivorous fish were sampled on the rocky reefs of temperate northern New Zealand and on the coral reefs of the northern Great Barrier Reef (GBR), Australia, and the San Blas Archipelago in the Caribbean. A pilot study established the most appropriate habitat setting and the scale and magnitude of replication for the sampling program in temperate waters. Herbivorous fishes, including members of families endemic to the southern hemisphere (Odacidae and Aplodactylidae), were most abundant in turbulent, shallow water (0 to 6 m) and had patchy distributions within this habitat. A hierarchical sampling program using 10-min transect counts within the 0 to 6 m depth stratum examined abundance patterns at a range of spatial scales including mainland and island coasts, localities separated by up to 100 km and sites separated by up to 10 km. This program identified a characteristic fauna of seven species of herbivorous fishes with mean total abundances ranging from 23 to 30 individuals per 10-min transect. Species composition of the fauna varied between islands and coasts. A similar methodology was used to sample the major families of herbivorous fish in a number of sites in each of the tropical regions. These sampling programs revealed a fauna dominated by acanthurids and scarids in both the GBR and Caribbean localities. Estimates of abundance from these regions were similar, with a mean of 108 individuals recorded on the GBR and 129 per 10-min transect in the Caribbean.

Species richness varied between each region, with 44 taxa recorded from the GBR and 11 from the Caribbean. Abundances of temperate water herbivores in New Zealand were found to be 75 to 80% lower than those recorded from shallow water habitats sampled on coral reefs. This was not related to species richness, since both New Zealand and the Caribbean locality had patterns of low richness. We suggest that the differences in abundance found by our study between temperate and tropical regions are not restricted to herbivorous fishes, but are representative of general latitudinal trends in reef fish faunas.

Introduction

Herbivory by marine fishes may have important ecological and evolutionary consequences. Their feeding provides pathways for the release of energy fixed by plants to higher trophic levels and in the cycling of nutrients (Horn 1989; Choat 1991). Herbivorous fishes may also control the local distribution and structure of plant communities (Lewis and Wainwright 1985; Horn 1989). On longer time scales, herbivory has been implicated in the evolution of the structural features of marine plants and their chemical composition, especially when individual plants are selected as food items (Horn 1989; Hay 1991).

The interactions between herbivorous fishes and marine plants have been viewed as a tropical phenomenon that is particularly characteristic of coral reef environments (Ogden and Lobel 1978; Gaines and Lubchenco 1982; Ebeling and Hixon 1991). The large numbers of herbivorous fishes that may be readily observed in the clear waters of coral reefs reinforce this view (Russ 1984a, b). Little is known of the abundance or role of herbivorous fishes in temperate waters.

Latitudinal comparisons of faunas of herbivorous fishes must take three problems into account: (1) most surveys of abundance patterns have occurred in the

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tropics and few data sets are available from temperate regions; (2) herbivorous fishes in temperate waters show marked latitudinal and biogeographic differences in diversity, species composition and possibly abundance (Choat 1991); (3) most comparisons between temperate and tropical regions rely on estimates obtained by studies using a wide variety of sampling methods.

In tropical regions, the majority of descriptions of abundance patterns of herbivorous fish have occurred on coral reefs. The equivalent habitats in temperate regions are rocky reefs dominated by macroscopic algae. While a number of herbivorous taxa occur in such environments, the limited information available suggests that they are restricted to shallow depths (Choat and Ayling 1987). In both hemispheres, shallow reefs are areas of strong wave surge and poor visibility which, in addition to their patchy distribution, has made it difficult to obtain reliable data on the abundance of herbivorous fishes.

The primary aim of the present study was to provide estimates of abundance of herbivorous fishes in temperate waters that could be directly compared to those from coral reef habitats. This information was obtained in the following sequence: (1) a pilot sampling program was developed on temperate reefs to establish habitat and site-associated variation in abundance; (2) a visual census technique appropriate for the turbulent environment of shallow reefs, but also applicable to coral reefs, was developed; (3) a sampling program designed to accommodate variation in abundance at several spatial scales on temperate reefs was implemented; (4) a comparative data set from coral reefs in two tropical regions was obtained using similar sampling methods.

Methods

Sampling localities and study species

Abundances of temperate herbivorous fishes were sampled on reefs in northeastern New Zealand (Fig. 1A). Tropical species were sampled at Lizard Island and on adjacent midshelf reefs on the northern Great Barrier Reef (GBR) and in the San Blas Islands in the western Caribbean (Fig. 1B, C).

Seven species of herbivorous fish were recorded in abundance estimates in New Zealand. These included members of the families Odacidae and Aplodactylidae, which are restricted to southern temperate waters, and members of cosmopolitan groups (Girellidae, Kyphosidae and Pomacentridae) that are widely distributed in shallow-reef environments. All species feed on large algae, although girellids will also consume some animal material (Russell 1983; Choat and Clements 1993).

All species of the four major families of herbivorous fishes (Acanthuridae, Kyphosidae, Scaridae and Siganidae) that occur on coral reefs were included in abundance estimates in tropical regions. At Lizard Island a total of 44 species was recorded. In the Caribbean locality, ten species, all of which were members of the families Acanthuridae, Kyphosidae and Scaridae, were recorded. Siganids are absent from this region. Small and/or cryptic species, mainly pomacentrids and blennies, were not counted in these surveys. Abundances of pomacentrids at Lizard Island were examined in a separate study (Meekan et al. 1995).

Sampling program, temperate reefs

Pilot study

A pilot study was used to determine patterns of habitat association and local-scale variation of herbivorous fishes at a coastal locality, the Cape Rodney to Okakari Marine Reserve at Leigh (Fig. 1A) in May 1985. At each of two sites maps of the bottom topography were made at three depths. Each map covered an area of approximately 3000 m² within the 0 to 6, 6 to 12, and 12 to 18 m depth zones. Total counts of herbivorous fishes were made by swimming over mapped areas and recording the positions of all individuals, with no part of the area repeatedly sampled during a single count. Three replicate counts were made at each combination of depth and site. As these counts were not independent, the results were analyzed graphically.

Main study

The construction of large maps of the bottom topography was inappropriate for a sampling program that required extensive within-site replication. Moreover, the surge and algal cover in shallow waters often made it impossible to deploy tapes to estimate areas and distances searched. Consequently, a count method utilizing time-based belt transects, similar to that used by Williams (1982) and Russ (1984a, b), was adopted for the main study. The duration of the count was determined by swims of varying time periods over mapped reef areas. A count duration of 10 min was found to cover an area of reef that allowed identification of all species of herbivorous fish present in the immediate area. During a swim, all fish within 5 m of either side of the diver were counted. The distance covered by a count varied depending on the wave surge and current but generally ranged between 150 and 200 m, so that the area sampled varied between 1500 and 2000 m². The method allowed a high level of replication within shallow water habitats. In this and all subsequent sampling programs, timed counts were conducted by the same observer during periods of calm seas and low current flow.

Previous studies of coastal fish faunas (Choat and Ayling 1987) identified differences among coastal localities and also between coastal and island localities. Accordingly, abundances of herbivorous fish were examined at two coastal (Tutukaka and Leigh) and two offshore island (Poor Knights and Great Barrier Islands) localities (Fig. 1A) during the period December 1985 to May 1986. General descriptions of coastal and island habitats are provided in Choat and Scheil (1982). Seven sites were sampled at each coastal and island locality. At Tutukaka and Leigh, sites were selected along rocky coastlines that were exposed to occasional northeasterly storms. Sites at the Poor Knights Islands were within bays on both the eastern and western sides of the islands. Those on Great Barrier Island were at the northern tip. Both island localities were exposed to storm conditions. Sites were separated by approximately 1 km, with the exception being Tutukaka, where weather conditions during sampling required a distance of approximately 5 km between sites. Within each site, fish abundances were estimated by four 10-min counts, all of which were done in shallow (less than 6 m depth) algal forests. Detailed descriptions of this shallow water habitat are given by Choat and Scheil (1982). Counts were run parallel to the low tide mark in a series of nonoverlapping, linear transects.

In order to examine the generality of depth-distributions of herbivorous fishes found in the pilot study, a further depth-stratified sampling program was conducted at a coastal and an island locality (Leigh and Poor Knights) in December 1985. In this program, three sites were sampled at each locality. Within each site, four 10-min swims were done at each of three depth zones; 0 to 6, 6 to 12, and 12 to 18 m. All counts recorded the number of individuals and an estimate of their standard length.

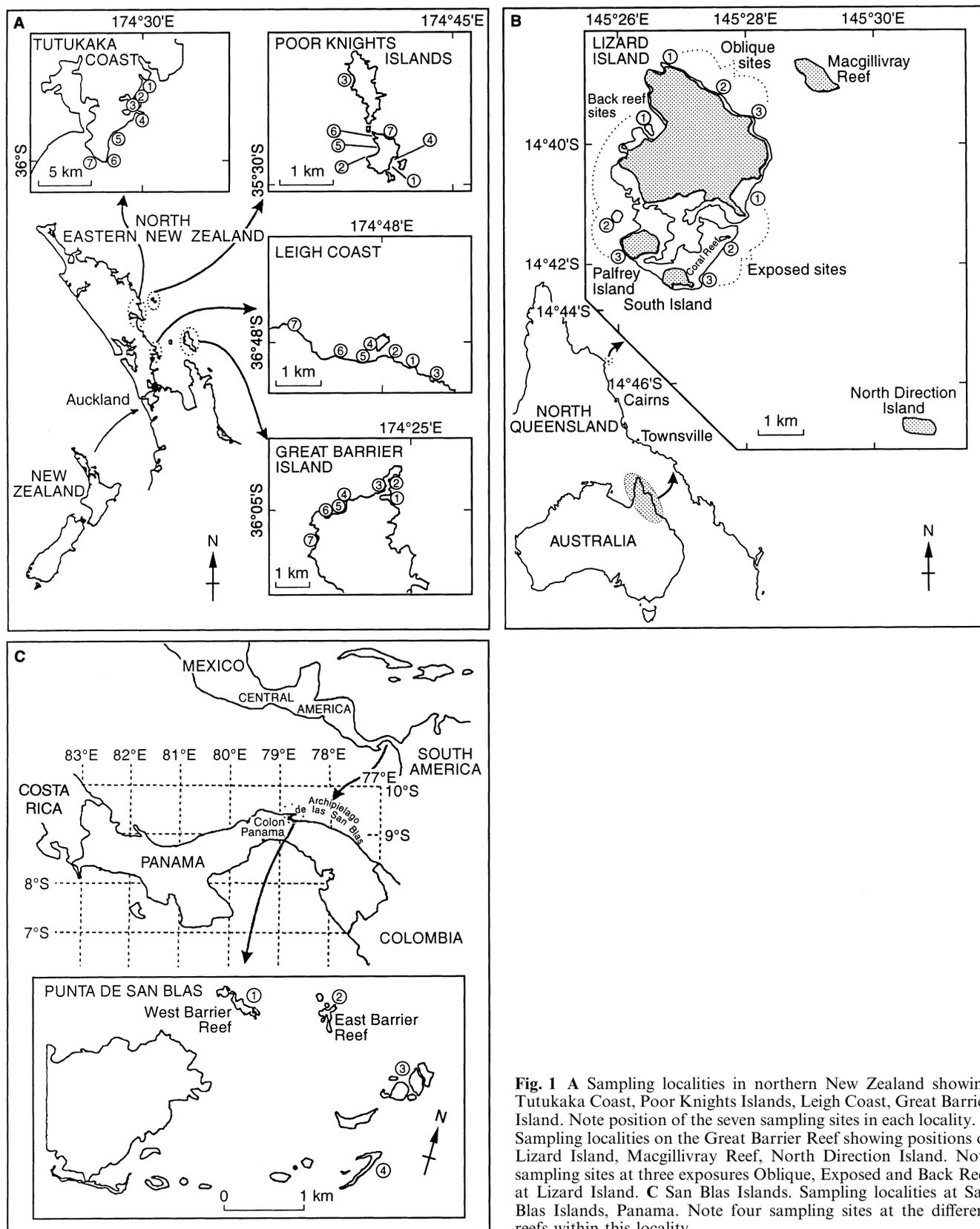


Fig. 1 A Sampling localities in northern New Zealand showing Tutukaka Coast, Poor Knights Islands, Leigh Coast, Great Barrier Island. Note position of the seven sampling sites in each locality. **B** Sampling localities on the Great Barrier Reef showing positions of Lizard Island, Macgillivray Reef, North Direction Island. Note sampling sites at three exposures Oblique, Exposed and Back Reef at Lizard Island. **C** San Blas Islands. Sampling localities at San Blas Islands, Panama. Note four sampling sites at the different reefs within this locality

Sampling program, tropical reefs

Lizard Island, GBR

Lizard Island lies 30 km off the mainland coast of northern Australia and 18 km from the edge of the continental shelf (Fig. 1B). Our sampling program was conducted during November 1986. Extensive surveys of midshelf reefs in the central region of the GBR by Russ (1984a, b) identified major trends in the abundance and composition of faunas of large, mobile herbivorous fish (acanthurids, scarids and siganids). Both diversity and abundance were influenced by exposure of habitats to wind and wave action and the structure of the reef. The abundance and composition of faunas also changed at the scale of hundreds of meters within a habitat, according to depth and reef profiles (Russ 1984a). These results were used to organise sampling at Lizard Island to ensure that we obtained robust abundance estimates. Our study divided the large fringing reef that surrounds Lizard Island into three habitats based on exposure to the prevailing southeasterly wind. These were the windward habitat, where the reefs faced southeast; the oblique habitat, where reefs were aligned parallel with the wind; and the backreef, where reefs were sheltered from the southeast wind. Three sites separated by 500 to 1000 m were sampled in each of these habitats. Within each habitat and site, reef topography and depth were combined to define three reef zones following the terminology of Choat and Bellwood (1985): the reef flat, crest and slope zones. The time-based count method developed in New Zealand was used to estimate abundances of herbivorous fishes. Three counts, each of 10-min duration, were done in each combination of zone and site. All species of mobile herbivorous fish within 5 m of either side of the diver were recorded, although individuals smaller than 100 mm standard length were not included in counts. To ensure that the estimates of abundance obtained from Lizard Island were representative of the region, two other reefs nearby were also sampled by our study. These were North Direction Island, 5 km to the southeast of Lizard Island; and Macgillivray Reef, 1 km to the northeast (Fig. 1B). As these reefs were small, only three sites could be accommodated around their periphery. At each site, the reef was divided into zones and abundances of herbivorous fish estimated by three counts in each zone. Finally, in order to provide more detailed information on species richness and relative abundances of herbivorous fishes, a fixed-belt transect (dimensions: 30 × 10 m) was sampled at each combination of site and depth at Lizard Island.

San Blas Islands, Panama

Counts were made at four sites that spanned a range of exposures to prevailing winds among the reefs surrounding the end of the San Blas Peninsula (Fig. 1C) during November 1993. As at Lizard Island, the reef was divided into flat, crest and slope zones in each site. Due to wave exposure and tides, only the reef crest and slope were sampled. At one site (3, Fig. 1C) where the reef had little vertical elevation, all counts were conducted at a single depth. In other sites, four timed counts of 5-min duration were used to estimate the abundance of herbivorous fish in both the crest and slope zones. The shorter count duration was used to accommodate the greater level of local scale patchiness in reef structure found at San Blas. Estimates of species richness and relative abundances of the fauna were obtained from 30 × 10 m belt transects sampled in each combination of site and zone.

Statistical analysis

Canonical discriminant analysis (CDA) (V6.03, SAS, Cary, N. C.) was used to examine abundance patterns of temperate herbivorous fish at the largest spatial scale of sampling. Abundances of each species and the total number of herbivores per count were analyzed using a hierarchical three-factor analysis of variance (ANOVA). Results of the depth survey were also examined using a three-factor

ANOVA. Plots of residuals and tests for normality were used to ensure that the assumptions of homogeneity of variance and normality made by the analyses were not violated. Details of the analyses and transformations are provided in the appropriate table headings. Variances for *Parma alboscapsularis* remained heterogeneous due to the absence of this species at one of the four localities. As the ANOVA procedure is relatively robust to departure from this assumption, the data set was included in the analysis.

For the data sets from tropical regions, variation in abundance was estimated for each of the major families and for total numbers of herbivorous fishes using factorial analysis of variance. Details of the analyses and of transformations of data sets are provided in table headings.

Results

New Zealand

Pilot study and depth distribution

The pilot study provided three important results: (1) most herbivorous fish were associated with shallow depths; (2) there were marked differences in abundance between the two sampling sites; and (3) at sites where fish were abundant, there was high variability in numbers between counts (Fig. 2). This was due to the tendency of common species to occur in monospecific schools that were highly mobile. Between-site differences were associated with differences in reef topography, with areas of high relief tending to harbor more individuals.

The more comprehensive sampling of depth-related abundance patterns undertaken at island (Poor Knights) and mainland coast (Leigh) localities confirmed a gen-

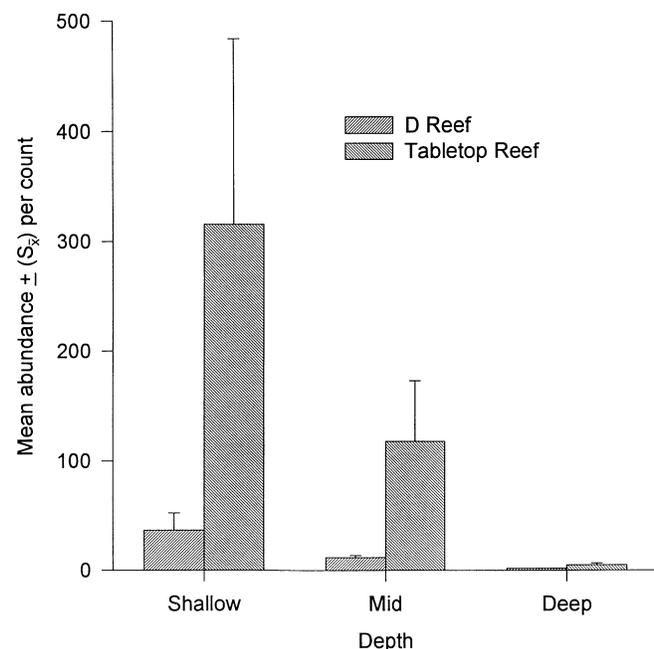


Fig. 2 Mean numbers of herbivorous fishes (\pm standard error, S_x) recorded in mapped areas of reef at three depths at Leigh, New Zealand ($n = 3$)

eral trend of declining abundances with depth in the five species sampled (Fig. 3A–E). There were some exceptions to this trend with *Kyphosus sydneyanus* being almost equally abundant at shallow and mid-depth strata. Subdivision of abundance data by size showed that small individuals were located only in shallow water. This was not due to a sampling bias as deeper waters, where there was less turbulence and lower algal cover, were more readily sampled. ANOVAs of these results revealed locality and site effects, which were expected from the results of the pilot study. Although the decline in abundance associated with depth occurred consistently at most sites, there was a significant depth–site interaction. This was attributable to a single site, where there was a more uniform distribution of schooling species among depths.

Main study

The timed counts of herbivorous fishes within the 0 to 6 m depth stratum at each of the two island and two mainland localities provided a total of 112 visual estimates of the abundance of herbivorous fishes in their main habitat. A summary of species abundance by locality is given in Table 1. The mean number of herbivorous fish was similar at all localities and ranged from 23 to 30 individuals per count. However, species composition of the fauna varied at this scale. These patterns were analyzed using CDA, which clearly differentiated the Poor Knights Islands from the coastal Leigh locality (Fig. 4A). The distinguishing features of the island locality were the high abundances of the large territorial pomacentrid *Parma alboscaphularis* and the presence of

Fig. 3 Mean numbers of **A** *Parma alboscaphularis* **B** *Girella tricuspidata* **C** *Kyphosus sydneyanus*, **D** *Odax pullus* and **E** *Aplodactylus arcidens* of differing size classes at three depths. **A–C** were recorded at only one locality, so that $n = 12$ for these species. For the remaining species, $n = 24$

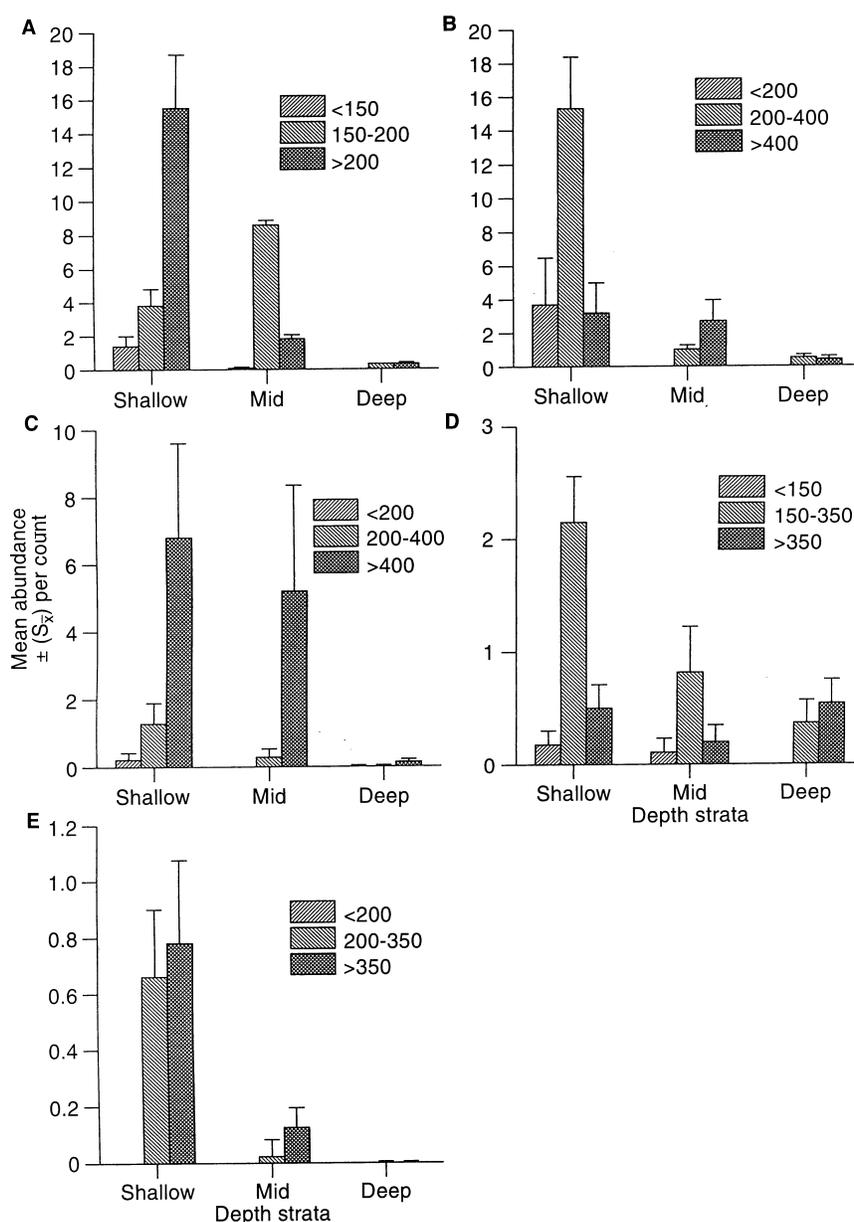


Table 1 Summary of abundance patterns of herbivorous fish at two mainland coastal (Tutukaka, The Marine Reserve at Leigh) and two island (Poor Knights Islands, Great Barrier Island) localities in northeastern New Zealand. Mean numbers per count \pm SD and range in abundance per count (parentheses) are shown ($n = 28$ for each locality)

Species	Tutukaka	Leigh	Poor Knights Islands	Great Barrier Island
<i>Parma alboscaphularis</i>	3.04 \pm 3.67 (0–13)	0.04 \pm 0.19 (0–1)	23.00 \pm 13.60 (5–54)	7.00 \pm 7.43 (0–26)
<i>Girella tricuspidata</i>	20.18 \pm 24.60 (0–132)	13.93 \pm 14.43 (0–63)	0.04 \pm 0.19 (0–1)	11.11 \pm 15.60 (1–62)
<i>Kyphosus sydneyanus</i>	3.04 \pm 11.57 (0–61)	4.36 \pm 7.89 (0–36)	1.93 \pm 4.48 (0–16)	2.39 \pm 3.45 (0–12)
<i>Kyphosus cyanea</i>	0	0	2.04 \pm 6.17 (0–30)	0
<i>Aplodactylus arcidens</i>	1.07 \pm 1.27 (0–4)	2.11 \pm 2.06 (0–8)	0.71 \pm 1.19 (0–4)	2.71 \pm 2.07 (1–10)
<i>Aplodactylus etheridgi</i>	0	0	0.07 \pm 0.26 (0–1)	0.04 \pm 0.19 (0–1)
<i>Odax pullus</i>	1.68 \pm 2.78 (0–11)	2.75 \pm 2.69 (0–12)	2.57 \pm 4.35 (0–22)	1.36 \pm 2.14 (0–9)
Total numbers	28.61 \pm 30.79 (0–107)	23.25 \pm 17.68 (3–68)	30.36 \pm 18.74 (7–73)	25.07 \pm 18.29 (1–84)

species such as *Girella cyanea*, which tends to be restricted to island localities (Choat and Ayling 1987; Choat et al. 1988). Coastal localities were characterised by relatively high abundances of *Girella tricuspidata*, *Odax pullus* and *Kyphosus sydneyanus*.

Analysis of the data sets at the level of sites (Fig. 4B) identified a number of patterns of local scale variation in abundance and composition of the fauna. Sites at the Poor Knights Islands formed a discrete group. Sites at

the remaining island locality were split between “island” and “coastal” assemblages. The sites with island affinities occurred at the northern tip of the locality and supported large numbers of *Parma alboscaphularis*. Sites where the assemblage of fishes was more typical of mainland coasts occurred on the central part of the western side of the island and were dominated by *Girella tricuspidata*. Tutukaka, a locality on the mainland coast adjacent to the Poor Knights, had a number of sites aggregated with island groupings, reflecting the presence of *P. alboscaphularis* at these sites. Sites at Leigh, the southern-most coastal locality, formed a discrete group and had a fauna dominated by *G. tricuspidata*.

Nested three-factor ANOVAs were used to examine the influence of spatial scale on the abundance of herbivorous fishes. Table 2 shows the distribution of significant effects by factors (scale of sampling) and the proportion of variation accounted for by each factor. Coastal type (islands and mainland coasts, Fig. 1A) was not a significant factor in any analysis, which was attributable to the mixture of assemblages found at sites at Tutukaka and Great Barrier Island. Significant terms at the level of localities were due to differences in the composition of the fauna among the Poor Knights Islands and the remaining localities, including Great Barrier Island. For all species analyzed, a significant site effect was identified. This confirmed the findings of the pilot study and appears to reflect differences in habitat structure, including reef profile, algal communities and exposure to prevailing weather conditions among sites.

The proportion of variation accounted for by each factor in the analysis differed among species. For *Parma alboscaphularis*, the proportion increased with the scale of sampling, reflecting the predictable association of abundances of this species with island habitats. At smaller scales, the sedentary, conspicuous nature and uniform distribution of this territorial species resulted in little variation in abundance between replicate counts within a site. In contrast, a major proportion of the variation in the abundance of the remaining species occurred at the spatial scale of sites. Such local vari-

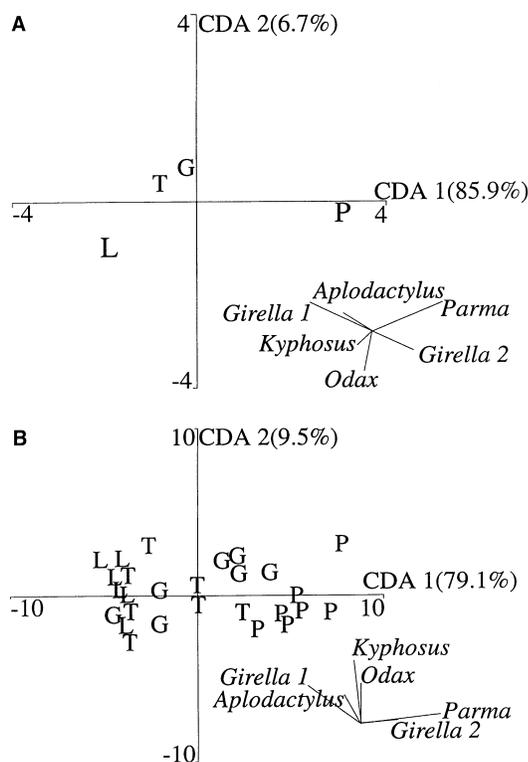


Fig. 4 Canonical discriminant analysis (CDA) of faunal composition and abundance at the levels of **A** locality and **B** sites within localities (P Poor Knights Islands; G Great Barrier Island; T Tutukaka; L Leigh) Relative contributions of each species to the differentiation of localities and sites on the CDA axes shown on bottom right (Girella 1, *Girella tricuspidata*; Girella 2, *Girella cyanea*; other species, as in Fig. 3)

San Blas Islands, Panama

At three sites the fauna was dominated by scarids and acanthurids, while large numbers of schooling kyphosids were recorded at the remaining site (Fig. 6). Mean total numbers of herbivores varied between 67 and 240 individuals per site. ANOVAs did not detect consistent differences in abundances of families or the total numbers of herbivorous fishes at any of the spatial scales examined by the study (two-factor ANOVA, all terms nonsignificant at $p > 0.05$). However, this is a preliminary result that may be due to the relatively limited replication at this locality.

Comparison of temperate and tropical regions

Data sets from each regional sampling program were pooled among localities and sites to provide an overall comparison between temperate and tropical regions (Fig. 7). In total, abundances of herbivorous fishes on temperate reefs were only 20 to 25% of those recorded in the two tropical regions. Estimates of abundance of herbivorous fishes from the Caribbean locality are preliminary, although the data suggest that they are similar to those recorded from Indo-Pacific reefs.

Differences in the abundance of herbivorous fishes between temperate and tropical regions were not related to species richness. Both New Zealand and the Caribbean have similar patterns of low richness (Fig. 8A, B, D). Species richness is much greater at Lizard Island, where a typical Indo-Pacific assemblage of species is found. Here, the frequency distribution of

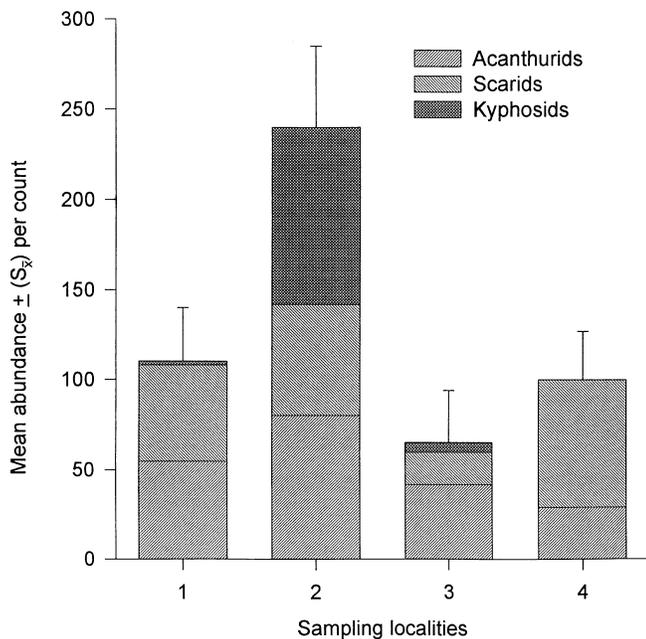


Fig. 6 Mean numbers of herbivorous fishes (\pm standard error) recorded in timed belt transects at four sites in the San Blas Islands, Panama. Means calculated from data sets pooled to give four counts of 10-min duration at each site

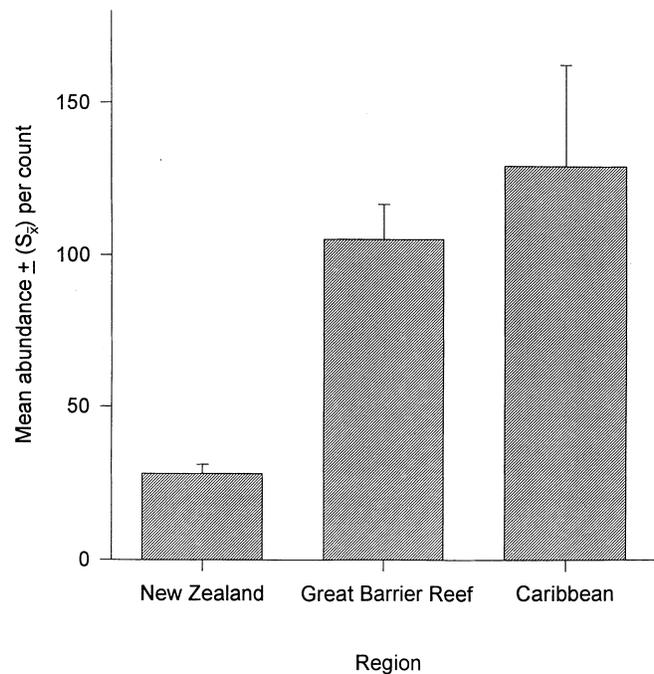


Fig. 7 Mean numbers of herbivorous fishes (\pm standard error) recorded in timed belt transects pooled among localities and sites to provide an overall comparison between temperate (New Zealand, $n = 112$) and tropical (GBR, $n = 135$; Caribbean, $n = 32$) regions. Means for the Caribbean region calculated from data sets pooled to give four counts of 10-min duration at each site

abundances is dominated by few species and has a long tail of increasingly rare species (Fig. 8C). Counts in both tropical regions were dominated by one or two abundant species of acanthurid.

Discussion

Horn (1989) summarized abundance patterns of herbivorous fishes from a number of temperate marine habitats. The range in abundance is considerable and varies from 15 to 7640 individuals per 1000 m². These results imply that, contrary to earlier assertions (Bakus 1969; Ogden and Lobel 1978; Gaines and Lubchenco 1982), herbivorous fishes may occur in large numbers in temperate waters. However, these data sets were obtained from a variety of habitats and include both recruit and adult fishes from species that may be either obligate or facultative herbivores. In addition, the methods used to sample abundances were often unique to each study. Such information provides little basis for the resolution of the question of the comparative abundance of herbivorous fish in temperate and tropical regions (Horn 1989).

The present study provides a better framework for comparisons among regions. Our data sets were produced by a standardized method that sampled fishes of a similar size within equivalent habitats in shallow water, where the greatest numbers of herbivorous fish were

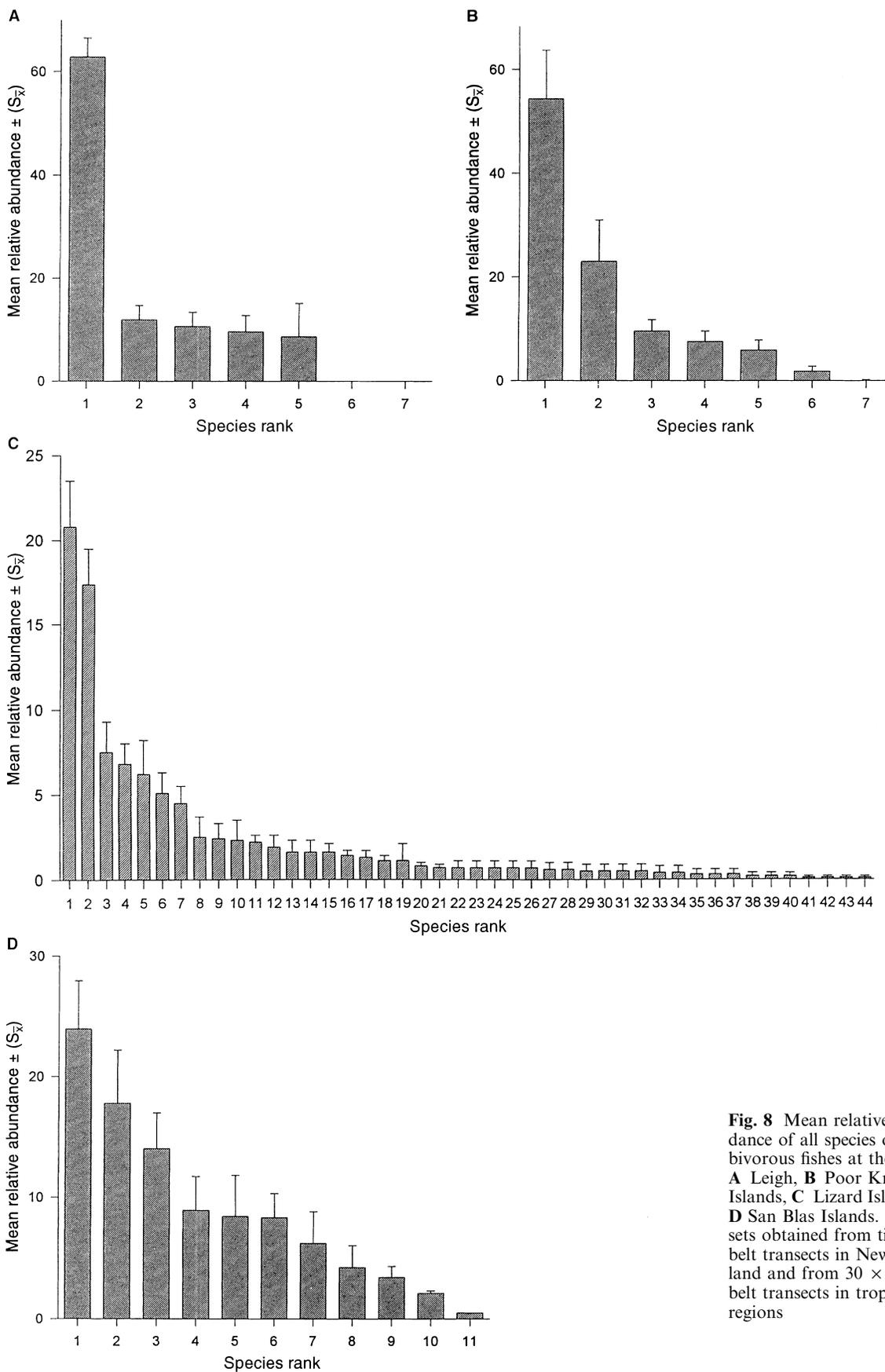


Fig. 8 Mean relative abundance of all species of herbivorous fishes at the **A** Leigh, **B** Poor Knights Islands, **C** Lizard Island and **D** San Blas Islands. Data sets obtained from timed belt transects in New Zealand and from 30×10 m belt transects in tropical regions

likely to occur (Choat and Ayling 1987; Steneck 1988). In these shallow depths, herbivorous fishes were consistently less abundant in our temperate localities than in tropical localities. On average, abundances recorded by counts in New Zealand were only 20 to 25% of those found at Lizard Island and San Blas. Previous estimates (Choat 1991) suggested that abundances of herbivores in temperate waters may be as low as 14 to 15% of those in tropical regions. Such differences may reflect the targeting of shallow habitats for sampling by our study.

In both tropical and temperate localities, counts had a lower size threshold of 100 mm SL. On reefs in northern New Zealand, it was not possible to obtain reliable estimates of the abundance of small sizes of some species, particularly odacids and aplodactylids. These cryptic individuals are associated with dense stands of macroalgae but may not be herbivorous. At small sizes, *Odax pullus* consume substantial amounts of animal material before switching to an exclusively herbivorous mode of feeding with increasing age (Clements and Choat 1993). For tropical assemblages, a threshold of 100 mm excluded recruit and juvenile fishes, in addition to many smaller herbivores such as pomacentrids and blennies. These small fishes could not have been counted without substantial modification of the sampling method. Furthermore, the degree to which such tropical taxa are herbivorous is not clear (Bellwood unpublished data). In New Zealand, pomacentrids were easily included in the timed counts since the single species that occurred in this region was relatively large, sedentary and tended to reside in the water column just above its territory. If the smaller and more cryptic blennies and pomacentrids of tropical localities had been counted, the difference in abundance found between our tropical and temperate localities would have been exaggerated. Thus, the fourfold change in numbers found by our study is likely to represent a conservative estimate of real differences in abundance of herbivorous fishes among latitudes.

In addition to the selective nature of our count technique, the use of a limited number of tropical and temperate localities by the study may restrict the generality of our findings. While our localities are not likely to be typical of all temperate or coral reefs, their biogeography and geographic setting made them the most appropriate choice for the comparison of herbivorous fish faunas at global scales. Faunas of temperate reefs of northern New Zealand are similar in composition to those of the temperate coasts of southeastern Australia. These southern regions harbor assemblages of herbivorous fishes that are species-rich in comparison to those of northern temperate localities such as the coastline of California (Choat 1991). Lizard Island lies in the Indo-West Pacific, a region that hosts the greatest diversity of tropical herbivorous fishes (Choat 1991). At this locality, the composition and abundance of the fauna of herbivorous fish is comparable to that found on midshelf reefs in the central section of the GBR, hundreds of kilometers to the south (Russ 1984a, b; Meekan et al.

1995). This implies that the fauna at Lizard Island is typical of many reefs on the GBR. There have, however, been few broad-scale descriptions of abundance patterns of herbivorous fishes in the Caribbean. Despite this problem, it is clear that the fauna recorded at San Blas is not unique to this locality, since Lewis and Wainwright (1985) and Lewis (1986) recorded assemblages of herbivorous fishes on the barrier reef in Belize that were similar to those found at San Blas, both in terms of species richness and relative abundance of the dominant families.

Our sampling programs suggested that the abundances of the major families of herbivorous fish were similar in both the Caribbean and on the GBR, despite marked differences in species richness of the assemblages. Abundance estimates from the San Blas Archipelago were more variable than those from Lizard Island, a reflection of the reduced sampling effort and patchy distribution of some taxa such as kyphosids in this region. High abundances were also recorded at some sites at San Blas due to large numbers of small individuals of *Scarus inserti*. While each region supported similar densities of herbivorous fishes, there were striking differences in the composition of assemblages. A total of 12 species were recorded at San Blas, of which seven species made up more than 5% of total numbers. In contrast, at Lizard Island, 44 species were recorded, but only six accounted for more than 5% of total numbers. In the latter region, most species were rare, resulting in a frequency distribution of relative abundances that was highly skewed. It seems unlikely that increasing the sampling intensity at San Blas, or including herbivorous pomacentrids would have substantially altered the difference in species richness between tropical regions.

In New Zealand, the composition of the fauna of herbivorous fishes was influenced by large-scale variation in habitats. Faunas on offshore islands had strong subtropical affinities (Choat and Ayling 1987) and were dominated by the large territorial pomacentrid *Parma alboscapsularis*. The shape of frequency distributions of relative abundance at offshore localities resembled those of the San Blas Archipelago. In contrast, faunas of mainland coasts were clearly dominated by a single species (*Girella tricuspidata*). The remaining species occurred in similar numbers, each accounting for approximately 10% of total numbers. The southern hemisphere endemics, *Odax pullus* and *Aplodactylus arcidens*, were only a small component of the fauna in northern New Zealand, although these species are more abundant at higher latitudes (Choat and Ayling 1987; Choat and Clements 1993).

Our study demonstrates that herbivorous fish are less abundant on shallow reefs in a temperate region than in equivalent habitats on some coral reefs. However, we lack the data to answer the more general question that relates our findings to the trophic structure of reef fish assemblages: do herbivorous fishes account for similar proportions of the total fauna of reef fishes in tropical

and temperate regions? A traditional response to this question would be that herbivorous fishes make up a smaller proportion of the fauna in temperate regions, implying that a different pattern of trophic organization exists on temperate reefs with a greater proportion of primary production passing through invertebrate food chains. Most explanations of this phenomenon (reviewed by Horn 1989; Choat 1991) suggest that changes in the relative abundance of herbivorous fishes reflect a gradient in the digestibility, palatability or productivity of algal communities between tropical and temperate regions. However, recent estimates of the composition of fish assemblages on temperate (Jones and Andrew 1990) and tropical reefs (Williams and Hatcher 1983) in the southern hemisphere imply that the proportions of herbivores in both systems may be similar. Additionally, Hobson (1994) noted that the abundance and diversity of both carnivorous and herbivorous fishes was lower in cold-temperate than warm-temperate regions on the Californian coast. The trend of declining abundance of herbivorous fishes with increasing latitude may therefore be representative of a pattern that occurs in all trophic groups of reef fish.

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