Habitat structure in soft-sediment environments and abundance of juvenile snapper *Pagrus auratus*

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ABSTRACT: Small-scale biogenic or physical features, such as depressions, burrows, shells, boulders, cobbles and sand waves, dominate soft-sediment coastal and shelf environments. Such structures may provide refuge from predation and feeding areas for juvenile fish. We investigated the potential for juvenile snapper *Pagrus auratus* to utilise areas characterised by small-scale structures by sampling soft-sediment habitats that varied in both sediment characteristics and biogenic structure. Juvenile snapper abundance was estimated at each site using opera house traps, while variations in small-scale benthic habitat structure were quantified from video transects of the seafloor. The captured fish had 172 ± 43 mm fork length, indicating that they were 1 to 2 yr old. Statistical modelling revealed that complex habitat structure had a positive influence on the abundance of juvenile snapper, suggesting that these areas are preferentially utilised. This finding highlights the potential for disturbance of such structures (by, for example, trawling or dredging) to affect the abundance of juvenile snapper.

KEY WORDS: Seafloor habitat · Juvenile fish · *Pagrus* · New Zealand · Sustainable fisheries · Sparidae

INTRODUCTION

The potential for complex seafloor habitats to influence the survivorship of juvenile life stages of exploited demersal fin-fish species has been implicitly acknowledged by the identification of nursery areas (e.g. Bradstock & Gordon 1983). The recent legislative framework for fisheries management explicitly recognises the need to determine ecological links between exploited fish populations and their environment (e.g. in the USA the Sustainable Fisheries Act [SFA] 1996 refers to 'essential fish habitat' and in New Zealand the 1996 Fisheries Act refers to 'habitat of particular significance for fisheries management'). However, knowledge of natural history and habitat requirements for different life stages of exploited populations is often unavailable. Auster et al. (1995) have demonstrated specific habitat associations for mobile megafauna

(demersal fishes and crustaceans). They observed that small-scale biogenic or physical features, such as depressions, burrows, shells, boulders cobbles and sand waves, were important elements providing structure in sedimentary habitats that dominate coastal and shelf environments. In contrast to the paucity of information on the ecology of exploited fish species, a number of ecological studies of fishes in lakes and marine reef and seagrass habitats have shown that habitat structure can play an important role in influencing juvenile survivorship (e.g. Heck & Thoman 1981, Persson & Eklov 1995, Rooker et al. 1998).

There is growing awareness of the need to broaden the scope of fisheries management by moving away from considering fish stocks in isolation and towards placing fish within an ecological and environmental context (e.g. Fluharty 2000). This implies that we need to develop an understanding of how a fish habitat is defined and the role that habitat structure can play in developing sustainable fisheries (Able et al. 1999).

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Describing fish-habitat relationships and understanding the underlying mechanisms is complicated by ontogenetic changes in habitat requirements and the spatial scales over which mobile individuals integrate habitats. In terrestrial ecosystems, there is a recognised relationship between spatial scales of mobility and body size (e.g. Addicot et al. 1987, Kotliar & Wiens 1990), but in fluid environments such movement and body size scaling rules are not so clear. For most commercially exploited species, there is insufficient information to define the spatial scales of their habitat. Nevertheless, given the 3D nature of biogenic features in sedimentary habitats, and the often high levels of predation on juvenile life stages, it is likely that if biogenic habitat structure plays a role in the population dynamics of a fish species, this role will be most important for juvenile life stages. As a first step to identifying the relationship between benthic habitat and fish, we aim to determine the importance of habitat structure in influencing the abundance of juvenile snapper.

Snapper *Pagrus auratus* (Sparidae) is one of the most intensively studied fish species in New Zealand; it supports a valuable recreational and commercial fishery (Francis & Williams 1995). Diver observations on the density of juvenile snapper within a small reef system have shown large differences in the density of fish over small spatial scales (10s of metres) that were broadly related to habitat (Kingett & Choat 1981). The highest densities of Year 0+ fish (i.e. fish in their first year of life) were found on sedimentary flats adjacent to rocky reef and kelp forest, and associated with turfing coralline algae *Corallina officinalis*. In contrast, low densities of fish older than Year 0+ were found in the reef system (Kingett & Choat 1981). Trawl surveys of juvenile snapper (Year 0+, 1+ and 2+ cohorts) have also demonstrated consistently high levels of spatial variation at the 1 km scale (Francis 1995). This pattern was explained as a preference by the juveniles for muddy substrates over muddy sand-shell hash substrates, although this could not be adequately tested due to insufficient spatial resolution of the trawl samples. These 2 studies emphasise the importance of shallow coastal sedimentary habitats for juvenile snapper of different ages over the summer months. However, neither of these previous studies was designed to identify relationships between the abundance of juvenile snapper and elements of habitat structure in soft-sediment environments that are susceptible to disturbance.

The present study was designed to explore whether habitat utilisation by juvenile snapper, at the >1 km scale, was related to the presence of small-scale habitat features. Although seafloor habitat biogenic features (e.g. presence of sponges, hydroids, suspension feeding bivalves) as well as heterogeneity created by physical features (e.g. cobbles, shell hash, sand waves)

have the potential to provide important habitat to juvenile fish, these elements are often removed by repeated fishing disturbance. These habitat features are often positively related to macrobenthic diversity (Thrush et al. 2001), and are often highly variable over small spatial scales (>1 km; e.g. Schneider et al. 1987). This heterogeneity limits the detection of ecological patterns based on traditional fish sampling strategies such as trawling, where the sampling gear sweeps over areas of the seafloor that are larger than important scales of variation in habitat structure. By determining the relationship between the abundance of juvenile snapper and the small-scale elements of habitat structure, we can identify the need for future work to elucidate mechanisms as well as providing information to resource managers on the importance of habitat diversity for juvenile life stages of exploited populations.

MATERIALS AND METHODS

Study site. The study was conducted in the vicinity of Kawau Bay (36° 24′ S, 174° 48′ E), a large, 10 to 20 m deep, embayment on the NE coast of the North Island of New Zealand (Fig. 1). Kawau Bay is comprised mainly of soft-sediment habitats that vary both in sediment characteristics and biogenic structure. Five sites were chosen to reflect this habitat variation and to encompass a range of geographic locations around the bay (Fig. 1, Table 1). Kawau Bay was chosen for this study as it enabled us to sample a variety of sedimentary habitats in close proximity, contained reasonable numbers of juvenile snapper and was the site of previous work (Francis 1993, 1994, 1995, Francis & Williams 1995). Comparative sampling in the Mercury Bay area (36° 37′ S, 175° 47′ E) was discontinued because of very low juvenile snapper abundance. While there has been extensive trawling and dredging in this region, data collected for management of the fishery generally indicate that the density of juvenile snapper is often much lower than at Kawau Bay (Langley 1993).

Sampling. Trapping, long lining or direct observations are the most appropriate methods of estimating fish abundance in relation to habitat features that vary on scales of 10s to 100s of metres. We used opera house traps and deployment procedures following the recommendations of Ferrell et al. (1994), who found these traps to be more effective than 3 other types of traps or long-lines. They found consistent catches could be achieved with soak times as low as 20 to 50 min, and were not able to detect a significant effect of time of day on catch rate. We supplemented this information with preliminary trials using different types of bait, soak times and diver and video observations of fish
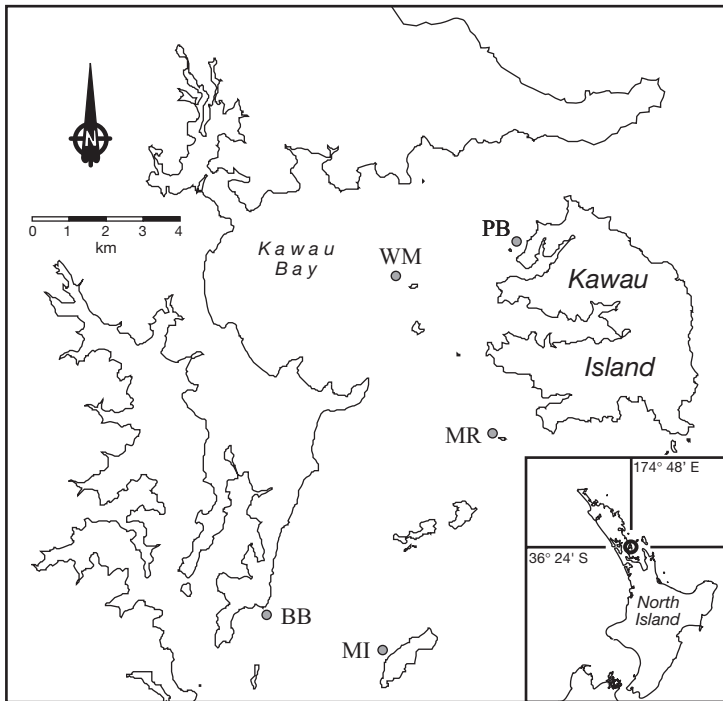
Fig. 1. Map of Kawau Bay, New Zealand, showing the location of the 5 sampling sites. Abbreviations explained in Table 1

behaviour in and around the opera house traps, as well as deploying the traps at a variety of sites. Traps used were 1.2 m long, 0.8 m wide and 0.6 m high. The traps were covered with red netting of 1 cm^2 mesh. The traps had entrances on either short side consisting of 0.25 m long tunnels that tapered in diameter from 40 to 14 cm. Each trap was baited with 2 dead pilchards *Sardinops neopilchardus*. The bait was held in a purse of plastic netting, making it impossible for the first fish to enter the trap to swallow the bait. At each site, 5 individual traps were lowered to the seabed, encompassing an area of about 100 to 200 m^2 and the total number of

juvenile snapper caught in all 5 traps was used in the subsequent statistical modelling. Soak times were similar across sites on each sampling occasion (1-way ANOVA: $F = 0.40$, df = 4, p = 0.8046), but varied between occasions (85 to 172 min) due to sea conditions and logistic problems. Samples were collected over the summer months of 1998/99 and 1999/2000. Sampling times when very low numbers of fish were caught (i.e. mean of <1 snapper at >2 of the 5 sites) were not used in the subsequent analysis. In total, 7 sampling occasions were used to relate juvenile snapper abundance to habitat structure (November and December 1998, January, February [2 dates] and April 1999, and February 2000).

Habitat structure. Seafloor habitat structure was quantified at 2 different spatial scales for each of the 5 sites. At the large scale, we used the acoustic technique QTC VIEW™ to provide a broad overview of the diversity of habitat structure. Potentially simple, single beam acoustic techniques, like QTC, enable habitats to be mapped cheaply and over broader spatial scales than achievable using traditional core or grab sampling techniques. Hamilton et al. (1999) compared this technique with another single beam acoustic technique (RoxAnn) and found QTC to be more consistent and reliable. Between February and March 1999, a 1 × 1 km square area was mapped at each site using a Simrad EA501P hydrographic sounder and QTC VIEW™ (Series 4) operating at 200 kHz with a ping-rate of 5 s^{-1}, to receive and decompose the sonar signal into 166 variables. All navigation was done using the software package HYDRO™ and a Trimble DSM212 dGPS, ensuring high spatial positioning accuracy (±5 m). The square area was mapped by pairs (50 m apart) of 1 km

Table 1. Site description, including sediment type and habitat. Shannon-Wiener diversity (H′) is derived for acoustic habitat elements sampled by QTC View in 1 × 1 km blocks. Small-scale habitat elements (number of elements) were counted on 4 transects per site. PB: Pembles; MR: Marteello Rock; WM: West Mayne; BB: Big Bay; MI: Moturoa Island

Site	Sediment type	Habitat description	H′	No. of elements
PB	Sand; patches of muddy sand; shell hash	Scallops, sponges, *Atrina zelandica*, chaetoperid tubes, spionid tube mats, burrows and mounds	1.62	3.9
MR	Sand; patches of muddy sand; pebbles; shell hash	Scallops, spionid tube mats, burrows, mounds	1.55	3.8
WM	Sand	*Atrina zelandica*, spionid tube mats, burrows, mounds and gastropod shells	1.24	4.3
BB	Sand; shell hash; patches of muddy sand	*Atrina zelandica*, sponges, seaweed, spionid tube mats, burrows	1.92	3.3
MI	Sand; few patches of shell hash	*Atrina zelandica*, chaetoperid tubes, holes	1.61	2.8

Table 2. Elements of habitat structure observed by video sampling

Immobile biological features	Sediment grain size characteristics	Miscellaneous
Ascidians	Boulder (256–4096 mm)	Sand ripples
Coralline algae	Cobble (64–256 mm)	Ray pits
Chaetopterid tubes	Gravel (2–4 mm)	Shells
Atrina zelandica	Sand	*Atrina zelandica*
Holes and burrows	Sandy mud	*Atrina zelandica* shells lying down
Hydroids	Muddy sand	*Atrina zelandica* upright and dead
Mounds	Mud	Scallop shells
Scallops *Pecten novae-zelandiae*		Dead sponge
Sponges		
Seaweed		
Spionid worm tube mat		

long transects separated by 200 to 250 m. The area sampled by each sonar ping varied in diameter from 0.18 m to 1.84 m, depending on water depth. Due to limited information transfer, each datum point that QTC VIEW™ records is an average of 5 consecutive pings.

A principal component analysis (PCA, mean centred) was run on the 166 variables collected from all 5 sites to reduce the number of variables. The first 5 of the PCA axes (which together comprised >95% of the variability) were then analysed by K-means clustering using the Calinski-Harabasz statistic to determine how to best partition the data into a number of different groups (Legendre et al. 2002). Once the optimum number of groups was decided, the diversity of habitats found at a site was determined using the Shannon-Wiener index: $H' = -\sum_i p_i(\log_2 p_i)$, where p represents the frequency distribution of habitat i.

To assess small-scale habitat complexity, 2 locations were haphazardly chosen within each site. At each location, two 20 m transects were laid on the seafloor at right angles to each other. One transect in each pair was always aligned with the tidal flow (typically ~ north-south). Each transect was videotaped using a digital video camera with the lens held perpendicular 0.7 m above the seabed. For visual classification, the transects were frame grabbed. Quadrats of 30 × 100 cm were selected from the grabbed strip, and depending on the number of habitat features observed along each transect, a maximum of five 30 × 100 cm quadrats were selected. On transects exhibiting no apparent change in habitat structure, quadrats were positioned at the start and end of the transect. For each quadrat, the number of different habitat features observed (see Table 2) was counted. Means were calculated from these values to produce a single estimate of small-scale habitat structure for each site (see Table 1).

Generalised linear modelling procedures (McCullagh & Nelder 1989, Crawley 1993) were used to relate the abundance and size of juvenile snapper to habitat structure and a number of other environmental/sampling variables (Table 3). Initially a model with normal error structure and no data transformations was run for each set of explanatory variables. Model fit was evaluated by visual inspection of half normal plots of residuals, together with plots of residuals vs predicted values. It proved unnecessary to transform the data or use other error structures. To develop regression models,

Table 3. Environmental variables and generalised linear models developed to explore patterns in the abundance of juvenile snapper *Pagrus auratus.* Variables in italics are categorical. Listing 'habitat structure' indicates the inclusion of both large- and small-scale variables. For details on model numbers, refer to text. CPUE: catch per unit effort

Model	Independent variables	Dependent variables	Interaction with *Date* included	2nd degree polynomial function included
1	Size	*Site*, *Date*	No	No
2	Abundance	*Site*, *Date*	No	No
3	Abundance	Time to nearest high tide, Tidal state, Direction and height, Soak time, *Date*	Yes	Yes for all continuous variables
4	CPUE	Soak time, *Date* Habitat structure	Yes	Yes for all continuous variables
5	Abundance	Soak time, *Date*, Habitat structure	Yes	Yes for all continuous variables
6	Abundance	Habitat structure, Potential food, Soak time, *Date*	Yes	Yes for all continuous variables

we used backwards variable selection with an exit level of p = 0.15. Even then, variables were dropped from the model only if their removal did not markedly affect the error sum of squares. After finding the most parsimonious model, a number of different orders of dropping variables were tested to make sure that the model produced was the best and most consistent.

RESULTS

The opera house traps sampled snapper between 40 and 315 mm fork length (mean ± 1 SD: 172.4 ± 43.3 mm), with no indication of changes in the size of fish caught with respect to site (p = 0.4187; Model 1, Table 3). Other species were rarely collected from the opera house traps (in total, 11 juvenile trevally *Caranax geogians*, 3 juvenile sweep *Scorpis lineotatus*, 10 juvenile goatfish *Upeneichthys lineatus* and 1 unidentified blennie); no decapods or cephalopods were collected. The low and sporadic occurrence of these fish was not considered to influence the numbers of snapper collected in the traps. However, changes in size with date were apparent (p = 0.0193), probably indicating growth over the summer. Over all times there were no significant differences in fish abundance between sites (p = 0.1335; Model 2, Table 3), due predominantly to high variability over time (Fig. 2). Sites MI and WM showed the most variability over time, while Site PB was the most consistent in fish abundance.

Initial modelling concentrated on determining whether changes in abundance over time and site could be explained by differences in tidal state and soak time (Model 3, Table 3). This model provided no evidence (p > 0.15) that the tide was an important

influence on the abundance of juvenile snapper. However, there was an indication that soak time might play a role (p = 0.15) and we were concerned with the potential for fish to behave differently towards cages in habitats with different levels of structure. Thus, in developing a generalised linear model to identify any relationship between habitat structure and the abundance of juvenile snapper, we maintained soak time in the model.

Initially this was done by normalising abundance by soak time (i.e. catch per unit effort [CPUE], Model 4, Table 3). However, there is the potential for interactions between soak time and habitat structure, so another model (Model 5, Table 3) was constructed that included continuous variables of habitat structure and soak time as 2nd-degree polynomial functions to account for potential non-monotonic responses. While both models resulted in significant positive relationships between fish caught and habitat structure, the model with normalised abundance had a lower adjusted R^2 (10 % less).

Lastly, a model (Model 6, Table 3) was investigated that included the density of potential food (macrofaunal densities calculated from Thrush et al. 2001), as well as habitat structure. However, the importance of macrofaunal density was lower than habitat structure and was always dropped from the model.

The final model accounted for 74 % of the variability in the abundance of juvenile snapper (Table 4), with a significant and positive influence of the variety and number of habitat structure elements, at both the small and large scale, on the abundance of juvenile snapper. No significant date interaction terms were found. Soak time was important, although this was not a simple monotonic relationship. Instead a complex interplay between increasing number of fish caught and increasing soak time, and a negative relationship between soak time and the habitat structure, measured at both the large and the small scale, was indicated.

DISCUSSION

Our results extend the natural history information available for the juvenile life-stage of a commercially important species. The interquartile size range for the juvenile snapper captured by the opera house traps was 136 to 200 mm fork length. The size for age characteristics described by Francis & Williams (1995), based on estimating age from otoliths (Francis 1994), indicates that the fish we sampled were a mixed assemblage of Year 1+ and 2+ fish. The effectiveness of the opera house traps in catching juvenile snapper was similar to that reported by Ferrell et al. (1994), with an overall mean of about 1 fish per trap. Our results
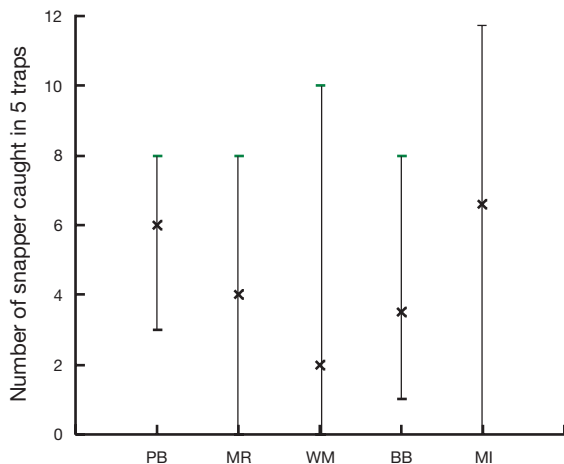

Fig. 2. *Pagrus auratus.* Median and interquartile range for the abundance of juvenile snapper found over time at each of the 5 sites. See Table 1 for definition of abbreviations

Table 4. Generalised linear model relating the abundance of juvenile snapper *Pagrus auratus* to habitat structure in Kawau Bay. $R^2 = 0.74$

	df	SS	F	p	Parameter estimates
Date	7	635.1	2.21	0.0743	
Soak time	1	374.5	9.09	0.0064	3.44
Small-scale habitat structure	1	210.8	5.12	0.0339	52.91
Large-scale habitat structure	1	277.8	6.74	0.0165	114.2
Soak time × Small-scale habitat structure	1	287.3	6.97	0.0149	−0.4595
Soak time × Large-scale habitat structure	1	365.9	8.88	0.0069	−0.9754
Model	12	2626.4	5.31	0.0004	
Error	22	906.6			

emphasise the importance of habitat structure in influencing the abundance of juvenile snapper. This result contrasts with Kingett & Choat (1981) who did not find a relationship between the abundance of Year 0+ snapper and topographic structure, although it is not clear how the authors quantified this variable. Our results refine the conclusions of Francis (1995), due to the finer scale sampling possible with traps rather than trawls, and the quantitative description of fine-scale habitat structure. Francis (1995) concluded that variation in the abundance of juvenile snapper in Kawau Bay result from higher juvenile snapper abundances associated with muddy sediments. Our analysis indicates that it is the habitat features nested within the broad-scale 'sand vs mud' type habitat classification that is important in influencing the abundance of juvenile snapper. This implies that seafloor habitats will need to be mapped at finer scales of resolution than simple measures of sediment type if maps are to be useful in defining and managing fish habitat.

We found no indication that the time of day or time of tide influenced the number of juvenile snapper caught. However, the role of soak time was more interesting: in combination with other sampling variables it only had a very weak influence, but in combination with habitat structure it became very important. This suggests that the effect of soak time on the abundance of juvenile snapper varies with habitat structure. Previous studies have demonstrated that trap and pot efficiency will vary with various factors including habitat (Blaustein 1989, Rozas & Minello 1997, Kneib & Craig 2001). Soak time involves the interaction of a number of factors, including changes in the influence of the bait-odour plume in attracting fish, rates of entry and exit of fish within the cage, and density of fish within the cage, which will influence the number of fish in the trap when it is pulled from the seabed. The identification of non-linear responses and interactions between soak time and habitat structure may well reflect behavioural responses of the fish to the cage structure, responses which are influenced by the surrounding habitat. Robichaud et al. (2000) reports that Antillean fish traps

were less effective at capturing fish adjacent to coral reef habitats in comparison to less structured habitats, even though fish densities were higher in the vicinity of the coral reef. In habitats with higher degrees of structure that provide refugia, fish may be less attracted to the cage structure than in more simple habitats. The negative interaction between soak time and both scales of habitat structure on juvenile snapper abundance in our model support the findings of Robichaud et al. (2000). Although research is needed on the behaviour of snapper, the implication of our statistical models is that such relationships between capture efficiency of trap and habitat would tend to weaken the strength of relationships between abundance and habitat structure.

Two mechanisms are commonly invoked to explain relationships between fish abundance and habitat structure: either the provision of refugia from predation or the provision of food. Gut analysis of some of the juvenile snapper caught in this study indicates they are eating a wide variety of macrofauna (authors' unpubl. data). We found no evidence for a relationship between potential food and the abundance of juvenile snapper when using macrofauna density estimates derived from Thrush et al. (2001). The spatial scale of sampling for macrofauna within sites integrates over small spatial heterogeneities such as ray pits that might include small accumulations of organic material. More general observations of the seafloor by divers and underwater video did not reveal any specific production hot spots that might be expected to increase fish numbers (Jenkins et al. 1993, Vetter & Dayton 1999). Thus, our work suggests that habitat structures providing refugia are important. The early life history (egg to larval stages) makes most exploited fish populations highly dynamic (see Francis 1993 and Zeldis 1993 for snapper). However, in theory at least one demographic rate must be density dependent, at some stage or location, to ensure population regulation (Hixon & Carr 1997). Predation is commonly considered as the mechanism inducing density-dependent mortality in juveniles of exploited fish populations (e.g.

Sissenwine 1984). Modifying the risk of predation for an individual involves searching out areas that reduce a predator's ability to locate and capture prey (Giske et al. 1998). A number of studies have demonstrated that survivorship of juvenile Atlantic cod *Gadus morhua* is related to habitat structure, which may at least partly explain the slow recovery of the stock after its collapse (Lough et al. 1989, Gotceitas & Brown 1993, Tupper & Boutilier 1995, Gregory & Anderson 1997, Lindholm et al. 1999). This implies that we need to understand the behaviour and ecology of fish over various space and time scales, as well as their recruitment dynamics, to sustainably manage populations (Bailey 1994).

Our work provides the first empirical evidence that small-scale habitat structure within soft-sediment habitats influences the abundance of juvenile snapper. The sites sampled in Kawau Bay spanned a range of habitats that differed both in sediment characteristics and the presence of a variety of epifauna. They do not reflect what is typically considered to be a highly structured seafloor habitat such as patch reefs. The variety of relatively low-density features observed create small-scale structures on the seafloor, typical of what could be expected over large expanses of coastal and shelf soft-sediment environments. These features can have an important and positive influence on macrobenthic diversity (Thrush et al. 2001), indicating the potential for positive interactions between maintaining both juvenile fish abundance and biodiversity. When the seafloor is disturbed by trawling or dredging, biogenic elements of habitat structure are usually removed, although the magnitude of effects will depend on the extent, frequency and intensity of disturbance. However, the sensitivity and resilience of resident species that contribute to habitat structure are also important (Thrush & Dayton 2002). Given the growth rate and dispersal of many of these organisms, recovery is likely to be sufficiently slow to result in long-term changes in fished areas (Dayton et al. 1995, Jennings & Kaiser 1998, Thrush et al. 1998, Auster & Langton 1999).

Our results highlight the potential links between fisheries and habitats, and the consequences of declines in habitat structure in soft-sediment environments that can occur as a result of anthropogenic disturbances such as trawling and dredging. In this paper we have identified a positive relationship between habitat structure and the abundance of juvenile snapper across a wide array of the soft-sediment habitats of Kawau Bay. Further research is needed to assess the generality of this relationship to encompass the spatial extent of the fishery, and most importantly to understand the mechanisms that generate this pattern and its influence on the population dynamics of this valuable fishery. The analysis of habitat does demonstrate that simplistic broad-scale classifications of seafloor habitats may be insufficient to describe the variability in abundance of juvenile demersal fish. Although gathering natural history and ecological information on exploited stocks to identify and assess the benefits of improved juvenile survivorship is difficult in coastal and shelf environments, evidence is growing of the links between habitat quality and fish stocks, at least for some species (Sainsbury 1988, Steves et al. 1999, Turner et al. 1999, Kaiser et al. 2000). This type of research is necessary if science is to support the policy initiatives in fisheries management that seek to identify and sustainably manage habitats of importance to exploited populations, while maintaining marine biodiversity.

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