

Effects of Poor Knights Islands Marine Reserve on demersal fish populations

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Christopher M. Denny, Trevor J. Willis, and Russell C. Babcock

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CONTENTS

Abstract	5
<hr/>	
1. Introduction	6
<hr/>	
2. Material and methods	9
<hr/>	
2.1 Study sites	9
2.2 Baited underwater video	10
2.3 Underwater visual census	11
2.4 Data analysis	11
3. Results	13
<hr/>	
3.1 Baited underwater video	13
3.1.1 Species richness	13
3.1.2 Seasonal variation	14
3.1.3 Density	14
3.1.4 Size	16
3.1.5 Reserve status	16
3.2 Underwater visual census	18
3.2.1 Species richness	18
3.2.2 Seasonal variation	20
3.2.3 Density	21
3.2.4 Size	25
4. Discussion	26
<hr/>	
4.1 Snapper	26
4.2 Other fish species	27
4.3 Seasonal variation	28
4.4 Species richness	28
4.5 Partial protection	29
4.6 Conclusion	30
5. Recommendations	30
<hr/>	
6. Acknowledgements	31
<hr/>	
7. References	31
<hr/>	

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Christopher M. Denny, Trevor J. Willis, and Russell C. Babcock

University of Auckland, Leigh Marine Laboratory, PO Box 349,
Warkworth, New Zealand

ABSTRACT

The responses of demersal reef fish to the establishment of the Poor Knights Islands Marine Reserve in northeastern New Zealand were investigated. The reserve and two reference locations (Cape Brett and the Mokohinau Islands) were sampled biannually over 3½ years using two survey methods: baited underwater video (BUV), and underwater visual census (UVC). Following the implementation of full marine reserve status at the Poor Knights Islands in 1998, both methods found that snapper (*Pagrus auratus*) dramatically increased in abundance (relative to fished reference locations): mean (\pm SE) snapper size also increased here from 274 (\pm 9) mm in autumn 1999 to 324 (\pm 5) mm in spring 2001 (BUV). BUV also found porae (*Nemadactylus douglasi*) increased in density at the Poor Knights Is and UVC found blue maomao (*Scorpiis violaceus*), pink maomao (*Caprodon longimanus*) and orange wrasse (*Pseudolabrus luculentus*) increased in density. Seven species decreased significantly in density in the reserve but only three at both reference locations. The drop in density of some species may result from competitive or predatory interactions with snapper or other species. Several seasonal trends were apparent. There was evidence that the earlier partial fishing regulations were inefficient at protecting targeted species. The increase in snapper density in particular, since full reserve status, has been rapid, probably resulting from immigrating adult fish rather than from recruitment. It is not yet clear whether snapper numbers have stabilised. Populations sustained by larval recruitment (e.g. pink maomao) may take longer to recover.

Keywords: Poor Knights Islands Marine Reserve, New Zealand, snapper, Cape Brett, Mokohinau Islands, spatial distribution, temporal variation, partial protection, pink and blue maomao, orange wrasse, porae

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1. Introduction

The Poor Knights Islands Marine Reserve, located 24 km off the east coast on Northland, was established in 1981 with the aim of protecting reef fish that are vulnerable to overfishing, are long-lived, or that have low reproductive rates. Special fisheries regulations existed until October 1998 at which time the Poor Knights Islands were given full no-take marine reserve status. From 1981 to 1998 all commercial fishing, and recreational nets and long-lines were prohibited. Recreational fishers were allowed unweighted, single-hook lines, trolling, and spearing to catch a permitted number of species within 95% of the marine reserve. The permitted species (Table 1) were all thought to be nomadic or pelagic at the time of the reserve creation, that is, they were not considered part of the resident demersal reef fish assemblage. However, the inclusion of these species was based on very limited knowledge of their biology and behaviour. Several species such as trevally (*Pseudocaranx dentex*), snapper (*Pagrus auratus*), pink maomao (*Caprodon longimanus*) and kingfish (*Seriola lalandi*) are now known to be wholly or partially resident around reefs (Saul & Holdsworth 1992; Francis 2001; Willis et al. 2001). Recreational fishers targeted these, particularly snapper—the most abundant demersal predatory fish species in northeast New Zealand.

Before October 1998, the Poor Knights Islands Marine Reserve was effectively a partial marine reserve or ‘marine park’. This is a common scenario in other countries where marine reserves or marine protected areas (MPAs) usually allow certain forms of fishing. For example, Francour et al. (2001) found that amateur and commercial fishing was allowed in half the MPAs in the Mediterranean, and Bohnsack (1997) pointed out that 99.5% of the Florida Keys Marine Sanctuary provided no protection for any species. The world’s largest MPA, the Great Barrier Reef Marine Park, has many levels of zoning: most of these allow fishing of some kind and less than 5% of the area is no-take (Anon. 2002). With growing worldwide pressure to increase the level of protection afforded to marine habitats, partial fishing closures are often advocated by groups with direct fishing interests as a ‘compromise’ solution allowing both protection and fishing. Despite the number of MPAs worldwide, the effectiveness of partial closures for either conservation or enhanced fishing has not been well evaluated (but see Francour et al. 1994; Vacchi et al. 1998; Denny & Babcock in press).

Before the expiry of the special fisheries regulations in 1994, the Department of Conservation (DOC) undertook a review of recreational fishing to assess whether this should continue in the marine reserve. The majority of submissions (73%) did not want fishing to continue so the Minister decided not to issue a further fishing notice. Following this decision, the Whangarei Deep Sea Anglers Club and the Tutukaka Boat Association were granted an interim order to allow continued fishing within the marine reserve. Further public consultation was initiated, the key issue relating to the debate over whether recreational fishing was having a substantial impact on the marine life of the Marine Reserve. During this time it was acknowledged by both sides that the ecology of the Poor Knights Is was by no means fully understood and the impact

TABLE 1. THE SPECIES, COMMON NAME, FAMILY AND LOCATION OF FISH OBSERVED DURING UVC AND BUY.

FAMILY	SCIENTIFIC NAME	COMMON NAME	LOCATION UVC	RECORDED BUY
Aplodactylidae	<i>Aplodactylus arctidens</i>	Marblefish	PK CB MK	
	<i>A. etberidgii</i>	Notch-head marblefish	PK CB MK	
Arripidae	<i>Arripis trutta</i>	Kahawai†	PK CB	CB
Berycidae	<i>Centroberyx affinis</i>	Golden snapper‡	PK CB MK	PK CB MK
Blenniidae	<i>Plagiotremus tapeinosoma</i>	Mimic blenny	PK CB MK	
Callanthidae	<i>Callanthis australis</i>	Northern splendid perch	PK CB	
Carangidae	<i>Decapterus koberu</i>	Koheru‡	PK CB MK	
	<i>Pseudocaranx dentex</i>	Trevally†	PK CB MK	PK CB MK
	<i>Seriola lalandi</i>	Kingfish†	PK CB MK	PK CB MK
	<i>Trachurus novaezelandiae</i>	Jack mackerel†	PK CB MK	MK
Carcharhinidae	<i>Carcharhinus brachyurus</i>	Bronze whaler†		PK
Chaetodontidae	<i>Ampbichaetodon howensis</i>	Lord Howe coralfish	PK CB	PK CB
Cheilodactylidae	<i>Cheilodactylus ephippium</i>	Painted moki	PK MK	
	<i>C. spectabilis</i>	Red moki‡	PK CB MK	PK CB MK
	<i>Nemadactylus douglasii</i>	Porae‡	PK CB MK	PK CB MK
	<i>N. macropterus</i>	Tarakihī‡	PK CB MK	PK CB MK
Chironemidae	<i>Chironemus marmoratus</i>	Hiwihiwī‡	PK CB MK	CB MK
Dasyatidae	<i>Dasyatis brevicaudata</i>	Short-tailed stingray	PK CB MK	PK CB MK
	<i>D. tbetidis</i>	Long-tailed stingray	PK CB MK	PK CB
Diodontidae	<i>Allomycterus jaculiferus</i>	Porcupinefish	CB MK	CB MK
Gempylidae	<i>Thyrstites atun</i>	Barracouta†	MK	PK MK
Girellidae	<i>Girella cyanea</i>	Bluefish	PK CB MK	
	<i>G. tricuspidata</i>	Parore	PK CB MK	
Kyphosidae	<i>Kyphosus bigibbus</i>	Grey drummer	PK	
	<i>K. sydneyanus</i>	Silver drummer	PK CB MK	CB MK
Labridae	<i>Anampses elegans</i>	Elegant wrasse	PK CB MK	PK CB MK
	<i>Bodianus unimaculatus</i>	Pigfish‡	PK CB MK	PK CB MK
	<i>Coris picta</i>	Combfish	PK CB MK	PK CB MK
	<i>C. sandageri</i>	Sandagers wrasse‡	PK CB MK	PK CB MK
	<i>Nototabrus celidotus</i>	Spotty‡	PK CB MK	PK CB MK
	<i>N. fucicola</i>	Banded wrasse‡	PK CB MK	PK CB MK
	<i>N. inscriptus</i>	Green wrasse‡	PK CB MK	PK CB MK
	<i>Pseudolabrus luculentus</i>	Orange wrasse	PK CB MK	PK CB MK
	<i>P. miles</i>	Scarlet wrasse‡	PK CB MK	PK CB MK
	<i>Suezichthys arquatus</i>	Rainbowfish	PK CB MK	
	<i>S. aylingi</i>	Crimson cleanerfish	PK CB MK	PK CB MK
Latridae	<i>Thalassoma amblycephalum</i>	Two-tone wrasse	PK	
	<i>T. lunare</i>	Moon wrasse	PK	
	<i>Latridopsis ciliaris</i>	Blue moki	PK MK	MK
	<i>L. forsteri</i>	Copper moki	PK CB	
Microcanthidae	<i>Atypichthys latus</i>	Mado	PK CB MK	PK CB MK
Monacanthidae	<i>Parika scaber</i>	Leatherjacket	PK CB MK	PK CB MK
	<i>Thamnaconus analis</i>	Morse-code leatherjacket	PK MK	
Moridae	<i>Lotella rbacinus</i>	Rock cod‡	PK CB MK	PK MK
Mullidae	<i>Parupeneus spilurus</i>	Black-spot goatfish	PK	
	<i>Upeneichthys lineatus</i>	Goatfish	PK CB MK	PK CB MK

Continued next page >>

† Species permitted to be caught prior to 1998 at the Poor Knights Is.

‡ Species known to be caught as bycatch.

PK = Poor Knights Is; MK = Mokohinau Is; and CB = Cape Brett.

TABLE 1. *Continued.*

FAMILY	SCIENTIFIC NAME	COMMON NAME	LOCATION UVC	RECORDED BUY
Muraenidae	<i>Enchelycore ramosa</i>	Mosaic moray‡	PK CB	PK
	<i>Gymnotborax nubilis</i>	Grey moray‡	PK CB MK	PK CB MK
	<i>G. obesus</i>	Speckled moray‡	PK CB	PK CB
	<i>G. prasinus</i>	Yellow moray‡	PK CB MK	PK CB MK
	<i>G. prionodon</i>	Mottled moray‡	PK CB MK	PK CB MK
Myliobatidae	<i>Myliobatus tenuicaudatus</i>	Eagle ray	PK CB MK	PK CB MK
Nototheniidae	<i>Notothenia angustata</i>	Maori chief	PK	
Odacidae	<i>Odax pullus</i>	Butterfish	PK CB MK	PK CB MK
Ophichthidae	<i>Opbisurus serpens</i>	Snake eel		CB
Pempheridae	<i>Pempheris adspersus</i>	Bigeye	PK CB MK	
Pentacerotidae	<i>Evistias acutirostris</i>	Striped boarfish	PK	
	<i>Paristiopterus labiosus</i>	Giant boarfish		CB
	<i>Zanclistius elevatus</i>	Long-finned boarfish	PK CB	
Pingupedidae	<i>Parapercis coltias</i>	Blue cod‡	PK CB MK	PK CB MK
Polyprionidae	<i>Polyprion oxygeneios</i>	Hapuku‡	PK MK	
Pomacentridae	<i>Chromis dispilus</i>	Demoiselle	PK CB MK	PK CB MK
	<i>C. fumea</i>	Yellow demoiselle	PK CB MK	
	<i>C. hypsilepis</i>	Single-spot demoiselle	PK CB MK	
	<i>Parma alboscapularis</i>	Black angelfish	PK CB MK	PK MK
Rajidae	<i>Raja innominata</i>	Skate		CB
Scorpaenidae	<i>Helicolenus percooides</i>	Sea perch		CB
	<i>Scorpaena cardinalis</i>	Northern scorpionfish	PK CB MK	PK CB MK
	<i>S. papillosus</i>	Dwarf scorpionfish‡		PK CB MK
Scorpidae	<i>Bathystetbus cultratus</i>	Grey knifefish	PK	
	<i>Labracoglossa nitida</i>	Blue knifefish	PK CB	
	<i>Scorpis lineolatus</i>	Sweep‡	PK CB MK	PK CB MK
	<i>S. violaceus</i>	Blue maomao‡	PK CB MK	PK CB MK
Scyliorhinidae	<i>Cephaloscyllium isabellum</i>	Carpet shark†	PK CB	PK CB
Serranidae	<i>Acanthistius cinctus</i>	Yellow-banded perch	PK CB	PK
	<i>Caesioperca lepidoptera</i>	Butterfly perch	PK CB MK	PK CB MK
	<i>Caprodon longimanus</i>	Pink maomao†	PK CB MK	PK CB MK
	<i>Epinephelus daemeli</i>	Spotted black grouper	PK	
	<i>Hypoplectrodes huntii</i>	Red-banded perch	PK MK	PK MK
	<i>Hypoplectrodes</i> sp. B	Half-banded perch	PK CB MK	PK CB MK
Sparidae	<i>Pagrus auratus</i>	Snapper†	PK CB MK	PK CB MK
Tetraodontidae	<i>Cantbigaster callisterna</i>	Clown toado	PK CB MK	PK CB MK
Triakidae	<i>Galeorhinus galeus</i>	School shark†		PK CB
Triglidae	<i>Chelidonichthys kumu</i>	Red gurnard‡		CB MK
Tripterygiidae	<i>Obliquichthys maryannae</i>	Oblique swimming triplefins	PK CB MK	
Zeidae	<i>Zeus faber</i>	John dory	PK CB MK	CB MK
Other permitted fish	Scombridae	Tuna—6 species†		
	Istiophoridae	Billfishes—6 species†		
	Carangidae	Mackerel—5 species†		
	Many families	Sharks—27 species†		

† Species permitted to be caught prior to 1998 at the Poor Knights Is.

‡ Species known to be caught as bycatch.

PK = Poor Knights Is; MK = Mokohinau Is; and CB = Cape Brett.

of permitted fishing not really known. Advocates for and against the establishment of full marine reserve status at the Poor Knights Is had no research with which to support their arguments. Although there have been previous studies conducted at the Poor Knights Is, none provided information of sufficient detail to allow an assessment of the impacts of recreational fishing activity on reef fish ecology (Schiel 1984; Ward & Roberts 1986; Choat & Ayling 1987; Choat et al. 1988; Kingsford & MacDiarmid 1988).

The present study examines the effects of full marine reserve protection on the demersal reef fish assemblage at the Poor Knights Islands Marine Reserve. It compares the results with two reference locations: Cape Brett and the Mokohinau Islands—reference locations which allow normal fishing and are used here as ‘fished controls’. In particular, snapper, *P. auratus* (Bloch and Schneider, 1801) was examined closely as it supports New Zealand’s most valuable commercial and recreational fishery. In our survey we used two different methods to provide quantitative estimates of fish abundance and size: underwater visual census (UVC) and baited underwater video (BUV). Very few studies on marine reserves have:

- Data prior to the establishment of a reserve
- Used two methods to assess the entire reef fish assemblage
- Data from inside and outside the marine reserve (but see Edgar & Barrett 1999)

The continual record of the rate of recolonisation of key fish species of our study also provides insights into the mechanisms of fish recovery in marine reserves.

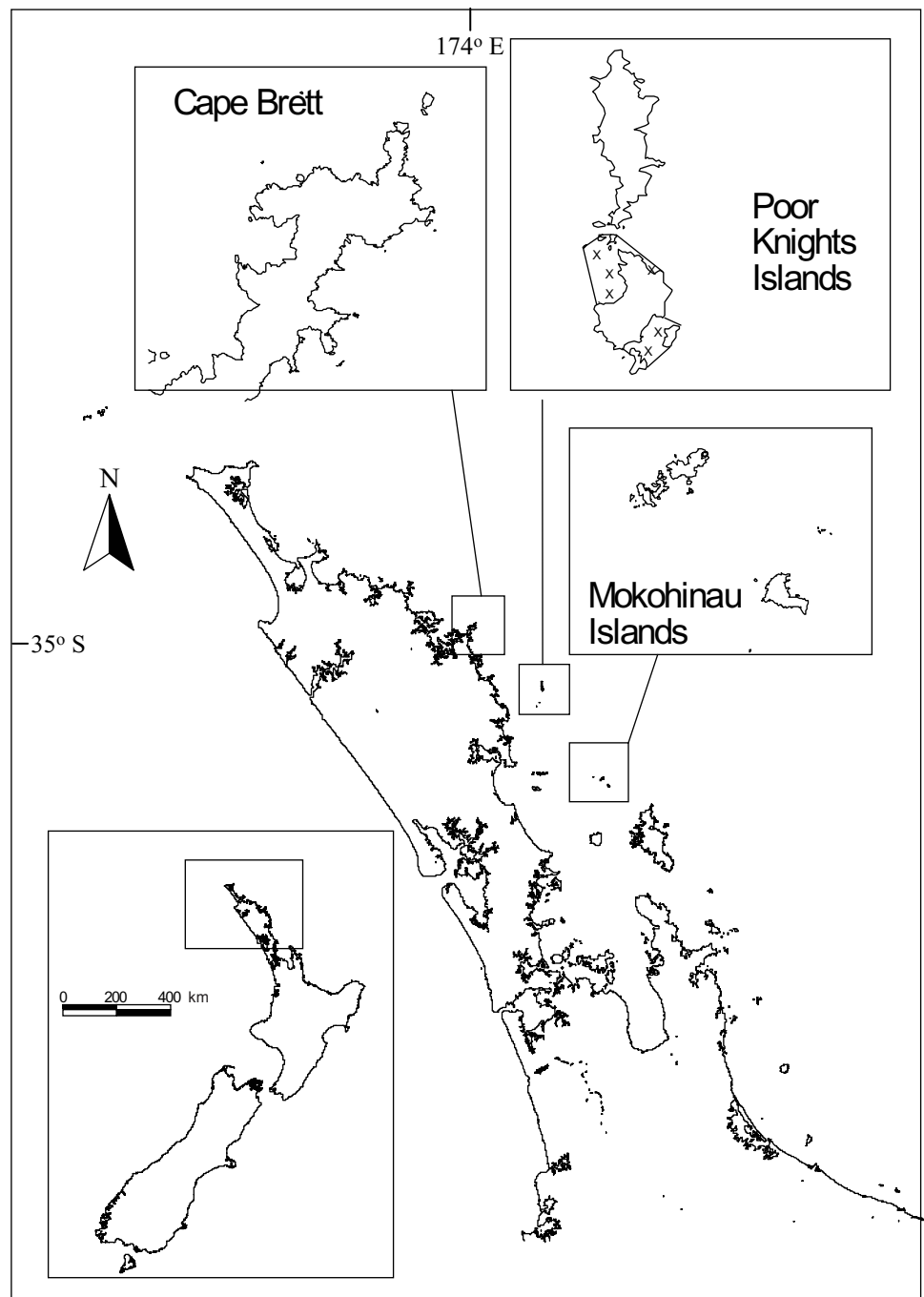
2. Material and methods

2.1 STUDY SITES

Three locations were surveyed in northeastern New Zealand: the Poor Knights Is, Cape Brett, and the Mokohinau Is (see Fig. 1). The Poor Knights Is and the Mokohinau Is (separated by 60 km) lie 50 km and 110 km southeast of Cape Brett, respectively. These locations are influenced by the East Auckland Current (EAC) (Stanton et al. 1997) and display temperate reef characteristics being dominated by laminarian and furoid algae (Choat & Schiel 1982). The initial survey at the Poor Knights Is was conducted in spring 1998 (September/October), prior to full marine reserve establishment, and has continued biannually until autumn 2002 (March/April). The two reference locations were surveyed biannually from spring 1999 to autumn 2002. Each survey period took approximately one month, but may have been spread over 6 weeks, depending on weather conditions.

It would have been desirable to include the reference sites in the study from the beginning, however this was not possible. Even so, the study still addresses whether trends in fish abundance differ between the Poor Knights from those at reference locations (Morrissey 1993; Underwood 2000).

Figure 1. Map of northern New Zealand showing the location of Cape Brett, the Poor Knights Islands and the Mokohinau Islands. The areas marked with X at the Poor Knights indicate areas that were fully protected prior to 1998.



2.2 BAITED UNDERWATER VIDEO

Use of the BUV technique allows sampling of carnivorous species that are not amenable to UVC methods and can sample at depths greater than where divers can operate. The BUV system (methodology: Willis & Babcock 2000) consists of a triangular stainless steel stand, with a Sony XC-777P high-resolution colour camera in a waterproof housing, positioned 1.5 m above a bait container with about 300 g of pilchard (*Sardinops neopilchardus*). The BUV was deployed from the research vessel to depths of up to 50 m, at sites at least 500 m from diving activities (so the presence of divers would not interfere with fish responses to the bait). Each location was divided into 3 to 4 areas with at least seven replicate drops conducted in each area. Each sequence was recorded for

30 minutes from the time the video assembly reached bottom. A 100 m long coaxial cable connected the underwater camera to a Sony GV-S50E video monitor and 8 mm recorder on the research vessel, enabling the scientist to ensure the stand was upright and over suitable substratum. Table 2 shows the number of BUV and UVC deployments conducted at each location.

At the laboratory, 8 mm videotapes were copied to 16 mm VHS tapes for analysis and archiving. Videotapes were played back with a real-time counter, and the maximum number of each species of fish observed during each minute was recorded (i.e. 30 counts were made during each 30-minute sequence). Only fish visible at any one time were recorded to avoid counting the same fish twice. The lengths of snapper, porae and tarakihi were obtained by digitising video images using the Sigmascan image analysis system. Measurements were made only of those fish present when the count of the maximum number of fish of a given species in a sequence was made. This means that some fish moving in and out of the field of view may not have been measured and avoids repeated measurements of the same individuals. This approach is likely to result in more conservative abundance estimates in high-density areas than low-density areas; and therefore differences between sites are likely to be conservative.

2.3 UNDERWATER VISUAL CENSUS

The distribution and abundance of reef fish were counted at the study locations using underwater visual census (UVC). This is a routine method for quantifying reef fishes, studying their distribution, and estimating their sizes. The advantages of UVC include the high levels of replication possible, the requirements of little bulky sampling equipment (apart from SCUBA gear), and being able to record other types of data in situ. The disadvantages include constraints of depth (less than 30 m), high levels of inter-observer variability, diving limitations due to currents and poor underwater visibility, and bias associated with diver positive/negative species. Despite these flaws it is acknowledged by most workers as the best method for non-destructive surveying of fish populations.

Between 15 and 23 sites were surveyed at each location and were conducted using 25 × 5 m (125 m²) transects (Table 2). Three divers surveyed each site, each of whom completed three transects, giving n = 9 transects per site (Denny & Babcock in press). To avoid overlap, divers decided which direction to swim prior to each dive. Transects were done by attaching the tape to the substratum and swimming the tape out while counting all fish and recording the size of all snapper within a 5 m corridor. A 5 m lead in was swum before commencing counts to avoid including fish attracted to the diver while the tape was being attached. During each transect observers recorded the depth (between 3–27 m) and the general habitat.

2.4 DATA ANALYSIS

Properties of the fish community calculated for each survey for both the BUV and UVC included total number of species, mean number of individuals and mean size. Temporal changes for the 24 most common species were graphed.

BUV and UVC data are counts and, therefore, do not satisfy the assumptions of normality and homogeneity of variance that are required by ANOVA. Therefore, the data were analysed using the Poisson distribution with a log-link using a generalised linear model (GENMOD) in SAS V8 (SAS 1999) to obtain unbiased estimates of the relative abundance of reef fish and to determine the ratio of reef fish change. 'Survey' 'Location' and 'Survey x Location' were the factors in the main model. To examine seasonal variation, the above technique was used with 'Season' added to the model. When species showed a statistically significant seasonal variation in density, to avoid seasonal bias, estimates comparing the initial and final spring surveys were used. To examine whether partial protection was effective at protecting snapper, the mean number of snapper per BUV and UVC from areas protected prior to 1998 and from areas with only partial protection prior to 1998, were analysed using the GENMOD procedure (T.J. Willis and C.M. Denny, unpublished report).

Because size data are continuous variables, changes in the size of snapper were analysed using the GLM procedure in SAS. This general ANOVA procedure will work with any unbalanced (i.e. unequal number of observations in each cell) or balanced design.

To investigate snapper recruitment the mean number of snapper in the 1+ category (14–22 cm) per BUV were recorded at each of the 3 locations and correlated with the mean coastal sea surface temperature (SST). The SST was obtained for the period 1995–2002 from the Leigh Marine Laboratory Climate Records and usually provides a good representation of trends in SST for Northland as a whole (Stanton et al. 1997).

Patterns in species composition were examined using constrained and unconstrained multi-dimensional scaling and as bi-plots in the Canonical Analysis of Principal coordinates (CAP) statistical package (Anderson & Willis 2003). CAP analyses were also conducted using data pooled at the location level, to obtain a single observation for each location at each time, based on Bray-Curtis dissimilarities with $\log(x+1)$ transformed data. There were 35 species of fish (variables) in the multivariate analyses. The following schooling

TABLE 2. TOTAL NUMBER OF UVC TRANSECTS AND SITES SURVEYED AND NUMBER OF BUV DROPS AT THE POOR KNIGHTS IS, CAPE BRETT, AND MOKOHINAU IS FROM SPRING 1998 UNTIL AUTUMN 2002.

SPECIES	POOR KNIGHTS IS			CAPE BRETT			MOKOHINAU IS		
	UVC TRANSECTS	SITES	BUV DROPS	UVC TRANSECTS	SITES	BUV DROPS	UVC TRANSECTS	SITES	BUV DROPS
1998 Spring	135	15	30						
1999 Autumn	190	20	31						
1999 Spring	180	20	29	199	22	35	180	20	31
2000 Autumn	170	19	30	180	21	31	210	23	33
2000 Spring	186	20	30	184	20	30	189	19	30
2001 Autumn	193	20	30	179	20	30	184	20	30
2001 Spring	184	21	32	192	21	30	199	21	30
2002 Autumn	184	20	31	184	20	32	184	20	29
Total	1422		243	1118		188	1146		183

species were not included: kahawai (*Arripis trutta*), demoiselles (*Chromis dispilus*), koheru (*Decapterus koheru*), trevally, blue knifefish (*Labracoglossa nitida*) and jack mackerel (*Trachurus novaezelandiae*).

Reef fish density estimates can be affected by small-scale spatial and temporal variability, caused in part by habitat patchiness as well as fish mobility. The statistical significance of a difference between two samples, therefore, does not necessarily imply a real biological change. In this report we only regard changes of a magnitude of 100% (i.e. a doubling or halving of density) as being indicative of a biologically significant difference.

3. Results

3.1 BAITED UNDERWATER VIDEO

3.1.1 Species richness

We recorded 61 species of fish from 33 families in all BUV deployments (Table 1). The largest number of species was recorded at the Mokohinau Is (52), slightly fewer at the Poor Knights Is (48), and Cape Brett (47). Except in spring 1999 and spring 2000, the number of species recorded in the BUV at the Poor Knights Is was lower or similar to those at the reference locations in each survey period (Fig. 2). The vast majority of these species were rare, recorded only once per survey. Changes in the mean densities of the eight main species attracted to the BUV are shown in Fig. 3 and the estimate of change between surveys are shown in Table 3. These eight species showed a strong attraction to the bait and are known to be vulnerable to angling.

TABLE 3. CHANGE IN CARNIVOROUS FISH DENSITY AT THE POOR KNIGHTS IS, MOKOHINAU IS AND CAPE BRETT ESTIMATED BY BUV BETWEEN THE INITIAL SURVEY AND SPRING 2001 FOR THE FIRST 5 SPECIES AND BETWEEN INITIAL SURVEY AND AUTUMN 2002 FOR THE FINAL 3 SPECIES.

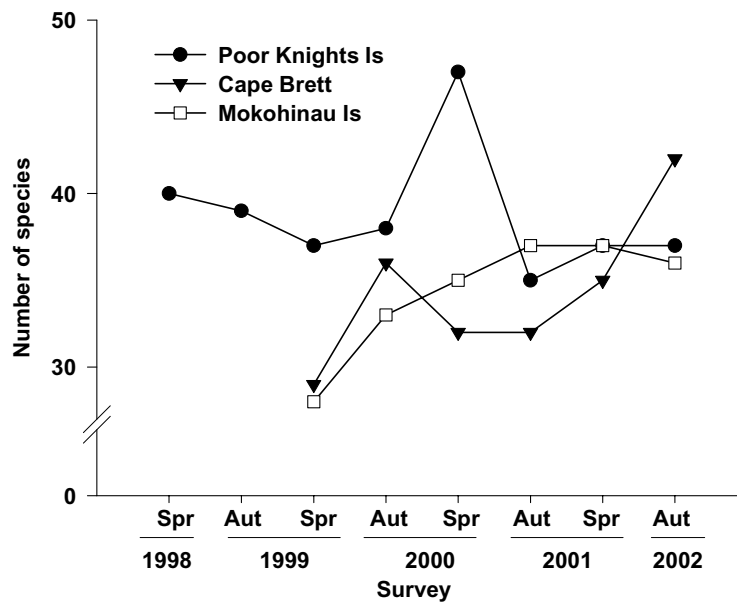
	POOR KNIGHTS IS			MOKOHINAU IS			CAPE BRETT		
	RATIO	95% CI	χ^2	RATIO	95% CI	χ^2	RATIO	95% CI	χ^2
	FOR RATIO			FOR RATIO			FOR RATIO		
Snapper	5.5	4.01-7.5	158.05	1	0.73-1.37	0.1	1.52	1.2-1.93	12.12
Porae	4.1	1.9-8.84	16.6	No fit			2.55	1.25-5.19	6.58
Tarakihi	1.87	1.05-3.36	4.48	0.39	0.15-0.99	3.92	1.02	0.52-1.98	0.1
Scorpionfish	1.76	1.07-2.88	4.98	No fit			1.55	0.35-6.95	0.33
Sandagers wrasse	0.61	0.3-1.23	1.93	0.62	0.14-2.59	0.43	2.33	0.58-9.33	1.44
Trevally	0.55	0.38-0.8	9.62	0.25	0.18-0.35	69.25	0.23	0.15-0.34	51.81
Pigfish	1.07	0.8-1.45	0.22	1.26	0.91-1.74	1.93	1.45	0.95-2.22	2.89
Moray eels	0.99	0.77-1.27	0.12	0.88	0.51-1.52	0.21	1.01	0.65-1.57	1.12

χ^2 Values in **bold** type indicate a statistically significant change ($p < 0.05$) in relative density.

Ratios in **bold** type we consider biologically significant (see text).

'No fit' means that the model algorithm did not converge.

Figure 2. Number of species from baited underwater video at the Poor Knights Is, Cape Brett, and the Mokohinau Is from spring 1998 to autumn 2002. Spr and Aut indicate spring and autumn, respectively.



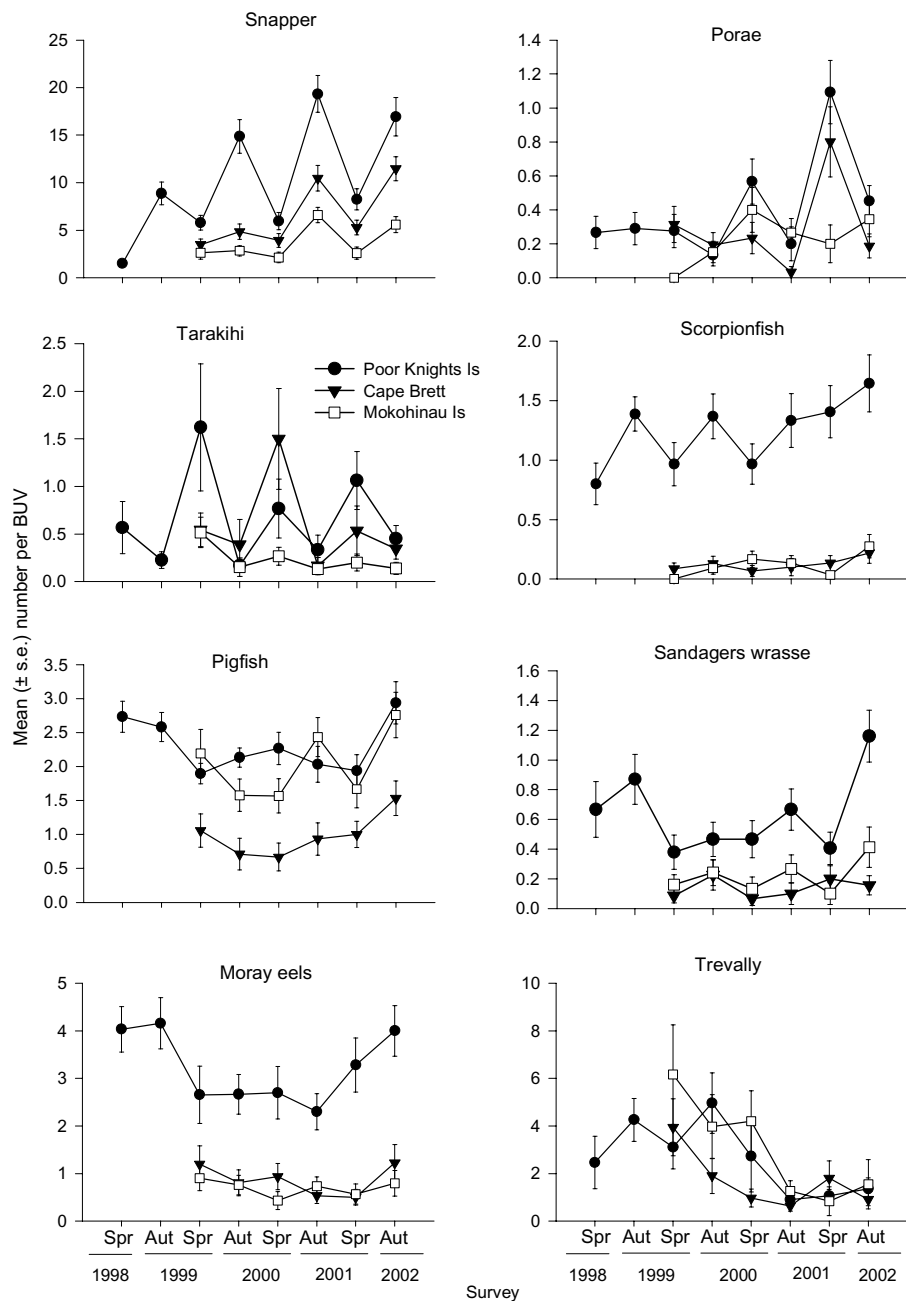
3.1.2 Seasonal variation

Five of the eight species showed a statistically significant difference in abundance with season. In autumn, snapper were over twice as common at all three locations compared to spring ($p < 0.001$) (Fig. 3). Scorpionfish were 1.3 times more common in autumn at the Poor Knights Is ($p = 0.008$) (Fig. 3). Sandagers wrasse (*Coris sandageri*) were also common in autumn at Poor Knights Is and Mokohinau Is ($p = 0.008$ and 0.03 , respectively) (Fig. 3). Conversely, porae (*Nemadactylus douglasii*) were 2 and 3.2 times more common in spring compared to autumn at the Poor Knights Is ($p = 0.0008$) and Cape Brett, respectively ($p = 0.0015$) (Fig. 3) and tarakihi (*Nemadactylus macropterus*) were 2.8 times more common in spring compared to autumn at the Poor Knights Is ($p = 0.0079$) (Fig. 3).

3.1.3 Density

To avoid the impact of seasonal variation in snapper density, we compared the initial and final spring surveys. The density of legal snapper at the Poor Knights Is had increased by 9.4 times ($p < 0.001$) with no difference in legal snapper between spring surveys at the reference locations (Fig. 4A). Sublegal snapper were 2.9 times more abundant in the final spring survey at the Poor Knights Is than initially survey ($p = 0.008$). The high numbers of sublegal snapper recorded at Cape Brett accounts for the high mean number of snapper observed in Fig. 3. The number of sublegal snapper at the Poor Knights Is has remained at a similar level throughout the surveys with near identical peaks during each autumn survey (Fig. 4B). The density of 1^+ snapper increased all three locations since the initial survey: 2.6 times more at Cape Brett ($p = 0.0005$), 3.1 times more at the Mokohinau Is ($p = 0.004$) and 25 times more at the Poor Knights Is ($p = 0.024$) (Fig. 4C). The large increase noted at the Poor Knights Is must be treated with caution as very low numbers of 1^+ snapper were recorded in the initial survey. There was a pulse observed in the 1^+ age class at Cape Brett and the Mokohinau Is in autumn 2001 and autumn 2002. The large increase in the abundance of small snapper in 2001 and 2002, particularly at Cape Brett, is likely to have resulted

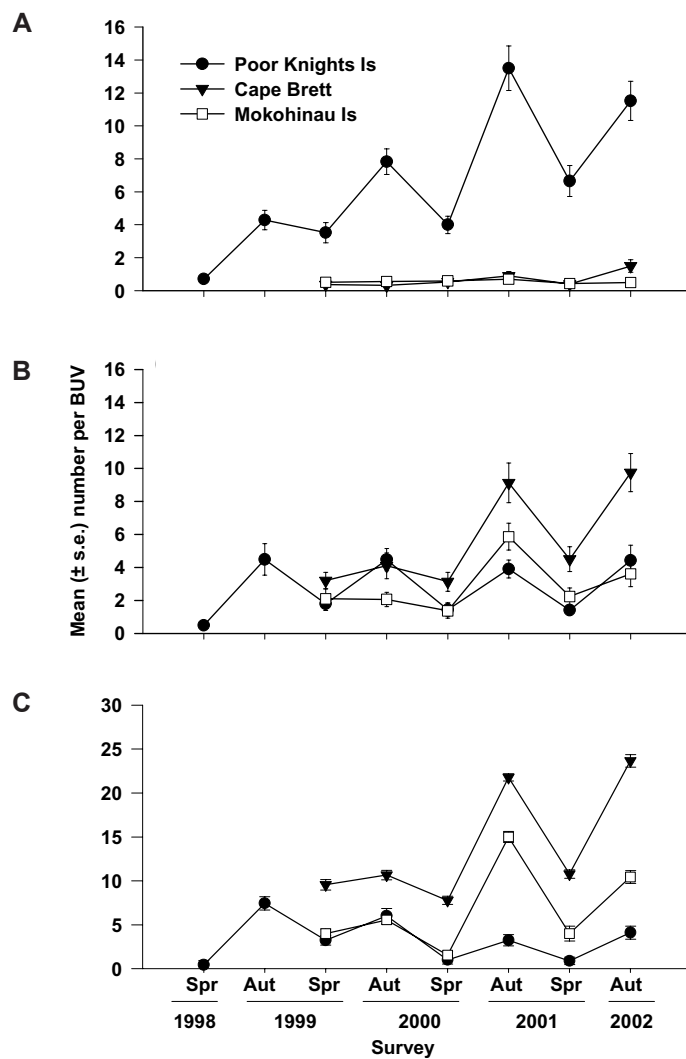
Figure 3. Mean (\pm s.e.) number of fish per BUV for eight common fish species at the Poor Knights Is from spring 1998 to autumn 2002 and at Cape Brett and the Mokohinau Is from spring 1999 to autumn 2002 (note the different y-axes).



from a successful recruitment of snapper in 1998 and 1999 when the SST was 0.5°C and 1.7°C warmer than the 30-year average (Fig. 5).

Along with snapper, the density of tarakihi, northern scorpionfish (*Scorpaena cardinalis*) and porae increased at the Poor Knights Is ($p < 0.05$) (Table 3, Fig. 3). Of these, only the increase in density of porae, by 4.1 times, was biologically significant (Table 3). At the Mokohinau Is the density of tarakihi showed a biologically significant decrease ($p = 0.036$) (Table 3). Snapper and porae density showed a statistically significant increase at Cape Brett, however only the increase in porae was biologically significant ($p = 0.007$) (Table 3). The above species changes must be treated with caution as there was a degree of variation in density over time (Fig. 3). Trevally showed a biologically significant decrease at both reference locations. There was no significant change in density for the remaining species.

Figure 4. Mean (\pm s.e.) number of (A) legal size snapper (> 270 mm), (B) sublegal snapper (< 270 mm) and (C) 1+ snapper per BUV at the Poor Knights Is from spring 1998 to autumn 2002 and at Cape Brett and the Mokohinau Is from spring 1999 to autumn 2002.



3.1.4 Size

The average snapper size increased at the Poor Knights Is (both, $p < 0.001$). From autumn 1999 until spring 2001, the mean (\pm s.e.) snapper size increased from 274 (± 9) mm to 324 (± 5) mm ($p < 0.001$). The mean snapper size dropped in the autumn 2002 survey as many more smaller fish were present (Fig. 6). At the reference locations the mean snapper size remained relatively stable over time, fluctuating from 200 to 221 mm at Cape Brett and from 215 to 258 mm at the Mokohinau Is. The number of large snapper (> 400 mm) has increased at the Poor Knights Is with the vast majority of snapper in the autumn 2002 survey over the minimum legal size (Fig. 6). This contrasts with the control locations where fish over the minimum legal size were rare.

3.1.5 Reserve status

To assess the effectiveness of the two previously fully protected areas at the Poor Knights Is in protecting snapper, the relative densities of legal snapper there were compared between the fully and partially protected areas prior to 1998 (Fig. 7). There was no difference found in the density of snapper between fully and partially protected areas in the initial survey, before the establishment

Figure 5. Mean monthly coastal sea surface temperature (SST) ($^{\circ}\text{C}$) for northeastern New Zealand from January 1998 to April 2002 (solid line). Arrows indicate the timing of surveys analysed in this report. The dashed line indicates average monthly SST temperatures from 1967 to 1996. Source: Leigh Marine Laboratory climate records.

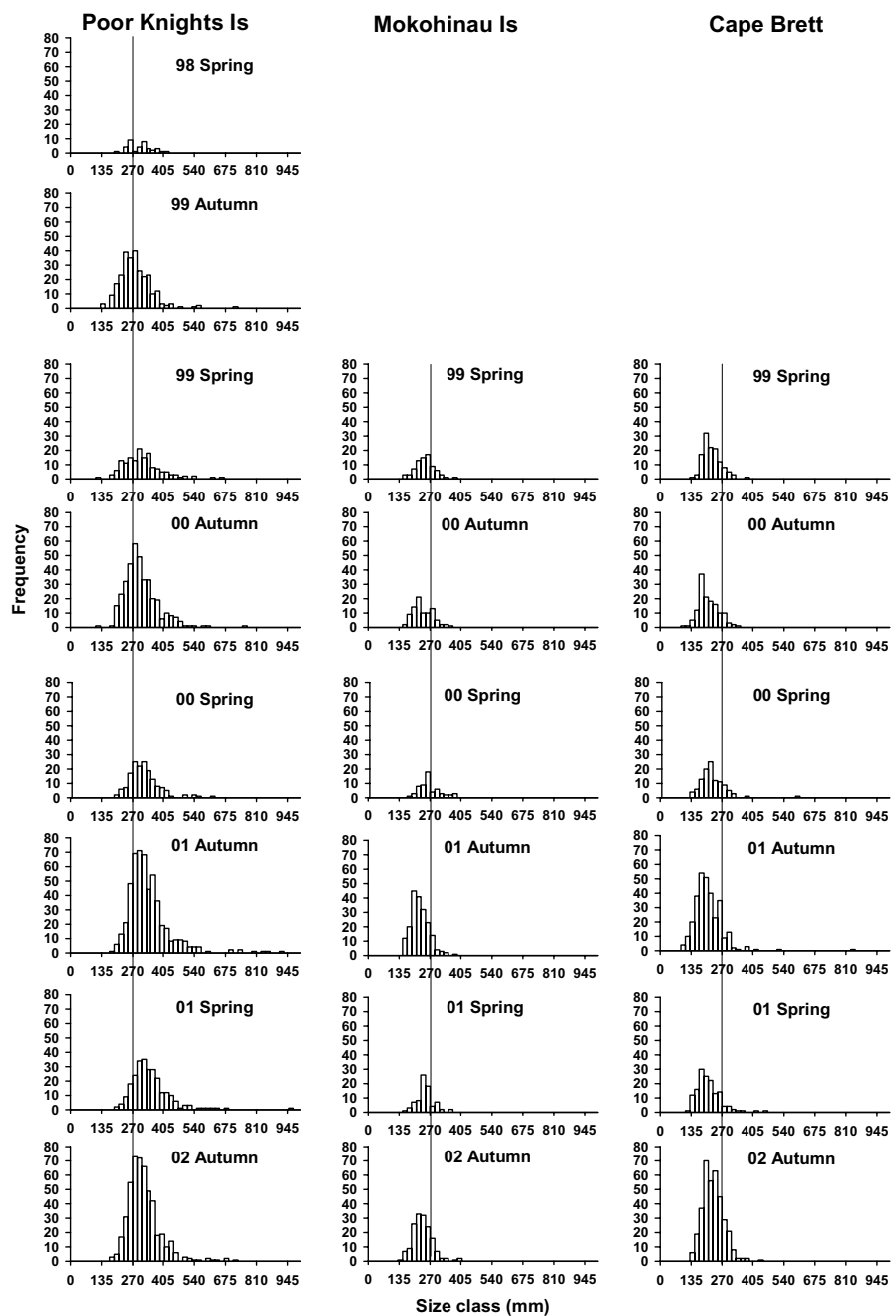
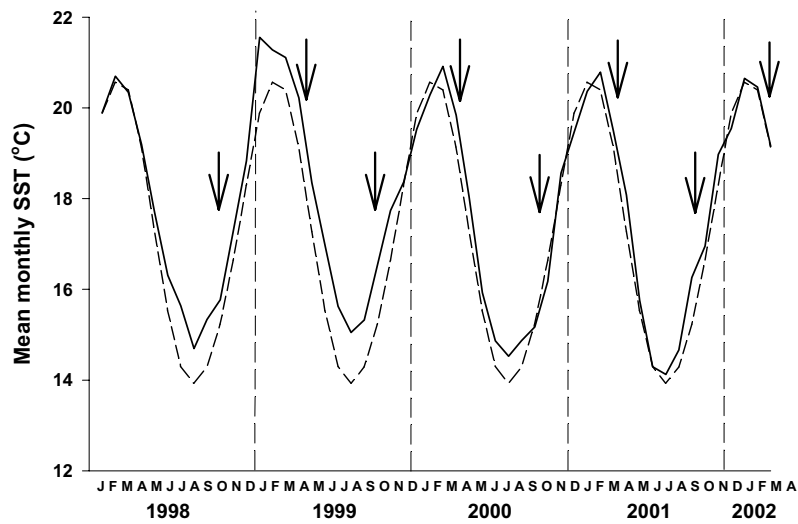


Figure 6. Size frequency graph of snapper from the BUV at the Poor Knights Is from spring 1998 to autumn 2002 and at Cape Brett and the Mokohinau Is from spring 1999 to autumn 2002. Line indicates the minimum legal size (270 mm).

of the marine reserve. Following this survey snapper density was always slightly higher in the fully protected areas, however this difference was only statistically significant in a few surveys, mainly in autumn when snapper density is its highest (Fig. 7). However, the magnitude of these differences is negligible compared to the overall increase in snapper density.

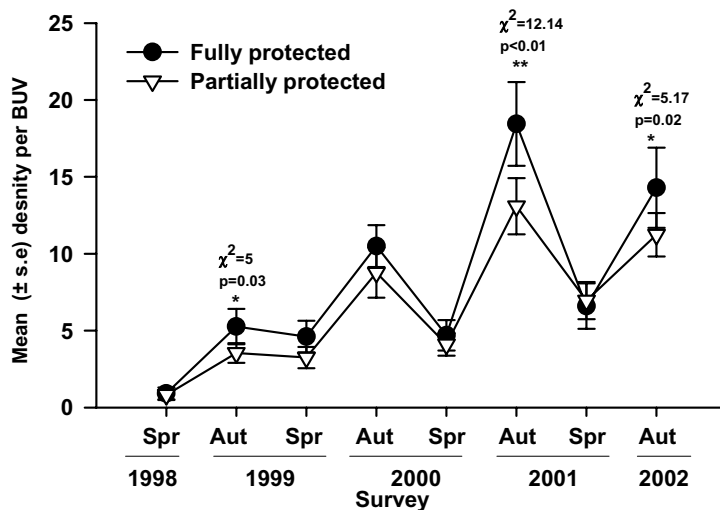


Figure 7. Mean (\pm s.e.) number of legal snapper per BUV from areas that were previously fully protected and areas that were partially protected at the Poor Knights Is. χ^2 and p values above an * indicate statistically significant differences at $P < 0.05$.

3.2 UNDERWATER VISUAL CENSUS

3.2.1 Species richness

From September 1998 until April 2002, we conducted 3687 UVC transects in all three locations (Table 2). We observed 78 species of fish (from 37 families) in all surveys, of which 76 species were recorded at the Poor Knights Is, 60 at the Mokohinau Is, and 64 at Cape Brett (Table 1). There were, on average, 8.1 ± 1.2 more species recorded per survey at the Poor Knights Is compared to the reference locations. The number of species at the reference locations followed a similar pattern to each other over time, although at Cape Brett we recorded slightly more species than at the Mokohinau Is (Fig. 8).

There was a statistically significant difference between locations for each survey ($p < 0.01$). The constrained multi-dimensional scaling showed a similar separation in the fish assemblages between locations (Fig. 9A); the Poor Knights Is and Mokohinau Is were more closely associated, Cape Brett being the most distinct. Correlations of species with both canonical analysis of principal coordinate axes are shown in a bi-plot (Fig. 9B). Species with an absolute correlation of less than 0.2 or that occurred in fewer than six observations, were not included (Anderson & Willis 2003). The bi-plot shows the species responsible for observed differences between locations. For example, species with positive x-values on the bi-plot characterise Cape Brett; red moki (*Cheilodactylus spectabilis*), parore (*Girella tricuspidata*), spotty (*Notolabrus celidotus*) and leatherjacket (*Parika scaber*).

Figure 8. Number of species from underwater visual census at the Poor Knights Is, Cape Brett, and the Mokohinau Is from spring 1998 to autumn 2002.

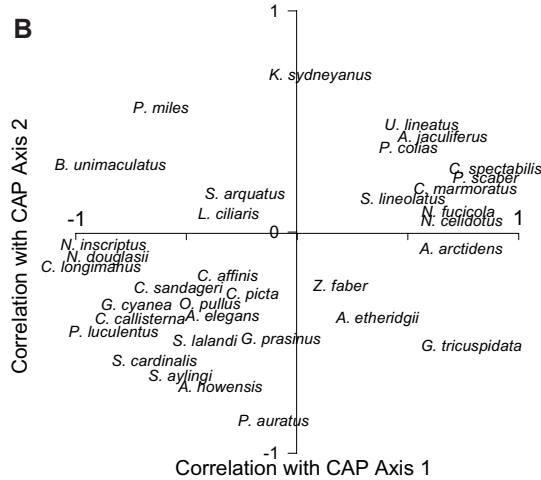
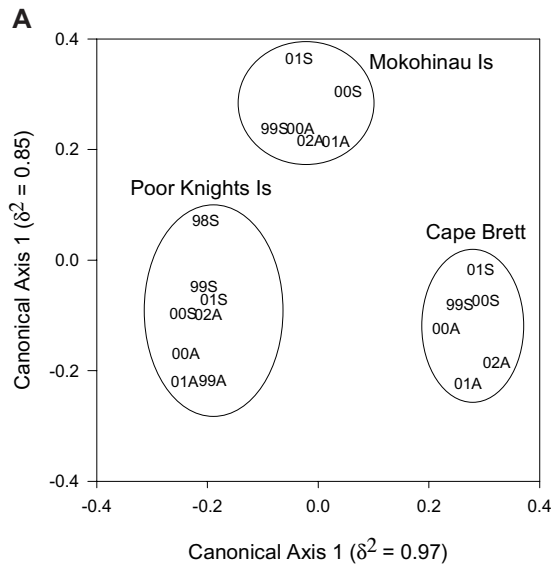
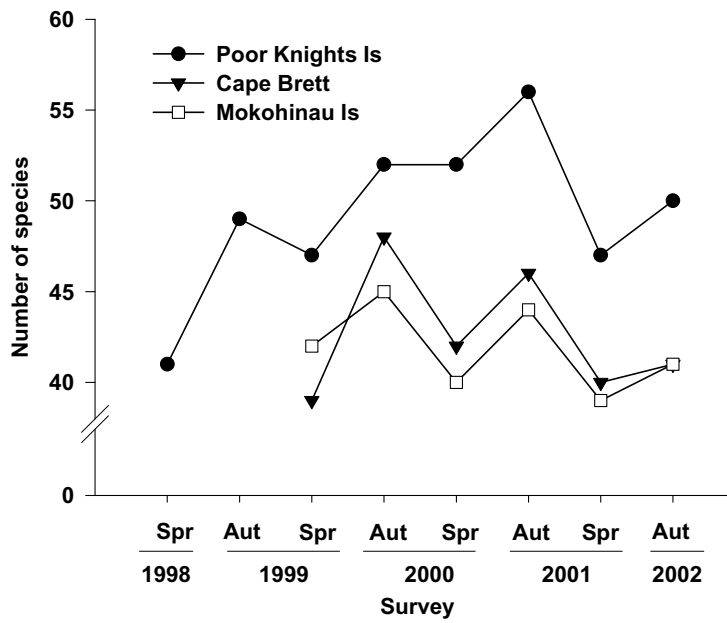


Figure 9. (A) Constrained MDS (CAP) of the reef fish assemblage pooled at the location level from spring 1998 to spring 2002 at the Poor Knights Is and from spring 1999 to spring 2002 at Cape Brett and the Mokohinau Is.

(B) A bi-plot showing the correlation of species with the two CAP axes.

3.2.2 Seasonal variation

Several species showed a seasonal variation in abundance (Fig. 10A-D). For example, snapper ($p < 0.001$), orange wrasse (*Pseudolabrus luculentus*) ($p = 0.002$), pigfish (*Bodianus unimaculatus*) ($p = 0.01$), sandagers wrasse ($p < 0.001$), and spotties ($p = 0.002$) were more abundant in autumn surveys. Conversely, banded wrasse (*Notolabrus fucicola*) ($p < 0.001$) (Fig. 10A), red moki ($p < 0.001$) (Fig. 10C), and tarakihi ($p = 0.036$) (Fig. 10D) were more common in spring. The seasonal trend was particularly noticeable for snapper (Fig. 10B), with noticeable differences between the high autumn peaks and lower spring numbers for both legal and sublegal fish.

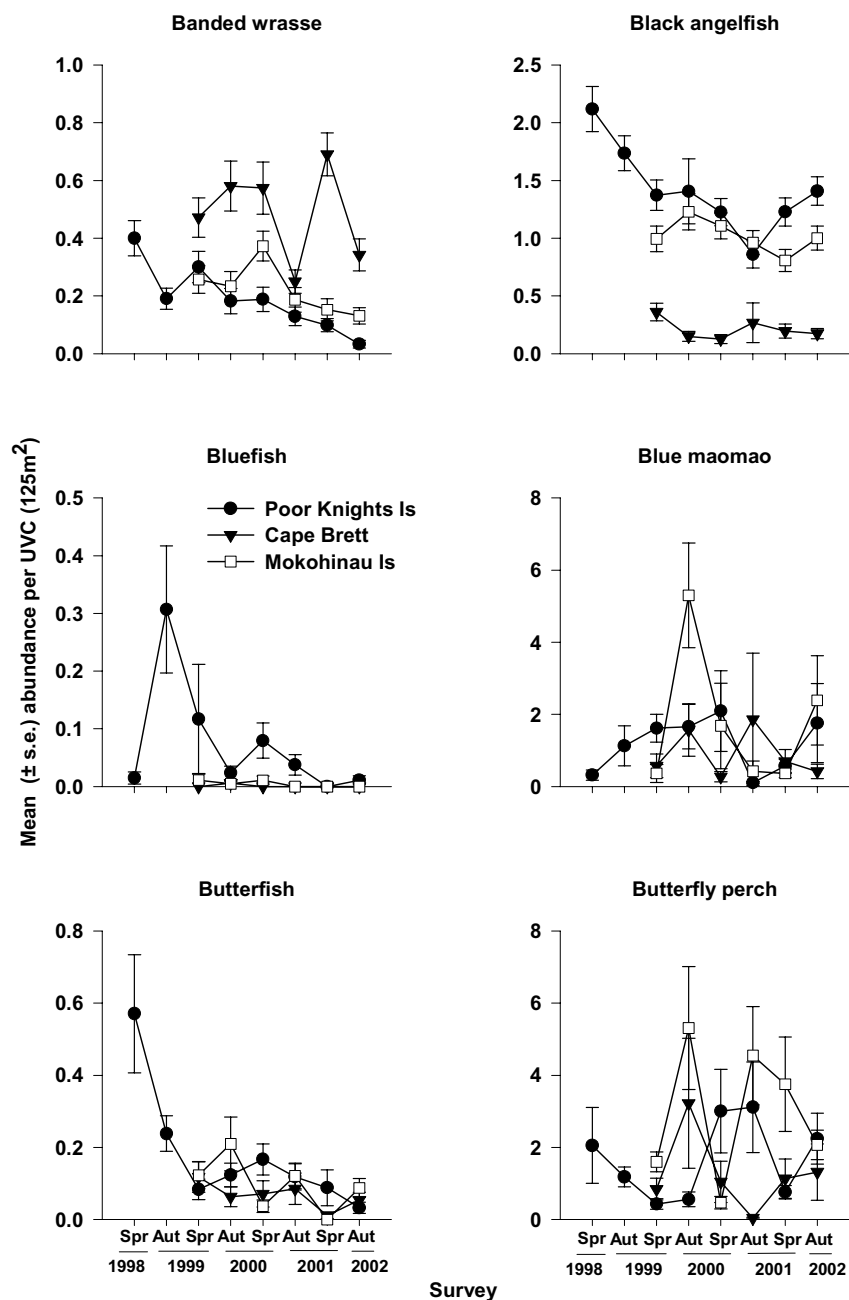


Figure 10A. Mean (\pm s.e.) number of banded wrasse, black angelfish, bluefish, blue maomao, butterfly perch and butterfly perch per UVC (125 m²) at the Poor Knights Is from spring 1998 until autumn 2002 and at the Mokohinau Is and Cape Brett from spring 1999 until autumn 2002.

3.2.3 Density

At the Poor Knights Is, 11 of the 20 species examined changed in density by > 100% relative to 1998, 4 species numbers increased (orange wrasse, blue maomao (*Scorpiis violaceus*), pink maomao, and snapper) and 7 species (banded wrasse, butterfish (*Odax pullus*), crimson cleanerfish (*Suezichthys aylingi*), goatfish (*Upeneichthys lineatus*), red moki, scarlet wrasse (*Pseudolabrus miles*) and spotties) decreased (Table 4). Recreational fishers exploited snapper and both maomao species. At the Mokohinau Is only pink maomao and sweep increased in density. No species increased by > 100% at Cape Brett. The density of spotties, orange wrasse and black angelfish (*Parma alboscapularis*) declined at the Mokohinau Is and Cape Brett, respectively (Table 4). Statistically significant declines were noted at several other locations, but these were not biologically significant.

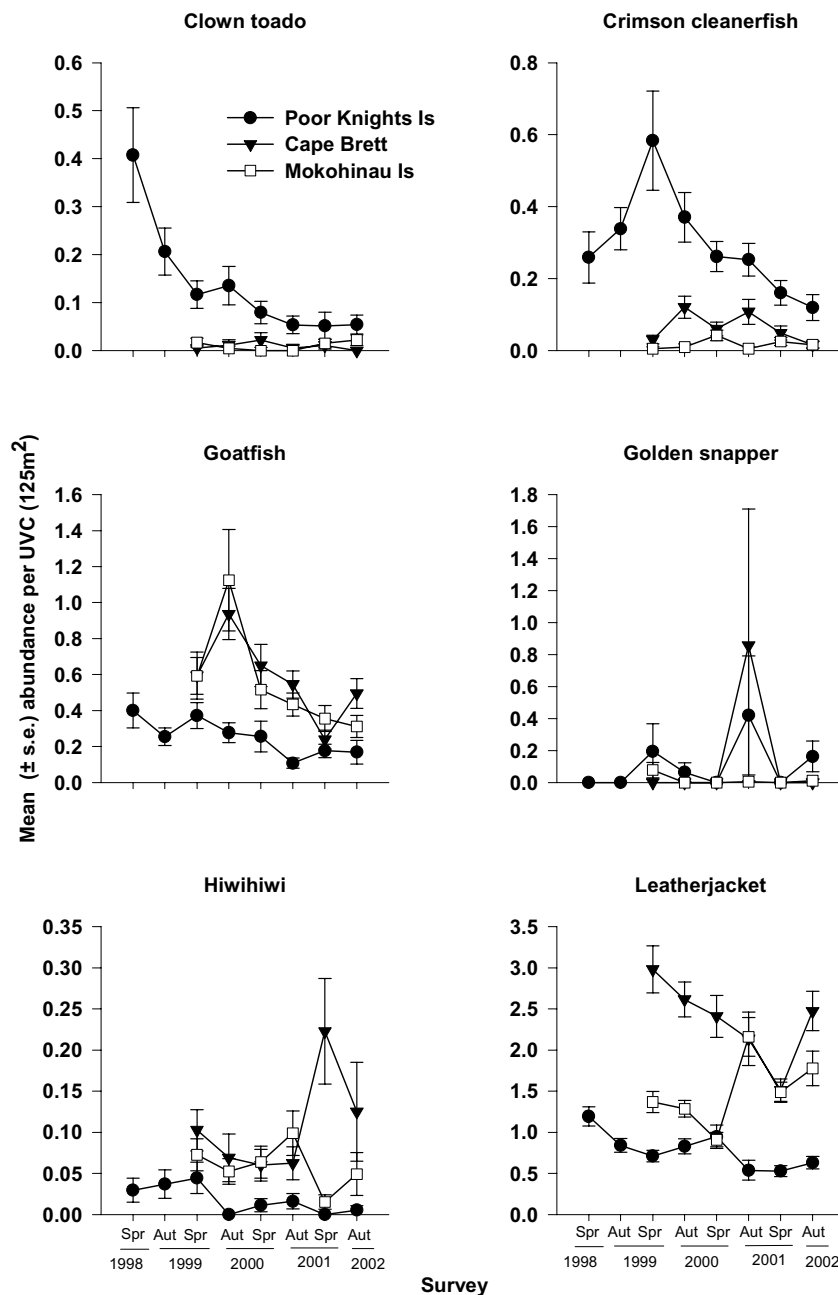


Figure 10B. (Continued)
Mean (± s.e.) number of clown toado, crimson cleanerfish, goatfish, golden snapper, hihihiwi and leatherjacket.

Since spring 2000, pink maomao numbers were higher than in the previous two years (6.6 times higher), and were found in higher numbers than pre-reserve survey ($p = 0.049$), albeit with a large standard error (Fig. 10C). Orange wrasse were common at the Poor Knights Is, compared to the reference locations, and increased in abundance by 6.9 times ($p < 0.001$) (Table 4, Fig. 10C). Pink maomao and sweep increased at the Mokohinau Is by 2.2 and 3.4 times ($p = 0.036$ and < 0.001 , respectively) (Table 4). However, it must be noted that the actual change in density at the Mokohinau Is was small compared to the large changes recorded at the Poor Knights Is.

When the spring 1998 survey and spring 2001 survey were compared at the Poor Knights Is, the density of all snapper had increased by 14.7 times ($p < 0.001$) (Table 4). However, the density of legal sized (> 270 mm) snapper only increased by 6.3 times ($p < 0.01$) (Fig. 11A). The large standard error for some surveys at the Poor Knights Is was a result of the presence of several large

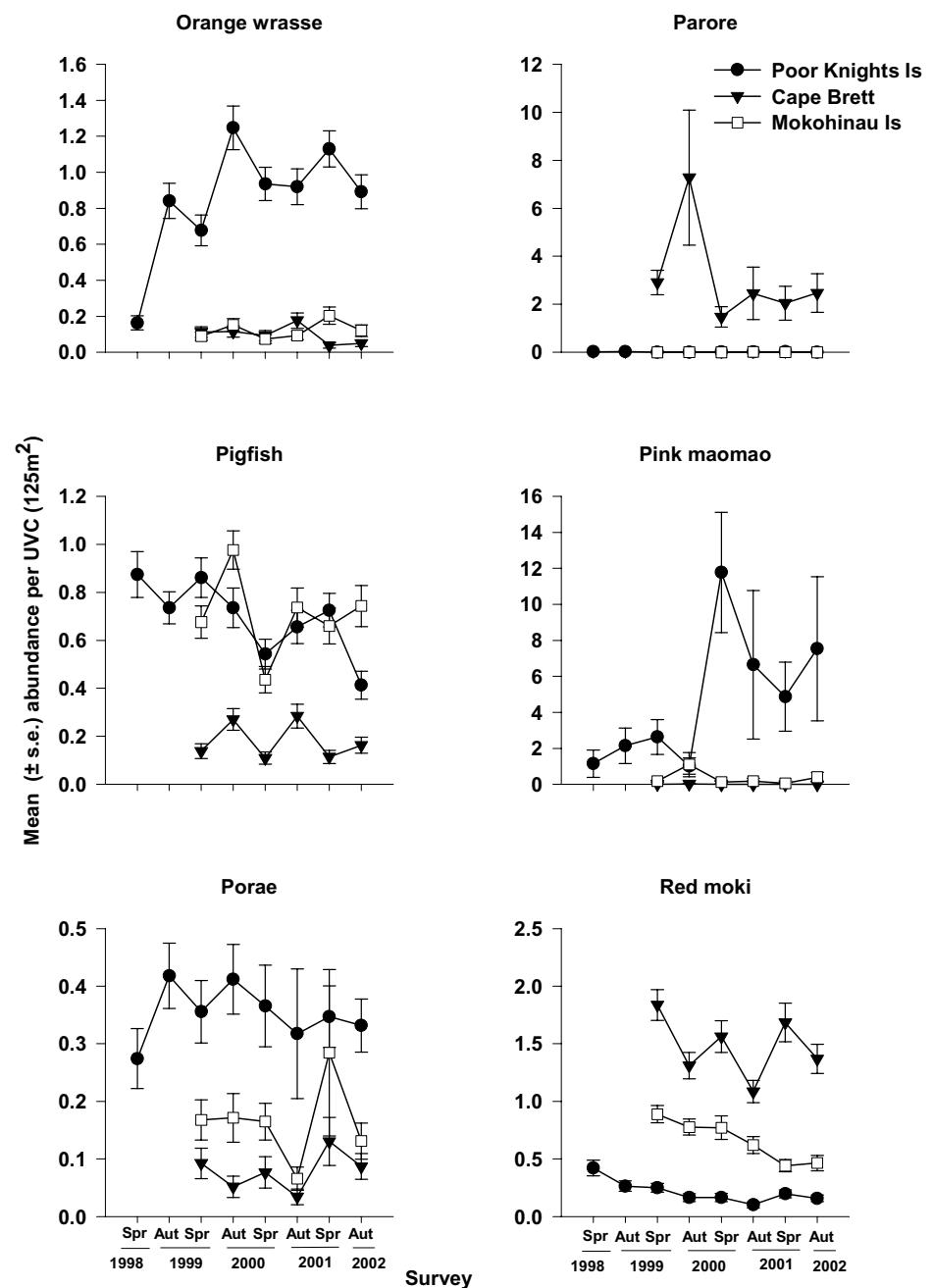


Figure 10C. (Continued)
Mean (\pm s.e.) number of orange wrasse, parore, pigfish, pink maomao, porae and red moki.

schools of adult snapper. When initial densities of snapper prior to no-take status at Poor Knights Is were compared to initial densities at the reference locations, there was no statistically significant difference. More importantly, there was also no statistically significant change in the density of legal snapper at either reference location over time. The density of sublegal snapper (< 270 mm) at both island locations remained relatively consistent, but there was considerable variation at Cape Brett (Fig. 11B).

Conversely, many species declined in numbers at the Poor Knights Is since the initial survey in spring 1998. Banded wrasse numbers steadily decreased at the Poor Knights Is and were 4.06 times lower than in the initial survey ($p < 0.001$). Black angelfish numbers were 1.5 times lower in autumn 2002 than in the initial survey in 1998 ($p < 0.001$) (Fig. 10A). Crimson cleanerfish numbers increased by 5 times in the first year ($p = 0.007$), but steadily declined after the peak in spring

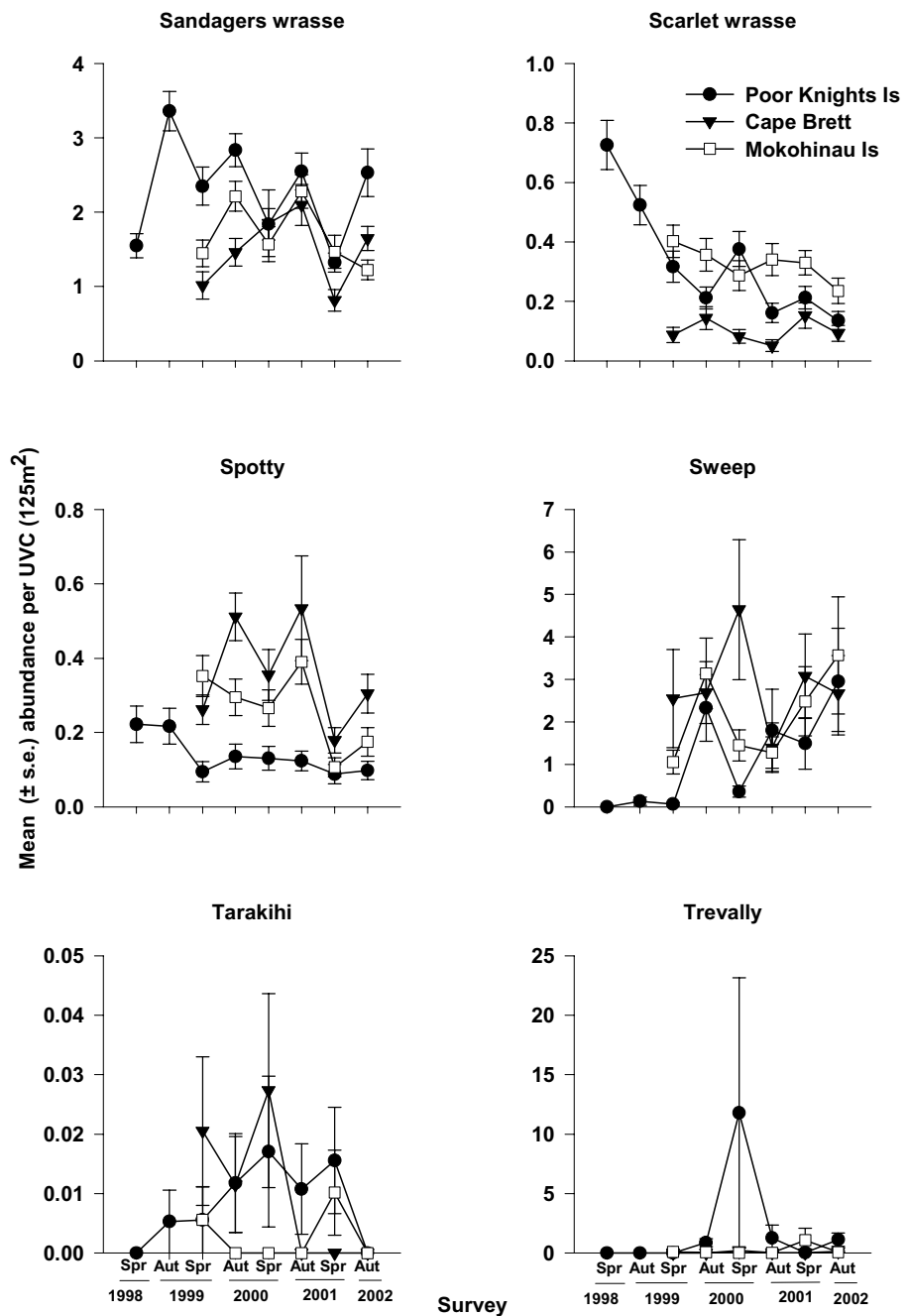


Figure 10D. (Continued)
 Mean (± s.e.) number of sandagers wrasse, scarlet wrasse, spotty, sweep, tarakihi and trevally.

TABLE 4. ESTIMATES OF CHANGE IN FISH DENSITY AT THE POOR KNIGHTS IS, MOKOHINAU IS, AND CAPE BRETT ESTIMATED BY UVC BETWEEN THE INITIAL SURVEY AND SPRING 2001 FOR THE FIRST 8 SPECIES AND BETWEEN INITIAL SURVEY AND AUTUMN 2002 FOR THE FINAL 12 SPECIES.

	POOR KNIGHTS IS			MOKOHINAU IS			CAPE BRETT		
	RATIO	95% CI FOR RATIO	χ^2	RATIO	95% CI FOR RATIO	χ^2	RATIO	95% CI FOR RATIO	χ^2
Banded wrasse	0.25	0.16-0.38	39.21	0.59	0.39-0.9	6.17	1.46	1.07-2	5.61
Orange wrasse	6.93	4.2-11.4	57.94	2.27	1.39-3.69	10.87	0.34	0.19-0.59	10.87
Pigfish	0.83	0.32-1.09	14.6	0.98	0.73-1.3	0.03	0.82	0.53-1.27	0.75
Porae	1.27	0.85-1.89	1.34	1.67	1.03-2.78	4.37	1.41	0.88-2.27	2.03
Red moki	0.47	0.32-0.69	14.6	0.5	0.32-0.69	23.7	0.92	0.73-1.15	0.57
Sandagers wrasse	1.17	0.89-1.54	1.32	0.99	0.73-1.33	0.01	1.25	0.87-1.77	1.48
Snapper	14.69	4.5-47.9	19.83	No fit			0.89	0.54-1.46	0.21
Spotty	0.39	0.25-0.64	14.48	0.4	0.25-0.64	28.2	0.69	0.47-1	3.68
Black angelfish	0.66	0.56-0.79	22.72	0.99	0.8-1.22	13.33	0.48	0.32-0.73	11.53
Blue maomao	5.51	4.01-7.58	110.6	6.57	5.06-8.53	200.72	0.72	0.55-0.97	4.57
Butterfish	0.06	0.02-0.13	45.58	0.71	0.37-1.35	1.07	0.46	0.22-0.97	4.18
Butterfly perch	1.09	0.93-1.27	1.34	1.3	1.11-1.51	10.97	1.56	1.28-1.91	19.54
Crimson cleanerfish	0.47	0.28-0.81	7.41	2.9	0.31-28.2	0.87	0.53	0.13-2.12	0.81
Goatfish	0.42	0.27-0.66	14.72	0.53	0.38-0.73	15.3	0.83	0.46-1.09	1.74
Golden snapper	No fit			0.14	0.03-0.61	6.78	No fit		
Leatherjacket	0.53	0.42-0.67	27.4	1.29	1.1-1.53	9.48	0.83	0.73-0.94	8.86
Parore	No fit			No fit			0.85	0.75-0.96	6.77
Pink maomao	6.56	5.56-7.75	493.3	2.23	1.47-3.4	14.33	No fit		
Scarlet wrasse	0.19	0.12-0.29	55.93	0.58	0.4-0.85	7.78	1.06	0.54-2.08	0.03
Sweep	No fit			3.4	2.87-3.97	217.4	1.05	0.92-1.19	0.52

χ^2 values in **bold** type indicate a statistically significant change ($p < 0.05$) in relative density.

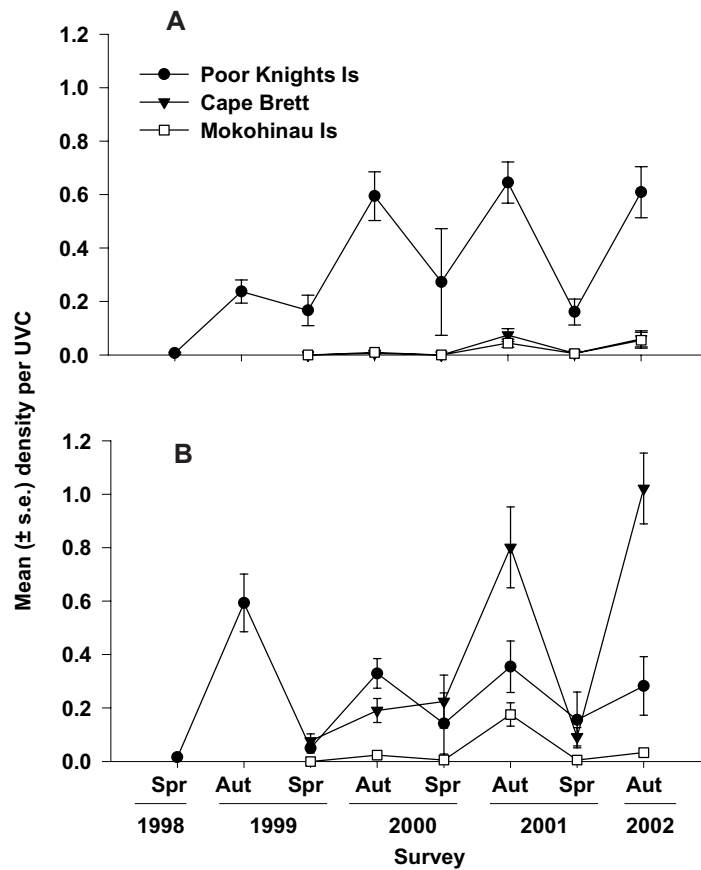
Ratios in **bold** type we consider biologically significant (see text).

'No fit' means that the model algorithm did not converge.

1999 and were 2 times lower in the final survey than the initial survey, although not statistically significant. Like crimson cleanerfish, numbers of combfish (*Cortis picta*) initially increased after the marine reserve was established, but steadily declined since autumn 2000 (not shown graphically). Numbers of scarlet wrasse steadily decreased at the Poor Knights Is and were 5.3 times lower in the final survey than the initial survey ($p = 0.02$). Likewise, spotties steadily decreased at the Poor Knights Is with densities 2.5 times lower in the final survey than the initial survey ($p < 0.006$) while butterfly numbers declined by 17 times ($p < 0.001$). Goatfish and leatherjackets were 2.4 and 1.9 times less abundant, respectively, at the Poor Knights Is in the autumn 2002 survey compared to the initial survey ($p = 0.015$ and 0.0153 , respectively) (Fig. 10B). At the Mokohinau Is, spotty density declined by 3.3 times ($p = 0.008$). The only species that declined at Cape Brett, black angelfish, did so by 2 times ($p = 0.04$) (Fig. 10A).

Numbers of porae and tarakihi (Figs 10C and 10D) increased following the initial survey at the Poor Knights Is, but there was no statistically significant difference in density between the initial and final survey. At the reference locations, the abundance of the vast majority of species did not vary over time. Of 18 species, 10 showed no statistically significant change at the Mokohinau Is and at Cape Brett, the abundance of 15 species did not vary over time (Table 4).

Figure 11. Mean (\pm s.e.) density of (A) legal size snapper ($>$ 270 mm), and (B) sublegal snapper ($<$ 270 mm) per UVC at the Poor Knights Is, Cape Brett, and the Mokohinau Is from spring 1999 to autumn 2002.



3.2.4 Size

The mean snapper size at the Poor Knights Is was usually greater than 300 mm in length, larger than at the reference locations ($p < 0.001$) (Fig. 12). The vast majority of snapper recorded by UVC at the reference locations were again under the minimum legal size, with very few large fish recorded at these locations. At Cape Brett, snapper were always less than 210 mm, whereas at the Mokohinau Is the mean size fluctuated between 120 mm and 290 mm, intermediate between the Poor Knights Is and Cape Brett (Fig. 12). This size fluctuation and the large standard error for some values usually reflected low number of snapper recorded. There was no increase in the mean size of snapper at any of the three locations when the initial and final surveys were compared.

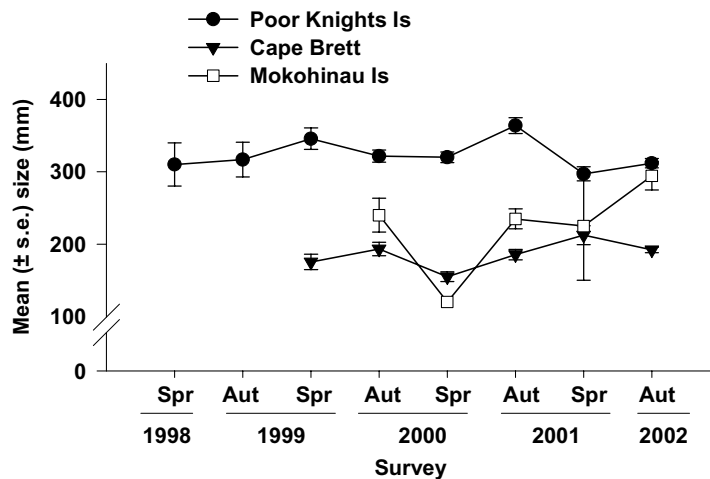


Figure 12. Mean (\pm s.e.) size (mm) of snapper per UVC at the Poor Knights Is from spring 1998 until autumn 2002 and at the Mokohinau Is and Cape Brett from spring 1999 until autumn 2002.

4. Discussion

4.1 SNAPPER

Following the implementation of full marine reserve status at the Poor Knights Is in 1998, the density of snapper showed a dramatic increase. The magnitude of increase in snapper in the marine reserve is consistent with many other studies that found an increase in the density and/or biomass of large predatory fish following no-take status (White 1988; McClanahan & Kaunda-Arara 1996; Russ & Alcalá 1996; Edgar & Barrett 1999). We found no statistically significant increase in abundance or size of snapper at either reference location. The increase in snapper abundance following protection was surprisingly rapid: some time lag period might be expected when fish populations are recovering from previous heavy fishing pressure (Polunin & Roberts 1993). For example, Russ & Alcalá (1996) found a slow increase in fish density in the first 3–5 years of protection, followed by a more rapid increase in the next 4 years. This time lag might be particularly noticeable where recovery is dependent on recruitment. Recovery rates are likely to be variable and can depend on other factors such as species, site and level of exploitation.

The rapid recovery of snapper at the Poor Knights Is, particularly in the first year, is due to the immigration of large fish rather than juvenile recruitment. These large fish arrive at the Poor Knights Is as a result of regular seasonal onshore migrations and remain if not subjected to fishing pressure. This is well supported by BUV data at the Poor Knights Is where fish present had a mode of 410 mm SL by autumn 2000. These fish would be approximately 14 years old (Millar et al. 1999) so cannot have grown to this size in the 2 years since full protection.

The higher SST throughout 1999 probably accounts for the high number of 1+ snapper recorded in autumn 2000 and autumn 2001, particularly at Cape Brett. Francis (1993) proposed that higher SST may lead to faster growth, shorter periods of exposure to each size class of predators, and a larger size class at the onset of winter. There may be many small snapper at Cape Brett because the current regime along the Northland coast may bring large numbers of larval snapper to this region, compared to the island locations.

Although only the BUV showed that the mean snapper size increased at the Poor Knights Is, snapper were usually larger here compared to the reference locations (usually greater than the minimum legal size) implying that populations at the Poor Knights Is are composed of generally smaller fish. The mean snapper size at the reference locations remained relatively stable over time, but large snapper (> 400 mm) were almost never recorded there. These larger snapper have become increasingly common at the Poor Knights Is. Larger snapper may be lacking at the reference locations because of a high level of recreational fishing that may, in turn, lead to a domination by a small number of young age classes (Francis 1993).

4.2 OTHER FISH SPECIES

The reef fish community at the Poor Knights Is appears to have changed rapidly following the establishment of the marine reserve. This is consistent with McClanahan (1994) who recorded rapid changes in the fish fauna within 1 year of the establishment of a marine reserve in Kenya. Recreational fishing, and the resulting incidental mortality of 'protected' species, has probably affected the structure of the fish community at the Poor Knights Is. Relatively little fishing pressure is needed to cause significant reductions in the density of targeted species and structural changes in the reef fish community (Russ & Alcala 1989; Polunin & Roberts 1993; Watson & Ormond 1994; Jennings & Polunin 1996, 1997). In Jamaica, the overall fish species composition of heavily exploited areas underwent a complete re-ordering over 13–17 years (Koslow et al. 1988). This suggests a 'compromise' solution, often touted by advocates of partial protection, is not an effective management solution as even the removal of a small proportion of biomass may cause significant changes in the community structure. Despite the changes in community composition there was no significant increase in species richness at the Poor Knights Is. This is similar to other studies of marine reserves elsewhere (Alcala 1988; Samoilys 1988; Galzin et al. 1990; Dufour et al. 1995; Roberts 1995). The community composition at the reference locations remained relatively stable.

At the Poor Knights Is, the density of other targeted species (besides snapper) increased, particularly porae as seen in BUV and pink maomao by UVC. However, our study failed to find increases in many non-targeted species, a result consistent with others (e.g. Jennings et al. 1995; Jennings & Polunin 1997). Targeted species, being sensitive indicators of fishing pressure, are more likely to respond to marine reserve protection once the main factor limiting their population density (i.e. fishing) has been removed (Carr & Reed 1993; Rowley 1994). The sudden increase in the density of pink maomao, 2 years after the start of monitoring at the Poor Knights Is, is consistent with a single localised recruitment pulse. However, prior to full no-take status this species was subjected to heavy fishing pressure, so their numbers could have been quickly lowered to a level observed in the initial pre-reserve survey. Unlike fishing for target species, it is climatic factors that will be responsible for changes in the density of some species not targeted or only incidentally caught by fishers, like orange wrasse.

Responses for some species that look like 'reserve effects' may be the result of the warmer sea-surface temperature during 1998 and 1999 (Fig. 5). Under these warmer conditions recruitment of subtropical fishes to the Poor Knights Is might be greater than in previous years (Francis & Evans 1993). Indeed, this is reflected by higher numbers of fish with subtropical affinities such as clown toado, crimson cleanerfish, and orange wrasse (Fig. 10). It is likely the East Auckland Current brought many of these species to the Poor Knights Is from the Three Kings Islands and Lord Howe Island, and thanks to the favourable conditions, they survived. Changes observed for some species at one location were often not recorded at another, probably because EAC affects each location differently. The Poor Knights Is are likely to receive a higher number of 'subtropical' recruits because of their location. Although the reference locations are influenced by the EAC and low densities of the same 'subtropical'

species were present, their data did not show the same increases in these species as at the Poor Knights Is.

Subsequent declines in the density of fishes with subtropical affinities, such as clown toado and crimson cleanerfish, may have been caused by natural mortality after the successful recruitment pulse in 1998 and 1999. Similar results were found by Choat et al. (1988) where warmer sea-surface temperatures in the 1970s resulted in the establishment of a more subtropical fauna at the Poor Knights Is. Subsequent declines in these species over time were attributed to recruitment failure and the effects of a severe storm. Alternatively, density of some species in this study may have dropped from competitive or predatory interactions (Watson et al. 1996). Tupper & Juanes (1999) attributed the low recruitment of juvenile grunts within the Barbados Marine Reserve to an increase in predator density. The large increase in the density of snapper at the Poor Knights Is may cause a decrease in potential prey or, alternatively, they may out-compete other species for food or space. For example, numbers of other benthic carnivores, banded wrasse and scarlet wrasse, have dropped by over 100% over time, a criterion for species replacement (Daan 1980). Observations around a bait source have shown that snapper can aggressively displace other species (C.M. Denny, unpubl. data). However, these interactions were not subject to controlled field experiments, so such explanations must remain speculative.

4.3 SEASONAL VARIATION

In our study, several species showed a seasonal trend in abundance, a well-known phenomenon among reef fish. This is typically because fish move from inshore shallow waters in summer to offshore deeper waters in winter (Beentjes & Francis 1999; Hyndes et al. 1999; Magill & Sayer 2002). This movement can be related to either spawning behaviour (Crossland 1977; Robertson 1983), changes in feeding patterns (Schmitt & Holbrook 1986), or to avoid adverse weather conditions (Walsh 1983). The seasonal variation in snapper abundance is consistent with other studies on snapper in New Zealand (Willis et al. 2003). Seasonal offshore migrations are less likely to occur for more strongly based reef fish like banded wrasse and spotties, that are seldom recorded in deep water (C.M. Denny unpubl. data). Seasonal variation may sometimes be explained by cooler water conditions in which activity becomes relatively low and some fish are therefore not recorded by divers as often (e.g. Costello 1991).

4.4 SPECIES RICHNESS

The lack of overlap in the ordination among locations in all seven surveys (see Fig. 9) shows that some elements of the fish assemblage are consistently different (either through composition or density). Fewer species were recorded at the reference locations in the UVC, compared to the Poor Knights Is where subtropical species are more common. The East Auckland Current may not have

such a heavy influence on the reference locations, but does supply low numbers of subtropical species. The number of species recorded in the BUV (61) was much higher than expected considering the BUV was aimed at carnivorous fish. Non-carnivorous species recorded may have been recorded as they swam into view under the BUV or if the stand happened to land in their territory.

4.5 PARTIAL PROTECTION

Our study provided evidence that partial fishing regulations are ineffective at protecting targeted species, at least where recreational and commercial fishers both target the same species. This presents a powerful argument against the widely held view that recreational fishing cannot affect fish populations. There was no build-up of snapper populations at the Poor Knights Is following the creation of the 'marine reserve' in 1981 that allowed partial harvest within 95% of the reserve. This was most likely due to recreational fishing pressure, as even limited fishing effort would maintain fish biomass at low levels (Jennings & Polunin 1997). Similar results were found at the Mimiwhangata Marine Park (identical fishing restrictions as were present at the Poor Knights Is prior to full reserve status) where no difference was found in snapper numbers between protected and adjacent unprotected areas (Denny & Babcock in press). Paradoxically, fishing pressure may have been higher in the 1980s and 1990s at the Poor Knights Is than at the Mokohinau Is or the adjacent coast. In the absence of commercial fishing there may have been a perception that fish were larger and more plentiful in the reserve area. Thus, 'marine reserve' status and fishing gear restrictions at the Poor Knights Is may initially have had exactly the opposite effect to what was intended.

There was no difference in relative snapper density between the small, fully protected areas and partially protected areas, prior to the islands receiving no-take status. The exclusion zones may have been too small to effectively protect snapper from fishing pressure: tagging studies suggest that some snapper move over moderate distances (> 100 km) (Paul 1967), although Willis et al. (2001) found snapper to have considerable site fidelity. This finding is important because recent meta-analyses (e.g. Mosquera et al. 2000; Halpern 2003) have made general statements about the uniformity of response to protection from fishing regardless of reserve size. However, their conclusions are not universal and will not apply to all species or all locations. There may also have been considerable edge effects because of the small size and configuration of the closed areas, resulting in fish being caught outside the areas. Edge effects have been demonstrated at the Leigh Marine Reserve (Willis et al. 2000), where recreational fishers commonly anchor and fish on the reserve boundary. After implementation of no-take protection at the Poor Knights, snapper numbers were usually higher in previously fully protected as opposed to partially protected areas. This difference probably reflects habitat: shallow reef and sand patches found in the previously fully protected areas are rare elsewhere in the reserve.

4.6 CONCLUSION

Our study has clearly demonstrated the effectiveness of the Poor Knights Islands Marine Reserve: the number and size of targeted fish species are increasing. The increase in snapper density in particular has been rapid, resulting from immigrating adult fish rather than from recruitment. It is not yet clear whether snapper numbers have stabilised. The large increase in snapper at the Poor Knights Is has the potential to enhance areas outside the reserve through the export of biomass (juveniles and adults) and planktonic dispersal. Furthermore, protection from fishing may protect stock from genetic changes, altered sex ratios, and other disruptions caused by selective fishing. This study demonstrates that the partial closures at Poor Knights Is were ineffective as conservation tools for snapper (i.e. through reduction in by-catch). Lastly, the choice of methodology has important implications in assessing populations for management purposes. Use of a single method will overlook important changes in fish abundance.

5. Recommendations

- Based on the data reported in this paper we recommend continued fish monitoring at the Poor Knights Is and the two reference locations for a further 3 years using the same methodology as employed in this study. Surveys should be conducted annually in autumn (when fish numbers are highest). The use of only a single method will overlook important changes in fish abundance. Frequency of monitoring should be reviewed after this time.
- Further monitoring will allow changes in long-lived species or species that rely on larval recruitment to be assessed and to examine whether snapper have reached carrying capacity at the Poor Knights Is.
- Any no-take marine reserve at Mimiwhangata should be incorporated in the sampling program to provide a fully-orthogonal design with crossed reserve/non-reserve and island/mainland sites. This will allow a more reliable differentiation of island and reserve trends in fish populations.
- Fish surveys should be combined with a benthic monitoring program to assess changes in the invertebrate and algae communities. Benthic habitats may affect the abundance of fish species (e.g. habitat associations), as well as being affected by fish (e.g. trophic cascades).

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