Protection of exploited fish in temperate regions: high density and biomass of snapper *Pagrus auratus* (Sparidae) in northern New Zealand marine reserves

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Summary

1. The use of marine reserves as tools either for conservation or fisheries management requires rigorous empirical evidence for the recovery of exploited species within them.
2. The relative density and size structure of snapper *Pagrus auratus* (Sparidae), an intensively exploited reef fish species, were measured, using baited underwater video, inside and outside three northern New Zealand marine reserves (Leigh Marine Reserve, Hahei Marine Reserve and Tawharanui Marine Park) every 6 months from October 1997 to April 1999.
3. Log-linear modelling showed that relative total density and egg production of snapper were higher in all three reserves than in fished areas. Snapper that were larger than the minimum legal size were estimated to be 14 times denser in protected areas than in fished areas, and the relative egg production was estimated to be 18 times higher. In the Leigh reserve, legal-size snapper were larger than legal-size snapper in fished areas.
4. At the Leigh reserve, snapper density consistently peaked at the reserve centre and declined towards either boundary, which suggests that snapper became increasingly vulnerable to fishing towards the reserve boundaries.
5. Inshore snapper density was significantly higher in autumn than in spring, supporting previous suggestions that snapper make regular onshore–offshore seasonal migrations that might be related to spawning. We suggest that the observed recovery of snapper populations within reserves is attributable to immigration of individuals from fished areas that take up residency within reserves, rather than juvenile recruitment.
6. *Synthesis and applications.* This study demonstrates the effectiveness of marine reserves for protecting an exploited species previously thought to be too mobile to respond to area-based protection. Although it is difficult to envisage significant enhancement of fished areas via adult emigration, it is likely that the reserves contribute significantly to local gamete production. In addition, the protection of fish populations within reserves might slow reductions in genetic diversity caused by size-selective mortality brought about by exploitation.

Key-words: baited underwater video, fishing, migration, no-take, recovery, replication.

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Introduction

It has been widely suggested that marine reserves (areas of sea permanently closed to all forms of fishing or disturbance), in addition to performing a conservation function, might be of long-term benefit to fished stocks. The potential benefits are many and have been described extensively (Roberts & Polunin 1991; Allison, Lubchenco & Carr 1998; Bohnsack 1998; Jennings 2000). In essence, the ideal is protection of a portion of an exploited stock, with the expectation that the biomass of targeted species within protected areas will rebuild to approach unfished densities. Density-dependent processes might then cause emigration of adults from the 'source' (reserve) population to fished areas, either by passive diffusion (Beverton & Holt 1957) or by displacement of individuals caused by space limitation

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(Kramer & Chapman 1999). Additionally, spawning activity within the reserve by greater numbers of large individuals should result in greater production of gametes than in similar, unprotected areas.

Various theoretical models have implied that increases in, or maintenance of, yield per recruit can be obtained from marine reserves (Polacheck 1990; DeMartini 1993; Attwood & Bennett 1995; Sladek Nowlis & Roberts 1999), but alternative models have implied that reserves may have little effect (Horwood, Nichols & Milligan 1998) and might even be detrimental to overall fishery yield (Parrish 1999). While the construction of such models provides a useful heuristic framework (Walters 1993), it does not provide a means of answering questions applicable to real fisheries (Attwood & Bennett 1995; McArdle 1996; Sladek Nowlis & Roberts 1999).

Many studies have reported on the effect of reserves on exploited species. While these effects are generally positive, on a case-by-case basis evidence for substantial recovery in populations is often limited (Jones, Cole & Battershill 1993; Rowley 1994; but see Russ & Alcala 1996a; Wantiez, Thollot & Kulbicki 1997; Edgar & Barrett 1999). There are three main reasons. First, exploitation in any geographical region tends to begin with large predatory species (Pauly *et al.* 1998) that are less common than species at lower trophic levels and therefore more difficult to monitor with sufficient statistical power (Cole, Ayling & Creese 1990; Paddack & Estes 2000). Moreover, larger predators tend to be slower to grow and reproduce, which means that population-level responses may be slow (Jennings, Reynolds & Mills 1998). Secondly, with few exceptions (Edgar & Barrett 1997, 1999; Wantiez, Thollot & Kulbicki 1997), the design of marine reserve surveys has often been spatially or temporally confounded (or both) so that the results must be interpreted cautiously. Finally, field methods used to assess fish density have sometimes been subject to biases caused by intra- or interspecific behavioural plasticity (Cole 1994; Jennings & Polunin 1995; Kulbicki 1998; Willis, Millar & Babcock 2000). Alternatives to traditional diver-based sampling methods, such as catch-and-release angling (Bennett & Attwood 1991, 1993; Millar & Willis 1999; Willis, Millar & Babcock 2000) or remote imaging (Ellis & DeMartini 1995; Willis & Babcock 2000), might provide more accurate relative density data.

The sparid snapper *Pagrus auratus* (Bloch & Schneider) (synonymous with *Chrysophrys auratus*, *C. unicolor* and *Pagrus major*) is the most sought after inshore teleost species in northern New Zealand waters, and supports valuable fisheries in Australia (McGlennon *et al.* 2000) and Japan (Paulin 1990). Snapper occur across the continental shelf from estuarine habitats to depths > 100 m (Paul 1976) and are generalist predators that take primarily invertebrate prey from both soft sediment (Colman 1972) and rocky reefs (Choat & Kingett 1982; Babcock *et al.* 1999). In north-eastern New Zealand, snapper recruit to the commercial fishery at 4–5 years of age (25-cm caudal fork length, FL). However, on inshore reefs most fishing pressure comes from the recreational line fishing sector, where a 27-cm FL minimum size limit applies.

Heavy levels of exploitation by both commercial and recreational fisheries place snapper under continuous pressure. The largest and most productive of the New Zealand stocks (SNA1) is currently estimated to be at 23% of virgin biomass and below the theoretical biomass required to maintain maximum sustainable yield (Gilbert *et al.* 2000). Risk assessment has been used to set allowable catches that will result in the SNA1 stock rebuilding with high probability. However, the high levels of uncertainty inherent in the specification and fitting of fishery models (Francis & Shotton 1997; Myers, Hutchings & Barrowman 1997; Seijo & Caddy 2000) mean that cautious approaches to management are warranted. There are data suggestive of recovery by sparids in marine reserves in other geographical regions (Bell 1983; Buxton & Smale 1989; Garcia-Rubíes & Zabala 1990; Dufour, Jouvenel & Galzin 1995; Harmelin, Bachet & Garcia 1995) but not within New Zealand (Cole, Ayling & Creese 1990; but see Willis, Millar & Babcock 2000).

In this study we examined the effects of marine reserve protection on the density and size of snapper at three coastal marine reserves of varying age in north-eastern New Zealand. The aim of the study was to assess the general effects of reserves by using spatially and temporally replicated surveys. Specifically, we wished to (i) determine the magnitude of differences in snapper density and size between reserve and adjacent fished areas, and (ii) quantify seasonal and interannual variability in snapper density and size.

Methods

STUDY AREAS

The three reserves were the Cape Rodney to Okakari Point (Leigh) Marine Reserve, Tawharanui Marine Park and Te Whanganui a Hei (Hahei) Marine Reserve (Table 1 and Fig. 1a). All three are complete no-take areas administered under different legislation and by separate government departments (the 'reserves' are controlled by the Marine Reserves Act 1971 and administered by the

Table 1. Location, area, and year of establishment of the three marine reserves surveyed in this study

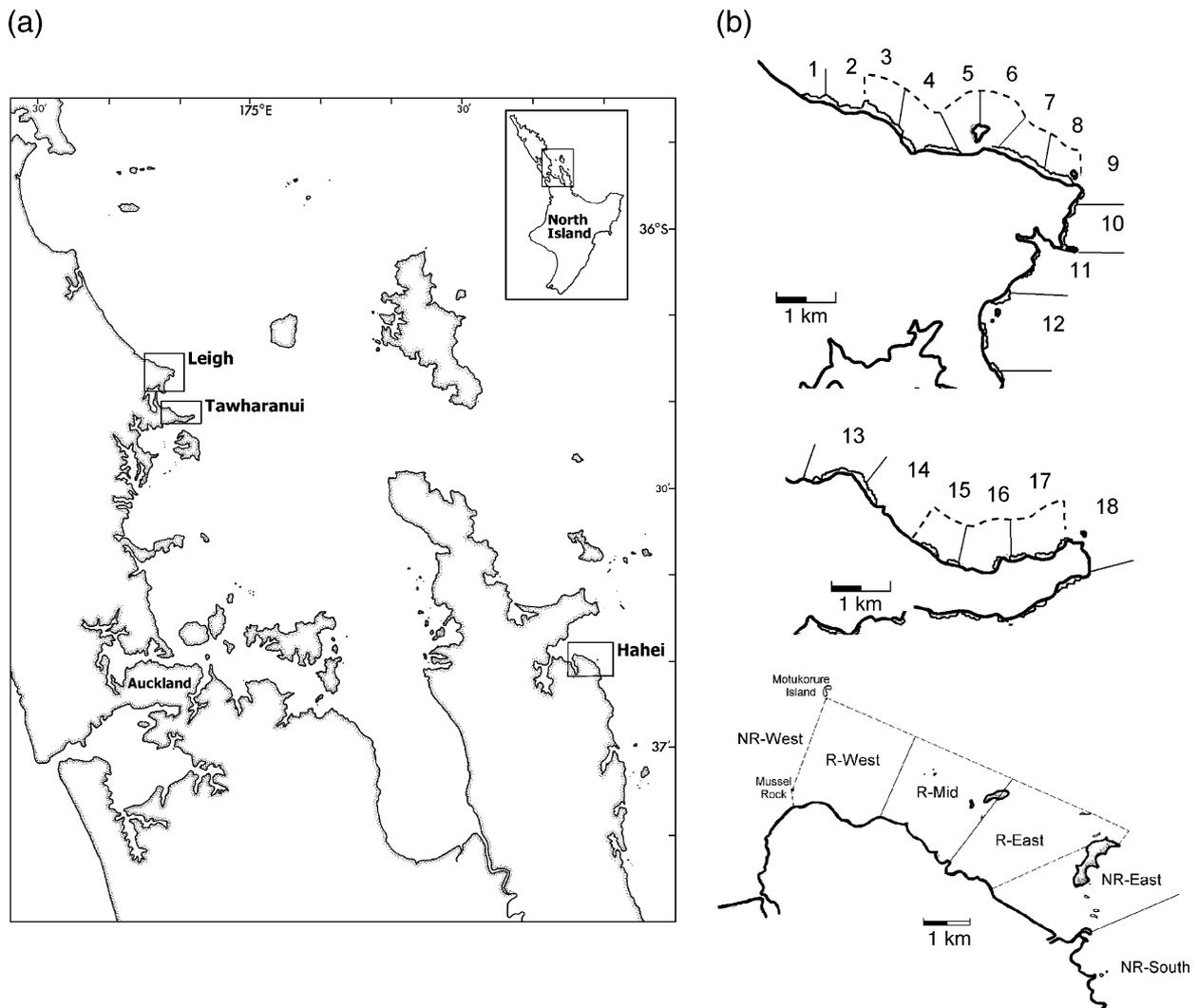| Reserve	Latitude	Longitude	Reserve area (ha)	Year established
Cape Rodney–Okakari Point (Leigh)	36°16′S	174°48′E	518	1977
Tawharanui Marine Park	36°22′S	174°50′E	350	1981
Te Whanganui a Hei (Hahei)	36°49′S	175°47′E	840	1992

Fig. 1. (a) Map of the Hauraki Gulf and environs, showing the location of the three reserves surveyed in this study. The inset shows the location of the area in the North Island of New Zealand. (b) Details of the three reserves surveyed, showing reserve boundaries (dashed lines) and survey areas. Top: Leigh; centre, Tawharanui; bottom, Hahei.

Department of Conservation, whereas the 'park' is controlled by the Fisheries Act 1983 and administered by regional authorities). The Tawharanui Marine Park has no nearby local community that can provide day-to-day surveillance to assist enforcement because the adjacent land is a regional park. The Leigh reserve is the oldest marine reserve in New Zealand and has a long history of research (Creese & Jeffs 1993) due to the presence of the Leigh Marine Laboratory (University of Auckland, Auckland, New Zealand).

The habitat structure of the sea floor at the three locations is similar within and adjacent to the reserve, each containing areas of coastal contiguous reef, patch reef and large areas of soft sediment. Subtidal reefs in northern New Zealand are generally dominated by the laminarian kelp *Ecklonia radiata* (Choat & Schiel 1982). General habitat types at Leigh and Tawharanui have been described by Babcock *et al.* (1999) and Shears & Babcock (2002).

SURVEY DESIGN

A true before-after-control-impact (BACI) design (Hurlbert 1984; Stewart-Oaten, Murdoch & Parker 1986; Underwood 1994) could not be implemented because of the absence of comparable data prior to reserve establishment, so the three reserves and their environs were surveyed four times at 6-monthly intervals in an attempt to encompass both seasonal and interannual variability in snapper density. Replication at reserve level meant that any intrinsic location-specific biases would be reduced by being averaged over the three reserves.

The reserves and adjacent non-reserve regions were divided into survey areas (Fig. 1b), and four or five sampling sites were located haphazardly within each area. True spatial randomization of sampling stations could not be obtained because of constraints caused by current or weather conditions and bottom topography.

Sampling commenced in October (austral spring) 1997, and the three locations were resurveyed in April 1998, October 1998 and April 1999. The exact position of sites was not repeated in consecutive surveys to reduce the risk of non-independence of samples.

SAMPLING METHODS

At each sampling site, observations of snapper relative density were made using a baited underwater video (BUV) system (Willis & Babcock 2000). This system was developed in response to difficulties in accurately sampling a species whose behavioural reactions to divers vary markedly between sites (Cole 1994; Willis, Millar & Babcock 2000). Fish feeding by visitors to the Leigh marine reserve has resulted in snapper exhibiting diver-positive behaviour at some sites, whereas elsewhere they are wary of divers, and outside the reserve they actively avoid divers. Use of a remotely deployed sampling method eliminates this source of bias.

The BUV system consisted of a Sony XC-999P high-resolution colour camera (Sony New Zealand, PO Box 100048, North Shore Mail Centre, Auckland, New Zealand) mounted on a stainless steel stand 115 cm above the substratum and faced straight down. A bait holder (containing *c*. 200 g of pilchard *Sardinops neopilchardus* Steindachner) was attached to the triangular base of the stand so that it lay in the centre of the camera's field of view. The base was marked with cable ties, and the distance between them was measured to allow spatial calibration of digitized images. This allowed accurate estimation of the lengths of fish responding to the bait (Willis & Babcock 2000; Willis, Millar & Babcock 2000).

Replicate deployments (*n* = 4 per survey area at Leigh and Tawharanui, and *n* = 5 per area at Hahei) were made on soft substrata, either immediately adjacent to or within 50 m of the reef. The BUV assembly was lowered to the sea floor from an anchored vessel, and deployed for 30 min from the time contact was made with the bottom. At the laboratory, video footage was analysed (frame-by-frame where necessary) to determine the maximum number of snapper (MAXsna) in the field of view during each 30-min sequence. Individual fish lengths (FL) were measured from calibrated images using the Mocha® image analysis software (Jandel Scientific, SPSS New Zealand, Box 4097, Auckland, New Zealand). Measurement error using this method was typically < 20 mm (Willis & Babcock 2000). Fish were generally only measured from images taken at the time MAXsna was recorded. On a few occasions fish that occurred elsewhere in the sequence were measured because they were obviously different fish, by virtue of size (i.e. differed from MAXsna measurements by > 100 mm). Small snapper that appeared early in the sequence were the most frequent additions to the data set, but sometimes one or two large fish were measured in this way. Although this meant that some fish were

not measured, it also avoided repeated measurement of the same individuals.

ESTIMATION OF BIOMASS AND EGG PRODUCTION

Biomass of individual snapper (*W*, g) was estimated from caudal fork length (FL, mm) using the formula listed by Taylor & Willis (1998):

$$W = 0.00007194 \times FL^{2.793}$$

Total deployment biomass was estimated as the sum of the individual weights, plus the estimated weight of those fish that could not be measured with accuracy because they appeared to be swimming too high above the calibrated plane. The biomass of unmeasured fish was estimated from the mean weight of measured snapper in each sample.

Snapper are serial spawners (Crossland 1977) that spawn batches of eggs daily (Scott, Zeldis & Pankhurst 1993) from late austral spring to late summer (Crossland 1977; Scott & Pankhurst 1992). We estimated snapper fecundity in order to determine the difference in reproductive output between reserve and fished areas. Egg production was expressed as daily batch fecundity (*F*) and calculated using the formula of Zeldis & Francis (1998):

$$F = 73.9 \times W - 7793$$

Zeldis & Francis's (1998) model was not based on fish any larger than 4·5 kg but it was assumed that larger fish conform to the model. No observations to date suggest that snapper undergo reproductive senescence as they age (J. Zeldis, National Institute of Water and Atmospheric Research Ltd, personal communication). The length of snapper at sexual maturity was assumed to be 230 mm FL, as 80% of fish are mature at this size (Scott 1991). Therefore, only fish larger than this were used in the analysis. It was not possible to obtain sex ratios of snapper as there is no external sexual dimorphism, so the sampled population was assumed to be 1 : 1, based on mean observed ratios from Zeldis & Francis (1998). We therefore calculated the sum batch fecundity of all mature snapper in a sample, and used half this value as the sample estimate. The number of egg batches produced by a snapper in a season is variable, and appears to increase with fish size (Crossland 1977; Scott, Zeldis & Pankhurst 1993), but this relationship has not been determined with any accuracy because of the difficulties associated with separating batches in continuously and asynchronously spawning fish. In this study batch fecundities were therefore compared only as a relative measure of reproductive output, but it should be noted that because the number of spawning episodes increases with fish size this is likely to underestimate seasonal fecundity where large snapper are present. All comparisons of egg production should therefore be treated as conservative.

STATISTICAL ANALYSES

Snapper relative density was quantified in four ways: the maximum number of fish per BUV deployment (MAXsna), biomass (kg) as calculated above, and two size-related components of MAXsna, being the number greater than the recreational minimum legal size (MLS) limit of 270 mm FL (LEGsna), and the number of undersize fish (JUVsna). The latter two categories were examined because it was expected that undersize fish should experience relatively little fishing mortality, and hence that JUVsna should be little affected by reserve protection, whereas snapper larger than MLS would exhibit the greatest response to protection.

Count data violate the assumptions of normality and constant variance, and are constrained at zero. Hence, the data were analysed with a generalized linear model under the assumption of a Poisson distribution or, more generally, as Poisson with possible overdispersion due to the fact that fish may not behave independently of each other (e.g. schooling behaviour). The log-linear model was fitted using maximum likelihood by the SAS procedure GENMOD (SAS 1997). The factors used were 'location', 'status' (reserve or non-reserve) and 'survey', all treated as fixed effects. Ratios describing the magnitude of differences between the main effects were calculated after non-significant interaction terms were removed progressively from the model.

Fishing in the non-reserve areas would diminish the extent of any seasonal changes in fish density. We therefore used data from reserve areas only to estimate the magnitude of seasonal change in snapper density. For this analysis, we assumed that the magnitude of the inshore seasonal migration was independent of the density of reef residents, i.e. the seasonal effect would be additive rather than multiplicative (as fitted by a log-linear model). This additive model was fitted using GENMOD for overdispersed Poisson data, but with the link function specified as the identity function rather than the log function. The model was fitted using the fixed factors location and season (spring and autumn).

Fish size frequency distributions from reserve and non-reserve areas were compared using pairwise Kolmogorov–Smirnov tests and analysis of variance (ANOVA). Data were tested for normality using the Shapiro–Wilks test and examination of residual plots. The observed differences between means were tested for statistical significance using Tukey's studentized range tests.

Statistical power of tests of reserve status was estimated using a procedure modified from the method of Zar (1984, his equation 9.24). The use of traditional forms of power analysis assumes homogeneity of variance, which does not hold for count data. For Poisson data the variance equals the mean but, more generally, the data may be overdispersed, with $\sigma^2 = \phi\mu$ where ϕ is the overdispersion parameter. Here, the overdispersion parameter was estimated by SAS as part of the log-linear model. If $k = \mu_2/\mu_1$ denotes the ratio of the two

specified means, then an approximate upper bound on type II error rate is given by the value β obtained as the probability of having standard-normal quantile z_β given by:

$$z_\beta = \frac{\log(k)}{\sqrt{\dfrac{\phi}{n\mu_1}\dfrac{k+1}{k}}} - z_{\alpha/2}.$$

Then, an approximate lower bound on power is given by $1 - \beta$. Here, μ_1 is taken to be the smaller of the two means (so that $\log(k) > 0$) and n is the sample size in each of the reserve and non-reserve areas. The quantile z_β is the value that a standard normal random variable exceeds with probability β. The value α is the level of the test (i.e. type I error rate) and is frequently taken to be 0·05, in which case we have $z_{\alpha/2} = z_{0·025} = 1·96$ (Appendix 1).

For any specified power and sample size, the above formula can be used to determine the necessary minimum value of the ratio k. Conversely, for a given value of k and a desired power, the necessary minimum sample size can be obtained. This can ensure that effort expended on future surveys is sufficient to detect reserve effects, where they exist.

Results

EFFECTS OF MARINE RESERVE PROTECTION ON *P. AURATUS* DENSITY, BIOMASS AND EGG PRODUCTION

Biomass per BUV deployment and density of legal-size snapper (LEGsna) were higher in the reserve than adjacent non-reserve areas at all three locations and for all four surveys (Figs 2 and 3). In particular, the Leigh reserve recorded the highest value of LEGsna on all four survey occasions, and the highest density of snapper of all sizes (MAXsna) on all but the April 1999 survey, when the Hahei reserve MAXsna was boosted by large numbers of sublegal fish.

The log-linear model fits resulted in significant location × survey interactions (Table 2) and non-significant status × survey interactions. These implied that, although the differences between locations varied by survey, the reserve effect did not. At all three locations MAXsna, LEGsna, biomass and egg production were all significantly higher (i.e. 95% confidence intervals lying entirely above unity) in the reserve than in the adjacent non-reserve region (Table 3). The relative density of undersize fish (JUVsna) varied between locations, with higher reserve densities at Hahei, lower reserve densities at Leigh, and no difference between reserve and non-reserve densities at Tawharanui (Table 3).

The analysis of LEGsna (Table 2) resulted in no significant location × status interaction, and thus status appeared as a main effect only. This estimated effect was a 14·3-fold higher density in LEGsna inside reserve areas compared with the adjacent non-reserve areas,
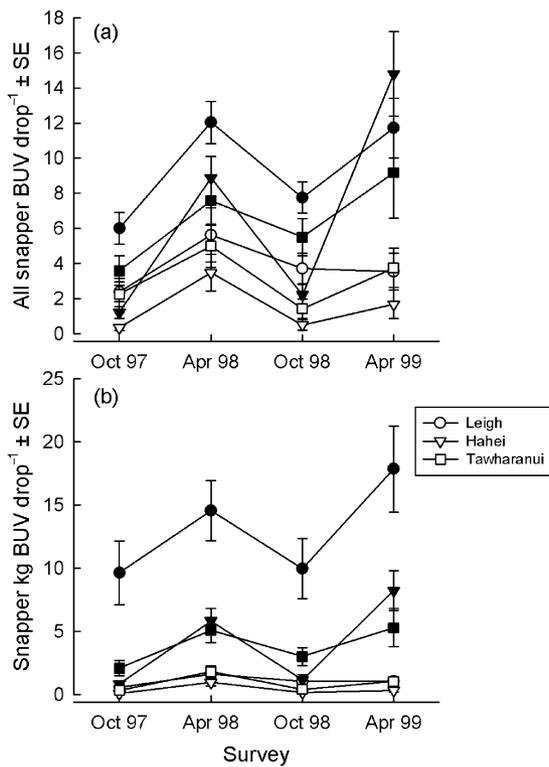
Fig. 2. Mean reserve (filled symbols) and non-reserve (open symbols) snapper *Pagrus auratus* relative density at Leigh, Hahei and Tawharanui from November 1997 to April 1999. (a) Total numerical relative density, all size classes (MAXsna); (b) relative biomass.
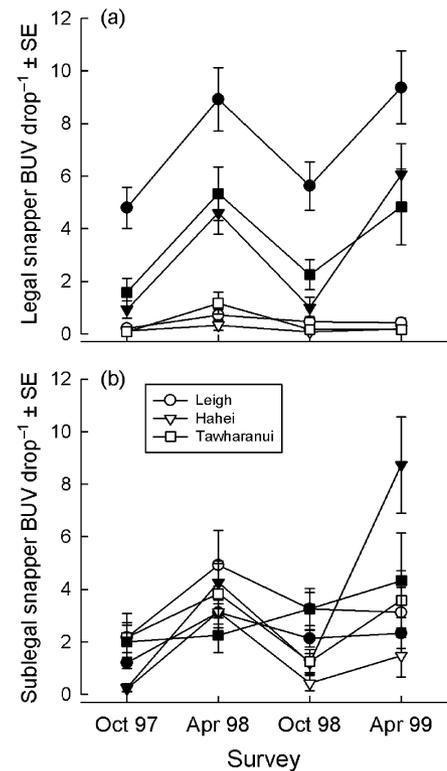

Fig. 3. Mean reserve (filled symbols) and non-reserve (open symbols) snapper *Pagrus auratus* numerical relative density at Leigh, Hahei and Tawharanui from November 1997 to April 1999. (a) Fish > minimum legal size (LEGsna); (b) fish < minimum legal size (JUVsna).

and it could be assumed to be common to all three locations. This ratio had 95% confidence limits (CL) of 10·0 and 20·5. Analyses of biomass and egg production resulted in a final model with the same terms as those fitted to LEGsna (Table 2). Reserve biomass per deployment was 9·9 times greater than in non-reserve areas, with 95% CL of 6·8 and 14·7, and egg production was 18·1 times higher in reserve areas than in non-reserve areas, with 95% CL of 10·7 and 30·6.

SMALL-SCALE VARIABILITY IN *P. AURATUS* DENSITY

Between-area (Fig. 1b) differences in *P. auratus* relative density were modelled separately for each of the three

locations. There were no significant area × survey interactions, indicating that, despite density varying between surveys, relative density was consistent between areas. Predicted counts and estimates of density were made for each survey area, scaled to the April 1999 survey. The division of the MAXsna data into LEGsna (Fig. 4) and JUVsna (Fig. 5) allowed the assessment of the relative contribution of fishable and sublegal fish to the overall patterns.

Survey areas within all three reserves had higher reserve than non-reserve densities of LEGsna (Fig. 4). Hahei and Tawharanui exhibited little between-area variability within reserves, but at Leigh the highest densities of snapper occurred consistently at the reserve centre (areas 5 and 6) and declined toward the

Table 2. Likelihood ratio statistics (type 3 analysis) for all (MAXsna), legal-size (LEGsna), undersize (< 270 mm fork length), biomass and egg production of *Pagrus auratus* at three reserve locations (Leigh, Hahei and Tawharanui) surveyed four times. Status = reserve, non-reserve. Non-significant (*P* > 0·05) interaction terms have been removed from the model

Source	d.f.	MAXsna		LEGsna		JUVsna		Biomass		Egg production	
		χ^2	*P*	χ^2	*P*	χ^2	*P*	χ^2	*P*	χ^2	*P*
Status	1	92·8	< 0·01	447·8	< 0·01	2·6	0·10	331·2	< 0·01	389·5	< 0·01
Location	2	42·0	< 0·01	82·9	< 0·01	15·1	< 0·01	134·6	< 0·01	151·6	< 0·01
Survey	3	88·4	< 0·01	81·0	< 0·01	57·5	< 0·01	54·7	< 0·01	45·0	< 0·01
Location × survey	6	28·9	< 0·01	17·8	< 0·01	32·9	< 0·01	17·5	< 0·01	15·2	0·02
Location × status	2	6·0	0·04			23·5	< 0·01				

Table 3. Relative density and egg production estimates of snapper *Pagrus auratus*. Estimate of relative density derived from log-linear models using data from four surveys at each of three reserve locations (Leigh, Hahei and Tawharanui). Reserve and non-reserve mean density and the magnitude of the difference (expressed as a ratio) with 95% CL are given. MAXsna are all size classes combined, LEGsna are those > 270 mm fork length, JUVsna those < 270 mm fork length; biomass is estimated from all snapper (kg), and egg production is daily batch fecundity. All are expressed in units per BUV deployment

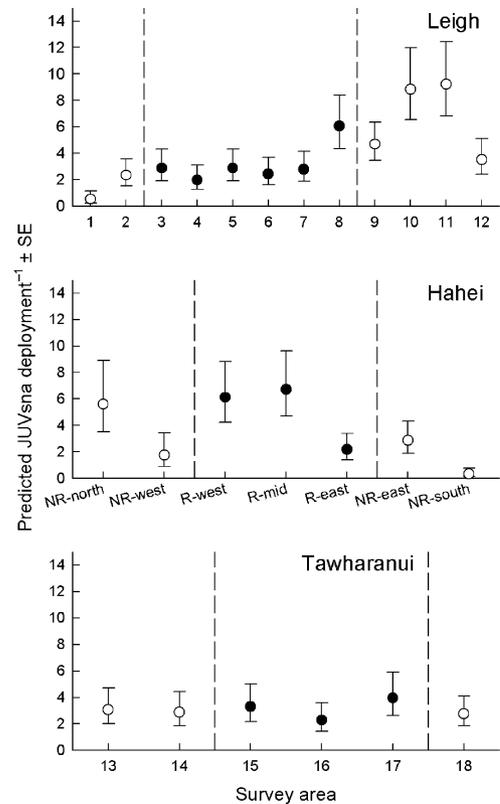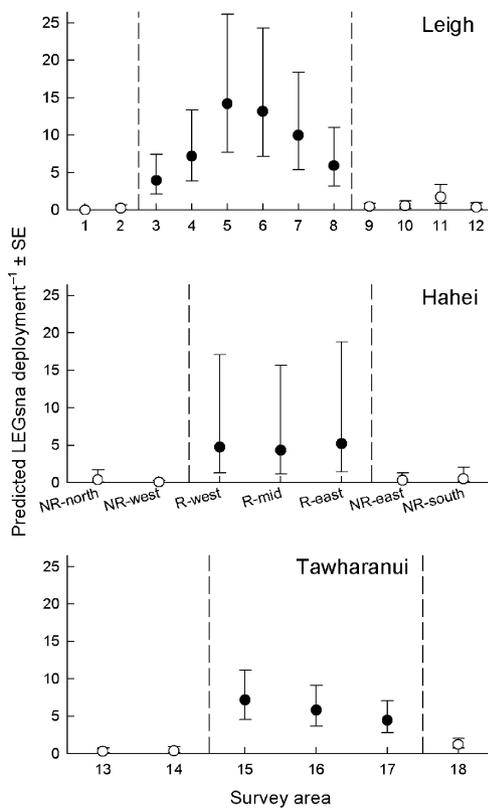|	Reserve mean	Non-reserve mean	Reserve:non-reserve ratio	Lower 95% CL for ratio	Upper 95% CL for ratio
MAXsna					
Leigh	9·38	3·81	2·5	1·84	3·29
Hahei	6·77	1·63	4·2	2·46	7·01
Tawharanui	6·46	3·10	2·1	1·37	3·17
LEGsna					
Leigh	7·18	0·45	16·0	9·30	27·69
Hahei	3·15	0·19	16·5	6·98	39·05
Tawharanui	3·50	0·40	8·8	4·18	18·76
JUVsna					
Leigh	2·20	3·36	0·6	0·46	0·93
Hahei	3·62	1·44	2·5	1·47	4·29
Tawharanui	2·96	2·71	1·1	0·68	1·75
Biomass					
Leigh	13·00	1·08	12·1	7·02	20·84
Hahei	4·02	0·42	9·6	4·84	19·07
Tawharanui	3·88	0·90	4·3	2·59	7·19
Egg production					
Leigh	440 691	18 934	23·3	11·03	49·29
Hahei	117 606	7 704	15·3	6·51	35·97
Tawharanui	112 792	16 696	6·8	3·61	12·67

Fig. 4. Predicted mean LEGsna by survey area at Leigh, Hahei and Tawharanui. Vertical dashed lines represent reserve boundaries, solid symbols are reserve (R) areas and open symbols are non-reserve (NR) areas.

Fig. 5. Predicted mean JUVsna by survey area at Leigh, Hahei and Tawharanui. Vertical dashed lines represent reserve boundaries, solid symbols are reserve areas and open symbols are non-reserve areas.

boundaries. The Tawharanui reserve areas had the lowest standard error estimates because of lower between-replicate variation, and a less pronounced seasonal change in density (relative to the mean) than the other two reserves. Error estimates around area means at Hahei were very high relative to the means because of the patchy distribution of large fish in the reserve, and the contribution of large seasonal fluctuations in density relative to the means.

At Tawharanui, the density of undersize fish was consistent in all six areas, regardless of reserve status. There was more between-area variation at Hahei, but little overall difference between reserve and non-reserve areas. At Leigh, high MAXsna means at the eastern end of the reserve were due to high counts of undersize fish from areas 8–12 (Fig. 5).

SEASONAL EFFECTS ON *P. AURATUS* DENSITY WITHIN RESERVES

For biomass and LEGsna, the location × season interaction term was not significant ($P > 0·20$ for both) so the analyses were re-run with location and season main effects only. The estimated additive effect of season within the three reserves was a spring to autumn mean increase of 5·07 ($± 1·83$ 95% CL) kg per BUV deployment, and for LEGsna an increase of 3·91 ($± 1·08$ 95% CL). For undersize snapper (JUVsna) and all snapper (MAXsna) there was considerable among-location variability (Figs 2 and 3) that was partly attributable to patchiness in the distribution of undersize fish. This caused a significant interaction between location and season ($\chi^2 = 11·62$, d.f. = 2, $P < 0·01$), so individual season estimates were obtained for each location. For JUVsna the increases were Leigh, $1·06 ± 0·91$; Hahei, $5·77 ± 1·76$; Tawharanui, $0·67 ± 1·92$ (95% CL); and for MAXsna they were Leigh, $5·00 ± 2·60$; Hahei, $10·13 ± 2·63$; Tawharanui, $3·83 ± 3·09$ (95% CL).

FISH SIZE

As previously indicated by the proportionally large differences in biomass relative to numerical density, the mean length of snapper was greater within reserves than in fished areas at all three locations (Table 4 and
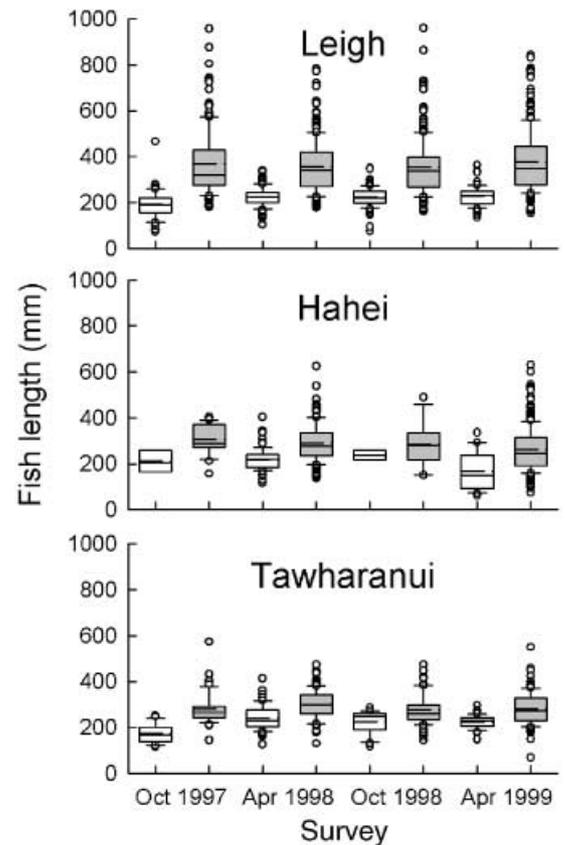

Fig. 6. Box-plots comparing the size of snapper *Pagrus auratus* inside and outside Leigh Marine Reserve, Hahei Marine Reserve and Tawharanui Marine Park, October 1997–April 1999. Solid and dashed horizontal lines are medians and means, respectively. Upper and lower box limits are 25th and 75th percentiles, and error bars represent the 10th and 90th percentiles. Data outside the 10th and 90th percentiles are plotted individually. Shaded boxes are marine reserve samples, and unshaded boxes are non-reserve samples.

Fig. 6). Log-transformed Hahei data passed formal tests for normality (Shapiro–Wilks test: $W = 0·99$, $P > 0·05$) but Leigh and Tawharanui data did not ($P < 0·01$ in both cases) due to a small number of outliers.

Kolmogorov–Smirnov tests run on fish ≥ 270 mm FL found a significant difference between the reserve and non-reserve size structure at Leigh ($D = 0·55$, $P < 0·01$) where almost all non-reserve fish were < 400 mm FL. The comparison was not significant at

Table 4. ANOVA comparisons of log-transformed fish size in reserve and non-reserve areas at three locations, including pairwise Tukey's studentized range test comparisons of mean (untransformed) *Pagrus auratus* size (fork length) from BUV data, with 95% confidence intervals (CI) for the difference estimate

Status comparison (reserve – non-reserve)	Error d.f.	*F*-value	Difference between means (mm)	95% CI	*P*
All snapper					
Leigh	1162	397·98	144·29	14·18	< 0·01
Hahei	481	57·98	64·80	17·79	< 0·01
Tawharanui	439	96·88	62·92	12·71	< 0·01
Legal snapper					
Leigh	682	41·66	103·97	36·80	< 0·01
Hahei	181	3·00	37·03	42·89	0·08
Tawharanui	183	3·67	24·21	25·53	0·06

either Hahei or Tawharanui (Fig. 6). The reserve vs. non-reserve difference in mean size of legal-size snapper at Hahei and Tawharanui was small relative to Leigh (Table 4).

All reserve vs. non-reserve comparisons of MAXsna and LEGsna were statistically significant (Table 2), hence the statistical power was sufficient. At Leigh and using the current design ($n = 24$), the minimum detectable difference (reserve:non-reserve ratio) in MAXsna was 2·3 for a power of at least 0·8, and for LEGsna the reserve density would have had to be 5·3 times the non-reserve density (for observed values see Table 3). At Hahei ($n = 15$) and Tawharanui ($n = 12$), for a power of at least 0·8, the MAXsna minimum reserve:non-reserve ratio differences were 4·4 and 3·2, respectively, and the LEGsna minimum reserve:non-reserve ratio differences were 14·0 and 8·7, respectively.

Discussion

Surveys of three marine reserves in northern New Zealand, repeated biannually for 2 years, have allowed estimation of the effects of protection on snapper populations, as well as location and seasonal effects. The design of the study reduced the risk of location-specific biases that may have been present due to the lack of 'before' data, which in marine reserve studies are often unobtainable. The data presented here demonstrate large differences in relative density of the heavily exploited sparid fish *P. auratus* between marine reserves and adjacent fished areas in northern New Zealand. Log-linear modelling indicated a common status (reserve or non-reserve) effect corresponding to a 14-fold increase of legal-size snapper in the reserve compared with the adjacent non-reserve areas, despite significant between-location and between-survey variability in densities.

Failure to detect significant differences between reserves and non-reserve areas in many previous studies has been attributed to lack of power in the survey design (Cole, Ayling & Creese 1990; Paddack & Estes 2000) but few attempts have been made to use pilot studies to determine minimum sample sizes for specified effect sizes (Peterman 1990; Fairweather 1991). While this study found statistically significant differences between reserve and non-reserve areas, it is instructive to consider the minimum effect size detectable using this design if future surveys are to attempt to detect small reserve effects in young or small reserves. Traditional power analyses (Cohen 1977; Zar 1984) assume that the variances of all observations are the same, and therefore not dependent on the means. This assumption does not hold for count data and it is more reasonable to assume that the variance is proportional to the mean (Zar 1984). The constant of proportionality can be estimated using the scale factor provided by the log-linear model output from a pilot study.

With the sample sizes employed in this study, we should expect effects to be detectable with power (by convention) set at 0·8 if the reserve:non-reserve ratio is greater than 2·3 for snapper. Edgar & Barrett (1997, 1999) suggested that, given the inherent variability of natural marine systems, a minimum biologically meaningful (as opposed to statistically significant) effect criterion might be a doubling or halving of abundance. This approach is akin to the 'equivalence testing' approach advocated by McBride (1999). Using this criterion, for the future examination of changes in snapper density in new reserves using BUV, it is recommended that $n \geq 25$ for each of the reserve and non-reserve areas. For individual reserves, the minimum detectable difference in reserve:non-reserve ratio for legal-size snapper ranged from 5·3 to 14·0 with statistical power of 0·8, therefore the level of sample replication used in this study should probably be regarded as a minimum.

At all three reserves, counts were much lower in the spring (October–November) surveys than in the autumn (April–May) surveys. This pattern agrees with previously recorded observations of seasonal increases in snapper density on reefs and soft sediment bottoms. Trawl surveys have indicated that the abundance of snapper at inshore Hauraki Gulf locations fluctuates seasonally (Paul 1976). Within the Leigh reserve, high densities of juvenile fish belonging to the 0+ and 1+ year classes have been described on reef habitats during spring and summer (December–March) but densities were very low in winter (Kingett & Choat 1981). Similarly, Francis (1995) suggested that observed seasonal changes in juvenile snapper density on soft sediment bottoms might be attributable to movement of fish onto reefs in early summer. Similar evidence for seasonal changes in snapper abundance has been recorded from Japan (Matsumiya, Endo & Azeta 1980; Kiso 1985). Interestingly, Kingett & Choat (1981) did not detect the seasonal fluctuations in the density of older fish that were found in this study, possibly due to bias caused by the presence of diver-habituated resident fish (Cole 1994; Willis, Millar & Babcock 2000). Similarly, the angling experiment of Millar & Willis (1999) did not detect seasonal variability (June vs. December) in snapper catch-per-unit-effort data at Leigh. This could be due to capture biases, but it is also likely that June and December are both part way through the emigration and immigration (respectively) of snapper to inshore reefs.

The large seasonal fluctuations in snapper density have implications for marine reserve monitoring and the prediction of potential reserve benefits to fisheries. First, there is need for standardization of the timing of surveys to determine reserve effects. If different reserves are surveyed at different times of year, the results will not be comparable, and will give misleading impressions of the relative effectiveness of the different reserves. This may apply to species other than snapper. Theoretical

reviews have predicted that migratory species, or species with moderate mobility, will not benefit significantly from marine reserve protection (Kramer & Chapman 1999). In this case, however, the density of a migratory species is much higher within reserves than in fished areas. It appears that most snapper are seasonally mobile, but some individuals have shown a marked degree of site fidelity (Willis, Parsons & Babcock 2001). Thus, generalizations about the entire species are inappropriate, and theoretical predictions made from such generalizations are likely to lead to incorrect conclusions. Similar behavioural variability between individuals of the same species has been recorded from other temperate fish species (Attwood & Bennett 1994, 1995), and the estimation of the proportions of a population subject to different behavioural traits might be a fruitful avenue of research to pursue. In the case of snapper it is likely that many (probably the majority) of the fish found within the reserve during winter are residents (Willis, Parsons & Babcock 2001) and that the increase in density seen during summer is entirely due to the migratory component of the population.

It is likely that most of the recolonization of snapper to reserves is not from new recruits but from the establishment of home ranges by seasonal immigrants. This conclusion is based on several observations. First, many of the snapper found within the reserves are older than the reserves. Secondly, the density of juveniles within the oldest (Leigh) reserve is actually significantly lower than outside (we do not know if this is due to habitat differences or whether high densities of large fish inside the reserve inhibit the colonization of juveniles). Thirdly, as, discussed above, 0+ snapper appear to be subject to similar seasonal migratory patterns as larger fish (Kingett & Choat 1981; Francis 1995): small juveniles are only seasonally common on reef habitats. If there is little or no aggregative or, conversely, territorial behaviour in snapper (i.e. the recolonization rate is independent of the density of fish present) then the abundance of fish in the reserve might be expected to build as a linear function of time. If, however, the presence of conspecifics encourages fish to remain, densities might increase exponentially in the early stages until space or resources become limiting.

The observed pattern of declining relative density towards the boundaries, which was noted in earlier surveys used for comparisons of methodology (Millar & Willis 1999; Willis, Millar & Babcock 2000), was consistent throughout these four surveys. There are several reasons why this pattern might have occurred. As suggested by Cole (1994), high abundance of snapper at the reserve centre might be a response to (i) differences in habitat quality, (ii) hand feeding of fish by the public or (iii) higher levels of surveillance at the reserve centre. It is also possible that these factors are of secondary importance to the relative vulnerability of site-attached fish (Willis, Parsons & Babcock 2001) to fishing pressure at the reserve boundaries. Kramer & Chapman (1999) predicted that the degree of exposure to the fishery of

individuals within reserves would increase with home range size. In addition, the probability of a fish making cross-boundary movements would be higher if the centre of its range was close to the boundary (Zeller & Russ 1998). As the actual extent of movements of home-ranging snapper have not yet been determined, the distance from a boundary that would provide zero vulnerability to fishing pressure is unknown, and densities at the centre might be higher still if the reserve was larger. Seasonal movements on and off reefs further reduce the likelihood that consistently high densities of snapper present at the centre of the Leigh reserve represent a possible 'virgin' (unfished) biomass level.

Furthermore, similar within-reserve patterns were not apparent at Tawharanui or Hahei, where reserve densities of snapper were much lower than at Leigh. This may have been because of insufficient spatial resolution in the survey design, as these reserves were divided into three, rather than six, survey areas. Alternatively, the spatial pattern of habitat distribution in relation to reserve boundaries differs at these reserves, producing different patterns of fish abundance. For example, if resident snapper orientate visually to reefs, areas of open sand may provide effective disincentives to cross-boundary movements (Kramer & Chapman 1999). Finally, such patterns may not exist at these reserves because of differences in the distribution of fishing effort.

Illegal fishing occurs at all three reserves (T.J.W., personal observation; P. Carter, Department of Conservation, personal communication), so the relative density estimates presented here are conservative estimates of fish responses to protection. As we lack information on the relative levels of non-compliance with the reserve regulations, it was assumed that poaching is consistent at the three reserves. It is notable that the Tawharanui reserve densities of both snapper and blue cod *Parapercis colias* (Pinguipedidae) are comparable to those recorded at Hahei (Willis 2001), despite the latter reserve having been established 11 years later. The low level response to protection (considering the time since the park was established) might be because of less compliance with the no-take regulations at Tawharanui.

There are two potential direct benefits of marine reserves to fisheries: (i) enhancement of spawning stock biomass and (ii) 'spillover' of adults to enhance local fisheries (Roberts & Polunin 1991; Rowley 1994; Allison, Lubchenco & Carr 1998; Bohnsack 1998; Horwood, Nichols & Milligan 1998). Seasonal peaks in inshore snapper density coincide with the spawning season and post-spawning period (Crossland 1977; Scott & Pankhurst 1992), implying that marine reserves protect both resident fish and some proportion of migratory fish during spawning, assuming that they spawn within reserves. However, greater output of eggs need not necessarily translate into production (Francis 1993). Variability in larval mortality means it has proven difficult to determine any relationship between spawner abundance and recruitment (Myers & Barrowman 1996;

Gilbert 1997), and increased contributions from reserves are likely to become important only when stocks are overfished to low levels. If reserves are to have measurable effects, they may have to be large, perhaps to the detriment of the fishery (Parrish 1999). However, the inability to detect a measurable effect on production or recruitment does not mean some beneficial contribution is not being made (Lauck *et al*. 1998). For example, our data suggest that a reserve the size of Leigh (*c*. 5 km of coastline) might conservatively produce a quantity of snapper eggs equivalent to that produced by *c*. 90 km of unprotected coastline.

The term 'spillover' implies that density-dependence (whether via resource limitation or territoriality) actively displaces fish across reserve boundaries, where they become available to the fishery (Kramer & Chapman 1999). In this study, the survey areas adjacent to the reserve boundaries generally contained the lowest overall density of *P. auratus* of non-reserve areas. This was most likely because of concentrated recreational fishing effort at those locations (especially area 9 at Leigh; authors' personal observation) caused by perceptions that catch rates next to the reserve are likely to be high. If emigration from the reserve has been occurring, numbers were too low to be detected with the current methodology. In this regard, the importance of knowing the distribution of fishing effort outside reserves cannot be understated. It is possible that the results of some previous studies that imply spillover (Rakitin & Kramer 1996; Chapman & Kramer 1999) could rather have reflected relatively low fishing effort near to the reserve. Several numerical simulations of fish stock dynamics (Polacheck 1990; DeMartini 1993; Attwood & Bennett 1995; Guénette & Pitcher 1999) and an empirical study (Russ & Alcala 1996b) suggest that fishery yield might be increased by temporary protection of individuals within reserves, which then become available to the fishery. In the case of snapper, the long-term site fidelity shown by some individuals, and our observations from BUV that indicate that larger fish tend to be behaviourally dominant, would contradict these simulations. Indeed, the distribution of juvenile snapper at Leigh did not match that of larger fish. If fish are displaced, it is more likely to be smaller individuals that emigrate, and increases to yield-per-recruit or even local yield brought about by small individual reserves could be negligible. However, the finding that marine reserves retain high densities of large, older snapper provides support for the concept of reserves as tools for mitigating losses in genetic diversity caused by overexploitation (Hauser *et al*. 2002).

Acknowledgements

References

Allison, G.W., Lubchenco, J. & Carr, M.H. (1998) Marine reserves are necessary but not sufficient for marine conservation. *Ecological Applications*, **8** (Supplement), 79–92.

Attwood, C.G. & Bennett, B.A. (1994) Variation in dispersal of galjoen (*Coracinus capensis*) (Teleostei: Coracinidae) from a marine reserve. *Canadian Journal of Fisheries and Aquatic Sciences*, **51**, 1247–1257.

Attwood, C.G. & Bennett, B.A. (1995) Modelling the effect of marine reserves on the recreational shore-fishery of the south-western Cape, South Africa. *South African Journal of Marine Science*, **16**, 227–240.

Babcock, R.C., Kelly, S., Shears, N.T., Walker, J.W. & Willis, T.J. (1999) Changes in community structure in temperate marine reserves. *Marine Ecology Progress Series*, **189**, 125–134.

Bell, J.D. (1983) Effects of depth and marine reserve fishing restrictions on the structure of a rocky reef fish assemblage in the north-western Mediterranean Sea. *Journal of Applied Ecology*, **20**, 357–369.

Bennett, B.A. & Attwood, C.G. (1991) Evidence for recovery of a surf-zone fish assemblage following the establishment of a marine reserve on the southern coast of South Africa. *Marine Ecology Progress Series*, **75**, 173–181.

Bennett, B.A. & Attwood, C.G. (1993) Shore-angling catches in the De Hoop nature reserve, South Africa, and further evidence for the protective value of marine reserves. *South African Journal of Marine Science*, **13**, 213–222.

Beverton, R.J.H. & Holt, S.J. (1957) *On the Dynamics of Exploited Fish Populations*. Facsimile reprint, 1993. Chapman & Hall, London, UK.

Bohnsack, J.A. (1998) Application of marine reserves to reef fisheries management. *Australian Journal of Ecology*, **23**, 298–304.

Buxton, C.D. & Smale, M.J. (1989) Abundance and distribution patterns of three temperate marine reef fish (Teleostei: Sparidae) in exploited and unexploited areas off the southern Cape coast. *Journal of Applied Ecology*, **26**, 441–451.

Chapman, M.R. & Kramer, D.L. (1999) Gradients in coral reef fish density and size across the Barbados Marine Reserve boundary: effects of reserve protection and habitat characteristics. *Marine Ecology Progress Series*, **181**, 81–96.

Choat, J.H. & Kingett, P.D. (1982) The influence of fish predation on the abundance cycles of an algal turf invertebrate fauna. *Oecologia*, **54**, 88–95.

Choat, J.H. & Schiel, D.R. (1982) Patterns of distribution and abundance of large brown algae and invertebrate herbivores in subtidal regions of northern New Zealand. *Journal of Experimental Marine Biology and Ecology*, **60**, 129–162.

Cohen, J. (1977) *Statistical Power Analysis for the Behavioural Sciences*. Academic Press, New York, NY.

Cole, R.G. (1994) Abundance, size structure, and diver-oriented behaviour of three large benthic carnivorous fishes in a marine reserve in northeastern New Zealand. *Biological Conservation*, **70**, 93–99.

Cole, R.G., Ayling, T.M. & Creese, R.G. (1990) Effects of marine reserve protection at Goat Island, northern New Zealand. *New Zealand Journal of Marine and Freshwater Research*, **24**, 197–210.

Colman, J.A. (1972) Food of snapper, *Chrysophrys auratus* (Forster), in the Hauraki Gulf, New Zealand. *New Zealand Journal of Marine and Freshwater Research*, **6**, 221–239.

Creese, R.G. & Jeffs, A.J. (1993) Biological research in New Zealand marine reserves. *Proceedings of the Second International Temperate Reef Symposium* (eds C.N. Battershill, D.R. Schiel, G.P. Jones, R.G. Creese & A.B. MacDiarmid), pp. 15–22. NIWA Marine, Wellington, New Zealand.

Crossland, J. (1977) Seasonal reproductive cycle of snapper *Chrysophrys auratus* (Forster) in the Hauraki Gulf. *New Zealand Journal of Marine and Freshwater Research*, **11**, 37–60.

DeMartini, E.E. (1993) Modeling the potential of fishery reserves for managing Pacific coral reef fishes. *Fishery Bulletin*, **91**, 414–427.

Dufour, V., Jouvenel, J.-Y. & Galzin, R. (1995) Study of a Mediterranean reef fish assemblage. Comparisons of population distributions between depths in protected and unprotected areas over one decade. *Aquatic Living Resources*, **8**, 17–25.

Edgar, G.J. & Barrett, N.S. (1997) Short term monitoring of biotic change in Tasmanian marine reserves. *Journal of Experimental Marine Biology and Ecology*, **213**, 261–279.

Edgar, G.J. & Barrett, N.S. (1999) Effects of the declaration of marine reserves on Tasmanian reef fishes, invertebrates and plants. *Journal of Experimental Marine Biology and Ecology*, **242**, 107–144.

Ellis, D.M. & DeMartini, E.E. (1995) Evaluation of a video camera technique for indexing abundances of juvenile pink snapper, *Pristipomoides filamentosus*, and other Hawaiian insular shelf fishes. *Fishery Bulletin*, **93**, 67–77.

Fairweather, P.G. (1991) Statistical power and design requirements for environmental effects studies. *Australian Journal of Marine and Freshwater Research*, **42**, 555–567.

Francis, M.P. (1993) Does water temperature determine year class strength in New Zealand snapper (*Pagrus auratus*, Sparidae)? *Fisheries Oceanography*, **2**, 65–72.

Francis, M.P. (1995) Spatial and seasonal variation in the abundance of juvenile snapper (*Pagrus auratus*) in the north-western Hauraki Gulf. *New Zealand Journal of Marine and Freshwater Research*, **29**, 565–579.

Francis, R.I.C.C. & Shotton, R. (1997) 'Risk' in fisheries management: a review. *Canadian Journal of Fisheries and Aquatic Sciences*, **54**, 1699–1715.

Garcia-Rubíes, A. & Zabala, M. (1990) Effects of total fishing prohibition on the rocky fish assemblages of Medes Islands marine reserve (NW Mediterranean). *Scientia Marina*, **54**, 317–328.

Gilbert, D.J. (1997) Towards a new recruitment paradigm for fish stocks. *Canadian Journal of Fisheries and Aquatic Sciences*, **54**, 969–977.

Gilbert, D.J., McKenzie, J.R., Davies, N.M. & Field, K.D. (2000) *Assessment of the SNA1 Stocks for the 1999–2000 Fishing Year*. New Zealand Fisheries, Assessment Report 2000/38, Wellington, New Zealand.

Guénette, S. & Pitcher, T.J. (1999) An age-structured model showing the benefits of marine reserves in controlling exploitation. *Fisheries Research*, **39**, 295–303.

Harmelin, J.-G., Bachet, F. & Garcia, F. (1995) Mediterranean marine reserves: fish indices as tests of protection efficiency. *PSZN Marine Ecology*, **16**, 233–250.

Hauser, L., Adcock, G.J., Smith, P.J., Bernal Ramirez, J.H. & Carvalho, G.R. (2002) Loss of microsatellite diversity and low effective population size in an overexploited population of New Zealand snapper (*Pagrus auratus*). *Proceedings of the National Academy of Sciences*, **99**, 11742–11747.

Horwood, J.W., Nichols, J.H. & Milligan, S. (1998) Evaluation of closed areas for fish stock conservation. *Journal of Applied Ecology*, **35**, 893–903.

Hurlbert, S.H. (1984) Pseudoreplication and the design of ecological field experiments. *Ecological Monographs*, **54**, 187–211.

Jennings, S. (2000) Patterns and predictions of population recovery in marine reserves. *Reviews in Fish Biology and Fisheries*, **10**, 209–231.

Jennings, S. & Polunin, N.V.C. (1995) Biased underwater visual census biomass estimates for target-species in tropical reef fisheries. *Journal of Fish Biology*, **47**, 733–736.

Jennings, S. Reynolds, J.D. & Mills, S.C. (1998) Life history correlates of responses to fisheries exploitation. *Journal of the Royal Society, London, Series B*, **265**, 333–339.

Jones, G.P., Cole, R.G. & Battershill, C.N. (1993) Marine reserves: do they work? *Proceedings of the Second International Temperate Reef Symposium* (eds C.N. Battershill, D.R. Schiel, G.P. Jones, R.G. Creese & A.B. MacDiarmid), pp. 29–45. NIWA Marine, Wellington, New Zealand.

Kingett, P.D. & Choat, J.H. (1981) Analysis of density and distribution patterns in *Chrysophrys auratus* (Pisces: Sparidae) within a reef environment: an experimental approach. *Marine Ecology Progress Series*, **5**, 283–290.

Kiso, K. (1985) On the feeding habit and mode of distribution of immature red sea bream (*Pagrus major*) in Shijiki Bay, Hirado Island, Japan. *Bulletin of the Seikai Regional Fisheries Research Laboratory*, **62**, 1–17.

Kramer, D.L. & Chapman, M.R. (1999) Implications of fish home range size and relocation for marine reserve function. *Environmental Biology of Fishes*, **55**, 65–79.

Kulbicki, M. (1998) How the acquired behaviour of commercial reef fishes may influence the results obtained from visual censuses. *Journal of Experimental Marine Biology and Ecology*, **222**, 11–30.

Lauck, T., Clark, C.W., Mangel, M. & Munro, G.R. (1998) Implementing the precautionary principle in fisheries management through marine reserves. *Ecological Applications*, **8** (Supplement), 72–78.

McArdle, B.H. (1996) Levels of evidence in studies of competition, predation, and disease. *New Zealand Journal of Ecology*, **20**, 7–15.

McBride, G.B. (1999) Equivalence tests can enhance environmental science and management. *Australian and New Zealand Journal of Statistics*, **41**, 19–29.

McGlennon, D., Jones, G.K., Baker, J., Jackson, W.B. & Kinloch, M.A. (2000) Ageing, catch-at-age and relative year-class strength for snapper (*Pagrus auratus*) in northern Spencer Gulf, South Australia. *Marine and Freshwater Research*, **51**, 669–677.

Matsumiya, Y., Endo, Y. & Azeta, M. (1980) Estimation of the abundance of 0-group red sea bream in Shijiki Bay. *Bulletin of the Seikai Regional Fisheries Research Laboratory*, **54**, 315–320.

Millar, R.B. & Willis, T.J. (1999) Estimating the relative density of snapper in and around a marine reserve using a log-linear mixed effects model. *Australian and New Zealand Journal of Statistics*, **41**, 383–394.

Myers, R.A. & Barrowman, N.J. (1996) Is fish recruitment related to spawner abundance? *Fishery Bulletin*, **94**, 707–724.

Myers, R.A., Hutchings, J.A. & Barrowman, N.J. (1997) Why do fish stocks collapse? The example of cod in Atlantic Canada. *Ecological Applications*, **7**, 91–106.

Paddack, M.J. & Estes, J.A. (2000) Kelp forest fish populations in marine reserves and adjacent exploited areas of central California. *Ecological Applications*, **10**, 855–870.

Parrish, R. (1999) Marine reserves for fishery management: why not. *California Cooperative Oceanic Fisheries Investigations*, **40**, 77–86.

Paul, L.J. (1976) *A Study on Age, Growth, and Population Structure of the Snapper,* Chrysophrys auratus *(Forster), in the Hauraki Gulf, New Zealand*. Fisheries Research Bulletin No. 13. New Zealand Ministry of Agriculture and Fisheries, Wellington, New Zealand.

Paulin, C.D. (1990) *Pagrus auratus*, a new combination for the species known as 'snapper' in Australasian waters (Pisces:

Sparidae). *New Zealand Journal of Marine and Freshwater Research*, **24**, 259–265.

Pauly, D., Christensen, V., Dalsgaard, J., Froese, R. & Torres, F. Jr (1998) Fishing down marine food webs. *Science*, **279**, 860–863.

Peterman, R.M. (1990) Statistical power analysis can improve fisheries research and management. *Canadian Journal of Fisheries and Aquatic Sciences*, **47**, 2–15.

Polacheck, T. (1990) Year around closed areas as a management tool. *Natural Resource Modeling*, **4**, 327–354.

Rakitin, A. & Kramer, D.L. (1996) Effects of a marine reserve on the distribution of coral reef fishes in Barbados. *Marine Ecology Progress Series*, **131**, 97–113.

Roberts, C.M. & Polunin, N.V.C. (1991) Are marine reserves effective in the management of reef fisheries? *Reviews in Fish Biology and Fisheries*, **1**, 65–91.

Rowley, R.J. (1994) Marine reserves in fisheries management. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **4**, 233–254.

Russ, G.R. & Alcala, A.C. (1996a) Marine reserves: rates and patterns of recovery and decline of large predatory fish. *Ecological Applications*, **6**, 947–961.

Russ, G.R. & Alcala, A.C. (1996b) Do marine reserves export adult fish biomass? Evidence from Apo Island, central Philippines. *Marine Ecology Progress Series*, **132**, 1–9.

SAS (1997) *SAS/STAT Software: Changes and Enhancements Through Release 6·12*. SAS Institute Inc., Cary, NC.

Scott, S.G. (1991) *The reproductive biology of the New Zealand snapper*; Pagrus auratus. MSc Thesis. University of Auckland, Auckland, New Zealand.

Scott, S.G. & Pankhurst, N.W. (1992) Interannual variation in the reproductive cycle of the New Zealand snapper *Pagrus auratus* (Bloch & Schneider) (Sparidae). *Journal of Fish Biology*, **41**, 685–696.

Scott, S.G., Zeldis, J.R. & Pankhurst, N.W. (1993) Evidence for daily spawning in natural populations of the New Zealand snapper *Pagrus auratus* (Sparidae). *Environmental Biology of Fishes*, **36**, 149–156.

Seijo, J.C. & Caddy, J.F. (2000) Uncertainty in bio-economic reference points and indicators of marine fisheries. *Marine and Freshwater Research*, **51**, 477–483.

Shears, N.T. & Babcock, R.C. (2002) Marine reserves demonstrate top-down control of community structure on temperate reefs. *Oecologia*, **132**, 131–142.

Sladek Nowlis, J. & Roberts, C.M. (1999) Fisheries benefits and optimal design of marine reserves. *Fishery Bulletin*, **97**, 604–616.

Stewart-Oaten, A., Murdoch, W.W. & Parker, K.R. (1986) Environmental impact assessment: 'pseudoreplication' in time? *Ecology*, **67**, 929–940.

Taylor, R.B. & Willis, T.J. (1998) Relationships amongst length, weight and growth of northeastern New Zealand reef fish. *Marine and Freshwater Research*, **49**, 255–260.

Underwood, A.J. (1994) On beyond BACI: sampling designs that might reliably detect environmental disturbances. *Ecological Applications*, **4**, 3–15.

Walters, C.J. (1993) Dynamic models and large scale field experiments in environmental impact assessment and management. *Australian Journal of Ecology*, **18**, 53–61.

Wantiez, L., Thollot, P. & Kulbicki, M. (1997) Effects of marine reserves on coral reef fish communities from five islands in New Caledonia. *Coral Reefs*, **16**, 215–224.

Willis, T.J. (2001) *Marine reserve effects on snapper (*Pagrus auratus: *Sparidae) in northern New Zealand*. PhD thesis, University of Auckland.

Willis, T.J. & Babcock, R.C. (2000) A baited underwater video system for the determination of relative density of carnivorous reef fish. *Marine and Freshwater Research*, **51**, 755–763.

Willis, T.J., Millar, R.B. & Babcock, R.C. (2000) Detection of spatial variability in relative density of fishes: comparison of visual census, angling, and baited underwater video. *Marine Ecology Progress Series*, **198**, 249–260.

Willis, T.J., Parsons, D.M. & Babcock, R.C. (2001) Evidence for long-term site fidelity of snapper (*Pagrus auratus*) within a marine reserve. *New Zealand Journal of Marine and Freshwater Research*, **35**, 581–590.

Zar, J.H. (1984) *Biostatistical Analysis*, 2nd edn. Prentice Hall, Englewood Cliffs, NJ.

Zeldis, J.R. & Francis, R.I.C.C. (1998) A daily egg production method estimate of snapper biomass in the Hauraki Gulf, New Zealand. *ICES Journal of Marine Science*, **55**, 522–534.

Zeller, D.C. & Russ, G.R. (1998) Marine reserves: patterns of adult movement of the coral trout (*Plectropomus leopardus*) (Serranidae). *Canadian Journal of Fisheries and Aquatic Sciences*, **55**, 917–924.

Appendix 1

CALCULATION OF STATISTICAL POWER FOR COMPARING TWO POPULATIONS USING COUNT DATA

Equation 9·24 of Zar (1984) is derived from the Wald test, whereby a statistic is normalized by subtracting its expected value (under H_0), dividing by its standard error, and then comparing to a t-distribution with appropriate degrees of freedom. This same normalization is used by the SAS procedure GENMOD (SAS 1997) in its analysis of parameter estimates table, except that the comparison is against the standard normal distribution (equivalently, comparing the square of the normalized statistic to a χ^2 with 1 degree of freedom). Thus, the power formula for count data is obtained from Zar's formula by using the appropriate specification of standard error and by replacing t-distribution quantiles with standard normal distribution quantiles.

Specifically, let μ_1 and μ_2 be the expected counts in populations 1 and 2. Then, $\mu_2 = k\mu_1$ where $k = \mu_2/\mu_1$. On the log scale this is $\log(\mu_2) = \log(k) + \log(\mu_1)$, i.e. we wish to find a difference between the log of population means of $\delta = \log(k)$.

For a log-linear model the test of H_0: $\mu_1 = \mu_2 \Leftrightarrow \log(\mu_1) = \log(\mu_2)$ normalizes the statistic $\log(\bar{X}_1) - \log(\bar{X}_2)$. If ϕ denotes the overdispersion factor (estimated by SAS as deviance/d.f; SAS 1997, p. 285), then it can be shown that:

$$\text{Var}(\log(\bar{X}_1)) \approx \frac{\phi}{n\mu_1} \text{ and Var}(\log(\bar{X}_2)) \approx \frac{\phi}{n\mu_2} = \frac{\phi}{nk\mu_1}$$

and hence

$$\text{Var}(\log(\bar{X}_1) - \log(\bar{X}_2)) = \text{Var}(\log(\bar{X}_1)) + \text{Var}(\log(\bar{X}_2))$$
$$\approx \frac{\phi}{n\mu_1}\frac{k+1}{k}.$$

Replacing the t-quantiles with z-quantiles, equation 9·24 of Zar (1984) can be written:

$$1 = \frac{\text{Var(statistic)}}{\delta^2}(z_{\alpha/2} + z_\beta)^2$$

which in our application gives:

$$1 = \frac{\text{Var}(\log(\bar{X}_1) - \log(\bar{X}_2))}{\log(k)^2}(z_{\alpha/2} + z_\beta)^2$$
$$= \frac{\dfrac{\phi}{n\mu_1}\dfrac{k+1}{k}}{\log(k)^2}(z_{\alpha/2} + z_\beta)^2.$$

Solving for n gives:

$$n = \frac{\dfrac{\phi}{\mu_1}\dfrac{k+1}{k}}{\log(k)^2}(z_{\alpha/2} + z_\beta)^2$$

and for z_β gives:

$$z_\beta = \frac{\log(k)}{\sqrt{\dfrac{\phi}{n\mu_1}\dfrac{k+1}{k}}} - z_{\alpha/2}.$$