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Detection of spatial variability in relative density of fishes: comparison of visual census, angling, and baited underwater video

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ABSTRACT: The ability to make accurate estimates of fish relative abundance is the basis of both ecological and environmental effects studies, and flawed sampling methods may give misleading results even in otherwise well-designed surveys. This paper compares surveys of snapper *Pagrus auratus* (Sparidae) and blue cod *Parapercis colias* (Pinguipedidae) conducted using 3 methods (underwater visual census, experimental angling, and baited underwater video) inside and outside the Cape Rodney-Okakari Point marine reserve in northeastern New Zealand. Angling and baited video consistently detected adult *P. auratus* at protected and fished sites, providing estimates of 36.7 and 39.2 times greater density of fishable *P. auratus* within the reserve, respectively. Visual surveys provided the least reliable measure of density of *P. auratus*, with adults only detected at the reserve centre where fish have been habituated to divers by hand-feeding. Measures of the size structure of *P. auratus* were consistent between angling and video, but mean size was significantly smaller using visual census methods. Relative density of *P. colias* was similar for all 3 methods, but angling estimated larger mean size, probably due to hook selectivity against smaller fish. The study indicates that methodological standardisation across all species is not always appropriate for environmental effects studies, and that different survey methods should be considered according to the biology and behaviour of the species of interest.

KEY WORDS: Angling · Baited underwater video · Exploited fishes · Behaviour · Log-linear model · Marine reserves · Recovery · Survey bias · Visual census

INTRODUCTION

There is an increasing global trend, instigated by the frequent failure of traditional single species fishery management practices (e.g. Myers et al. 1997, Pauly et al. 1998), to approach sustainability of the marine environment in a more holistic fashion (Dayton et al. 1995, Roberts 1997, Allison et al. 1998). The concept of marine reserves (the complete closure of an area of seabed to all forms of fishing or disturbance) was originally regarded as a tool for conservationists, but is now slowly gaining credence with fisheries biologists as a useful hedge against '... the limitations of science in comprehending and controlling... the marine environment' (Lauck et al. 1998).

The potential for marine reserves to act as both conservation and fishery management tools is often discussed (Roberts & Polunin 1991, Dugan & Davis 1993, Allison et al. 1998) but seldom substantiated by rigorously collected data (Roberts & Polunin 1991, Jones et al. 1993, Edgar & Barrett 1997). The enumeration of commercially and recreationally exploited fish species (which are those most expected to benefit from reserve protection) has been problematic in many cases. Difficulties in effectively demonstrating reserve effects and predicting outcomes of reserve implementation have been attributable to 3 factors: inadequate sampling methodology, inadequate survey design, and failure to obtain a suitable time series of data (both before and after reserve closure) using consistent methods.

Survey design problems have generally been caused by deficiencies in both spatial and temporal replica-

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tion (Jones et al. 1993, Edgar & Barrett 1997). Spatial patchiness in fish distribution means that the study of a limited number of sites inside and outside a reserve may not necessarily reflect changes in density across the entire area. Within-reserve variability can then cause high variances which confound formal comparisons of reserve effects (e.g. Cole et al. 1990 for the sparid snapper *Pagrus auratus*). Additionally, many studies lack data collected prior to reserve closure (Roberts & Polunin 1991, Jones et al. 1993, Edgar & Barrett 1997), meaning that natural site-related and temporal variations in density cannot be easily differentiated from a 'reserve effect'. This problem is not always easily remedied because reserve establishment is a political process, and funding agencies may be reluctant to fund surveys of proposed reserve areas until conferment of reserve status is certain. This usually results in little time being available for 'before' surveys.

Before concerns regarding sampling design can be addressed, it should be ensured that the sampling methodology is effective and unbiased. Most attempts to enumerate fish in marine reserves have used underwater visual census (UVC) methods (e.g. Cole et al. 1990, Russ & Alcala 1996a,b, Edgar & Barrett 1997). While UVC provides useful data for some groups of fish (e.g. *Sebastes* spp. [Paddack & Estes in press] or *Cheilodactylus* spp. [Leum & Choat 1980, McCormick 1989]), those exploited by commercial or recreational fishers tend to be behaviourally adaptable predatory species which may rapidly alter their response to divers (e.g. Chapman et al. 1974, Chapman & Atkinson 1986). This can cause severe bias in between-site comparisons based on diver surveys where fishing pressure is significant (Jennings & Polunin 1995, Kulbicki 1998). In marine reserves, positive, rather than negative changes in diver approachability tend to occur (Cole 1994). To counter the biases introduced by changes in fish behaviour, remote (surface-based) sampling methods such as experimental angling, potting or underwater video are needed. These can provide useful relative density data unobtainable by traditional methods in reef environments (Bennett & Attwood 1991, 1993, Rakitin & Kramer 1996, Millar & Willis 1999).

A variety of electronic media have been used for assessing relative fish density with varying success, including time-lapse still cameras for work in abyssal depths (e.g. Armstrong et al. 1992, Priede et al. 1994), stereo-photography for improving the accuracy of *in situ* size measurements (Klimley & Brown 1983, van Rooij & Videler 1996), and a variety of underwater television and video configurations for estimating fish density and behaviour (Alevizon & Brooks 1975, Michaloponlos et al. 1992, Posey & Ambrose 1994, Ellis & DeMartini 1995, Priede & Merrett 1996, Gledhill et al. 1996). Some of the latter were remotely deployed and some were diver operated, using various combinations of equipment configuration and deployment method. The quality of data provided by these studies was variable, with the effectiveness of particular techniques sometimes being equivocal.

Much of the previous work using remote underwater video cameras has been designed primarily to provide a means of visually enumerating fish in habitats or depths not accessible to divers (e.g. Ellis & DeMartini 1995, Priede & Merrett 1996, Gledhill et al. 1996). The present study aims to evaluate the use of remotely operated baited underwater video (BUV), to quantify local densities of predatory reef fish in shallow reef environments.

Biases in underwater surveys can vary between methods, as well as between species. These biases can be sufficiently strong to produce erroneous conclusions and/or inconsistencies across survey methods, therefore it is of vital importance that the survey method be chosen with this in mind. To illustrate this, we compare estimates of density and population size structure of snapper *Pagrus auratus* (Sparidae) and blue cod *Parapercis colias* (Pinguipedidae) obtained by BUV to UVC and rod-and-line angling data in and around a temperate marine reserve.

METHODS

Study area. The Cape Rodney-Okakari Point (CROP) Marine Reserve in the northwestern Hauraki Gulf (36°16'S, 174°48'E) is New Zealand's oldest marine reserve, having been gazetted in 1975 and fully established in 1977. No fishing, extractions, construction, or discharge are permitted in such a reserve. The 518 ha reserve has been a focus for subtidal ecological studies (Creese & Jeffs 1993), and the ecology of the subtidal reef has been described elsewhere (e.g. Ayling 1981, Choat & Schiel 1982, Choat & Ayling 1987).

For the current surveys, the reserve was divided into 6 areas of similar size, and compared with 4 fished areas (2 at either end of the reserve). The areas sampled were numbered sequentially from northwest to southeast, with Areas 1 and 2 being outside of the reserve in the northwest direction, Areas 3 through 8 in the reserve, and Areas 9 and 10 outside of the reserve in the southeast direction (Fig. 1). All relative density estimates were made by survey area. Sampling by all methods was restricted to daylight hours (08:00 to 16:00 h).

UVC. Three divers estimated densities of *Pagrus auratus* and *Parapercis colias* throughout the survey areas during September 1996 using 25 × 5 m strip tran-

sects (after McCormick & Choat 1987). Two or three sites were chosen haphazardly within each survey area (specific dive sites were influenced by weather conditions at the time of the survey). Three replicate transects were completed at each site, so that each survey area contained at least 6 transects. When weather limited diving activities, extra transects were completed at sheltered locations. Sampling was limited to depths <15 and >3 m, and to times when underwater visibility exceeded 5 m. In total, 83 transects were successfully completed.

At each site divers decided in which direction they would swim prior to the dive so that transects did not overlap. After attaching a fibreglass tape to a kelp plant, or weighting it with a rock, each diver swam 5 m before commencing counts to avoid censusing fish attracted by diver activity. The observer then swam 25 m, counting fish within a strip estimated 2.5 m either side of the centre of his path. Only snapper *Pagrus auratus* and blue cod *Parapercis colias* were included in the counts. Fish size was estimated in 50 mm size classes. Before the survey, the divers practiced size estimation using plastic fish models to avoid systematic bias. Mean densities are expressed in units of fish 125 m^{-2}.

Angling surveys. Sampling within a no-take marine reserve carries the proviso that disturbances be minimised. Hook-and-line angling as a sampling method presents a risk of incidental mortality occurring as a result of fish completely ingesting the hook (gut-hooking), and causing damage to the gills or viscera. To ensure sampling was as non-intrusive as possible, all survey angling was done using Mustad size-7 beak hooks modified by the addition of a 30 mm appendage of fine wire, attached to the shank and projecting obliquely opposite the barb. The appendage was designed to inhibit the passage of the hook past the lip area, ensuring that landed fish were minimally damaged. Comparative trials had indicated that modified hooks were less likely than normal hooks to allow snapper to become gut-hooked on hook-and-line rigs, without significantly reducing the catch rate (T.J.W. unpubl. data).

Area estimates of snapper and blue cod relative densities were made by conducting a series of angling surveys using boats crewed by volunteer anglers fishing simultaneously in the 10 sampling areas. The surveys were conducted on the 4 days of 15 June, 29 June, 7 December and 15 December, 1996. Fishing rig configuration was standardised so that all anglers used a single-hook Ochanneloe rig, consisting of a size-7 modified beak hook on a 50 cm trace tied to a swivel below a free-running 28 g lead-ball sinker. Bait was arrow squid *Notodarus sloanii* cut to approximately 2 × 5 cm. The anglers were supervised by an observer on each

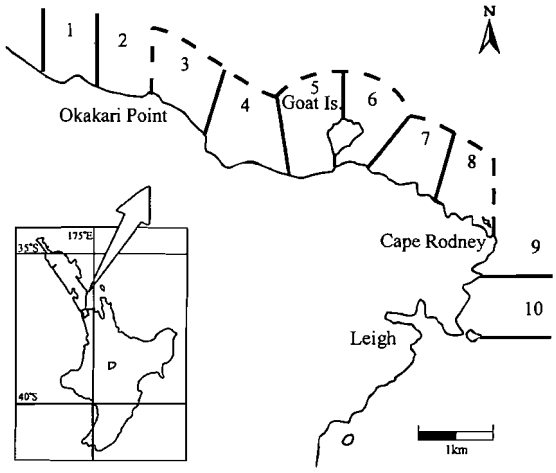

Fig. 1. Cape Rodney-Okakari Point marine reserve, showing the division of reserve (3 to 8) and non-reserve survey areas (1 to 2, 9 to 10). The inset shows the location of the reserve in the northeastern North Island of New Zealand

boat, who recorded bait soak time (the length of time for which each fisher had a baited hook in the water) and the species and size (± 1.0 mm fork length) of all fish caught. Each boat was assigned to fish in a specified area in the morning, and assigned to a different area in the afternoon. The skippers were instructed to choose sites 'haphazardly' within the assigned area, and to fish at that location for 30 min. This permitted a maximum of 6 sites within an area to be fished by a boat in any given morning or afternoon session. In total, 322 sites were fished during the course of the study.

Fish captured during the surveys were tagged using the visible implant fluorescent elastomer tagging system (Willis & Babcock 1998), and released immediately. Relative snapper density was expressed as fish h^{-1} of fishing effort.

BUV. Video data were obtained using a Q1 Corporation FV-100 black and white video camera, mounted at the apex of a pyramidal stand. The camera was pointed vertically downward toward the base of the stand, which formed a 1 m^2 quadrat with calibration marks placed at 5 cm intervals along the edges. A plastic bait holder (35 × 14 cm) was mounted in the centre of the base quadrat, which contained 4 whole pilchards *Sardinops neopilchardus*. The mantle of an arrow squid *Notodarus sloanii* was attached to the outside of the bait holder with cable ties. Sampling consisted of 30 min deployments made from an anchored boat. Deployment time of 30 min was used because previous trials indicated that maximum numbers of *Pagrus auratus* and *Parapercis colias* were usually detected by 25 and 15 min, respectively (T.J.W. unpubl. data). The camera was cabled to a Sony GV-S50E video monitor and 8 mm recorder on the support vessel, enabling the crew to ob-

serve the substratum during deployment to ensure the stand was stable upon reaching the bottom. Between 4 and 7 replicate deployments were made haphazardly throughout each of the 10 survey areas (Fig. 1), and a total of 54 deployments were successfully completed between 17 June and 7 August 1996.

Videotapes were played back on a VCR with a real-time counter, and the number of each species of fish present at the bait enumerated at 30 s intervals. Footage was continuously monitored to establish the maximum number of snapper (MAXsna) and the maximum number of blue cod (MAXcod) present at the bait during each 30 min sequence. Maxima were used as density measures because they provided the best estimate of 'true' density in earlier trials (T.J.W. & R.C.B. unpubl. data). Individual fish were measured by digitising video images using the Mocha® image analysis system, and obtaining a 3-point calibration (to compensate for wide-angle distortion) for each image using the marks visible on the base quadrat. Measurements were only made of those fish present within the quadrat when the count of the maximum number of fish of a given species in a sequence (e.g. MAXsna) was made. While this meant that some fish moving in and out of the field of view may not have been counted or measured, it also avoided repeated measurement of the same individuals.

Statistical analyses. The data are counts and hence do not satisfy the assumptions of normality and homogeneity of variance that are required by ANOVA. Such data are best modelled using the Poisson distribution, or more generally, as Poisson with possible overdispersion due to the fact that fish may not behave independently of each other.

In the angling and UVC surveys, overdispersion can also arise due to pseudoreplication (sensu Hurlbert 1984), that is, due to correlation between replicates that arises from the sampling design. For example, with the UVC method, the 3 transects taken at each site cannot be considered as truly independent replicates from the survey area because of between-site variability. Similarly, in the angling survey, each boat fished several sites successively in the same area and hence between-boat differences in fishing skill will cause counts at these sites to be correlated. Here, the overdispersion induced by the sampling design was explicitly accounted for in the analyses of the UVC and angling data by using a mixed-effects model.

A log-linear model was used to describe the expected counts and was fitted using maximum likelihood. This expresses the fish counts, Y, as

$$Y \sim Poisson(\lambda)$$

where $Poisson(\lambda)$ denotes a (possibly overdispersed) Poisson distribution with expected value of λ, and $\log(\lambda)$ is modelled as a linear function of the effects. For example, in the analysis of the video data the expected count of fish in replicate j in area i is modelled by

$$\log(\lambda_{ij}) = \alpha_i$$

The mixed effects analyses of the visual and angling data also use the log-linear formulation, but with the inclusion of random effects terms to model the pseudoreplication described above. These models add random coefficients to the right-hand side of the above equation. In the angling analysis it is necessary that inference is not conditional on the particular boats deployed, and hence boat was a random effect. This accounts for the component of overdispersion due to correlation of observations within each boat. A comprehensive explanation of this methodology can be found in Millar & Willis (1999). In the UVC analysis, site and diver were treated as random effects.

All analyses were conducted using SAS. The model for video data was fitted using the GENMOD procedure, while the more complicated analyses of the visual and angling data made use of the GLIMMIX macro (Littell et al. 1996). Both of these approaches allow for overdispersion in each observed count, that is, due to the lack of independence in the behaviour of individual fish.

Because juveniles may occur around inshore reef environments seasonally, regardless of reserve status (Kingett & Choat 1981, Francis 1995), *Pagrus auratus* was modelled using the entire dataset, and also using only fish > minimum legal size (MLS), which for this species is 270 mm fork length (FL).

The expected counts are not directly comparable across sampling methods. The UVC analysis estimates the number of fish expected in a 125 m^2 transect, whereas the angling analysis estimates the number of fish caught by an hour of standardised fishing effort, and the BUV analysis estimates the maximum number to be seen during a 30 min period of filming. Thus, for each method, the expected counts for each area can only be viewed as relative estimates of fish density.

The areas are all of similar size and hence the average of the expected counts in Areas 3 to 8 was used as a measure of the relative density of fish in the entire reserve. Similarly, averaging over the 4 non-reserve areas provided the relative density of the combined non-reserve area. The ratio of reserve to non-reserve relative density was calculated and a 95% confidence interval was computed using Fieller's method for computing confidence intervals for ratios (Seber 1977). This ratio is a dimensionless quantity that can be compared across the different methods.

Student's t-tests and ANOVA were used to test whether fish in fished areas were of the same expected size as fish in the reserve, and to test whether the 3

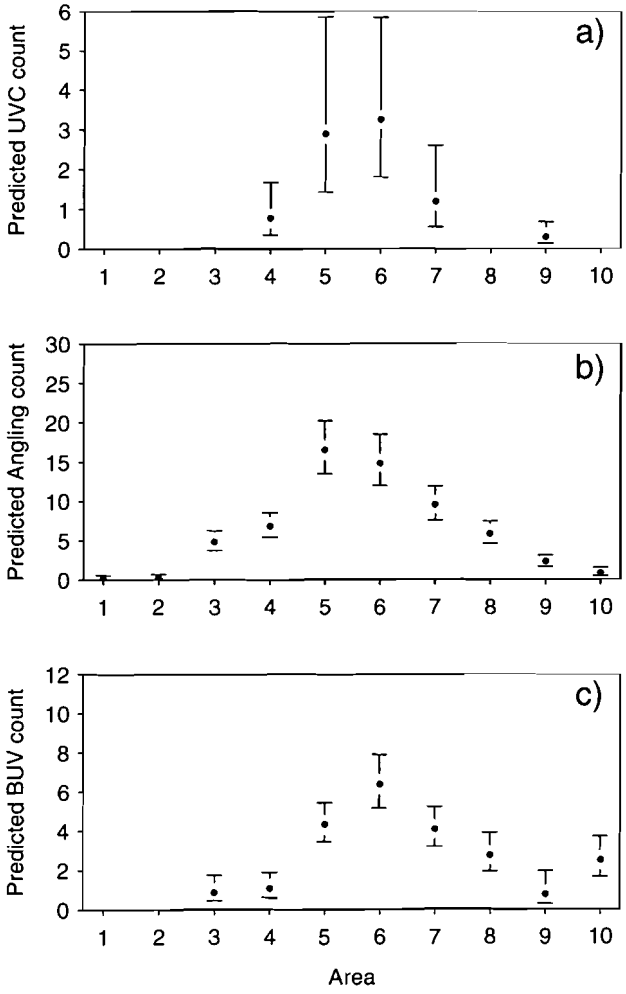

Fig. 2. Relative density of *Pagrus auratus* predicted by log-linear modelling in the 10 study areas (refer to Fig. 1) ±1 SE. (a) Underwater visual census (UVC) counts, expressed as fish 125 m^{-2}, (b) angling catch per unit effort (CPUE), expressed as fish h^{-1} fishing time, (c) baited underwater video (BUV) index, expressed as maximum fish 30 min^{-1} deployment. Error bars are of unequal length about the point estimate because the SE are calculated on the log scale, and hence are multiplicative on the arithmetic scale

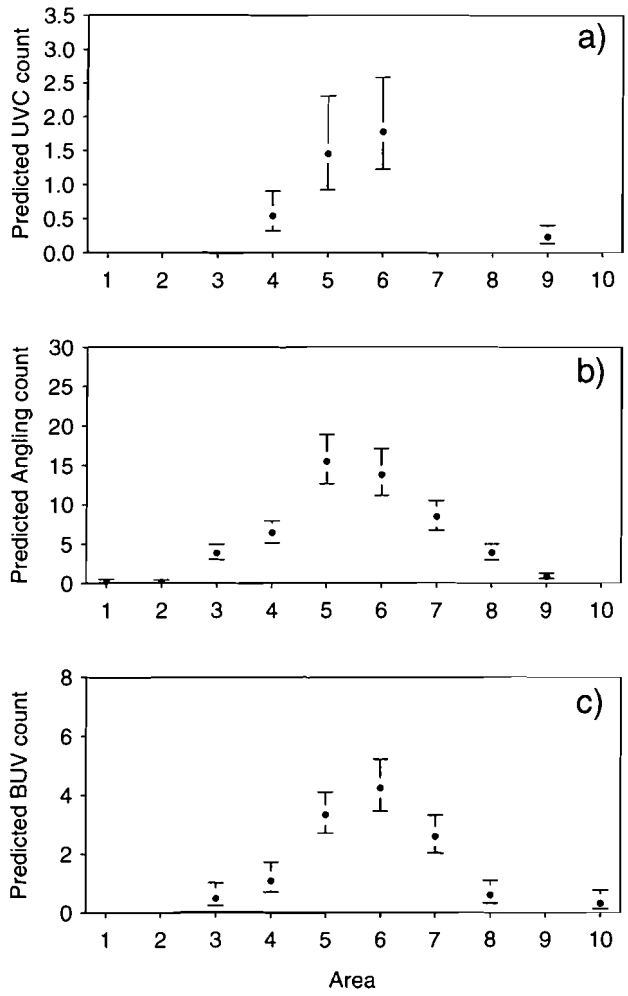

Fig. 3. Relative density of *Pagrus auratus* > minimum legal size (270 mm fork length) predicted by log-linear modelling in the 10 study areas ±1 SE. See Fig. 2 for explanation of *y*-axis units

methods produced consistent measurements of size. The length data were first natural-log transformed to attain approximate normality and variance homogeneity. Tukey's multiple comparison test was used whenever multiple hypotheses were simultaneously tested.

RESULTS

UVC survey

Density estimates of *Pagrus auratus* were highest at the reserve centre, and only 1 fish (in Area 9) was detected outside of Areas 4 to 7 (Fig. 2a). Transect means are certainly underestimates, particularly in Areas 5 and 6, where on the occasions when counts of just 2 or 3 fish were made there were usually more than 20 *P. auratus* following behind the diver (and hence not included in the count). Removal of sub-legal fish from the dataset reduced the estimates for Areas 4 to 6 by ~50%. The Area 7 estimate dropped to zero because all snapper seen there were assessed to be sub-legal size (Fig. 3a). Estimates of *Parapercis colias* density were similar between areas inside the reserve, but variable and generally lower in fished areas (Fig. 4a). In all cases, the ratio of reserve to non-reserve density had a 95% confidence interval with lower bound in excess of unity (Table 1), thereby establishing that density was higher in the reserve than in the fished areas ($p < 0.05$).

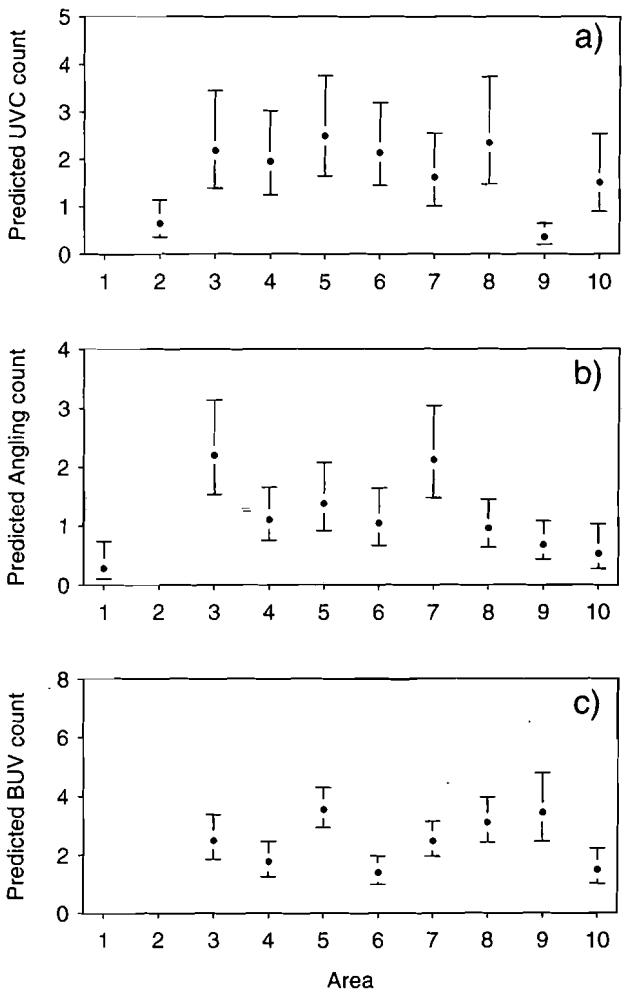

Fig. 4. Relative density of *Parapercis colias* predicted by log-linear modelling in the 10 study areas ±1 SE. See Fig. 2 for explanation of *y*-axis units

Comparison of *Pagrus auratus* size distributions between the reserve and fished areas was not possible because only 1 fish was seen outside the reserve. Of *P. auratus* seen within the reserve, 57% were >300 mm FL (Fig. 5). Large *Parapercis colias* (>300 mm) were found regularly within the reserve, but were practically absent in fished areas, and mean size differed significantly with protection status (t_{26} = 3.69, $p < 0.001$, Fig. 6).

Angling surveys

Catch per unit effort (CPUE) based estimates of *Pagrus auratus* density from angling surveys showed strong between-area variability within the reserve. The estimates of area means were highest at the reserve centre, and declined toward the boundaries at either end (Fig. 2b). Removal of sub-legal fish reduced the area estimates slightly, but made little difference to relative comparisons (Fig. 3b). There was no significant effect of season (June vs December) on catch rates (t_{130} = 0.54, p = 0.588). Although there was considerable variation in modelled mean catch rates between sampling days (up to 43%), this was not statistically significant because of high standard errors caused by catch variability within sampling areas. Angling estimates of *Parapercis colias* density were variable between areas (Fig. 4b), but all reserve estimates were higher than non-reserve estimates. In all 3 cases, density was significantly higher ($p < 0.05$) in the reserve than outside (Table 1).

Pagrus auratus caught inside the marine reserve were significantly larger than those from fished areas (t_{934} = 7.43, $p < 0.0001$, Fig. 5), as were *Parapercis colias* (t_{134} = 2.32, $p < 0.05$, Fig. 6). The differences in

Table 1. Log-linear model estimates of fish density. Reserve and non-reserve mean (standard deviation) *Pagrus auratus* and *Parapercis colias* relative density, and the magnitude of the difference (expressed as a ratio) with 95% confidence interval bounds. Legal *P. auratus* are those >270 mm fork length. The units of relative density are fish 125 m^{-2}, fish h^{-1} fishing effort, and maximum number of fish deployment^{-1}, for underwater visual census (UVC), angling and baited underwater video (BUV) respectively

	Reserve mean (SD)	Non-reserve mean (SD)	Reserve:non-reserve ratio	Lower 95% CI for ratio	Upper 95% CI for ratio
All *P. auratus*					
UVC	1.35 (0.24)	0.07 (0.03)	19.4	2.18	>200
Angling	9.73 (1.00)	0.87 (0.21)	11.1	7.02	23.20
BUV	3.16 (0.41)	0.77 (0.35)	4.1	2.04	35.50
Legal *P. auratus*					
UVC	0.63 (0.16)	0.07 (0.05)	9.1	1.95	>200
Angling	8.63 (0.91)	0.25 (0.09)	34.6	18.55	174.60
BUV	1.96 (0.27)	0.05 (0.07)	39.2	9.70	>200
P. colias					
UVC	2.12 (0.62)	0.62 (0.20)	3.4	1.55	25.29
Angling	1.47 (0.20)	0.37 (0.11)	3.9	2.03	14.11
BUV	2.36 (0.27)	1.18 (0.33)	2.0	1.20	4.47

mean size were estimated to be 102.6 ± 26.9 mm (95% CI) and 39.6 ± 35.0 mm (95% CI) respectively. There was no significant difference for either species ($p > 0.4$ in both cases) between mean size with season (Table 2) and no significant interaction between reserve status and season ($p > 0.8$).

BUV survey

Density of *Pagrus auratus* measured by the MAXsna and MAXcod indices varied markedly between areas (Fig. 2c). No snapper were detected in the non-reserve areas west of the reserve (Areas 1 and 2), while reserve mean densities (Areas 3 to 8) were approximately bell shaped about a peak at Area 6. Area 10 was the only non-reserve area to exhibit densities comparable with reserve areas, which was due to the presence of schooling juvenile snapper in the samples. This is illustrated by comparison with the estimates of legal-sized fish (Fig. 3c). The reserve had a higher density ($p < 0.05$) of snapper than the fished areas (Table 1).

Blue cod also appeared to be absent from Areas 1 and 2 (Fig. 4c), but were present in variable but similar densities throughout the rest of the sampled area regardless of reserve status. There is possible bias in these blue cod density estimates at areas within the reserve due to interspecific interactions with snapper, which were frequently observed to behave agonistically towards cod around the bait. In the presence of large snapper (i.e. in the reserve), densities of blue cod may therefore be slightly underestimated. Density of blue cod was higher ($p < 0.05$) in the reserve than outside (Table 1).

Large *Pagrus auratus* found within the reserve were absent from non-reserve areas (Fig. 5). The mean size of measurable reserve snapper was 351.9 mm (±21.2 SE), which was significantly higher ($t_{21} = 8.43$, $p < 0.001$) than the non-reserve mean of 197.6 mm (±13.6 SE). Thirty-two *P. auratus* (mostly from the reserve)

Table 2. Fish size comparisons based on angling data. Sample size, mean length and standard deviation of *Pagrus auratus* and *Parapercis colias* size by season, inside and outside the Cape Rodney-Okakari Point Marine Reserve

Sample	*P. auratus* n	Fork length (mm)	SD	*P. colias* n	Total length (mm)	SD
Reserve						
Jun	489	356.6	95.1	53	340.7	78.0
Dec	409	364.3	93.5	69	322.7	61.8
Non-reserve						
Jun	26	253.0	54.7	9	296.1	40.8
Dec	21	262.1	65.7	7	284.3	29.0

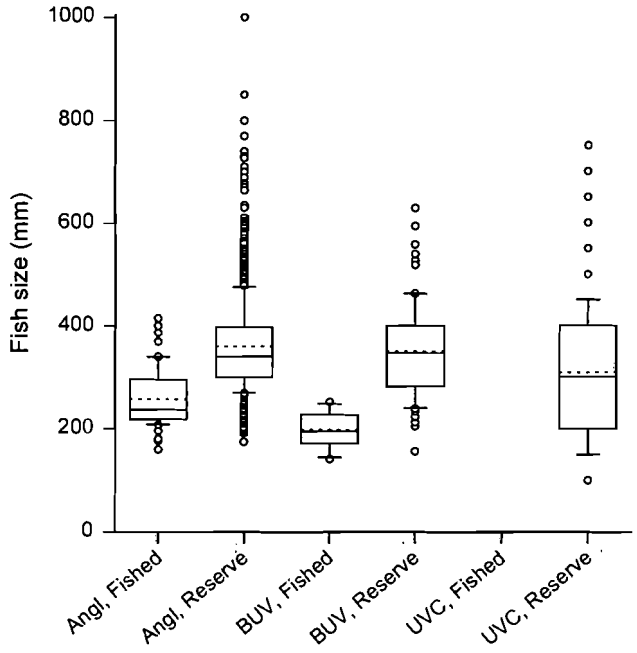

Fig. 5. Box-plots comparing the size distribution of *Pagrus auratus* in the CROP marine reserve and adacent fished areas, as measured by angling, baited underwater video (BUV) and underwater visual census (UVC). Solid and dashed horizontal lines are medians and means, respectively. Upper and lower box limits are 25th and 75th percentiles, and error bars represent the 10th and 90th percentiles. Data points outside the 10th and 90th percentiles are plotted individually

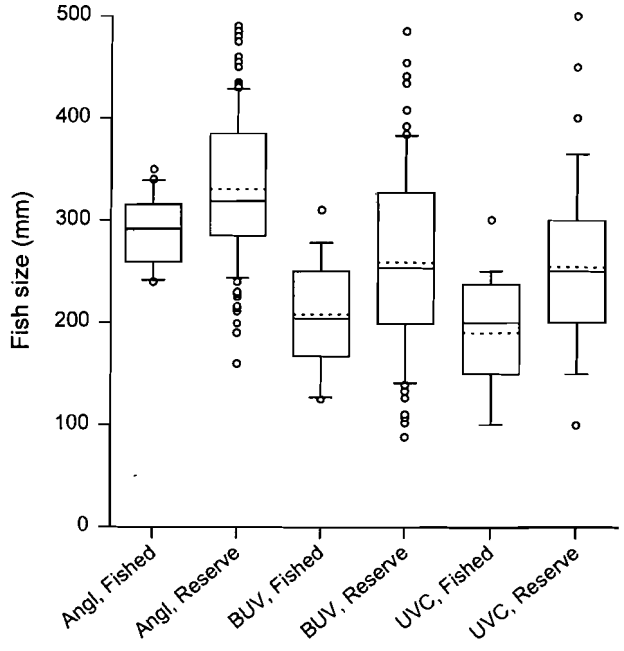

Fig. 6. Box-plots comparing the size distribution of *Parapercis colias* in the CROP marine reserve and adacent fished areas, as measured by angling, BUV and UVC. See Fig. 5 for explanation of percentile bounds

Table 3. Comparison of fish size estimates using different methods. Pairwise Tukey's studentised range comparisons of mean *Pagrus auratus* and *Parapercis colias* size (fork length and total length, respectively) obtained by underwater visual census (UVC), baited underwater video (BUV), and angling within the CROP marine reserve. ns = not significant, *p < 0.05; **p < 0.01; ***p < 0.001

Method comparison	Difference	95% CI	Significance
P. auratus			
UVC-angling	-57.87	23.19	***
UVC-BUV	-44.22	36.15	*
Angling-BUV	13.65	30.25	ns
P. colias			
UVC-angling	-80.51	23.95	***
UVC-BUV	-6.47	25.95	ns
Angling-BUV	74.04	24.56	***

were omitted from the analysis as they were not measurable, either because of problems with calibration or fish being obscured by kelp *Ecklonia radiata*. An additional unknown number of fish which may have been attracted to the bait were omitted as they were not in view during the measurement period.

The marine reserve supported larger *Parapercis colias* than fished reefs. Blue cod >300 mm were common inside the reserve, but practically absent from unprotected areas (Fig. 6). The mean size of the measured fish was 256.9 mm (±10.1 SE) and 200.5 mm (±13.4 SE) for reserve and non-reserve populations respectively. The reserve mean was significantly higher (t_{44} = 3.35, p < 0.001).

Comparison of methods for density and size estimates

Comparison of area-based relative density estimates of all *Pagrus auratus* (Fig. 2) and legally fishable *P. auratus* (Fig. 3) using the 3 survey methods indicated that the angling and BUV studies returned more precise (i.e. lower variability) estimates than UVC. Figs. 2 to 4 were scaled such that the mean estimate for the highest density area would have approximately the same height on the *y*-axis for each method. Thus, direct visual comparison of the error bars effectively compares the magnitude of the standard error relative to the mean.

The SEs depend critically on the amount of sampling effort expended on each methodology because confidence increases as sample size increases. It is particularly notable that the BUV method gave the lowest SEs on the *Pagrus auratus* estimates despite having the smallest sample size—54 video sites, compared to 83 UVC transects and 322 angling sites.

The high error estimates associated with the UVC method and its failure to detect fish in some areas (where angling and BUV had shown them to be present) suggest that the results of UVC are likely to be less reliable than remote-sampling methods for this species. The estimated UVC ratio of overall reserve: non-reserve density for legal-sized *Pagrus auratus* was considerably lower than those generated by BUV and angling (Table 1), whereas it was higher for all *P. auratus*. This is due to the ratios being extremely unreliable, with 95% confidence intervals with a lower bound of approximately 2 and an upper bound in excess of 200. These wide CIs arise because only 1 snapper was counted outside the reserve during the entire UVC study (and it happened to be of legal size).

Estimates of *Parapercis colias* density obtained by UVC had slightly higher modelled SEs (relative to the mean) than BUV or angling (Fig. 4). Reserve means for UVC and BUV were similar, but BUV gave the lowest reserve: non-reserve ratio (Table 1) because proportionally more *P. colias* were detected in fished areas.

ANOVA tests comparing *Pagrus auratus* size estimates between sampling methods (using data from Areas 4 to 7, where sample sizes were >10 in all cells) produced significant results for area ($F_{3,916}$ = 9.72, p < 0.0001), method ($F_{2,916}$ = 25.32, p < 0.0001), and the area × method interaction ($F_{6,916}$ = 3.51, p < 0.002) using Type III SS. Pairwise multiple comparison tests (Tukey's) showed that significant ANOVA results were due to generally lower mean size estimates made from UVC data (Table 3), and that the significant area × method interaction was caused by low UVC estimates in Area 7. *Pagrus auratus* size estimates from angling and video data were not significantly different.

Size comparisons of *Parapercis colias* from the 3 methods used data from Areas 3 to 10. There were significant differences between areas ($F_{7,341}$ = 3.27, p < 0.002) and the 3 sampling methods ($F_{2,341}$ = 28.97, p < 0.0001), but no significant interaction between them ($F_{14,341}$ = 0.98, p = 0.4706). Mean *P. colias* size from angling was consistently higher than area estimates obtained from either video or visual methods (Table 3), which was likely to be due to hook selectivity against smaller fish commonly detected by the non-intrusive methods.

DISCUSSION

Comparison of methods

The objective of this study was to compare data obtained from baited underwater video, a non-intrusive, non-extractive method of assessing predatory reef fish density, with density estimates familiar to both

fishers (angling) and ecologists (UVC). Most workers utilise SCUBA-based transect or point-count methods for estimating between-site differences in fish density, but documented site-related changes in fish behaviour (Cole 1994) and the failure to establish the statistical significance of increases in density of snapper within a marine reserve of long standing (Cole et al. 1990) caused such surveys to be viewed as equivocal. In tropical environments, the relative density of large predatory fishes has been shown to provide a useful measure of the effectiveness of protection from fishing (Alcala & Russ 1990, Polunin & Roberts 1993, Russ & Alcala 1996b), and indeed those species targetted by fishers would be most expected to become more abundant in protected areas. In temperate regions, relatively high turbidity coupled with variability in fish behaviour make extensive dive surveys less effective. If unbiased relative density estimates of targeted species inside and outside marine reserves can be obtained, the data may be used to test the efficacy of various theoretical models generated for predicting reserve recolonisation rates and the likelihood of supplementing local fisheries (e.g. Polachek 1990, DeMartini 1993, Attwood & Bennett 1995, Lauck et al. 1998).

Without a complete census of the study area, there is no absolute baseline against which differing sampling methods can be compared. The approach taken here was to survey the same areas using different methods, and critically compare the results in the light of existing knowledge of the biology of the species examined. Baited remote video appeared to be a useful method for simultaneously assessing relative density of both snapper and blue cod. The method does not rely on fish being caught, they must only appear within the field of view to be counted and measured. This avoids many of the problems associated with variable catchability (Arreguín-Sánchez 1996) and size selectivity (Millar & Fryer 1999) inherent in capture techniques. There is undoubtedly an upper limit to the number of fish that can simultaneously occur in the BUV field of view, which would cause underestimates of abundance to be made at high density sites. This may be problematic when attempting to detect differences between areas of high fish abundance, but is likely to make comparison of marine reserve versus fished areas conservative.

While angling methods gave similar results to BUV for snapper density, interspecific competition for hooks may have depressed angling-based estimates of blue cod density where snapper were common. It also appeared that small blue cod were under-sampled by angling. Conversely, while UVC appeared to provide good estimates of blue cod mean size (assuming diver error was negligible) and density, it was the least effective method for obtaining reliable snapper relative density data, due to the extreme between-site variability in responses of some fish species of fish to divers. With the exception of just 1 snapper in Area 9, snapper were detected by divers only in reserve areas where fish are known to exhibit diver-positive behaviour (Cole 1994). Both angling and BUV showed that snapper were present in all of the fished areas, albeit in lower densities.

The actual numbers of both *Pagrus auratus* and *Parapercis colias* detected by BUV were higher than those counted using UVC, and while behavioural bias certainly plays a part in this difference, the area sampled differs between the methods. A single UVC transect covered only 125 m^{-2}, whereas a single video deployment would have attracted fish from 314 m^{-2} if the radius of bait attraction was only 10 m. In reality, the dispersion of bait odour from a point source will be influenced by prevailing rates of advection and turbulent diffusion (Sainte-Marie & Hargrave 1987), and may cover much larger areas. The higher estimates resulting from larger samples generally result in more powerful between-site comparisons using BUV.

Non-baited cameras are perhaps less intrusive than baited systems (in that they may not actively affect fish behaviour), but, given the sparse nature of the data obtained (Posey & Ambrose 1994), require much greater field time and more expensive equipment in order to have any chance of providing statistically testable results. The system employed here uses relatively short deployments which, when suitably distributed, can supply spatially and temporally independent replicate samples. It may eventually be possible to model the radius of attraction of the bait plume (Sainte-Marie & Hargrave 1987, Priede & Merrett 1996) which, when combined with knowledge of fish reactions to bait and their swimming speeds, will allow more direct density estimates as well as between-site relative density comparisons.

Angling had 3 main advantages over video surveys: provision of accurate (±1.0 mm) size data, no post-survey laboratory analysis, and low likelihood of time-related bias because all areas were surveyed simultaneously. Capture methods also provide the opportunity to tag or weigh specimens, assess fish condition, or obtain other morphometric measurements. Video surveys required a large commitment of field time (40 to 60 min per replicate), a large amount of post-survey laboratory time (average 60 min per replicate, depending on fish density), and high capital outlay for underwater camera and recording equipment and spatial analysis software. On the other hand, video surveys were logistically much simpler to organise, require only 2 personnel, and fewer 'man-hours' in the field (our angling survey involved the coordination of more than 80 anglers and boat supervisors, and training the latter).

This study illustrates how the degree of statistical inference available from field data can be affected by the sampling method used. It should be apparent from pre-survey observations (as well as *a priori* assumptions about fishing impacts) which species are likely to be affected by fishing activities (and hence by marine reserve protection) in a particular region. Furthermore, fish surveyors and ecologists are often exhorted to use standardised methodology for all species (Sale 1980) so as to obtain data which provide 'unbiased' comparative estimates of relative density. Rather, variability in the behaviour and habitat requirements of species means that survey methodology must be tailored to the individual species of interest (Connell et al. 1998).

Lincoln Smith (1989) recognised the difficulties associated with attempting to conduct multi-species fish counts using visual survey methods, and highlighted the fact that some species were easier to count accurately than others. A species-by-species approach to methodology increases the amount of time workers must spend in the field, and therefore increases survey costs, but it is likely to reduce the incidence of inconclusive results often blamed on lack of statistical power which may really be primarily due to inappropriate sampling methods (Andrew & Mapstone 1987). Marine reserve surveys can become even more complex where reserve protection, for whatever reason, causes resident fish to be behaviourally distinct from those in fished areas (Cole 1994). Detection of a reserve effect then requires behavioural differences to be accounted for in the survey method chosen.

Marine reserve effects

Because of the absence of data collected using identical methods prior to reserve establishment, the density patterns revealed during these surveys cannot be, strictly speaking, attributed directly to marine reserve establishment. However, while it is possible that observed elevations in density of *Pagrus auratus* toward the reserve centre might be due to intrinsic differences in habitat quality, the sheer magnitude of change makes it difficult to accept this explanation. Similar extensive shallow patch reef areas are found within the fished areas sampled (particularly Area 10), but these contain only a fraction of the snapper density found in the vicinity of Goat Island. Variation within the reserve is not explained by differences in substratum type, as similar habitats are found throughout (Ayling 1978). Declining densities towards the reserve boundaries by a relatively mobile species are more likely to be manifestation of an 'edge effect' (Rakitin & Kramer 1996, Woodroffe & Ginsberg 1998), as home ranges of resident *P. auratus* may extend to several hundred metres (Berquist 1994), and fishing pressure at the reserve edges is intense (author's pers obs.). It is likely that such sustained pressure may prevent the build-up of resident populations near to reserve margins. This observation indicates that where fishing pressure is high, its effects may encroach inside a reserve, and supports the model of Kramer & Chapman (1999, their Fig. 2), which indicates increasing exposure to fishing mortality nearer to boundaries. This implies that the effectiveness of marine reserves in maintaining populations of target species is dependent upon establishing reserves of sufficient size to encompass the natural home range of those species (Attwood & Bennett 1994, Holland et al. 1996, Woodroffe & Ginsberg 1998, Zeller & Russ 1998). Thus, to optimise reserve design, detailed knowledge of short- and long-term movements of target species will be required.

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