

LETTER

Using marine reserves to estimate fishing mortality

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Abstract

The proportion of a fish stock that is killed by fishing activity is often calculated as the catch divided by the estimated stock biomass. However, stock biomass is notoriously difficult to estimate reliably, and moreover, the catch may be uncertain or misreported and does not include losses due to discarding. In all too many fisheries, these difficulties have led to underestimates of total fishing mortality and the commercial demise of the fishery. No-take marine reserves eliminate fishing mortality from within their boundaries and, for species that exhibit seasonal migratory behaviour, comparison of reserves with fished areas can provide direct estimates of the proportion killed by fishing. For an important exploited species in New Zealand, seasonal changes in density of sub-legal fish at three marine reserves were similar in both reserve and adjacent non-reserve areas. However, this result did not hold for legal-size fish, and the difference in seasonal change between reserved and non-reserved areas was used to obtain direct estimates of the total localized fishing mortality in the non-reserve area over 6-month periods. Estimates of the percentage of legal-size fish killed by fishing ranged from 70 to 96%. These results demonstrate an unanticipated practical benefit from marine reserves that goes beyond their ecological role.

Keywords

Fishing mortality, marine reserves, migration, New Zealand, snapper, *Pagrus auratus*.

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INTRODUCTION

While debate continues over the ability of appropriately designed no-take marine reserves to help rebuild depleted fisheries (Hastings & Botsford 1999; Roberts *et al.* 2001; Hilborn 2002; Pauly *et al.* 2002; Polunin 2002; Gell & Roberts 2003; Hilborn *et al.* 2004), a lack of empirical data currently limits the ability of fishery managers to make decisions about their efficacy for this purpose (Russ 2002; Willis *et al.* 2003b). Most of the research emphasis on the effectiveness of marine reserves with regard to fishery management has been on this potential role for enhancing or maintaining exploited populations, with relatively little attention given to the more immediate and tangible benefits arising from the availability of unfished areas with which to assess fishing effects (Macpherson *et al.* 2000; Schroeter *et al.* 2001; Jennings & Blanchard 2004). Since no fishing of any kind is permitted in no-take marine reserves, opportunities arise to test the efficacy of some of the assumptions upon which fishery assessment models depend so heavily (Schnute & Richards 2001).

Typically, estimates of the fishing mortality of exploited fishes are indirectly obtained from various complex models

fitted to lengthy time-series of fisheries data (Shepherd & Pope 2002). If the fishery is of high economic value then the fisheries data will often be supplemented by data from research surveys. These models are highly sensitive to many required assumptions. Unfortunately, the assumptions cannot always be validated by the available data. For example, the devastating collapse and subsequent closure of the Grand Banks cod fishery has been attributed to the assumption that the oldest age-classes were less vulnerable to the trawl gear. In fact, those older fish were simply not there in any great number because the vast majority of them had already been caught (Myers & Cadigan 1995). Another difficulty faced by fisheries models is that total fishing mortality is composed of several components: landed catch, discards, incidental mortality, illegal catch and misreported catch, which occur within both commercial and recreational or artisanal fisheries. Of these, only landed catch is relatively simple to measure, and the others are usually estimated with varying accuracy (Chopin *et al.* 1996).

In contrast, here we are able to obtain direct estimates of localized total fishing mortality. Note that this is not the instantaneous fishing mortality (F) as used in yield-per-recruit models, but rather the proportion of fish killed by

fishing activity over a given period. This is done by comparing the seasonal arrival rate of migratory snapper [*Pagrus auratus* (Bloch & Schneider 1801): Sparidae] within three marine reserves with that of adjacent fished areas.

MATERIALS AND METHODS

Relative density of snapper on inshore reefs can be reliably measured by the use of baited underwater video (BUV) (Willis & Babcock 2000; Willis *et al.* 2000). BUV measurements of relative snapper density were taken inside and outside the Cape Rodney–Okakari Point (CROP) Marine Reserve, Te Whanganui a Hei (Hahei) Marine Reserve, and Tawharanui Marine Park (see Willis *et al.* 2003a for background information). At the first two reserves, sampling was done at 6-monthly intervals between November 1997 and May 2002, with the exception of November 1999. At Tawharanui only four surveys were done, between 1997 and 1999. On each sampling occasion, a minimum of 12 BUV measurements were taken in each of the reserve and adjacent non-reserve areas.

Snapper outside of marine reserves are subject to both commercial and considerable recreational fishing effort, particularly over the summer months from December to March when fish migrate inshore (Crossland 1976; Willis *et al.* 2003a). Elevated densities of snapper within marine reserves occur because some migratory fish become seasonally resident on inshore reefs, and establish relatively small home ranges (Willis *et al.* 2001; Parsons *et al.* 2003). If it is assumed that all snapper present inside the reserve in austral spring (October/November) are year-round residents, the difference between the reserve densities in spring and the following autumn provides an estimate of the arrival rate of seasonally resident snapper to the reserve. These rates were applied to the adjacent non-reserve area to give an expected snapper density after onshore migration. The proportion of non-reserve snapper killed by fishing activity between the spring and autumn surveys was then estimated from their observed spring density (with an allowance for natural mortality), arrival rate and autumn density.

Let $\lambda_{\text{spring}}^R$ and $\lambda_{\text{spring}}^{NR}$ be the relative density of snapper in the reserve and non-reserve areas, respectively, in spring (October/November). Assuming that instantaneous natural mortality (m) is the sole source of snapper mortality within the reserve, the proportion of snapper within the reserve that survive the 6 month period between austral spring and the following austral autumn is given by $e^{-m/2}$. The relative density of snapper in the reserve in autumn can, therefore, be written as

$$\lambda_{\text{autumn}}^R = e^{-m/2}\lambda_{\text{spring}}^R + \lambda_{\text{arrival}} \quad (1)$$

where λ_{arrival} is the relative density of snapper arriving in the reserve and surviving through to austral autumn. Assuming

equal arrival rate of snapper outside the reserve as within, the relative density of snapper outside the reserve in autumn is given by the analogous equation, multiplied by the proportion that survive fishing:

$$\lambda_{\text{autumn}}^{NR} = s \left(e^{-m/2}\lambda_{\text{spring}}^{NR} + \lambda_{\text{arrival}} \right) \quad (2)$$

Rearranging eqn 1 for the relative density of fish arriving gives:

$$\lambda_{\text{arrival}} = \lambda_{\text{autumn}}^R - e^{-m/2}\lambda_{\text{spring}}^R \quad (3)$$

Rearranging eqn 2 gives:

$$s = \frac{\lambda_{\text{autumn}}^{NR}}{e^{-m/2}\lambda_{\text{spring}}^{NR} + \lambda_{\text{arrival}}}$$

and substituting eqn 3 gives:

$$s = \frac{\lambda_{\text{autumn}}^{NR}}{\lambda_{\text{autumn}}^R - e^{-m/2}(\lambda_{\text{spring}}^R - \lambda_{\text{spring}}^{NR})} \quad (4)$$

Replacing the λ values in eqn 4 by the mean observed BUV count, $\hat{\lambda}$, gives the estimate of s :

$$\hat{s} = \frac{\hat{\lambda}_{\text{autumn}}^{NR}}{\hat{\lambda}_{\text{autumn}}^R - e^{-m/2}(\hat{\lambda}_{\text{spring}}^R - \hat{\lambda}_{\text{spring}}^{NR})}$$

Confidence intervals for s were calculated on the log scale. Note that

$$\begin{aligned} \log(\hat{s}) &= \log\left(\frac{\hat{\lambda}_{\text{autumn}}^{NR}}{\hat{\lambda}_{\text{autumn}}^R - e^{-m/2}(\hat{\lambda}_{\text{spring}}^R - \hat{\lambda}_{\text{spring}}^{NR})}\right) \\ &= \log\left(\hat{\lambda}_{\text{autumn}}^{NR}\right) - \log\left(\hat{\Lambda}_{\text{autumn}}^{NR}\right), \end{aligned}$$

where $\hat{\Lambda}_{\text{autumn}}^{NR} = \hat{\lambda}_{\text{autumn}}^R - e^{-m/2}(\hat{\lambda}_{\text{spring}}^R - \hat{\lambda}_{\text{spring}}^{NR})$ denotes our estimate of the relative density of snapper that would be present in the non-reserve in May if no fishing activity took place. Using the delta method (Azzalini 1996),

$$\text{Var}[\log(\hat{s})] \approx \frac{\text{Var}\left(\hat{\lambda}_{\text{autumn}}^{NR}\right)}{\left(\hat{\lambda}_{\text{autumn}}^{NR}\right)^2} + \frac{\text{Var}\left(\hat{\Lambda}_{\text{autumn}}^{NR}\right)}{\left(\hat{\Lambda}_{\text{autumn}}^{NR}\right)^2} \quad (5)$$

The sampling occasions can be considered independent, and so

$$\begin{aligned} \text{Var}\left(\hat{\Lambda}_{\text{autumn}}^{NR}\right) &= \text{Var}\left(\hat{\lambda}_{\text{autumn}}^R\right) \\ &\quad + e^{-m} \left[\text{Var}\left(\hat{\lambda}_{\text{spring}}^R\right) + \text{Var}\left(\hat{\lambda}_{\text{spring}}^{NR}\right) \right] \end{aligned} \quad (6)$$

The variance of $\log(\hat{s})$ was calculated using eqns 5 and 6, with the variances of the $\hat{\lambda}$ values estimated using their sample variance.

Under the above model, s is of course constrained to be between 0 and unity. However, the estimated survival, \hat{s} , can exceed unity due to statistical variability in the BUV data. This can be verified by a test of the hypothesis that $s = 1$. If not rejected then an unfeasibly large value of \hat{s} is not significantly different from unity.

RESULTS

The relative density of legal-sized (> 27 cm fork length) snapper was much higher inside the three reserves than outside (Willis *et al.* 2003a), and exhibited marked and consistent seasonality (Figs 1a,c,e). Sublegal sized snapper density did not differ markedly inside and outside the reserve, and density changes in time were similar in both fished and unfished areas (Figs 1b,d,f). Our estimates of survival rate (\hat{s})

assumed a natural mortality value of $m = 0.075$, currently used in stock assessments of snapper in New Zealand (Gilbert *et al.* 2000). Natural mortality was assumed to be the same both inside and outside the marine reserves. The percentage of snapper killed by fishing activity during the interval between surveys [denoted by $\hat{p} = (1 - \hat{s})100\%$] was estimated for both legal and sublegal snapper, with the latter expected to have near zero \hat{p} .

For legal-size snapper at CROP, values of \hat{s} varied from 0.20 over November 2000 to May 2001, to 0.09 over November 1998 to May 1999 (Table 1). The average \hat{p} over the 4 years was 85%, which is remarkable as most of the fishing effort in the surveyed area is non-commercial. For undersized fish, the hypothesis that $P = 0$ was not rejected (Wald test, P -value > 0.05) for any year. Similar results were obtained from Tawharanui (Table 1), with an overall

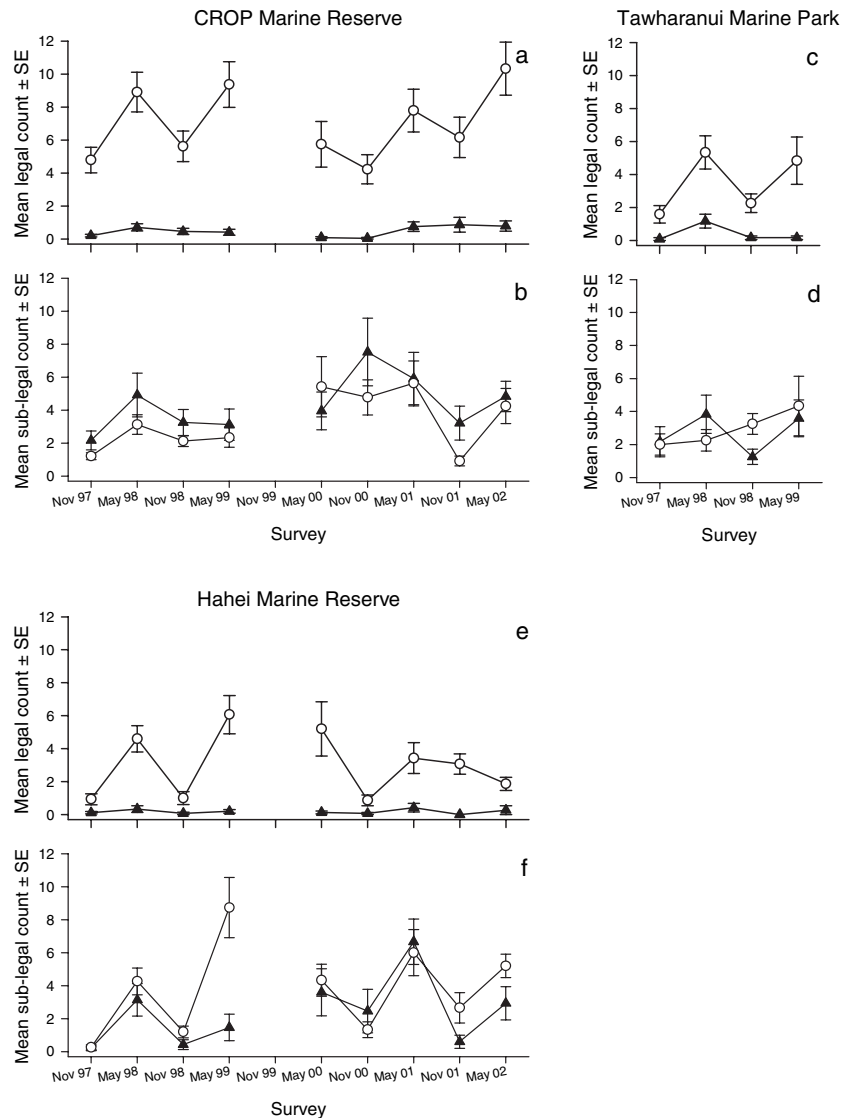


Figure 1 The effects of fishing mortality at CROP Marine Reserve, Tawharanui Marine Park, and Te Whanganui a Hei (Hahei) Marine Reserve. Relative density of *Pagrus auratus* inside (circles) and outside (triangles) the marine reserves for a, c, e fish subject to fishing mortality and b, d, f undersized fish not subject to fishing mortality.

Location	Year	Legal snapper [\hat{f} (95% CL)]	Sub-legal snapper [\hat{f} (95% CL)]
CROP	1997/1998	0.16 (0.07–0.38)	1.21 (0.63–2.36)
	1998/1999	0.09 (0.03–0.29)	0.91 (0.40–2.10)
	2000/2001	0.20 (0.07–0.60)	0.72 (0.32–1.60)
	2001/2002	0.15 (0.05–0.45)	0.75 (0.42–1.34)
Tawharanui	1997/1998	0.30 (0.12–0.75)	1.59 (0.49–5.17)
	1998/1999	0.06 (0.01–0.32)	1.49 (0.27–8.20)
Hahei	1997/1998	0.09 (0.02–0.31)	0.74 (0.36–1.54)
	1998/1999	0.04 (0.01–0.12)	0.18 (0.06–0.59)
	2000/2001	0.16 (0.04–0.65)	0.94 (0.48–1.85)
	2001/2002		0.91 (0.34–2.47)

Legal snapper are those > 27 cm fork length, and sub-legal snapper < 27 cm fork length.

average \hat{p} of 82%. The estimated survivorship of undersize fish at Tawharanui was greater than unity, but not significantly so (Wald test, P -value > 0.05).

Results from Hahei were generally similar to the two more northern reserves, except for two instances. Mortality of undersize (and therefore theoretically unfished) fish was estimated to be very high over the summer of 1998/1999 (Table 1). This was the result of very high densities of small snapper within the reserve in May 1999. Second, the seasonal arrival of legal snapper was not observed in 2001/2002 (Fig. 1e). That is, the arrival rate was estimated to be negative, and therefore it was not possible to estimate survivorship.

The average percentage of *P. auratus* killed by fishing activity in shallow coastal habitats of northern New Zealand between November and May was estimated to be $86 \pm 8\%$.

DISCUSSION

We estimated the seasonal (November to May) fishing-related mortality of *P. auratus* in coastal waters of northern New Zealand to be consistently greater than 70%, and as high as 96%. These are 'worst-case' estimates as the habitats surveyed are, by virtue of relative ease of access, the most intensively fished. However, they reflect the combined impact of the commercial and (relatively unregulated) recreational fisheries. The contribution of the latter to total fishing mortality is notoriously difficult to estimate, but our high mortality estimates are in line with the rapid recolonization of snapper after complete closure of the Poor Knights Islands Marine Reserve (Denny *et al.* 2004) which was previously open only to recreational fishers.

The assumptions associated with these estimates generally lead to conservative estimates of fishing mortality, that is, it is more likely that survivorship will be overestimated. If not all winter fish are resident, or poaching occurs within the reserves, then p will be higher than our estimate of 86%. Both of these assumptions may be violated. Some snapper that are 'resident' may in fact move over sufficiently large

Table 1 Estimates of snapper *Pagrus auratus* survival probabilities (\hat{f}) and 95% confidence limits in fished areas adjacent to three marine reserves, based on seasonal comparisons of fished and unfished densities

scales to be available to the fishery for part of the time (Egli & Babcock 2004). However, these would eventually be caught, so that the only truly non-migratory fish remaining in the reserve would have home ranges that do not cross the boundaries (e.g. Parsons *et al.* 2003). The degree of illegal fishing is unknown, although known to occur. It is possible that higher levels of poaching within the Hahei reserve during the summer of 2002 may explain the absence of the expected arrivals of legal-size fish. However, this and the unusual disparity between sublegal estimates in May 1999 might also be explained by sampling error, as the Hahei reserve had the lowest sampling effort per unit area of the three reserves. Higher sampling effort may negate the influence of chance patchiness in snapper distribution having large effects on the estimates.

Although we assume that natural mortality rates do not differ between protected and fished areas (Macpherson *et al.* 1997), our survivorship estimates are insensitive to uncertainty in natural mortality, and do not differ greatly if the expression is omitted from the model.

Our estimates depend on the assumption that the observed rate of onshore migration within a reserve reflects that occurring outside the reserve. However, if migratory snapper are concentrated within reserves, or migrant snapper survive the year and home to the same place, p will be overestimated. Concentration of migratory legal-size snapper in reserves is considered to be unlikely, since there is no such pattern occurring in undersized fish (Fig. 1), and numbers arriving onshore seasonally have been previously found not to differ between locations regardless of the original reserve density (Willis *et al.* 2003a). It is as yet unknown whether migratory snapper home back to the reefs where they were previously temporary residents.

Some sublegal snapper will grow to legal size over the November to May period. Our model does not explicitly consider this source of legal-sized snapper, however, it does so implicitly because these fish can be included amongst the arrivals. There are no systematic differences in the density of sublegal snapper between the reserve and non-reserve areas

(Fig. 1) and hence the rate at which sublegal snapper reach legal size will be similar in both.

The direct estimation of fishing mortality in this instance resulted from a serendipitous combination of biological circumstances. Such benefits are difficult to foretell and have thus never been included in models of the efficacy of marine reserves. More generally, using no-take marine reserves for establishing population parameters reduces the uncertainty associated with the 'shifting baseline' syndrome (Pauly 1995), and allows fishery biology to utilize fishery-independent controls for the first time (Schroeter *et al.* 2001). There are caveats, however. First, the efficacy of reserves for this purpose is limited primarily by their geographical extent, and the degree to which reserves represent the entire range of habitats occupied by an exploited species. Representativeness becomes even more important if reserves attract fishers to their boundaries, as comparisons of only adjacent areas with reserves will return inflated estimates of mortality. Approaches to designing reserve networks for conservation purposes (Mangel 2000; Sala *et al.* 2002) can be equally applied for fishery management purposes. Second, if density-dependent processes are brought into play by elevated densities of animals within reserves, parameters such as natural mortality and growth estimated in protected areas may not accurately reflect those of fished populations (Macpherson *et al.* 2000). Thus, reserves can augment our research toolbox in much the same way they may provide conservation benefits – without replacing existing methods (Allison *et al.* 1998).

Seasonal migrations are not uncommon in marine fishes around the world, particularly in temperate zones (e.g. Shimada & Kimura 1994; Hyndes *et al.* 1999; Hunter *et al.* 2003). We consider it likely that no-take marine reserves may be generally useful for estimating population parameters in other locales, and this method may be applicable elsewhere for species with similar seasonal migration patterns. Representative reserves will, however, be needed in offshore areas to provide unbiased estimates for entire stocks. Alternatively, if the distribution of fishing effort is known across the entire stock area, local estimates of p could be used to provide weighted estimates for regions lacking reserves. Our results show that in nearshore coastal environments, overall fishing-associated mortality may be considerably higher than previously thought.

Fisheries managers will likely be interested in annual mortality rates, rather than mortality over the period of a seasonal migration. The estimation of annual mortality rates can be made using information about the relative fishing effort expended within and outside the migration period. Specifically, the proportion of fish killed during the migration period can be converted into a rate of instantaneous fishing-related mortality (Quinn & Deriso 1999). This instantaneous mortality can be assumed proportional to

fishing effort, and hence the instantaneous mortality that occurred outside the period of study can be inferred from the relative efforts.

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REFERENCES

- Allison, G.W., Lubchenco, J. & Carr, M.H. (1998). Marine reserves are necessary but not sufficient for marine conservation. *Ecol. Appl.*, 8, S79–S92.
- Azzalini, A. (1996). *Statistical Inference Based on the Likelihood*. Chapman & Hall, London.
- Chopin, F., Inoue, Y. & Arimoto, T. (1996). Development of a catch mortality model. *Fish. Res.*, 25, 377–382.
- Crossland, J. (1976). Snapper tagging in north-east New Zealand, 1974: analysis of methods, return rates, and movements. *N. Z. J. Mar. Freshw. Res.*, 10, 675–686.
- Denny, C.M., Willis, T.J. & Babcock, R.C. (2004). Rapid recolonisation of snapper *Pagrus auratus*: Sparidae within an offshore island marine reserve after implementation of no-take status. *Mar. Ecol. Prog. Ser.*, 272, 183–190.
- Egli, D.P. & Babcock, R.C. (2004). Ultrasonic tracking reveals multiple behavioural modes of snapper (*Pagrus auratus*) in a temperate no-take marine reserve. *ICES J. Mar. Sci.*, 61, 1137–1143.
- Gell, F.R. & Roberts, C.M. (2003). Benefits beyond boundaries: the fishery effects of marine reserves. *Trends Ecol. Evol.*, 18, 448–455.
- Gilbert, D.J., McKenzie, J.R., Davies, N.M. & Field, K.D. (2000). Assessment of the SNA 1 stocks for the 1999–2000 fishing year. *N. Z. Fish. Assess. Rep.* 2000/38.
- Hastings, A. & Botsford, L.W. (1999). Equivalence in yield from marine reserves and traditional fisheries management. *Science*, 284, 1537–1538.
- Hilborn, R. (2002). Marine reserves and fisheries management. *Science*, 295, 1233–1234.
- Hilborn, R., Stokes, K., Maguire, J.-J., Smith, T., Botsford, L.W., Mangel, M. *et al.* (2004). When can marine reserves improve fisheries management? *Ocean Coast. Manage.*, 47, 197–205.
- Hunter, E., Metcalfe, J.D. & Reynolds, J.D. (2003). Migration route and spawning area fidelity by North Sea plaice. *Proc. R. Soc. Lond. B.*, 270, 2097–2103.
- Hyndes, G.A., Platell, M.E., Potter, I.C. & Lenanton, R.C.J. (1999). Does the composition of the demersal fish assemblages in temperate coastal waters change with depth and undergo consistent seasonal changes? *Mar. Biol.*, 134, 335–352.

- Jennings, S. & Blanchard, J.L. (2004). Fish abundance with no fishing: predictions based on macroecological theory. *J. Anim. Ecol.*, 73, 632–642.
- Macpherson, E., Biagi, F., Francour, P., García-Rubies, A., Harmelin, J., Harmelin-Vivien, M. *et al.* (1997). Mortality of juvenile fishes of the genus *Diplodus* in protected and unprotected areas in the western Mediterranean Sea. *Mar. Ecol. Prog. Ser.*, 160, 135–147.
- Macpherson, E., García-Rubies, A. & Gordo, A. (2000). Direct estimation of natural mortality rates for littoral marine fishes using populational data from a marine reserve. *Mar. Biol.*, 137, 1067–1076.
- Mangel, M. (2000). On the fraction of habitat allocated to marine reserves. *Ecol. Lett.*, 3, 15–22.
- Myers, R.A., Cadigan, N.G. (1995). Was an increase in natural mortality responsible for the collapse of northern cod? *Can. J. Fish. Aquat. Sci.*, 52, 1274–1285.
- Parsons, D.M., Babcock, R.C., Hankin, R.K.S., Willis, T.J., Aitken, J.P., O'Dor, R.K. *et al.* (2003). Snapper *Pagrus auratus* (Sparidae) home range dynamics: acoustic tagging studies in a marine reserve. *Mar. Ecol. Prog. Ser.*, 262, 253–265.
- Pauly, D. (1995). Anecdotes and the shifting baseline syndrome of fisheries. *Trends Ecol. Evol.*, 10, 430.
- Pauly, D., Christensen, V., Guénette, S., Pitcher, T.J., Sumaila, U.R., Walters, C.J. *et al.* (2002). Towards sustainability in world fisheries. *Nature*, 418, 689–695.
- Polunin, N.V.C. (2002). Marine protected areas, fish and fisheries. In: *Handbook of Fish and Fisheries, Vol. 2, Fisheries* (eds Hart, P.J.B. & Reynolds, J.D.). Blackwell Science, Oxford, pp. 293–318.
- Quinn, T.J. II & Deriso, R.B. (1999). *Quantitative Fish Dynamics*. Oxford University Press, New York.
- Roberts, C.M., Bohnsack, J.A., Gell, F., Hawkins, J.P. & Goodridge, R. (2001). Effects of marine reserves on adjacent fisheries. *Science*, 294, 1920–1923.
- Russ, G.R. (2002). Yet another review of marine reserves as reef fish management tools. In: *Coral Reef Fishes: Dynamics and Diversity in a Complex Ecosystem* (ed. Sale, P.F.). Academic Press, San Diego, pp. 421–443.
- Sala, E., Aborto-Oropeza, O., Paredes, G., Parra, I., Barrera, J.C. & Dayton, P.K. (2002). A general model for designing networks of marine reserves. *Science*, 298, 1991–1993.
- Schnute, J.T. & Richards, L.J. (2001). Use and abuse of fishery models. *Can. J. Fish. Aquat. Sci.*, 58, 10–17.
- Schroeter, S.C., Reed, D.C., Kushner, D.J., Estes, J.A. & Ono, D.S. (2001). The use of marine reserves in evaluating the dive fishery for the warty sea cucumber (*Parastichopus parvimensis*) in California, USA. *Can. J. Fish. Aquat. Sci.*, 58, 1773–1781.
- Shepherd, J.G. & Pope, J.G. (2002). Dynamic pool models I: interpreting the past using Virtual Population Analysis. In: *Handbook of Fish and Fisheries, Vol. 2, Fisheries* (eds Hart, P.J.B. & Reynolds, J.D.). Blackwell Science, Oxford, pp. 127–163.
- Shimada, A.M. & Kimura, D.K. (1994). Seasonal movements of Pacific cod, *Gadus macrocephalus*, in the eastern Bering Sea and adjacent waters based on tag-recapture data. *Fish. Bull. U.S.A.*, 92, 800–816.
- Willis, T.J. & Babcock, R.C. (2000). A baited underwater video system for the determination of relative density of carnivorous reef fish. *Mar. Freshwater Res.*, 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. *Mar. Ecol. Prog. Ser.*, 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. *N. Z. J. Mar. Freshwater Res.*, 35, 581–590.
- Willis, T.J., Millar, R.B. & Babcock, R.C. (2003a). Protection of exploited fishes in temperate regions: high density and biomass of snapper *Pagrus auratus* (Sparidae) in northern New Zealand marine reserves. *J. Appl. Ecol.*, 40, 214–227.
- Willis, T.J., Millar, R.B., Babcock, R.C. & Tolimieri, N. (2003b). Burdens of evidence and the benefits of marine reserves: putting Descartes before des horse? *Environ. Conserv.*, 30, 97–103.

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