

COMMENT

Burdens of evidence and the benefits of marine reserves: putting Descartes before des horse?

An extensive literature has appeared since 1990 on the study of ‘no-take’ marine reserves and their potential to make significant contributions to the conservation and management of fisheries, especially in tropical environments (see Polunin 1990; Roberts & Polunin 1991; DeMartini 1993; Roberts 1997; Allison *et al.* 1998; Guénette *et al.* 1998). The literature describes many potential benefits of marine reserves to fisheries, including increases in spawner-biomass-per-recruit and increases in larval supply from protecting ‘source’ populations (Jennings 2000). The important word here is ‘potential’. Some claims made by advocates of marine reserves might be regarded as optimistic, whereas critics of reserves might sometimes have been unduly harsh. Conservation goals for marine reserves are often poorly defined, and differences of opinion regarding the efficacy of reserves for fulfilling any of their stated goals can frequently be attributed to a lack of good information with which to predict their effects. Here, we critically examine the literature from 1990–2001 to determine (1) the relative effort put into empirical and theoretical approaches to predict reserve effects, and (2) the quality of empirical evidence available to support theoretical predictions. It is not the purpose of this article to single out particular studies for criticism (although this is sometimes inevitable to provide examples), nor to draw conclusions concerning the efficacy of marine reserves.

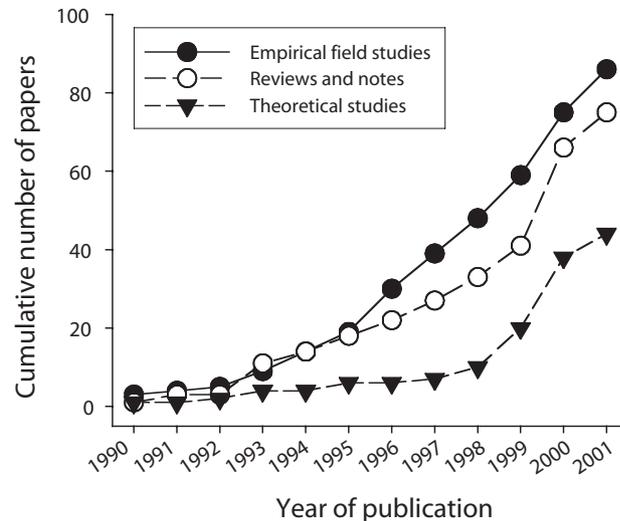
Our purpose is to examine the science, rather than politics, of the field of ‘marine reserves’. We examined the relevant peer-reviewed primary literature from 1990–2001 by searching the Current Contents and Science Citation Index (ISI) databases using the keywords ‘marine reserve’ found anywhere in a paper. Also included were papers that were not in the search databases but were cited in papers that were (these included refereed proceedings of symposia, but excluded book chapters and unpublished reports). Only studies that directly investigated the effects of reserves were included. Many articles that explored specific biological issues mentioned marine reserves incidentally in the discussion. These were removed from the analysis, as were those concerned solely with policy, management or advocacy. The remaining papers ($n = 205$) were classified into three groups, namely empirical (presenting field data from existing reserves), theoretical (conceptual or numerical modelling studies) and review (including notes and ideas papers based on other literature). With few exceptions, empirical papers reported some positive impact of the marine reserve or reserves under study, so these were carefully examined to determine (1) the robustness of the survey design, and (2) the effect size.

Approaches to reserve study: trends in the literature

We found that the number of empirical field studies has been climbing at a fairly consistent rate over the last ten years, but has recently been lagging behind the combined publication rate of reviews and theory (Fig. 1). Reading the latter papers, it is apparent that much of their *raison d'être* is advocacy for the establishment of marine reserves in parts of the world that lack them, rather than real attempts to contribute to the science of the field. The difference between science and advocacy in this field is becoming increasingly blurred (Polunin 2002), and we may soon be in the unusual situation of being faced with a greater number of reviews than there is reviewable material.

The amount of attention given to theoretical work has also increased markedly since 1997. Despite the increasing number of fisheries models that infer potential consequences of marine reserves (see Polacheck 1990; Dugan & Davis 1993; Rowley 1994; Allison *et al.* 1998; Bohnsack 1998), published evidence to empirically judge these models and their underlying assumptions is considerably rarer than might be expected. We regard science as a process for learning about nature in which competing ideas about how the world works are tested against systematic

Figure 1 Publications concerned with the effects of marine reserves in the primary literature, 1990–2001: comparison of the number of field and desktop studies



observations and experiments (Feynman 1985; Hilborn & Mangel 1997). Unfortunately, because of this dearth of data the models have little opportunity to compete against one another under the scientific process. Furthermore, the proliferation of models and reviews has resulted in model assumptions evolving into accepted paradigms, a case of ‘What everybody says must be true’ (Simpson 1993).

The speculative conclusion that marine reserves will be effective management tools can be obtained from simple behavioural and demographic assumptions. These include:

- (1) Where movement range of individuals is small relative to the size of the reserve, those individuals are spatially isolated from fishing mortality, and density within the reserve will be higher than in comparable fished areas.
- (2) Elevated densities within the reserve will result in net emigration of biomass from the reserve to fished areas, either by random diffusion (Beverton & Holt 1957) or density-dependent processes (specifically ‘spillover’) (Kramer & Chapman 1999).
- (3) Unfished populations of fishes are composed of relatively larger individuals, which have greater fecundity, and hence reserves will act as more productive sources of gametes than comparable fished areas.

The magnitude of the effect may also be speculated on in some cases. For example, if adult fish are sedentary then it could be postulated that density in reserves will increase to carrying capacity (see Hastings & Botsford 1999).

While such speculations are intuitive, they often appear in the literature as logically true assertions. However, these deceptively reasonable speculations are each dependent on underlying assumptions about behaviour, ecology and the fishery. It is logically true that preventing fishing in particular areas will eliminate direct fishing mortality and stop the destruction of habitat caused by contact fishing gears (Collie *et al.* 2000). However, it is imprudent to make untested assertions about the primary consequences of reserve protection on fish population dynamics, and then to extrapolate those effects to fishery-level predictions. Typical predictions of fishery enhancement could be invalidated for a number of reasons, including displaced fishing effort around the reserve boundary (Parrish 1999), recruitment limitation (Doherty & Fowler 1994), self-recruitment rather than larval export (Leis 2002), irreversible changes in species assemblages, and any number of unknown causes due to the underlying complexity of the ecosystem. Without empirical substantiation, predictions of fishery enhancement are deductions based on circumstantial evidence and ancillary information. Furthermore, even if model assumptions are logically correct, it is not sufficient to test only for the existence of reserve effects. Of real relevance is the magnitude of an effect and the certainty (or lack thereof) that surrounds estimates of it.

We use the issue of recovery of density within reserves (assumption 1 above) as an example of how little evidence exists to substantiate the basic responses of fish populations to reserve protec-

tion. We note here that this does not mean to imply that reserves fail in their objectives (we have ourselves documented large responses of exploited fishes to reserve protection), but that the quantity of good scientific evidence is not as extensive as a cursory examination of the literature might indicate.

The quality of empirical evidence for recovery within reserves

Many recent papers contain statements within their introductions along the lines of 'It is well known that exploited species exhibit increases in density and mean size within reserves', supported by a number of citations. A closer look at the cited papers shows that many are review articles (which themselves rely on reference to earlier reviews such as Roberts & Polunin 1991; Rowley 1994). Of the empirical studies cited, most present ambiguous evidence for recovery (see Jones *et al.* 1993; Rowley 1994; Edgar & Barrett 1997).

Detection of recovery of fish density in marine reserves often suffers from lack of rigour in the design of field surveys (Hurlbert 1984; Stewart-Oaten *et al.* 1986; Underwood 1990, 1993). As Underwood (1990) pointed out, studies lacking replication cannot be logically interpreted. In the marine reserve context there are many reasons why researchers might have limits on their sampling designs. However, a critical evaluation of the experimental designs employed by many published studies brought to light the following problems with replication and lack of control sites:

- (1) insufficient sample replication (for example only one site sampled inside and outside a reserve, or no control sites sampled at all);
- (2) spatial confounding (for example all control sites located only at one end of the reserve, so that comparisons are confounded by unknown location effects);
- (3) lack of temporal replication (most studies consist of surveys done at only one time);
- (4) lack of replication at the reserve level limiting the generality of results (although in many cases this reflects the number of reserves available); and
- (5) non-random placement of reserves, i.e. often reserves are sited to include 'special' or unique features, which causes difficulties in selecting valid control sites (this is obviously no fault of the researchers).

To date, there are no well-designed studies that avoid the above problems as well as possessing a time series of 'before' and 'after' data. However, some might be used as examples of attempts to fulfil good design criteria (Table 1). In addition, the power to detect effects can be affected by the choice of sampling method (Willis *et al.* 2000), especially when the target species are large carnivores that can exhibit fishing-related behavioural plasticity between sites (Cole 1994; Jennings & Polunin 1995; Kulbicki 1998).

Traditional approaches to fisheries stock assessment are often unable to provide useful predictions because of the lack of information in the data, and the resulting inability to verify model assumptions or to accurately estimate model parameters (Ulltang 1998). Indeed, such models can not reliably estimate sustainable levels of harvest without first overexploiting the resource, and this

Table 1 Some examples of marine reserve effects studies replicated both temporally and spatially (i.e. at the reserve level). *This study used a marine reserve as a control for examining the effects of fishing. It was unique in containing a long time-series of data prior to the beginning of the experiment. †Studied once prior to and once after reserve establishment.

<i>Reference</i>	<i>Location</i>	<i>No. reserves</i>	<i>No. times</i>	<i>Study focus</i>
Edgar & Barrett (1999)	Tasmania, Australia	4	9	algae, invertebrates fishes
Ferreira & Russ (1995)	Great Barrier Reef, Australia	2	4	coral trout, <i>Plectropomus leopardus</i>
Macpherson <i>et al.</i> (1997)	Western Mediterranean	3	2–3	sparid mortality
Schroeter <i>et al.</i> (2001)	California, USA	1*	18	sea cucumber, <i>Parastichopus parvimensis</i>
Wantiez <i>et al.</i> (1997)	New Caledonia	5	2†	reef fishes
Willis <i>et al.</i> (2003)	Northern New Zealand	3	4	snapper, <i>Pagrus auratus</i>

arises from the impossibility of performing controlled and replicated experiments on a large scale (Ludwig *et al.* 1993). There seems to be a trend to approach the issue of marine reserves in a similar fashion, partly because most countries so far have few of them. This is unfortunate, because a marine reserve is a large-scale manipulation that can be assessed in a more rigorous, less equivocal fashion. It will, however, require good lines of communication between management agencies and scientists; studies should begin well in advance of reserve implementation, and there must also be a commitment from management agencies to ensure compliance with reserve regulations (Paddack & Estes 2000).

How many studies unambiguously demonstrate significant within-reserve increases in the density of exploited species? Edgar and Barrett (1997) recognized that, with a sufficiently large sample size, a statistically significant difference between two sites (separated either spatially or temporally) can almost always be obtained due simply to true natural biological variability between the sites. That is, the null hypothesis of no difference between two biological entities is necessarily false. They therefore proposed a 100% increase in density as a minimum criterion for claiming the existence of a 'reserve effect'. This type of approach is more generally known as bio-equivalence testing, in which an effect is not considered biologically significant unless it exceeds a pre-specified threshold (McBride 1999). If we use the 100% threshold, and ignore flaws in sampling design, then there were only a handful of instances where differences in density of individual species between reserve and fished areas can be regarded as biologically significant (Polunin & Roberts 1993; Francour 1994; Harmelin *et al.* 1995; Russ & Alcala 1996; Edgar & Barrett 1997, 1999; Willis *et al.* 2003). In many other cases, slight trends towards higher reserve densities were described, but these were of insufficient magnitude to confidently attribute them to reserve effects, rather than real biological variability at the spatial or temporal level (Roberts & Polunin 1992; Chapman & Kramer 1999; Paddack & Estes 2000). If we consider only those studies that are replicated in both time and space, to our knowledge there are only a few that establish increases in excess of 100%: Ferreira and Russ (1995), Wantiez *et al.* (1997), Edgar and Barrett (1997, 1999), the long term studies of McClanahan (for example, McClanahan & Arthur 2001), and Willis *et al.* (2003).

Several theoretical studies have indicated that marine reserves can provide increases or equivalence in yield under the assumed model and parameter values (Polacheck 1990; DeMartini 1993; Attwood & Bennett 1995; Sladek Nowlis & Roberts 1999). However, if management decisions are based upon models built on unquestioned assumptions then we may find ourselves making costly errors. We reinforce this point by noting that the model of Parrish (1999) produces a contrary result; it suggests that the large reserves that are believed to be required to contribute to the Californian groundfish fishery might actually be to the detriment of the fishery, due to the displacement of fishing effort onto the remaining fishing grounds. In contrast, Horwood *et al.* (1998) conclude that reserves will have little effect on fishery yield. Yet, the model of Hastings and Botsford (1999) concludes that, even with arbitrarily high fishing effort outside of large reserves, marine reserves will return fisheries yields equivalent to traditional fisheries management for a wide variety of groundfish. Taken together, the conflicting conclusions from various plausible models lead us back to the beginning, where we must admit that, at present, we cannot predict what the effects of marine reserves might be.

Concluding remarks

It is ironic that we must appear to bemoan the proliferation of marine reserve comments and reviews by writing yet another comment. However, the intention is not so much to complain about such activities (very useful ideas have been published in this way), but to highlight the imbalance in research effort brought about by a lack of rigorous empirical science. Theoretical models (mathematical or not) are useful in developing our ideas, but they are just that: ideas. Returning to the philosophical reference in the title, just because 'we think', does not mean 'they are'. Indeed, it would appear that a lot of thinking has gone into specification of competing models of marine reserves. That is, the models and prior hypotheses about the nature of marine reserves have been put forward in abundance. It is now time to test them with data.

This comment is not intended to imply criticism of those working for the establishment of marine reserves, and it is not intended to counteract the precautionary principle (Lauck *et al.*

1998). Nor should this comment be interpreted as ‘anti-reserve’; our own research has demonstrated the potential of reserves for science and conservation (Babcock *et al.* 1999; Willis *et al.* 2000, 2003; Shears & Babcock 2002, 2003). Rather, it is a plea for researchers to apply the same rigour to examination of the fisheries-related efficacy of marine reserves as they would apply to other environmental effects studies. Perhaps more importantly, this plea also goes out to those in a position to fund this research. They must ensure that adequate planning and resources are allocated to make it possible to implement rigorous survey designs, and that this is done far enough in advance of reserve establishment so that effects outside their boundaries can be detected. In the meantime, advocates might more convincingly point to the use of reserves as controls for the understanding of ecosystem function (Babcock *et al.* 1999; Pinnegar *et al.* 2000; Schroeter *et al.* 2001; Shears & Babcock 2002).

Acknowledgements

Thanks to C.G. Attwood, W.J. Ballantine, N.V.C. Polunin, R.B. Taylor and the referees for helpful suggestions, criticisms and disagreements. Our own efforts to get data have been funded by the New Zealand Department of Conservation. Part of the title of this article was borrowed from *Fitterbug Perfume* by Tom Robbins, Random House Publishing.

References

- Allison, G.W., Lubchenco, J. & Carr, M.H. (1998) Marine reserves are necessary but not sufficient for marine conservation. *Ecological Applications* **8** (Suppl.): 79–92.
- 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.
- Beverton, R.J.H. & Holt, S.J. (1957) *On the Dynamics of Exploited Fish Populations*. London, UK: Chapman and Hall (facsimile reprint, 1993).
- Bohnsack, J.A. (1998) Application of marine reserves to reef fisheries management. *Australian Journal of Ecology* **23**: 298–304.
- 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.
- 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.
- Collie, J.S., Hall, S.J., Kaiser, M.J. & Poiner, I.J. (2000) A quantitative analysis of fishing impacts on shelf-sea benthos. *Journal of Animal Ecology* **69**: 785–798.
- DeMartini, E.E. (1993) Modeling the potential of fishery reserves for managing Pacific coral reef fishes. *Fishery Bulletin* **91**: 414–427.
- Doherty, P. & Fowler, T. (1994) An empirical test of recruitment limitation in a coral reef fish. *Science* **263**: 935–939.
- Dugan, J.E. & Davis, G.E. (1993) Applications of marine harvest refugia to coastal fisheries management. *Canadian Journal of Fisheries and Aquatic Sciences* **50**: 2029–2042.
- 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.
- Ferreira, B.P. & Russ, G.R. (1995) Population structure of the leopard coral grouper *Plectropomus leopardus*, on fished and unfished reefs off Townsville, Central Great Barrier Reef, Australia. *Fishery Bulletin* **93**: 629–642.
- Feynman, R.P. (1985) *‘Surely You’re Joking, Mr. Feynman!’: Adventures of a Curious Character*. New York, USA: W. W. Norton.
- Francour, P. (1994). Pluriannual analysis of the reserve effect on ichthyofauna in the Scandola natural reserve (Corsica, northwestern Mediterranean). *Oceanologica Acta* **17**: 309–317.
- Guénette, S., Lauck, T. & Clark, C. (1998) Marine reserves: from Beverton and Holt to the present. *Reviews in Fish Biology and Fisheries* **8**: 251–272.
- Harmelin, J.-G., Bachet, F. & Garcia, F. (1995) Mediterranean marine reserves: fish indices as tests of protection efficiency. *PSZN: Marine Ecology* **16**: 233–250.
- Hastings, A. & Botsford, L.W. (1999) Equivalence in yield from marine reserves and traditional fisheries management. *Science* **284**: 1537–1538.

- Hilborn, R. & Mangel, M. (1997) *The Ecological Detective: Confronting Models with Data*. New Jersey, USA: Princeton University Press.
- 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.
- Jones, G.P., Cole, R.G. & Battershill, C.N. (1993) Marine reserves: do they work? In: *Proceedings of the Second International Temperate Reef Symposium*, ed. C.N. Battershill, D.R. Schiel, G.P. Jones, R.G. Creese & A.B. MacDiarmid, pp. 29–45. Wellington, New Zealand: NIWA Marine.
- 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** (Suppl.): 72–78.
- Leis, J.M. (2002) Pacific coral-reef fishes: the implications of behaviour and ecology of larvae for biodiversity and conservation, and a reassessment of the open population paradigm. *Environmental Biology of Fishes* **65**: 199–208.
- Ludwig, D., Hilborn, R. & Walters, C. (1993) Uncertainty, resource exploitation, and conservation: lessons from history. *Science* **260**: 17 and 36.
- Macpherson, E., Biagi, F., Francour, P., García-Rubies, A., Harmelin, J., Harmelin-Vivien, M., Jouvenel, J.Y., Planes, S., Vigliola, L. & Tunesi, L. (1997) Mortality of juvenile fishes of the genus *Diplodus* in protected and unprotected areas in the western Mediterranean Sea. *Marine Ecology Progress Series* **160**: 135–147.
- McBride, G.B. (1999) Equivalence tests can enhance environmental science and management. *Australian and New Zealand Journal of Statistics* **41**: 19–29.
- McClanahan, T.R. & Arthur, R. (2001) The effect of marine reserves and habitat on populations of East African coral reef fishes. *Ecological Applications* **11**: 559–569.
- Paddock, 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 and Fisheries Investigations* **40**: 77–86.
- Pinnegar, J.K., Polunin, N.V.C., Francour, P., Badalamenti, F., Chemello, R., Harmelin-Vivien, M.-L., Hereu, B., Milazzo, M., Zabala, M., D'Anna, G. & Pipitone, C. (2000) Trophic cascades in benthic marine ecosystems: lessons for fisheries and protected-area management. *Environmental Conservation* **27**: 179–200.
- Polacheck, T. (1990) Year around closed areas as a management tool. *Natural Resource Modelling* **4**: 327–354.
- Polunin, N.V.C. (1990) Marine protected areas: an expanded approach for the tropics. *Resource Management and Optimization* **7**: 283–299.
- Polunin, N.V.C. (2002) Marine protected areas, fish and fisheries. In: *Handbook of Fish and Fisheries, Volume II*, ed. P.J.B. Hart & J.D. Reynolds, pp. 293–318. Oxford, UK: Blackwell Science.
- Polunin, N.V.C. & Roberts, C.M. (1993) Greater biomass and value of target coral-reef fishes in two small Caribbean marine reserves. *Marine Ecology Progress Series* **100**: 167–176.
- Roberts, C.M. (1997) Ecological advice for the global fisheries crisis. *Trends in Ecology and Evolution* **12**: 35–38.
- 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.
- Roberts, C.M. & Polunin, N.V.C. (1992) Effects of marine reserve protection on northern Red Sea fish populations. In: *Proceedings of the 7th International Coral Reef Symposium. Volume 2*, ed. H.A. Lessios & I.G. Macintyre, pp. 969–977. Panama: Smithsonian Tropical Research Institute.
- Rowley, R.J. (1994) Marine reserves in fisheries management. *Aquatic Conservation: Marine and Freshwater Ecosystems* **4**: 233–254.
- Russ, G.R. & Alcala, A.C. (1996) Marine reserves: rates and patterns of recovery and decline of large predatory fish. *Ecological Applications* **6**: 947–961.
- 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. *Canadian Journal of Fisheries and Aquatic Sciences* **58**: 1773–1781.

- Shears, N.T. & Babcock, R.C. (2002) Marine reserves demonstrate top-down control of community structure on temperate reefs. *Oecologia* **132**: 131–142.
- Shears N.T. & Babcock, RC (2003) Continuing trophic cascade effects after 25 years of no-take marine reserve protection. *Marine Ecology Progress Series* **246**: 1–16.
- Simpson, J. (1993) *The Concise Oxford Dictionary of Proverbs, Second Edition*. Oxford, UK: Oxford University Press.
- 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.
- Ulltang, Ø. (1998) Explanations and predictions in fisheries science – problems and challenges in a historical and epistemological perspective. *Fisheries Research* **37**: 297–310.
- Underwood, A.J. (1990) Experiments in ecology and management: their logics, functions and interpretations. *Australian Journal of Ecology* **15**: 365–389.
- Underwood, A.J. (1993) The mechanics of spatially replicated sampling programmes to detect environmental impacts in a variable world. *Australian Journal of Ecology* **18**: 99–116.
- 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., 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., Millar, R.B. & Babcock, R.C. (2003) Protection of exploited fishes in temperate regions: high density and biomass of snapper *Pagrus auratus* (Sparidae) in northern New Zealand marine reserves. *Journal of Applied Ecology* **40**: 214–227.

T. J. WILLIS^{1,2*}, R. B. MILLAR², R. C. BABCOCK¹, N. TOLIMIERI^{1,3}

¹Leigh Marine Laboratory, University of Auckland, PO Box 349, Warkworth, New Zealand,

²Department of Statistics, University of Auckland, Private Bag 92019, Auckland, New Zealand,

³School of Biological Sciences, University of Auckland, Private Bag 92019, Auckland, New Zealand

* Correspondence: Dr Trevor Willis, Centro Interdipartimentale di Ricerca per le Scienze Ambientali di Ravenna, Università di Bologna, Via Tombesi dall’Ova 55, I-48100 Ravenna, Italy.
e-mail: willis@ambra.unibo.it