CEE review 06-002

ARE MARINE PROTECTED AREAS EFFECTIVE TOOLS FOR SUSTAINABLE FISHERIES MANAGEMENT? I. BIODIVERSITY IMPACT OF MARINE RESERVES IN TEMPERATE ZONES

Systematic Review

STEWART, G.B., CÔTÉ, I.M., KAISER, M.J., HALPERN, B.S., LESTER, S.E., BAYLISS, H.R., MENGERSEN, K. & PULLIN, A.S.

Centre for Evidence-Based Conservation - School of the Environment and Natural Resources - Bangor University – Bangor – Gwynedd - LL57 2UW - UK

Correspondence: g.stewart@bangor.ac.uk
Telephone: +44(0)1248 382452

Draft protocol published on website: 01 December 2006 - Final protocol published on website: 28 March 2007 - Draft review published on website:13 November 2007 – Final review posted on website: 10 April 2008

Cite as: Stewart, G.B., Cote, I.M., Kaiser, M.J., Halpern, B.S., Lester, S.E., Bayliss, H.R., Mengersen, K. & Pullin, A.S. 2008. Are marine protected areas effective tools for sustainable fisheries management? I. Biodiversity impact of marine reserves in temperate zones. CEE review 06-002 (SR23). Collaboration for Environmental Evidence: www.environmentalevidence.org/SR23.html.

SYSTEMATIC REVIEW SUMMARY

Background
Marine Protected Areas (MPAs) have been proposed and designated as a mechanism to address the problem of achieving sustainable fisheries, while simultaneously preserving biodiversity. However, empirical studies and research syntheses indicate that there is considerable variation in the ecological effects of MPAs and there is considerable debate over whether they can produce fisheries benefits. Of the various types of MPAs, marine reserves (no-take areas) have been perhaps the best studied. Furthermore, by focusing on marine reserves, it is possible to eliminate protection level as a co-variate. Consequently, as a first review in a proposed series on the effectiveness of MPAs for sustainable fisheries management, we objectively collated data to ascertain the impacts of temperate zone no take areas on the density, biomass and species richness of marine biota within reserve borders (as reflected in the subtitle).

Objectives
- To determine the impacts of establishing temperate zone no take areas on density, biomass and species richness of marine biota within reserve boundaries.
- To ascertain whether the impacts of no take areas vary in relation to taxon, reserve parameters or organism parameters.

Search strategy
Multiple electronic sources were searched using a range of keywords. Bibliographies, expert contacts and website searches were performed to access grey literature. Information from soft sediment systems was explicitly sought as well as the more common reef-based assessments. Foreign language searches were not performed.

Selection criteria

Relevant subject(s): All marine biota
• **Types of intervention:** Temperate Marine Protected Areas (Marine Reserves) defined as geographically defined areas subject to no fishing activity (no take areas).
• **Types of comparator:** No restriction on fishing activity.
• **Types of outcome:** Density (other abundance measures), biomass, species richness.
• **Types of study:** Any primary study providing measures before and after implementation of a reserve, or comparing reserves to adjacent geographical areas without no-take protection.

Data collection and analysis

Data extraction was undertaken using a review-specific data extraction form. Random effects meta-analysis was used to examine species level data, reserve level data, and species-reserve interactions. Subgroup analyses and meta-regression were used to explore variation in effectiveness in relation to species and reserve level co-variates.

Main results

Density of marine biota is 23% to 196% higher within marine reserve no take zones than outside. Gains in biomass within no take are 20% to 422%, but there is uncertainty surrounding these results due to lower sample sizes. Species richness within marine reserves is 10% to 130% higher within no take areas than outside reserves, although this too is based on a small sample. Fish species density is 35% to 81% higher in marine reserves than in adjacent areas and variation in fish density response is not strongly linked to any species or reserve level parameters. Furthermore, it is not clear if these differences are due to marine reserve effects or other differences between the marine reserve and comparator, such as habitat variation. This lack of distinction is the primary reason for contention regarding marine reserve effectiveness and can only be resolved by improved monitoring.

Meta-analyses indicate that differences in the response of specific species, genera or functional groups are often small with effect sizes of <0.2. Power analysis indicates that detection of statistically significant differences for these small effects requires co-ordinated monitoring across a large number of marine reserves.

Conclusions

Implications for *management / policy / conservation:* The available evidence suggests that temperate MPAs that impose no-take zones may achieve higher densities, biomass and species richness of marine biota within the boundaries of the no-take zone than outside. The evidence for higher densities and biomass of fish is notable in this context. However, considerable uncertainty and low predictive power arises from small sample sizes and possible confounding factors such as habitat quality.

Implications for research: Lack of data is a hindrance in the development of an evidence-base regarding the effectiveness of MPAs. Small sample sizes result in high uncertainty about the impacts on specific taxa. In particular, algae and invertebrates are understudied; insufficient data are available regarding biomass, species richness, deep water no take areas, pelagic fish species and soft sediment systems. It is also very difficult to distinguish habitat effects from reserve effects without integrated experimental monitoring programs that present data regarding the baseline condition. Before After Control Impact studies are required to allow comparison of rates of change from the same baseline condition. Large numbers of marine reserves require monitoring if small effects are to be detected. Data regarding the intensity of resource use are required alongside biological metrics for monitoring to be effective.

1. BACKGROUND

Marine Protected Areas (MPAs) are becoming widely established across the globe (Halpern 2003) in response to two related policy drivers. Firstly, many traditional forms of fisheries stock management have proved to be unsustainable arising from a lack of appropriate implementation and compliance (FAO 1994). Secondly, traditional management such as not exceeding maximum sustainable yield estimates do not entirely address the multiple anthropogenic impacts on marine biota. Marine reserves (no take areas) have been proposed as a mechanism to address both these problems through their suggested capacity to contribute to the development and maintenance of sustainable fisheries, whilst simultaneously preserving aspects of biodiversity (Plan Development Team [PDT] 1990, Ballantine 1992, Dugan & Davis 1993, Bohnsack 1996, Nowlis & Roberts 1997, Allison *et al.* 1998, Lauck *et al.* 1998).

MPAs have variable levels of protection and are not synonymous with marine reserves or no-take areas that are subject to no fishing, although variation in enforcement impacts on the intensity of exploitation even within no-take areas. This review is concerned with no-take areas which are often established for conservation purposes irrespective of their potential role in sustainable fisheries (Halpern & Warner 2002; Halpern 2003). No-take areas are located in coastal (Micheli *et al.* 2004) and offshore habitat (Halpern 2003), in temperate and tropical biomes, and are designed to protect a wide range of habitats and taxa from seagrass meadows to coral reefs, and from plants and invertebrates (Edgar & Barrett 1999) to whales (Gerber *et al.* 2005), and particularly target species of commercial importance (Mosquera *et al.* 2000). Their effects have been monitored using a range of outcome measures. Recent quantitative reviews of the effects of no-take areas have synthesised parameters such as biomass, species richness, density (and other abundance measures), and organism size (Mosquera *et al.* 2000, Halpern 2003, Micheli *et al.* 2004). Theoretical models have also been employed to predict impacts on fish populations (Steele & Beet 2003; Gerber *et al.* 2005). The general consensus to emerge from this work is that marine reserves can increase the density, biomass and richness of marine biota within reserve boundaries (COMPAS and NCEAS 2001, Halpern 2003). In such instances marine reserves have the potential to rebuild stocks through enhanced recruitment and spill-over effects, maintain biodiversity, buffer marine systems from human disturbances, and maintain the ecosystems upon which fisheries rely (MEA). However, some studies have found that no take areas fail to effectively maintain biodiversity (Hilborn et al. 2004; Edgar and Barrett 1999; Willis et al. 2003). In many cases, failure was reportedly due to a lack of integration with broader coastal management systems or a lack of management funding or enforcement (MEA). In addition no-take areas could simply displace fishing effort and increase the vulnerability of other stocks and endangered species (Coleman et al. 2004; Kaiser 2005).

Despite the meta-analyses of effects of no-take zones undertaken to date, questions regarding their effectiveness remain unresolved, particularly with respect to temperate systems and the impact of ecological and methodological co-variables or effect modifiers (Mosquera *et al.* 2000, Halpern 2003, Micheli *et al.* 2004). Taxa (Halpern 2003), trophic groups (Froese & Pauly 2006, Micheli *et al.* 2004), and genera (Mosquera *et al.* 2000) have all explained variation in species response to no-take areas. Different groupings of species produce different results because weak responses of individual species may result in greater effect sizes when species are pooled in functional groups, and conversely strong response of individual taxa may be obscured (Micheli *et al.* 2004). Reserve size (Halpern 2003), adult mobility (range) (Kramer & Chapman 1999), community composition (as represented by a community similarity index, Bray &Curtis 1957) (Micheli *et al.* 2004) organism size (Mosquera *et al.* 2000), fishing intensity (Mosquera *et al.* 2000), life-history (Blyth-Skyrme *et al.* 2006) and habitat (Nilsson 1998) have also been proposed as variables that might influence the effectiveness of no take areas. Interestingly, there is general agreement among the studies undertaken to date, that spatial size of reserves has little or no proportional impact (with the exception of Claudet et al. 2008), although there are lots of arguments (with theoretical support) for the creation of larger rather than smaller reserves. Furthermore, this observation is probably linked to confounding variables such as habitat type and species' habitat association effects.

Here we synthesise all available published data on species density, biomass and richness in temperate zone marine reserves using systematic review methodology (Pullin & Stewart 2006) to evaluate the effectiveness of temperate no-take zones as an intervention to maintain sustainable fisheries.

2. OBJECTIVES

2.1 Primary objective

- What are the effects of establishing temperate no take areas on density, biomass and species richness of marine biota?

Table 1. Definition of components of the primary systematic review question.

Subject	Intervention	Outcome	Comparators	Designs
All marine biota	*Establishing an MPA involving implementation of a no take zone	Density (or other abundance measures) Biomass Species richness	No (or limited) restriction on fishing activity	Any primary studies providing measures before and after implementation of a reserve, or comparing no take areas to adjacent geographical areas without no take areas.

* Geographically defined areas subject to no fishing established for any purpose.

2.2 Secondary objective

- How do the effects of no take areas vary in relation to taxon, reserve parameters or organism parameters?

Reserve parameters are defined as latitude, habitat type, age and size. Organism parameters as adult size (maximum length), resilience (K), environment, mobility and utility (*sensu* Froese & Pauly 2006).

3. METHODS

3.1 Question formulation

The Joint Nature Conservation Committee (UK government body) proposed the question at a stakeholder meeting of the Natural Environment Research Council Knowledge Transfer, Science into Policy group. Definition of question elements and development of a protocol was subsequently undertaken under the guidance of the JNCC and with wider consultation of the scientific community. Scoping searches revealed that the question required further definition. There was a lack of literature regarding spillover effects and the definition of protected area became unmanageable in the context of sustainable fisheries. It was also very difficult to establish the objective of the MPA (sustainable fisheries or habitat protection). The question elements were therefore refined and although the original title (Are marine protected areas effective tools for sustainable fisheries management?) was retained the hypotheses addressed by the review are directly relevant to species and habitat protection rather than sustainability as reflected in the subtitle.

3.2 Search strategy

Searching was carried out across a range of resources in order to access both grey literature and the more readily available published literature to minimise the possibility of publication and related biases.

General sources
The following general resources were searched. All results were recorded and exported into EndNote Libraries.

1) ISI Web of Knowledge (Web of Science and Proceedings)
2) Science Direct
3) Copac
4) Scopus
5) Index to Theses
6) Digital Dissertations Online
7) Agricola
8) CAB Abstracts
9) Conservation Evidence (www.conservationevidence.com)

Search terms used were based on the following phrases, and modified according to the search functionality of the resources:

marine protected area
marine reserve
marine AND no take
marine AND fish* AND protect*
(benth* OR pelagic OR “soft sediment”) AND fish* AND protect*

The third term, marine AND no take, caused some problems as “no” and “take” are considered stop words in many resources and so the search had to be modified to account for this e.g. using “no take” or “no take zone”.

Web resources
The following web resources were searched using the above terms.

www.alltheweb.com
www.google.com
scholar.google.com
www.scirus.com (all journal sources)
knb.ecoinformatics.org/knb/metacat

The first fifty hits for each search were checked for relevant pages or documents containing data.

Bibliographies
Bibliographies of all articles accepted for viewing at full text were hand searched to identify any additional evidence. Web based bibliographies identified during the web searching phase were also checked for additional references.

3.3 Study inclusion criteria

All studies retrieved through the searching were assessed for relevance at title and abstract level. Any articles not relevant to the search were rejected. The following criteria were used to accept articles for viewing at full text. In cases where it was not clear whether an article met these criteria, for example when no abstract was available or it was not apparent whether data was presented, then it was automatically accepted for viewing at full text

- **Relevant subject:** All marine biota
- **Types of intervention:** Temperate Marine Protected Areas (Marine Reserves) defined as geographically defined areas subject to no fishing (no take zones).
- **Types of outcome:** Density (or other abundance measure), biomass, species richness.

All studies retrieved were assessed for relevance at title and abstract. A Random subset of 300 articles was assessed using the same criteria by a second reviewer, and a kappa analysis performed. The result of the kappa analysis was 0.79, indicating significant agreement between the two reviewers.

Studies accepted for viewing at full text were assessed using *a priori* criteria to determine relevance and suitability for meta-analysis. When viewing the selected articles at full text, an article was accepted for meta-analysis when it fulfilled the above criteria with an appropriate comparator and variance measures.

3.4 Study quality assessment

Variation in the quality of evidence hierarchy (Stevens & Milne 1997) could not be explored as marine reserve data is almost wholly based on site-comparisons. The most important variation in study quality with respect to derivation of effect sizes concern pseudo-replication and temporal autocorrelation. Additionally, different sampling methodologies are replicated to different degrees and have different precision (see Mosquera *et al.* 2000). These data quality elements all impact on the variance of a study. Rather than attempting complex standardised recording of design flaws and multiple subgroup analyses with concurrent loss of power, we dealt with study quality by running sensitivity analyses to compare Hedge's *d* with the response ratio (*RR*), which can be calculated without knowledge of sample variances (Rosenberg *et al*., 2000, Adams *et al*., 1997).

RR is defined as the ratio of the means measured in experimental and control areas (i.e., density, biomass or richness inside and outside each no take area). The statistical properties of *RR* have been examined thoroughly (Hedges *et al*., 1999), and the natural logarithm of the RR is usually recommended since it behaves better statistically (Rosenberg *et al*., 1997). The metric we used for sensitivity analysis in lieu of study quality assessment is thus defined as: ln *RR*=ln (*X* I) (*X* O) _1 where *X* I and *X* O are the means of the density or richness estimates in the experimental (inside reserve) and control (outside reserve) areas (or before and after when such situations occurred). Hedge's *d* is defined as the mean difference divided by the pooled standard deviation with a constant correction factor to account for small sample sizes.

3.5 Data extraction

Data extraction was undertaken using a review-specific data extraction form *sensu* Lipsey & Wilson (2001). A single reviewer performed data extraction but multiple iterations of the extraction form were piloted by the authors prior to extraction commencing. Density, biomass and species richness were treated as continuous metrics. Sample sizes, means and standard deviations were either extracted as presented or calculated from raw data or the statistics presented in the study. Different taxa were disaggregated as far as possible. Multiple non-independent data-sets were extracted for example where different depths or habitats within a no take area and adjacent control were surveyed, but data were also aggregated at a reserve level to maintain independence.

3.6 Data synthesis

Meta-analysis is performed using a range of effect size metrics (Osenberg *et al.* 1999). Our initial analyses were based on Hedge's adjusted *d* effect size with lnRR utilised in a quality sensitivity analysis using the program metawin (Rosenberg *et al.* 1997).

Data were pooled and combined across studies using DerSimonian and Laird random effects meta-analysis based on standardised mean difference (SMD; DerSimonian & Laird 1986; Cooper & Hedges 1994). The random effects model assumes that there is variation among the true study effects, and the aim of the analysis is to quantify such variation in the effect parameters; it is therefore appropriate for ecological questions for which the true effect is likely to vary between studies (Hedges & Gurevitch 1999). Failsafe numbers (Rosenthal 1979) were used to calculate the number of additional studies with a mean effect size of zero needed to reduce significance to $p>0.05$. When the failsafe number is larger than 5n +10 observed results, even with some publication bias, it can be considered a reliable estimate of the true effect (Rosenberg et al 2000).

Overall biota in relation to density, biomass and species richness

The effect of no-take areas on density, biomass and species richness was examined via visual inspection of Forrest plots of the estimated mean effects from the studies along with their 95% confidence intervals, and by formal tests of heterogeneity undertaken prior to meta-analysis (Thompson & Sharp 1999). Publication bias was investigated by examination of funnel plot asymmetry (Egger et al. 1997). These analyses provide estimates of the impact of no-take areas on the density, biomass and species richness of all biota at a reserve level (ecological bias arising from aggregation of multiple species within a reserve) and at a species level (quasi-replication arising from disaggregation of multiple species from one reserve).

Density

The relationships between differences in density and categorical subgroups were explored separately for each taxon (algae, invertebrates, and fish). Taxon density-reserve interactions were examined by pooling species within no take areas by taxon prior to combining data across independent marine reserves. Fish species were analysed in further subgroups relating to migratory status, environment, habitat and utility of fish species (based on commercial fishing status). Continuous variables (maximum length and resilience expressed as K *sensu* Froese & Pauly 2006) were analysed using random effects SMD meta-regression in Stata version 8.2 (Stata Corporation, USA, 2003) in the program Metareg (Sharp 1998). These analyses explore variation in the density of fish species in relation to species covariates. Fish species density-reserve interactions were examined for the environmental subgroups

Fish density data were also pooled by reserve and related to reserve-level characteristics. Continuous variables (reserve age, size, latitude, depth, monitoring period and number of taxa sampled) were analysed using random effects SMD meta-regression in Stata version 8.2 (Stata Corporation, USA, 2003) in the program Metareg (Sharp 1998).

Biomass

The relationships between differences in biomass and categorical subgroups were explored separately for each taxon. Small sample sizes and potential for bias precluded further analyses to explore variation in the fish species' biomass response in relation to species covariates. However, fish biomass data was pooled by reserve and related to reserve-level characteristics. Continuous variables (reserve age, reported body-size, latitude, depth, and monitoring period) were analysed using random effects SMD meta-regression in Stata version 8.2 (Stata Corporation, USA, 2003) in the program Metareg (Sharp 1998).

Species richness

Variation in species richness was explored separately for fish and invertebrates (no data on algae). Small sample sizes precluded further analyses.

Taxonomic quasireplication

Fish density data were pooled by fish genera to ascertain the impact of quasi-replication for density, biomass and species richness.

Power analysis

Power analyses were undertaken to explore the relationship between effect size and sample size at the reserve level. This was undertaken to provide insight into the number of no-take zones that would be required to detect a certain effect size. Such an output provides a rigorous basis from which to consider the number of individual no-take zones required to achieve a given effect with a reasonable probability of assessing the performance of such a management measure.

4. RESULTS

4.1 Review statistics

Of 3531 references examined, 34 present data on temperate no-take areas that fulfilled all the inclusion criteria. It should be noted that many studies were excluded because they have no comparator. However, otherwise relevant studies were also excluded where the marine protected area conferred only partial protection (e.g. Blyth-Skyrme et al. 2006; Bradshaw 2001; Murawski et al. 2000; Wolff 1992). Thus less than one percent of published material concerning no-take areas compared temperate no-take areas to exploited areas with (pseudo)replicated sampling. Of these studies 20 occurred in the Mediterranean with the remaining 14 split between Australasia, Africa, and America.

4.2 Description of studies

The 34 studies report differentially on taxa and outcome measure within no take areas. The studies report on 30 temperate reserves with 29 metrics relating to fish, 13 to invertebrates and nine to algae (Table 2). Density was measured in 29 reserves but only 11 reserves have biomass data and eight report on species richness (Table 2)
None of these studies, with the exception of Claudet et al. (2006), present Before/After/Control/Impact [BACI] data, but rather are based on comparison of no-take areas and adjacent areas [i.e. fished areas].

The reported characteristics of the reserves are variable. Median values are: latitude 37.4 (39° S to 23° 26′ 21″ S and 49.2° N to 23° 26′ 21″ N), year of establishment 1986 (1963 – 1998), size 3km^2 (0.01 – 300), depth 14.5m (3 – 230), number of taxa studied 7 (1-202) (Table 2). The studies used variable sampling methodologies and examine different numbers and types of taxa. The majority of studies are based on visual dive transects. All studies with the exception of Paddack & Estes (2001), Tuya (2006) and Willis & Millar (2005) were based upon repeated (pseudo-replicated) observations in single no take areas.

It is important to note the existence of large knowledge gaps in the evidence base. No studies were retrieved for any no-take areas in sand or mud habitats (although some include reserves with mixed sand and rock substrata). Likewise, no studies were retrieved concerning commercially important, highly migratory, northern hemisphere fish species, and the data regarding pelagic fish species are based on only two no-take areas. Furthermore, sample sizes are very small for algae and invertebrates. Species richness and to a lesser extent biomass data are also limited.

Table 2. Reserve characteristics and measured outcomes of no take zones presented in the included studies.

References	Reserve name	latitude	longitude	year of establishment	Size (Km^2)	Depth (m)	taxon				Outcome measures		
							n	algae	invertebrata	fish	Density	Biomass	Species richness
Macpherson et al (1997)	Banyuls	38.20	-0.48	1974	2	7	7			☺	☺		
Bell (1983)	Banyuls-Cerbere	42.30	3.07	1974	2	15	74			☺	☺		☺
Tuya et al (2000)	Bell Island and Lime Kiln No take areas	48.33	122.00	1997	15	20	3		☺		☺		
Paddack & Estes (2001)	Big Creek Marine Ecological Reserve	35.68	-121.30	1994	7	14	10			☺	☺	☺	
Harmelin et al. (1995)	Carry-le-Rouet	43.15	5.10	1982	0.01	14	9			☺	☺		☺
Claudet et al.(2006)	Courome no take zone in Cote Bleue Marine Park	43.30	4.50	1995	0.2	16	2			☺	☺		☺
Branch & Odendaal. (2003), Lasiak (1999)	Dwesa	-32.18	28.50	1963	5	10	3		☺		☺		☺
Duran & Castilla (1989)	Estacion costera de investigaciones marinas	-33.30	-71.38	1982	4	3	6	☺	☺		☺		
Borja et al (2006)	Gaztelugatxe	43.44	-2.78	1998	2	5	2		☺		☺	☺	
Paddack & Estes (2001)	Hopkins	36.60	-121.90	1984	3	9	10			☺	☺	☺	
Tuya et al. (2006)	Isla La Graciosa e islotes del norte de lanzarote (Chinijo)	28.06	15.24	1995	1	30	8	☺		☺	☺	☺	
Shears & Babcock (2003), Willis & Anderson. (2003), Willis & Millar. (2005), Willis et al (2003)	Leigh	-36.16	174.48	1977	5	17	21	☺	☺	☺	☺	☺	
Garcia-Rubies & Zabala (1990), Sabates et al. (2003), Sala et al. (1988)	Medes Island	41.60	2.90	1983	1	15	202	☺	☺	☺	☺		
Moreno et al (1986)	Mehuin	-39.24	-73.13	1978	15	8	8		☺		☺		

Guidetti et al (2005)	Miramare mpa	45.50	13.30	1986	1	7	13			☺	☺		☺
Lasiak (1999)	Mkambati	-31.18	30.00	?	15	5	1		☺		☺		☺
Schroeder & Love (2002)	Platform Gail	-34.00	-119.50	1988	0.02	230	3			☺	☺		
Paddack & Estes (2001)	Point Lobos	36.50	-121.90	1963	3	12	10			☺	☺	☺	
Bevilacqua (2006)	Punta Campanella MPA	40.34	14.23	1997	12	6	16	☺	☺		☺		☺
Castilla & Bustamante (1989)	Punta El Lacho	-33.30	-71.38	1982	3	10	3	☺	☺		☺	☺	
Tuya et al (2006)	Punta la Restinga-Mar de las Calmas (El Hierro)	28.06	15.24	1996	1	30	8	☺		☺	☺	☺	
Francour (1996)	Scandola	42.29	8.40	1975	6	17	3			☺	☺	☺	
Bordehore (2003)	Tabarca Island Marine Reserve	38.50	0.60	1989	1	39	32	☺	☺		☺		
Babcock et al (1999), Willis & Millar (2005)	Tawharanui Marine Park	-36.22	174.50	1981	4	22	4		☺	☺	☺	☺	
Willis & Millar (2005)	Te Whanganui a Hei (Hahei)	-36.49	175.47	1992	8	20	2			☺	☺	☺	
Guidetti. (2006)	Torre Guaceto Marine Reserve	40.71	17.79	1992	22	10	26	☺	☺	☺	☺		
Buxton & Smale (1989)	Tsitsikamma	-34.59	23.34	1964	300	25	3			☺	☺		
Michelli et al. (2005)	Tuscan archipelago (Capraia and Giannutri)	43.00	10.30	1989	3	10	1			☺	☺		
Vacchi et al (1988)	Urtica	38.7	13.18	1996	1	30	?			☺			☺
Martell et al (2000)	Whytecliff/Porteau cove no take areas	49.20	-123.30	1993	1	33	1			☺	☺		

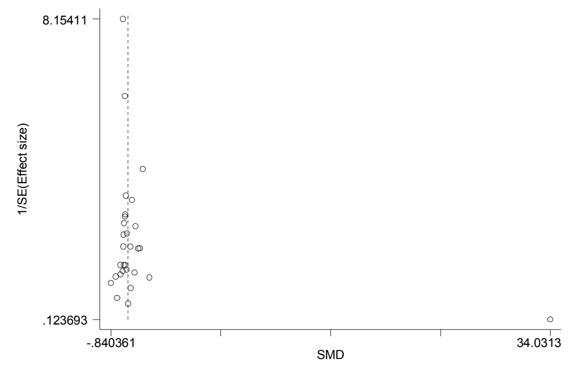
4.3 Meta-analysis

Overall, when data were pooled across species and no-take areas (all species) or average values from each marine reserve were pooled (all reserves), meta-analyses on all biota and outcome measures illustrate moderate to large statistically significant effects and heterogeneity irrespective of the effect-size metric (Table 3). Averaging species (and deriving variance across species within a reserve) prior to pooling always increased the magnitude of the effect.

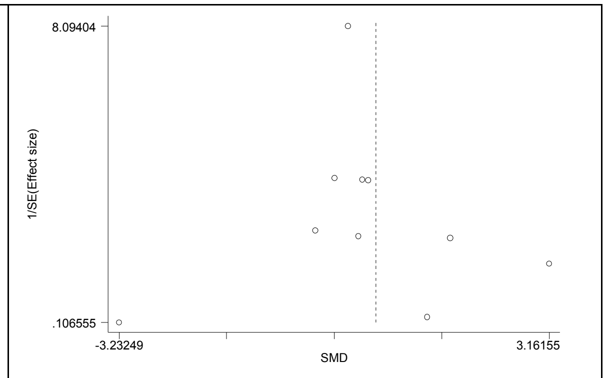
Density is 24% - 58% higher within no-take areas than outside reserves at the species level. The reserve-level estimate of 23% - 196% may be an overestimate as failsafe n is low and there is some evidence of funnel plot asymmetry with fewer small negative studies than positive studies (Figure 1). Both estimates of the difference in biomass are potentially overestimates as the failsafe n was low and there is evidence of funnel plot asymmetry (fewer small negative studies than positive studies: Figure 1). However, both point estimates indicate differences in biomass of >100% with the lowest 95% CI indicating a 20% increase. Species richness is 10% - 48% higher within no-take areas than outside at the species level. The reserve level estimate of 23% - 130% may be an overestimate as failsafe n is low and there is evidence of funnel plot asymmetry (fewer small negative studies than positive studies: Figure 1).

Table 3. Species level and Reserve level pooled effects summary statistics, density, biomass, species richness. N in parentheses indicates sample sizes for lnRR analysis. asterix indicate failsafe number > 5n + 10.

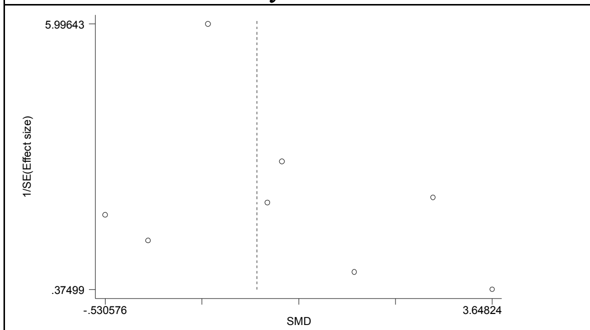
Model		Pooled effects					Heterogeneity		Fail safe
	n	Hedge's *d*	95% CI	*p*	lnRR	95% CI	*Q*	*p*	n
Density-all species	481 (360)	0.293	0.21 - 0.376	<0.001	0.335	0.213 - 0.457	1366.50	<0.001	3848*
Density-all reserves	29	0.529	0.262 - 0.796	<0.001	0.645	0.206 - 1.085	76.96	<0.001	64
Biomass-all species	29 (23)	0.571	0.277 – 0.865	<0.001	1.0327	0.413 - 1.653	92.74	<0.001	70
Biomass-all reserves	10 (8)	0.585	0.125 – 1.044	<0.013	0.727	0.184 - 1.27	40.35	<0.001	18
Species richness-all species	13	0.804	0.311 – 1.296	<0.001	0.242	0.094 - 0.390	59.16	<0.001	87*
Species richness-all reserves	8	1.109	0.308 – 1.91	<0.007	0.521	0.208 - 0.834	41.91	<0.001	50*



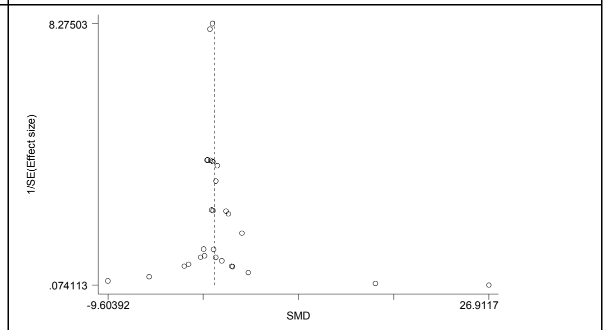
Reserve level: density



Reserve level: biomass



Reserve level: Species richness



Species level: biomass

Figure 1. Funnel plots illustrating the relationship between effect size and inverse variance for parameters where failsafe number ≠ 5n + 10 (N.B. species richness is borderline).

Density

Subgroup analyses illustrate overlap between the pooled effects of algae (Hedge's *d*, 0.302, 95%CI 0.021 – 0.584, *p<0.035*), invertebrates (Hedge's *d*, 0.161, 95%CI -0.124 – 0.447, *p*<0.267) and fish (Hedge's *d*, 0.317, 95%CI 0.229 – 0.406, *p<0.001*). The confidence intervals for invertebrates cross zero but statistically significant heterogeneity remains present within each group (*p<0.001,* Figures 2, 3, 4).

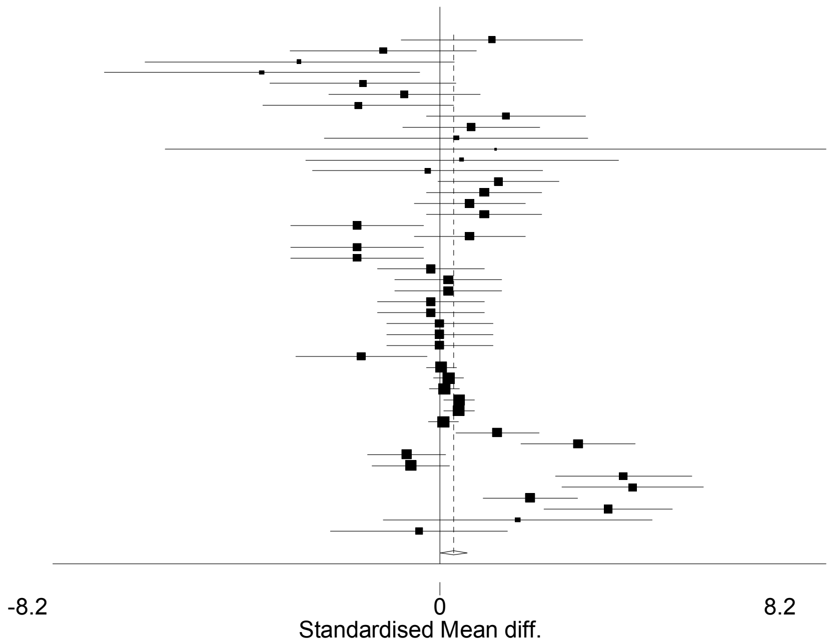


Figure 2. Forrest plot illustrating the variation in individual species effect sizes based on algal density. The x axis is standardised mean difference. The solid vertical line represents the line of no effect (0); the stippled line and diamond indicate the pooled effect. Box size is related to sample size, error bars are 95% confidence intervals.

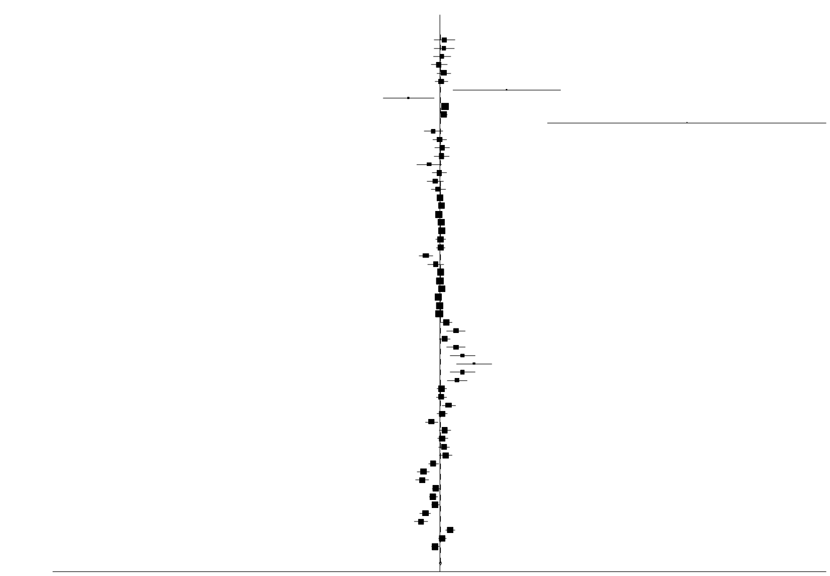


Figure 3. Forrest plot illustrating the variation in individual species effect sizes based on invertebrate density. The x axis is standardised mean difference. The solid vertical line represents the line of no effect (0); the stippled line and diamond indicate the pooled effect. Box size is related to sample size, error bars are 95% confidence intervals.

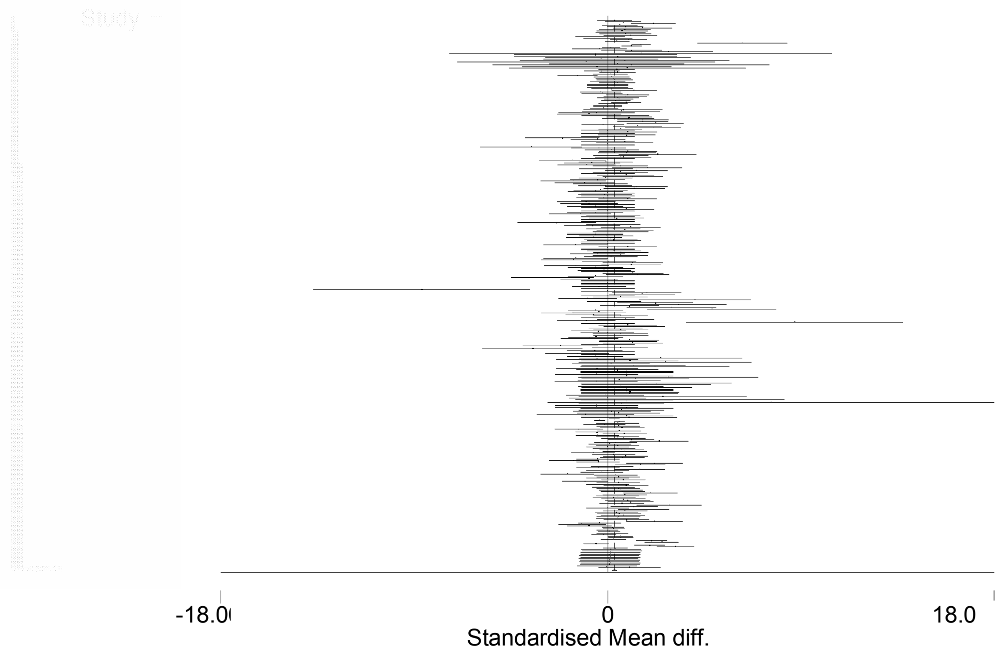


Figure 4. Forrest plot illustrating the variation in individual species effect sizes based on fish density (3 outliers not displayed). The x axis is standardised mean difference. The solid vertical line represents the line of no effect (0); the stippled line and diamond indicate the pooled effect. Box size is related to sample size, error bars are 95% confidence intervals.

Analysis based on aggregating taxa (n=number of taxa) within reserves for algae, invertebrates and fish results in non-significance for both algae (Hedge's *d* 0.103, 95%CI -0.349 – 0.555, $p > 0.65$) and invertebrates (Hedge's *d* 0.271, 95%CI -0.14 – 0.683, $p > 0.19$). The effect size for fish density alone remains biologically significant (Hedge's *d* 0.311, 95%CI 0.107 – 0.513, $p < 0.004$, Figure 5). This is equivalent to ln rr 0.448 (95%CI 0.303 - 0.593, n=260, failsafe 3340), or a 57% increase in fish density (based on the point estimate).

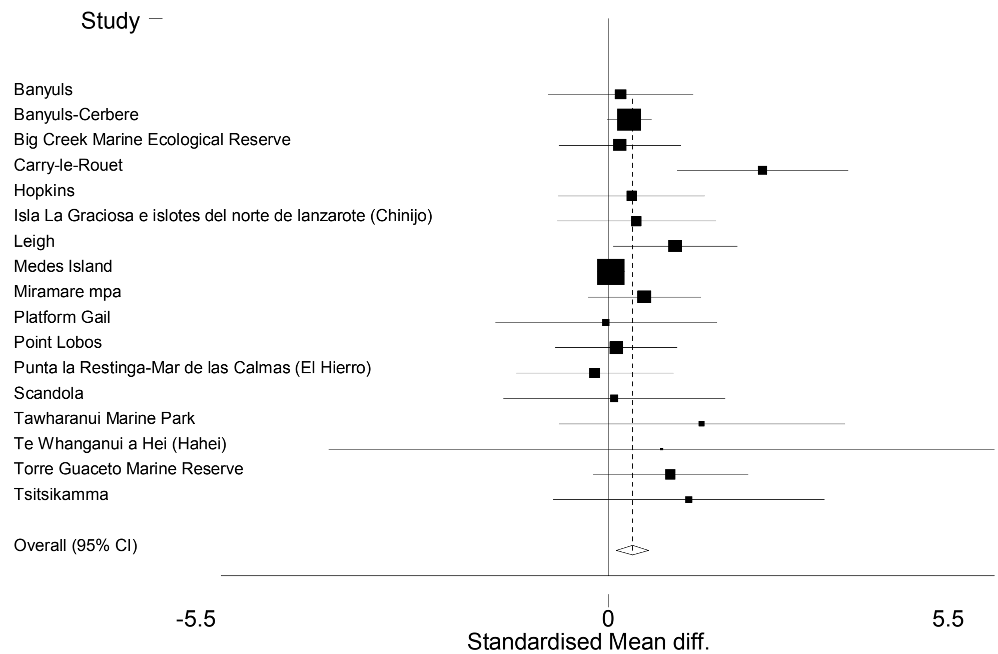


Figure 5. Forrest plot illustrating the variation in reserve density effect sizes based on fish effects sizes pooled (n=taxon) (3 outliers not displayed). . The x axis is standardised mean difference. The solid vertical line represents the line of no effect (0); the stippled line and diamond indicate the pooled effect. Box size is related to sample size, error bars are 95% confidence intervals.

Further subgroup analyses did not reveal any meaningful variation in fish species pooled effect size in relation to mobility ('migratory' Hedge's *d* 0.460, 95%CI 0.151 – 0.77 and 'non-migratory' Hedge's *d* 0.308, 95%CI 0.217 – 0.40). Aggregating migratory species that occur multiple times increases the magnitude of the effect but does not change this relationship (Hedge's *d* 0.791, 95%CI 0.204 – 1.38).

No-take zones did not have significantly increased densities of pelagic fish species. Benthopelagic, demersal and reef associated fish species show significantly greater densities in no-take zones but cannot be distinguished from each other due to overlapping confidence intervals (benthopelagic Hedge's *d* 0.5, 95%CI 0.260-0.740; demersal Hedge's *d* 0.263, 95%CI 0.111-0.415; pelagic Hedge's *d* 0.164, 95%CI -0.110-0.438; reef associated Hedge's *d* 0.266, 95%CI 0.094-0.438). However, analysis based on aggregating taxa (n=number of taxa) within no take areas results in confidence intervals crossing zero for all groups except demersal species, partly due to small sample sizes, with only two no-take areas (Banyuls-Cerebere and Medes Island) containing pelagic species (Pelagic Hedges *d* 0.214, 95%CI -0.331 - 0.76, benthopelagic Hedges *d* 0.065, 95%CI -0.397 - 0.528, reef associated Hedges *d* 0.023, 95%CI -0.271 - 0.317, demersal Hedges *d* 0.275, 95%CI 0.037 – 0.513, $p<0.025$) (Figure 6).

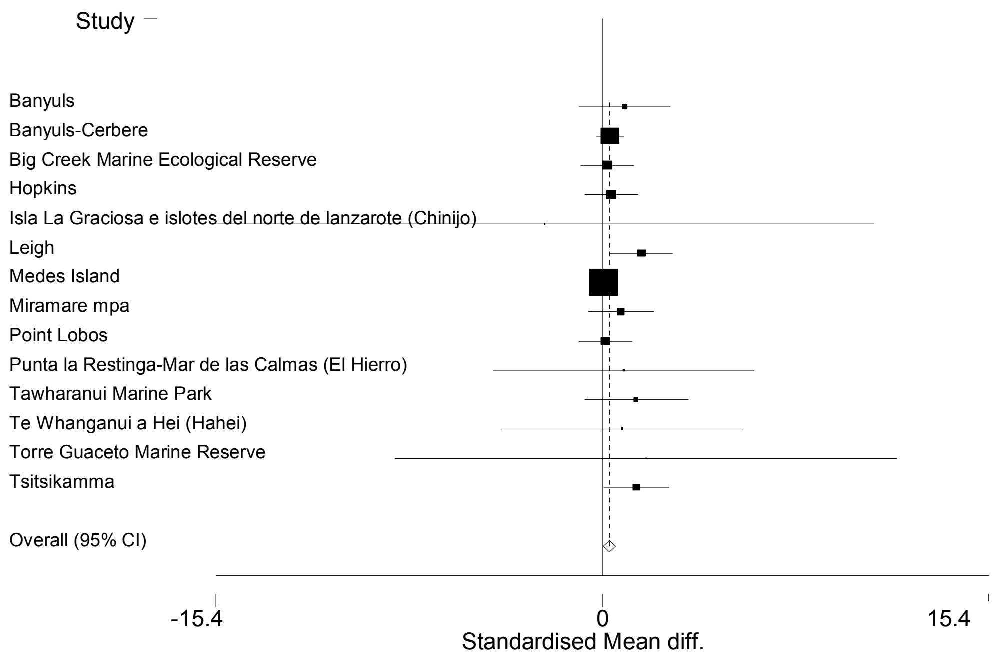


Figure 6. Forrest plot illustrating the variation in reserve level effect sizes based on Demersal fish species density. Demersal species within no take areas were pooled (n=number of taxa) prior to meta-analysis. . The x axis is standardised mean difference. The solid vertical line represents the line of no effect (0); the stippled line and diamond indicate the pooled effect. Box size is related to sample size, error bars are 95% confidence intervals.

Similarly, no-take areas did not show significantly increased densities of highly commercial species. Subsistence fished, minor commercial and commercial species all show significantly increased densities within no-take zones, but cannot be distinguished from each other as the confidence intervals overlap (subsistence Hedge's *d* 0.457, 95%CI 0.143 – 0.772; minor commercial Hedge's *d* 0.231, 95%CI 0.043 – 0.419; commercial Hedge's *d* 0.448, 95%CI 0.287 - 0.609; highly commercial Hedge's *d* 0.21, 95%CI -0.191 – 0.610) (Figure 8). Aggregating highly commercial species that occur multiple times increases the magnitude of the effect but does not change this relationship (Hedge's *d* 0.871, 95%CI -0.07 – 1.814).

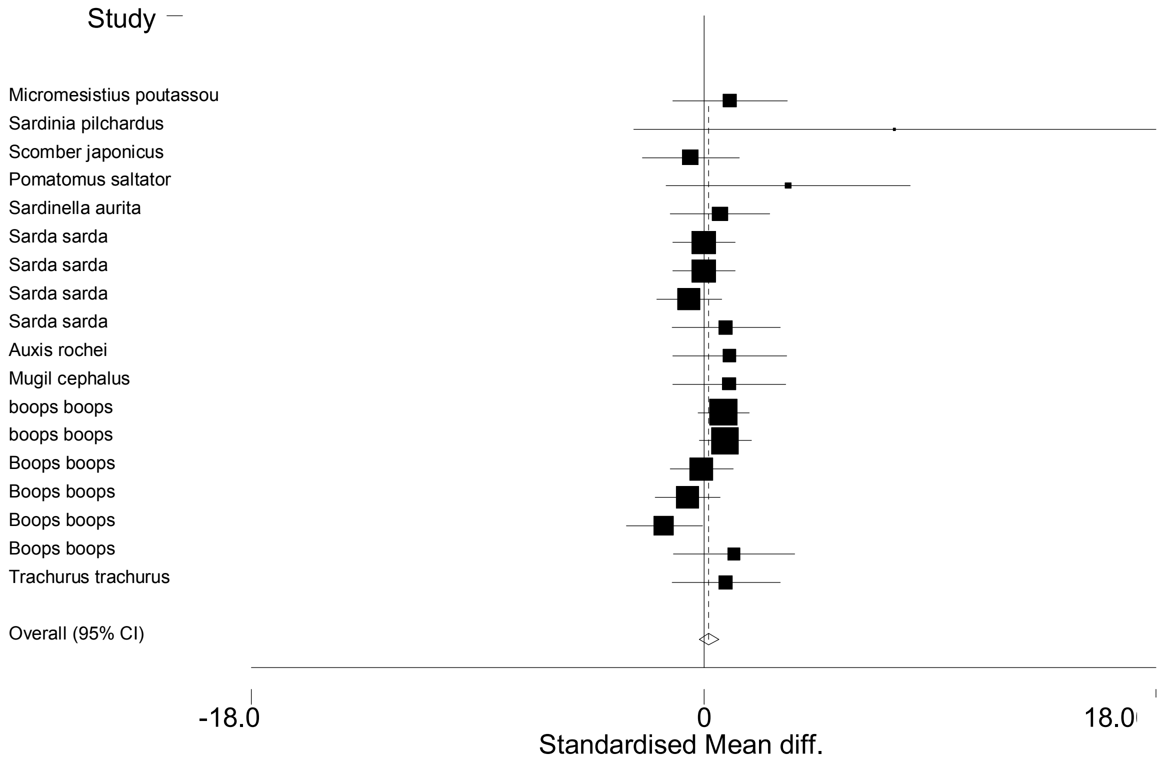


Figure 8. Forrest plot illustrating the effect sizes of highly commercial species (note that many of these species are also pelagic). The x axis is standardised mean difference. The solid vertical line represents the line of no effect (0); the stippled line and diamond indicate the pooled effect. Box size is related to sample size, error bars are 95% confidence intervals.

No-take areas did not significantly increase the density of species that inhabit artificial reefs or breakwaters. Reefs, rock and sand, and non-reef rock habitats were all associated with an increase in the density of fish. There is little evidence of variation in effectiveness between different habitats although non-reef rock habitats have larger effects than sand and rock or reef habitats (artificial Hedge's d 0.189, 95%CI -0.043 – 0.421; reef Hedge's d 0.244, 95%CI 0.168 – 0.321; non reef rock Hedge's d 0.739 (95%CI 0.503 - 0.975 df 127), sand and rock Hedge's d 0.375, 95%CI 0.250 – 0.500).

Variation in the effect size of fish species was statistically related to maximum body length (median 44.5cm, range 4.3-200) but the coefficient is so small as to be biologically meaningless (coeff 0.003, $p<0.02$), whereas resilience (measured as K *sensu* Froese & Pauly 2006), median 0.28, range 0.05-2.9) has a moderate coefficient but lacks statistical significance (coeff -0.289, $p<0.123$). Fish species-level variation therefore remains largely unexplained.

Reserve-level co-variates were explored in relation to species density effect sizes averaged across no-take areas. A very small but statistically significant relationship exists between the size of no-take areas and reserve-level effect size (coeff 0.004, 95% CI 0.001 – 0.007, z 2.82, n 29, *p*<0.006) All other reserve parameters were not statistically significant and coefficients were all <0.1.

Biomass

Biomass subgroup analyses illustrated overlap between the pooled effects of algae (Hedge's *d* 0.97, 95%CI -0.33 – 2.26, n=7, *p<0.144*), invertebrates (Hedge's *d* 1.755, 95%CI 1.275 – 2.235, n =2, *p<0.001*) and fish (Hedge's *d* 0.302, 95%CI 0.201 – 0.403, *p<0.001*). The confidence intervals for algae cross zero but statistically significant heterogeneity remains present within each group (*p<0.001*).

Reserve level co-variates were explored in relation to fish biomass effect sizes averaged across reserves. A small negative and statistically significant relationship exists between reserve size and reserve level effect size (coeff -0.223, 95% CI -0.42 – -0.26, z 2.22, n 10, *p*<0.026). There is also a small negative relationship with depth (coeff -0.117, 95%CI -0.21 –0.024, z -2.47, n 10, *p<0*.015). Insufficient data were available to ascertain if this relationship is confounded by fish length or resilience.

Species richness

Species richness subgroups demonstrate overlap between the pooled effects of invertebrates (Hedge's *d* 2.459, 95%CI 0.111 – 4.807, n=2, *p*<0.04) and fish (Hedge's *d*, 0.753, 95%CI -0.225 – 1.529, *p<0.056*). The confidence intervals for fish cross zero. No further analyses were undertaken due to the small sample sizes.

Taxonomic quasi-replication

Taxonomic quasi-replication was explored using the large fish density dataset. Pooling fish species density within genera results in an increased effect size compared to the integration of all species across reserves or averaging species and pooling across reserves: (hedges *d* 0.471 (95% CI 0.204 – 0.739), *p*<0.001, lnrr 0.621 (95% CI 0.307 – 0.935) n 50, failsafe n 277.8) equating to an 86% increase in density (Figure 10). Disaggregation of the data to species level is therefore a conservative method of estimating reserve effects.

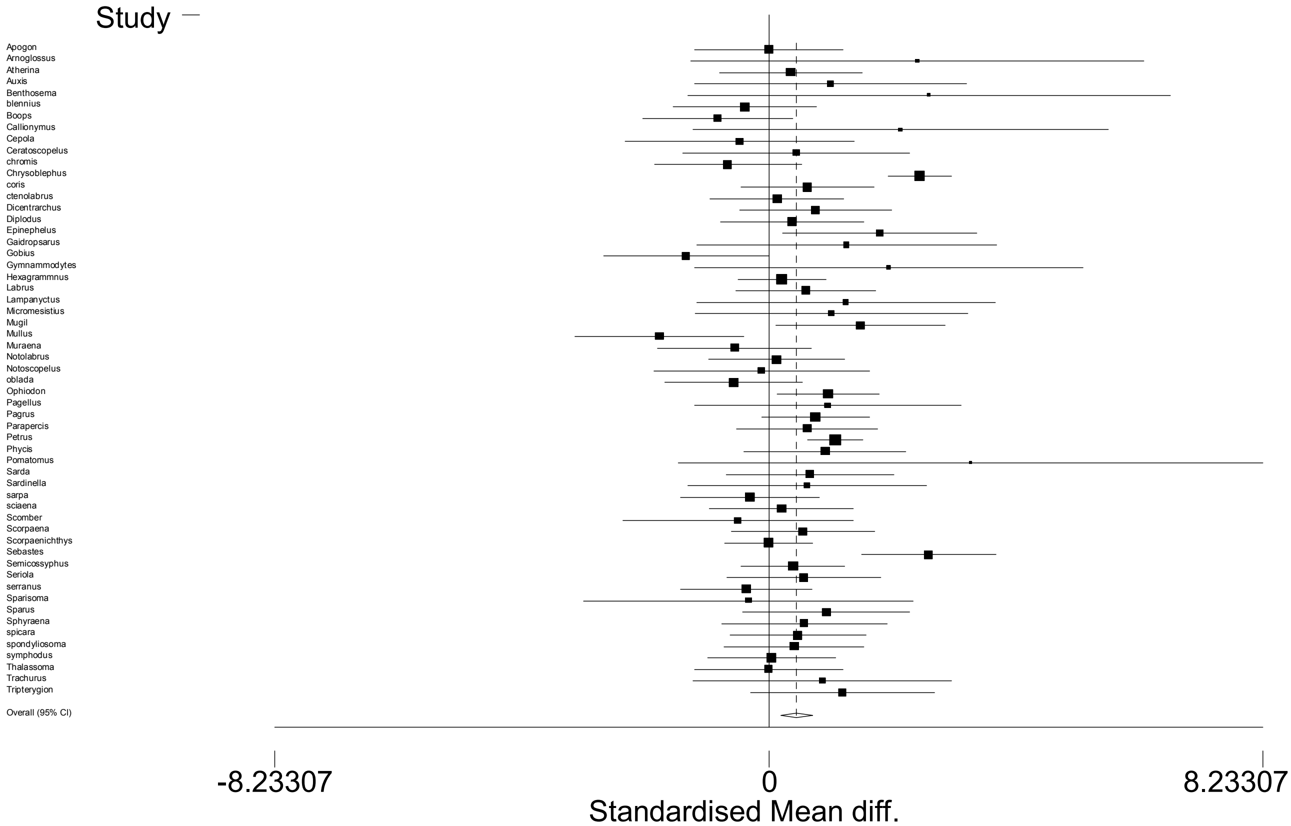


Figure 10: Forrest plot aggregating species by genera. *Sardinella* outlier has been removed from the plot for clarity. The x axis is standardised mean difference. The solid vertical line represents the line of no effect (0); the stippled line and diamond indicate the pooled effect. Box size is related to number of taxa, error bars are 95% confidence intervals.

Power analysis

Power analyses demonstrated that 30 marine reserves areas are sufficient for the detection of an effect size of 0.83 at alpha 0.05, beta 0.7 based on a single tailed distribution without meta-analytical pooling (Figure 11). However, >1000 no-take areas would be needed to detect small effects (0.2) at alpha 0.01 with beta 0.8. Alternatively, >400 no take areas are needed to detect small effects at alpha 0.05 with beta 0.7 based on conservative single tailed analysis (Figure 11).

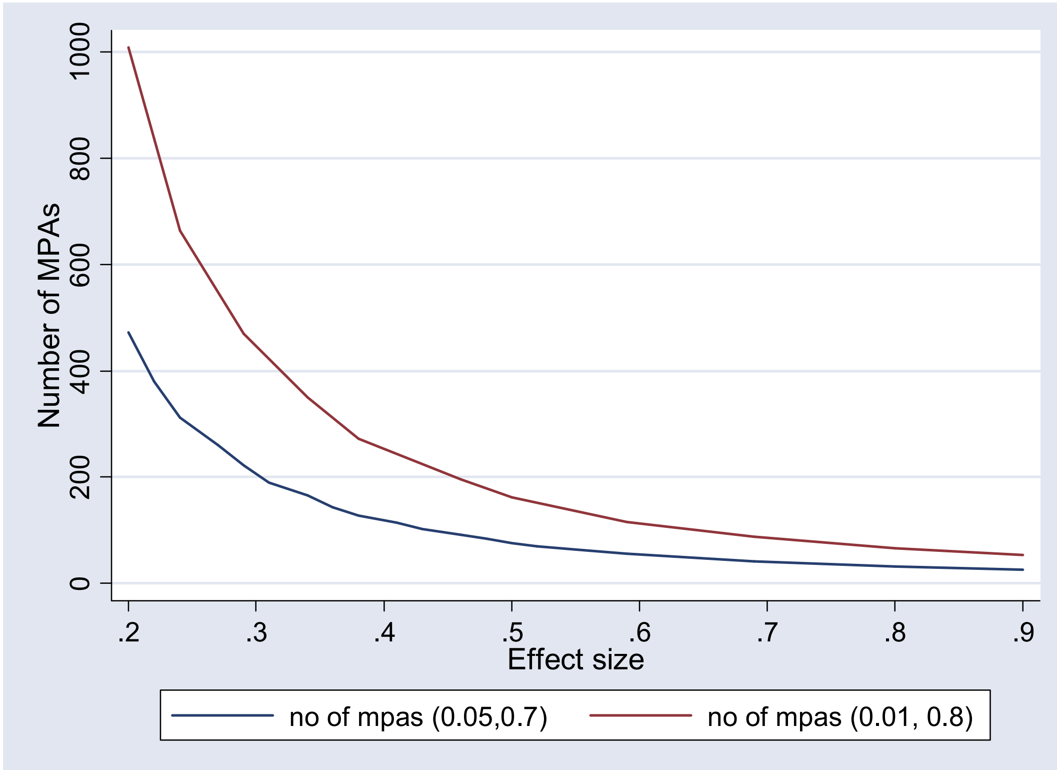


Figure 11. Power curves illustrating the ability of a single tailed test to detect statistically significant differences (p<0.05) at power 0.7/0.8 with differing numbers of marine protected areas.

5. DISCUSSION

5.1 Evidence of effectiveness

In the context of the original review question the available evidence is insufficient to evaluate the effectiveness of temperate no-take zones for maintaining sustainable fisheries through the provision of overspill effects. There are biologically and statistically significant differences between the density, biomass and richness of biota inside and outside no take areas. Density and biomass of fish species are both higher in no-take than in adjacent areas. Other relationships are less clear. It is immediately apparent that few of the studies undertaken to date have been designed to address the potential for no-take areas to enhance adjacent fisheries. Here we assess the strength of evidence based on consideration of the following six areas:

1. Study quality:

Only one of the studies included in the analysis presented BACI data. As a result, it is problematic to attribute the differences between no-take areas and adjacent controls to the establishment of the reserve. Confounded baselines have been identified as barriers to the interpretation of MPA studies previously (Willis et al. 2003) and they remain a hindrance in this analysis. Proponents of MPAs argue they are effective citing the large effects (e.g. Halpern 2003; Halpern *et al.* 2004) whilst others cite the potential for habitat confounding (Willis et al. 2003; Edgar et al. 2004). This controversy can only be satisfactorily addressed by further monitoring incorporating assessment of change from baseline conditions. Results of analyses based on standardised mean difference and response ratios are generally consistent and suggest that variation in sampling methods and pseudoreplication do not distort the pooled effect although they may hinder interpretation of individual reserve estimates and limit inference to individual reserves unless meta-analyses are used to combine the data.

2. The size and significance of the observed effects:

Overall pooled effect sizes are moderate to large and biologically as well as statistically significant. However, small sample sizes are problematic particularly with respect to algae, invertebrates, biomass and species richness metrics. Fish density data are more robust but even here there are confounding effects (e.g. pelagic species cannot be separated from highly commercial species) and small sample sizes limit the ability to generalise across specific groups (e.g. only two studies provide data on pelagic species and no reserves are located within entirely soft sediment systems).

Pooling increases the magnitude of effect sizes for both taxonomic and reserve level analyses. This suggests that genera with large responses integrate only a few species, whereas genera with small responses incorporate many species. Likewise, studies that quantified the responses of a few species have smaller species responses than studies that measure many species. However, the number of taxa was not related to effect size in density meta-regressions. An alternative explanation is that pooling across species increases the pooled effect by reducing variance. This suggests that combining different species is combining “apples and oranges” as individual species have unique responses. Nonetheless, quasi-replicated data has smaller effect sizes than ecologically biased (aggregated) data and thus offers a conservative estimate of the pooled effects which remain moderate to large.

3. The consistency of effects across reserves

There is considerable heterogeneity between reserves and this is largely unexplained by reserve or species level parameters. It is therefore difficult to predict the impact of a proposed no-take area based on any physical, geographic or biological parameter reported in the available studies. This uncertainty is expressed in the wide confidence intervals of the pooled effects of subgroups and subsequent lack of distinction between them.

4. Confounding effects of unknown exploitation levels

The intensity of the resource exploitation before reserve implementation, in the surrounding waters, and within the reserve where enforcement is variable is generally unknown or unreported. It is probable that this is a major cause of some of the unexplained variation among studies.

5. Inference of observed effects

There is no substantial **indirect** evidence that strongly supports or refutes the inference that temperate marine reserves increase the density, biomass and species richness of marine biota within the reserve. However, studies of partially protected marine reserves provide evidence that enhancement occurs as a result of excluding certain types of fishing (Blyth-Skyrme et al. 2006; Murawski et al. 2000). Furthermore protected areas can increase the density of marine biota outside the reserve boundaries (Gell & Roberts 2003).

6. The lack of other plausible competing explanations of the observed effects

Habitat effects alone could explain the observed results reported herein. Marine Reserves and no-take zones are often established to protect specific habitats and associated species. If these species or habitats are not present in the adjacent control areas, large differences in density, biomass and richness are to be expected that may be entirely attributed to a 'habitat' effect. The negative relationship between reserve size and biomass may be a weak indicator that a habitat effect is plausible as only a small proportion of larger no-take areas is preferred habitat. However, the lack of distinction between reef associated species and habitat, and other species and habitats suggests that habitat effect is not overriding. Lack of power is an alternative explanation for the latter relationship.

5.2 Reasons for variation in effectiveness

Despite considerable heterogeneity between reserves and species very few statistically significant relationships were found between species or reserve parameters and effect size. We speculate that this may be due to confounded fishing effort baselines.

Small sample sizes and lack of power are clearly problematic in some instances, for example pelagic species. Confounding is also an issue. Some confounding factors are known (e.g. there is a large degree of overlap between pelagic and highly commercial species). Others are speculative (e.g. the lack of difference between migratory and non-migratory fish density could be due to juvenile migratory species being attracted into the reserve).

There is a small statistically significant relationship between reserve size and the magnitude of difference in density between MPA and adjacent fished area at a reserve level. The coefficient is very small but reserve size is measured in large units (km^2) and conversion to small units (cm^2) would change the size of the coefficient. Objective interpretation of the ecological significance of this (and the other) statistically significant small coefficients is therefore difficult. These relationships may merit investigation in further work.

5.3 Review limitations

The primary limitations of the review have been imposed by the nature of the evidence-base (see above). However there are also some methodological issues.

No non-English publications were specifically sought and the grey literature search was deliberately designed as a sampling exercise rather than as an exhaustive compilation of all grey literature regarding marine reviews. Funnels plots indicate some potential for publication and language related biases suggesting that we may be overestimating the magnitude of the effects to some degree.

Data extraction was performed by a single reviewer due to resource constraints. Ideally two reviewers would extract data independently to ensure repeatability. In some instances decisions regarding which data to extract and how to combine them may not be repeatable because they involve subjective judgement. Furthermore, although attempts were made to contact authors for missing data, further efforts to obtain and to disaggregate raw data would increase both the quality and repeatability of the analyses.

Additional analyses would also be beneficial. In particular, hierarchical Bayesian meta-analysis could increase the precision of the effect estimates, particularly at a reserve level by "borrowing" strength from the distributions of related species parameters when an individual species was not present in a reserve. Using individual species variance estimates as priors for aggregated species variance estimates at different taxonomic levels could also provide further insights. These analyses are being pursued as a separate work.

Extensions of the dataset to include partially protected marine reserves would allow resource exploitation to be added as a co-variate. Disaggregating data to explore variation in the rate of change might also be fruitful in this context.

6. REVIEWERS' CONCLUSIONS

6.1 Implications for *management / policy / conservation*

The available evidence suggests that temperate MPAs that impose no-take zones may achieve higher densities, biomass and species richness of marine biota within the boundaries of the MPA or no-take zone. The evidence for higher densities and biomass of fish is notable in this context. However, considerable uncertainty and low predictive power arises from small sample sizes and possible confounding factors such as habitat quality.

6.2 Implications for research

Lack of data is a hindrance in the development of an evidence-base regarding the effectiveness of marine protected areas. Small sample sizes result in high uncertainty about the impacts on specific taxa. In particular, algae and invertebrates are understudied; insufficient data are available regarding biomass, species richness, deep water no take areas, pelagic fish species and soft sediment systems. It is also very difficult to distinguish habitat effects from reserve effects without integrated experimental monitoring programs that present data regarding the baseline condition. Large numbers of marine protected areas require monitoring if small effects are to be detected. Data regarding the intensity of resource use are required alongside biological metrics for monitoring to be effective.

7. ACKNOWLEDGEMENTS

The authors would like to thank CEBC colleagues particularly Lisette Buyung-Ali and Diana Bowler for their input. Numerous authors and marine subject experts helpfully responded to our enquiries especially Nick Dulvy and Stuart Rogers. Trevor Willis also contributed useful email exchanges as well as raw data. We also thank the NCEAS meta-analysis working group for many interesting discussions.

8. POTENTIAL CONFLICTS OF INTEREST AND SOURCES OF SUPPORT

There are no potential conflicts of interest to be declared. This review was funded by the UK Natural Environment Research Council.

9. REFERENCES

Adams, D. C., Gurevitch, J. & Rosenberg, M. S. (1997). Resampling test for meta-analysis of ecological data. *Ecology,* **78:** 1277–1283.

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

Ballantine, W.J. (1992). *The practicality and benefits of a marine reserve network. Submitted to the workshop on managing marine fisheries by limiting access*. Center for Marine Conservation and the World Wildlife Fund. Annapolis, U.S.A.

Blyth-Skyrme R.E., Kaiser M.J., Hiddink J.G., Edwards-Jones G. & Hart P.J.B. (2006). Conservation benefits of a marine protected area vary with fish life-history parameters. *Conservation Biology,* **20:** 811-820. doi: 10.1111/j.1523-1739.2006.00345.x

Bohnsack, J.A. (1996). "Maintenance and recovery of reef fishery productivity". Pp. 283-313, in: Polunin & C.M. Roberts (eds.) *Reef Fisheries*. N.V.C., Fish and Fisheries Series 20, Chapman and Hall, London, U.K..

Bradshaw, C., Veale, L.O., Hill, A.S. & Brand, A.R. (2001). The effect of scallop dredging on Irish Sea Benthos: experiments using a closed area. *Hydrobiologia,* **465:** 129-138.

Bray, J.R. & Curtis, J.T. (1957). An ordination of the upland forest communities of southern Winsconsin. *Ecological Monographs*, **27**: 325-349.

Claudet, J., Osenberg, C.W., Benedetti-Cecchi, L. et al. (2008). Marine reserves: size and age do matter. *Ecology Letters*, doi:10.1111/j.1461-0248.2008.01166.x

Coleman, F.C., Baker, P.B. & Koenig, C.C. (2004). A review of Gulf of Mexico marine protected areas: Successes, failures, and lessons learned. *Fisheries,* **29**(2): 10–21.

Cooper, H. & Hedges, L.V (Eds.). (1994). *The Handbook of Research Synthesis*. Russell Sage Foundation, New York.

COMPASS and NCEAS (National Center for Ecological Analysis and Synthesis), (2001). *Scientific Consensus Statement on Marine Reserves and Marine Protected Areas.* Available at: http://www.nceas.ucsb.edu/Consensus

Conner, D.W., Allen, J.H., Golding, N., Howell, K.L., Lieberknecht, L.M., Northen, K.O., & Reker, J.B. (2004). *The Marine Habitat Classification for Britain and Ireland Version 04.05*. JNCC, Peterborough. ISBN 1 861 07561 8 (internet version).

DerSimonian, R., & Laird, N. (1986). Meta-analysis in clinical trials. *Controlled. Clinical Trials* 7: 177-188.

Dugan, J. E. & Davis, G.E., (1993). Applications of marine refugia to coastal fisheries management. *Canadian Journal of Fisheries and Aquatic Sciences,* **50**: 2029-2042.

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 (1): 107-144.

Edgar, G. J., Bustamante, R.H., *et al*. (2004). Bias in evaluating the effects of marine protected areas: the importance of baseline data for the Galapagos Marine Reserve. *Environmental Conservation,* **31**(3): 212-218.

Egger, M., Davey-Smith, G., Schneider, M. & Minder, C. (1997). Bias in meta-analysis detected by a simple graphical test. *British Medical Journal* **315**: 629-34.

FAO (1994). Review of the state of world marine fishery resources. *FAO Fisheries Technical Paper*, **335**: 1-136.

Froese, R. & Pauly. D. (eds.). (2006). FishBase. http://www.fishbase.org.

Gerber, L.H., Hyrenbach, D., Zacharias, M.A. (2005). Do the largest protected areas conserve whales or whalers? *Science,* **307**: 525-526.

Gell, F.R. & Roberts, C.M. (2003). Benefits beyond boundaries: the fishery effects of marine reserves and fishery closures. *Trends in Ecology and Evolution,* **18**: 448-455.

Goldberg, D.E., Rajaniem, T., Gurevitch, J. & Stewart-Oaten, A. (1999). Empirical approaches to quantifying interaction intensity: competition and facilitation along productivity gradients. *Ecology,* **80**: 1118-1131.

Halpern, B.S. & Warner, R.R. (2002). Marine Reserves have rapid and lasting effects. *Ecology Letters*, **5**: 361-366.

Halpern, B.S. (2003). The impact of marine reserves: Do reserves work and does reserve size matter? *Ecological Applications,* **13**(1): 117-137.

Halpern, B.S., Gaines, S.D., & Warner, R.R. (2004). Confounding effects of the export of production and the displacement of fishing effort from marine reserves. *Ecological Applications,* **14**: 1248-1256.

Harvey, P. H. & Pagel, M.D. (1991). *The comparative method in evolutionary biology*. Oxford University Press, Oxford.

Hedges, L. V., Gurevitch, J. & Curtis, P. S. (1999). The meta-analysis of response ratios in experimental ecology. *Ecology,* **80:** 1150–1156.

Hilborn, R., Stokes, K., Maguire, J.J., Smith, T., Botsford, L.W. *et al.* (2004). When can marine reserves improve fisheries management? *Ocean & Coastal Management,* **47**(3–4): 197–205.

Kaiser M.J**.** (2005). Are Marine Protected Areas a red herring or fisheries panacea? *Canadian Journal of Fisheries and Aquatic Science,* **62:** 1194-1199.

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.

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

Lipsey, M.W., & Wilson, D.B. (2001). *Practical Meta-analysis*. Sage Publications, California, U.S.A.

Lizaso, J.L., Goni, R., Renones, O., Garcia Charton, J.A., Galzin, R., Bayle, J.T., Sanchez Jerez, P., Perez Ruzafa, A. & Ramos, A.A. (2000). Density dependence in marine protected populations: a review. *Environmental Conservation,* **27**: 144-158.

Lourie, S.A. & Vincent, A.C.J. (2004). Using Biogeography to Help Set Priorities in Marine Conservation. *Conservation Biology,* **18** (4): 1004–1020.

Micheli, F., Halpern, B.S., Botsford, L.W. & Warner, R.R. (2004). Trajectories and correlates of community change in no-take reserves. *Ecological Applications,* **14**: 1709-1723.

Millenium Ecosystem Assessment (2005). *Marine Fisheries Systems.* Chapter 18. 479-506. Available at: http://www.maweb.org.

Mosquera, I., Côté, I.M.,, Jennings, S., & Reynolds, S (2000). Conservation benefits of marine reserves for fish populations *Animal Conservation,* **3**: 321-332.

Murawski, S.A., Brown, R., Lai, H.-L., Rago, P.J. & Hendrickson, L. (2000). Large-scale closed areas as a fishery management tool in temperate marine systems: the Georges Bank experience. *Bulletin of Marine Science*, **66**(3):775-798.

Nilsson, P. (1998). *Criteria for the selection of marine protected areas: Report 4834*. Swedish Environmental Protection Agency, Stockholm, Sweden.

Nowlis, J.S. & Roberts, C.M. (1997). “You can have your fish and eat it too: theoretical approaches to marine reserve design”. Pp. 1907-1910, in: H. Lessios & I.G. Macintyre (eds.), *Proceedings of the eighth international coral reef symposium Smithsonian (2)*. Tropical Research Institute, Balboa, Republic of Panama.

Osenberg, C.W., Sarnelle, O., Cooper, S.D. & Holt, R.D. (1999). Resolving ecological questions through meta-analysis: goals, metrics and models. *Ecology* **80**: 1105–1117.

PDT [Plan Development Team] (1990). The potential of marine fisheries reserves for reef fish management in the U.S. Southern Atlantic. Contribution no. CRD/89-90/04. *NOAA Technical Memorandum NMFS-SEFC-261.*

Pullin, A.S. & Stewart, G.B. (2006). Guidelines for systematic review in conservation and environmental management. *Conservation Biology,* **20**(6): 1647-1656.

Rosenberg, M.S., Adams, D.C. & Gurevitch, J. (2000). *MetaWin: statistical software for meta-analysis with resampling tests.* Sunderland, MA: Sinauer Associates.

Rosenthal, R. (1979). The file drawer problem and tolerance for null results *Psychological Bulletin,* **86**: 638-641.

Sharp, S. (1998). Meta-analysis regression: statistics, biostatistics, and epidemiology. *Stata Technical Bulletin* **42**: 16–22.

Steele, JH & Beet, AR (2003). 'Marine protected areas in 'nonlinear' ecosystems', *Proceedings of the Royal Society of London*, 270 B: S230-S3.

Stevens, A. & Milne, R. (1997). “The effectiveness revolution and public health”. Pp. 197-225, in: G. Scally (ed.), *Progress in Public Health*. Royal Society of Medicine Press, London.

Thompson, S. G., & Sharp, S.J. (1999). Explaining heterogeneity in meta-analysis: a comparison of methods. *Statistics in Medicine* 18: 2693-708.

Williams, J.C., ReVelle, C.S. & Levin, S.A. (2004). Using mathematical optimization models to design nature reserves. Frontiers in Ecology and the Environment, 2: 98–105.

Willis, T.J., Millar, R.B., Babcock, R.C. & Tolimieri, N. (2003) Burdens of evidence and the benefits of marine reserves: putting Descartes before des horse? *Environmental Conservation,* **30**(2): 97–103.

Wolff, W. J. 1992. Ecological developments in the Wadden Sea until 1990. *Netherlands Institute for Sea Research Publication Series*, **20**:23-32.

Studies included in Meta-analysis

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

Bell, J.D. (1983). Effects of depth and marine reserve fishing restrictions on the structure of a rocky reef fish assemblage in the northwestern Mediterranean. *Journal of Applied Ecology,* **20**: 357-69.

Bevilacqua, S., Terlizza, A., Fraschetti, S., Russo, G.F., & Boero, F. (2006). Mitigating human disturbance: can protection influence trajectories of recovery in benthic assemblages? *Journal of Animal Ecology,* **75**: 908-920.

Bordehore, C., A. A. Ramos-Espla, and R. Riosmena-Rodriguez. (2003). Comparative study of two maerl beds with different otter trawling history, southeast Iberian Peninsula. *Aquatic Conservation - Marine and Freshwater Ecosystems,* **13**:S43-S54.

Borja, A., I. Muxika, and J. Bald. (2006). Protection of the goose barnacle Pollicipes pollicipes, Gmelin, 1790 population: the Gaztelugatxe Marine Reserve (Basque Country, northern Spain). *Scientia Marina,* **70**: 235-242.

Branch, G. M., and F. Odendaal. (2003). The effects of marine protected areas on the population dynamics of a South African limpet, Cymbula oculus, relative to the influence of wave action. *Biological Conservation*, **114**: 255-269.

Buxton, C.D., Smale, M.J. (1989). abundance and distribution of three temperate marine reef fish in exploited and unexploited areas off the southern cape coast. *Journal of Applied Ecology,* **26**: 441-51

Buxton, C.D., Smale, M.J. (1989). Abundance and distribution of three temperate marine reef fish in exploited and unexploited areas off the southern cape coast. *Journal of Applied Ecology*, **26**: 441-52.

Castilla, J.C. and Bustamante, R.H. (1989). Human exclusion from rocky intertidal of Las Cruces, central Chile: effects on Durvillaea Antarctica (Phaeophyta, Durvilleales). *Marine Ecology Progress Series*, **50**: 203-214.

Castilla, J.C. and Durán, L.R. (1985).Human exclusion from the ocky intertidal zone of central Chile: the effects on Concholepas concholepas (Gastropoda). *Oikos,* **45**: 391-399.

Claudet, J. Et al. (2006). Assessing the effect of mpa on a reef fish assemblage in a NW Mediterranean reserve: identifying community based indicators. *Biological Conservation*, **130**: 349-369.

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

Duran, L.R., & Castilla (1989). Variation and persistence of the middle rocky intertidal community of central Chile, with and without human harvesting. *Marine Biology*, **103**: 555-562.

Francour, P. (1996). L'Ichtyofaune de l'herbier à Posidonia oceanica dans le reserve marine de Scandola (Corse, Méditerranée Nord-Occidentale): Influence des mesures de protection. *Journal de Recherche Océanographique*, **21**: 29-34.

Garcia-Rubies, A., & Zabala, M. (1990). Effects of total fish prohibition of the rocky fish assemblages of Medes Islands Marine Reserve (NW Mediterranean). *Scienta Marina,* 54: 317-328.

Guidetti, P. (2006). Marine reserves re-establish lost predatory interactions and cause community changes in rocky reefs. *Ecological Applications,* **16**:963-976.

Guidetti, P., L. Verginella, C. Viva, R. Odorico, and F. Boero. (2005). Protection effects on fish assemblages, and comparison of two visual-census techniques in shallow artificial rocky habitats in the northern Adriatic Sea. *Journal of the Marine Biological Association of the United Kingdom,* **85**(2): 247-255.

Guidetti, P. L. (2007). Potential of Marine Reserves to cause community wide change changes beyond their boundaries. *Conservation Biology,* **21**(2):540-545.

Harmelin, J.-G., Bachet, F. and García, F. (1995). Mediterranean marine reserves: Fish indices as tests of protection efficiency. *Marine Ecology Progress Series*, **16**: 233-250.

Lasiak, T. (1999). The putative impact of exploitation on rocky infratidal macrofaunal assemblages: A multiple-area comparison. *Journal of the Marine Biological Association of the United Kingdom*, **79**: 23-34.

Macpherson, E., Biagi, F., Francour, P., García-Rubies, A., Harmelin, J., Harmelin-Vivien, M., Jouvenel, J. Y., Planes, S., Vigliola, L. and Tunesi, L.(1997). Mortality of juvenile fishes of genus Diplodus in protected and unprotected areas in the western Mediterranean Sea. *Marine Ecology Progress Series,* **160**: 135-47.

Martell, S. J. D., C. J. Walters, and S. S. Wallace. (2000). The use of marine protected areas for conservation of lingcod (*Ophiodon elongatus*). *Bulletin of Marine Science,* **66**: 729-743.

Michelli, F.,Benedetti-Cechi, L., Gambaccini, S., Bertocci,J., Borsini, C., Chato Osio, G. and Romano, F. (2005). Cascading impacts, marine protected areas, and the structure of Mediterranean reef assemblages. *Ecological Monographs,* **75**: 81-102.

Moreno, C.A., Lunecke, K.M. and Lépez, M.I. (1986). The response of an intertidal Concholepas concholepas (Gastropoda) population to protection from Man in southern Chile and the effects on benthic sessile assemblages. *Oikos*, **46**: 359-364.

Paddack, M.J., & Estes, J.A. (2001). Kelp forest fish populations in marine reserves and adjacent exploited areas of central California. *Ecological Applications,* **10**: 855-870.

Sabates, A., M. Zabala, and A. Garcia-Rubies. (2003). Larval fish communities in the Medes Islands Marine Reserve (North-west Mediterranean). *Journal of Plankton Research*, **25**:1035-1046.

Sala, E., Ribes, M., Hereu, B., Zabala, M., et al (1998). Temporal variability in abundance of the sea urchins *Paracentrotus lividus* and *Arbacia lixula* in the northwestern Mediterranean: comparison between a marine reserve and an unprotected area. *Marine Ecology Progress Series*, **168**: 135-145.

Schroeder, D. M., and M. S. Love. (2002). Recreational fishing and marine fish populations in California. *California Cooperative Oceanic Fisheries Investigations Reports,* **43**:182-190.

Shears, N. T., and R. C. Babcock. (2003). Continuing trophic cascade effects after 25 years of no-take marine reserve protection. *Marine Ecology-Progress Series*, **246**: 1-16.

Tuya, F., C. Garcia-Diez, F. Espino, and R. J. Haroun. (2006). Assessment of the effectiveness of two marine reserves in the Canary Islands (eastern Atlantic). *Ciencias Marinas*, **32**:505-522.

Tuya, F.C., Soboil, M.L., & Kido, J. (2000). An assessment of the effectiveness of Marine Protected areas in the San Juan Islands, Washington USA. *ICES Journal of Marine Science*, **57**: 1218-1226

Vacchi, M., Bussotti, S., Guidetti, P., & La Mesa, G. (1998). Study of the coastal fish assemblage in the marine reserve of the Ustica Island (southern Tyrrhenian Sea) *Italian Journal of Zoology*, **65**: 281-286.

Willis, T. J., and M. J. Anderson. (2003). Structure of cryptic reef fish assemblages: relationships with habitat characteristics and predator density. *Marine Ecology-Progress Series*, **257**:209-221.

Willis, T. J., and R. B. Millar. (2005). Using marine reserves to estimate fishing mortality. *Ecology Letters,* **8**: 47-52.

Willis, T. J., R. B. Millar, and R. C. Babcock. (2003). Protection of exploited fish 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.