

Biological effects within no-take marine reserves: a global synthesis

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Marine Ecology Progress Series 384:33–46 (2009)

Table S1. Marine reserve area and percent change in reserve means for the 4 biological variables: biomass, density, organism size and diversity

Country	Marine reserve	Reserve size (km ²)	Bio-mass	Density	Organism size	Species richness	Source
Temperate reserves							
Argentina	Islote Lobos	16		58	-7		Narvarte et al. 2006
Australia	Crayfish Point			23			Pederson & Johnson 2006
	Governor Island	0.6	2300	62	26	-11	Edgar & Barrett 1999
	Maria Island	7	464	131	15	15	Edgar & Barrett 1999, Pederson & Johnson 2006
	Merrett Rifle Range	0.3			5		Keough & Quinn 2000
	Ninepin	0.59	1375	20	14	19	Edgar & Barrett 1999
	Tinderbox	0.53	240	314	17	-3	Edgar & Barrett 1999
Canada	'Ecological reserve'			11	-1		Wallace 1999
	'Prison reserve'			22	15		Wallace 1999
	Duck Islands			4	8		Rowe 2002
	Round Island			522	5		Rowe 2002
	Whytecliff			0			Martell et al. 2000
Chile	Las Cruces	0.044	478	2206	153	100	Oliva & Castilla 1986, Duran & Oliva 1987, Castilla & Bustamante 1989, Duran & Castilla 1989, Manriquez & Castilla 2001, Loot et al. 2005
France	Mehuin	0.006		-77			Moreno et al. 1986
	Carry-le-Rouet	0.85		78		16	Harmelin et al. 1995
	Cerbère-Banyuls	6.5		372	17	17	Bell 1983, Jouvenel & Pollard 2001, Lecchini et al. 2002, Lloret & Planes 2003
	Couronne, Côte Bleue Marine Park	2.1	119	78		120	Jouvenel et al. 2004, Claudet et al. 2006
Italy	Scandola	0.72	112	24	80	15	Francour 1991, 1994, 1996, 2000
	Capraia	15.75		63		-6	Benedetti-Cecchi et al. 2003, Micheli et al. 2005
	Cinque Terre	0.79		60		21	Tunesi et al. 2006
	Giannutri			-6		-2	Benedetti-Cecchi et al. 2003, Micheli et al. 2005
	Miramare	1.21		43		17	Guidetti et al. 2005a,b
	Molarotto Island	5.29		747			Ceccherelli et al. 2006
	Torre Guaceto	1.83		219			Ceccherelli et al. 2006, Guidetti 2006
	Ustica Island	0.65		96		23	Milazzo et al. 2000, La Mesa et al. 2006
New Zealand	Cape Rodney-Okakari Point/Leigh	5.49	442	379	36	-3	McCormick & Choat 1987, Davis 1989, Cole et al. 1990, Babcock et al. 1999, Millar & Willis 1999, Willis et al. 2000, 2003, Shears & Babcock 2002, 2003, Willis & Anderson 2003, Langlois et al. 2005, Willis & Millar 2005

Table S1 (continued)

Country	Marine reserve	Reserve size (km ²)	Percent change			Source
			Bio-mass	Density	Organism size	
					Species richness	
South Africa	Hahei	8.4	555	307	47	Willis & Babcock 2000, Willis et al. 2003, Langlois et al. 2005, Willis & Millar 2005
	Long Island-Kokomohua	6.19		51	27	Cole et al. 2000, Davidson 2001
	Poor Knights Island	18.9	1209	277		MacDiarmid & Breen 1992, Denny et al. 2004
	Tawharanui	3.5	1215	967	20	Babcock et al. 1999, Shears & Babcock 2002, Willis et al. 2003, Langlois et al. 2005, Willis & Millar 2005, Shears et al. 2006
	Tonga Island	18.35		33	24	Davidson et al. 2002
	Betty's Bay	7.41		37		Mayfield et al. 2005
	De Hoop	230		264		Bennett & Attwood 1991
	Dwesa-Cwebe	39	439	139	22	-27 Siegfried et al. 1985, Hockey & Bosman 1986, Lasiak 1993, 2006, Branch & Odenaal 2003
	Hluleka	4				-17 Hockey & Bosman 1986
	Isi laka			-17		-37 Hockey & Bosman 1986
Spain	Tsitsikamma	300	1291	598	20	Buxton & Smale 1989, Buxton 1993, Cowley et al. 2002
	Cabo de Gata	122	152	-15		-9 Garcia-Charton et al. 2004
	Cabo de Palos	18.98	974	95		19 Garcia-Charton et al. 2004
	Cabrera	87.03	232	5		24 Garcia-Charton et al. 2004
	Columbretes Islands	44		714		Goñi et al. 2001
	Gaztelugatxe	1.58	194	248	-3	Borja et al. 2006
	Isla La Graciosa e islotes del norte de Lanzarote	0.01	423	348		Tuya et al. 2006
	Medes Islands	3	178	1270	25	Garcia-Rubies & Zabala 1990, Sala & Zabala 1996, Macpherson et al. 2000, Hereu et al. 2005, Tsounis et al. 2006
	Punta La Restinga-Mar de Las Calmas	1.55	88	127		Tuya et al. 2006
	USA	Anacapa Island, CA	0.137		-23	21
Big Creek, CA		8	-23	72	-1	Paddack & Estes 2000, Yoklavich et al. 2002
Gerstle Cove, CA		0.2		27	27	Fanshawe et al. 2003
Hopkins Marine Station, CA		2.75	188	50	21	Paddack & Estes 2000
Naranganset Bay, RI		1.07		144	100	Rice et al. 1989
Platform Gail de facto reserve, CA		0.129		-22		Schroeder & Love 2002
Point Lobos, CA		3.14	107	27	24	Paddack & Estes 2000
San Diego-La Jolla, CA		2.16		578	15	Parnell et al. 2005
Tropical reserves						
Australia	Heron Island	12		277	12	Craik 1981
	Keppel Islands	1.04	423	17		Evans & Russ 2004
	Lizard Island	9.9		20		Zeller & Russ 1998
	Mandu sanctuary zone	13.49	112	35	33	Westera et al. 2003
	Maud sanctuary zone	21.51	182	-3	15	Westera et al. 2003
	Osprey sanctuary zone	95.13	73	-10	6	Westera et al. 2003
	Palm Islands		194	17		Graham et al. 2003, Evans & Russ 2004, Williamson et al. 2004
Bahamas	Tripcony Bight	5.7		108	3	Pillans et al. 2005
	Whitsunday Islands	4.26	174	19		Graham et al. 2003, Evans & Russ 2004, Williamson et al. 2004
	Willes Island	1.9		221	4	Pillans et al. 2005
Bahamas	Exuma Cays Land and Sea Park	456	344	155	14	Stoner & Ray 1996, Sluka et al. 1997, Chiappone et al. 2000, Lipcius et al. 2001, Mumby et al. 2006
Barbados	Barbados	2.3		68	24	6 Rakitin & Kramer 1996, Chapman & Kramer 1999, Tupper & Juanes 1999
Belize	Glover's Reef	74	1987	55		Acosta & Robertson 2003
	Half Moon Caye	39.25		107	10	Carter & Sedberry 1997
	Hol Chan	2.6	106	79		Polunin & Roberts 1993, Roberts & Polunin 1993, Carter & Sedberry 1997, Williams & Polunin 2000

Table S1 (continued)

Country	Marine reserve	Reserve size (km ²)	Percent change			Source		
			Bio-mass	Density	Organism size		Species richness	
Brazil	Arquipelago	802		10		Floeter et al. 2006		
	Fernando de Noronha	18.2		282		Garla et al. 2006		
Cayman Islands	Cayman Islands marine park zones	0.7		1		Williams & Polunin 2000		
Costa Rica	Manuel Antonio	6.82		65	34	Ortega 1987		
Cuba	Parque Nacional Punta Frances	46		20		Williams & Polunin 2000		
Egypt	Dagal/El-dakal			1		Galal et al. 2002, Ashworth et al. 2004		
	Nakhlet El Tal			5		Galal et al. 2002		
	Ras Atantour/Tantor			65		Galal et al. 2002, Ashworth et al. 2004		
	Ras Mohamad NP	21.1	-34	-15		-7	Roberts & Polunin 1992	
	Ras Nasrani			-20			Galal et al. 2002	
	South Ghargana			83	6	Galal et al. 2002, Ashworth et al. 2004, Ashworth & Ormond 2005		
France	Mayotte Island	5.25	154	-17		1	Letourneur 1996	
Israel	Coral Beach	0.016		-16	102		Epstein et al. 1999	
Jamaica	Pedro Bank		76	22	100		Koslow et al. 1988	
Kenya	Kisite	15	446	277			Watson & Ormond 1994	
	Malindi	6.3		831	9		McClanahan & Muthiga 1988, Kaunda-Arara & Rose 2004	
	Mombasa	10	-4	32	104	100	McClanahan 1994, McClanahan & Kaunda-Arara 1996	
	Watamu	10		587	8		Kaunda-Arara & Rose 2004	
Netherlands Antilles	Saba	0.9	50				Polunin & Roberts 1993	
New Caledonia	Abore Reef	150		79			Ferraris et al. 2005	
	Amedee	2.8	221	171		50	Wantiez et al. 1997	
	Bailly	2.4	44	100		29	Wantiez et al. 1997	
	Larégnère islet	8.5	168	39		30	Wantiez et al. 1997, Chateau & Wantiez 2005	
	Maitre	9	850	350		143	Wantiez et al. 1997	
	Signal	4.3	270	329		90	Wantiez et al. 1997	
Papua New Guinea	Tamane Puli	0.02		45		7	Jones et al. 2004	
Philippines	Alegre	0.2	809	25			Russ et al. 2005	
	Apo Island	0.225	684	141		26	White 1988, Clark et al. 1989, Russ & Alcala 1996, 1998, 2003, Russ et al. 2003, 2004, 2005, Walmsley & White 2003, Abesamis & Russ 2005, Alcala et al. 2005, Abesamis et al. 2006a	
	Balicasag	0.08		35		7	White 1988, Clark et al. 1989, Walmsley & White 2003, Abesamis et al. 2006b	
	Binaliwan	0.085		9			Russ et al. 2005	
	Bolisong	0.1		5			Russ et al. 2005	
	Bongalonan	0.2	2800	10			Russ et al. 2005	
	Cangmating	0.06		-22			Russ et al. 2005	
	Canlucani	0.09		-64			Russ et al. 2005	
	Carbin Reef	2		805	69		Maliao et al. 2004	
	Maca Reef	10		410	80		Maliao et al. 2004	
	Masaplod	0.06		222			Russ et al. 2005	
	Pamilacan Island	0.3		147		27	White 1988, Clark et al. 1989, Walmsley & White 2003	
	Sumilon	0.125	502	122		31	Russ 1985, Alcala 1988, Russ & Alcala 1996, 1998, 2003, Alcala et al. 2005, Russ et al. 2005	
		Sumilon 'outside' ^a	0.375	370	610			Russ & Alcala 1996, 1998
		Tambobo	0.08		1			Russ et al. 2005
	Tandayag	0.06		87			Russ et al. 2005	
Seychelles	Cousin Island	1.2	150				Jennings et al. 1996	
	Sainte Anne	10	67				Jennings et al. 1996	
Solomon Island	Arnavon Islands	83		145	9		Lincoln-Smith et al. 2006	
St. Lucia	Anse Chastanet	0.026	100				Roberts & Hawkins 1997	

Table S1 (continued)

Country	Marine reserve	Reserve size (km ²)	Percent change				Source
			Bio-mass	Density	Organism size	Species richness	
	Soufriere	3.06	62	-3	7	0	Roberts et al. 2001, Hawkins & Roberts 2004, Hawkins et al. 2006
USA	Fort Jefferson, FL	19		55			Davis 1977
	Kealakakua, HI	1.28	24	6		-4	Grigg 1994
	Looe Key Reef, FL	15.54		158			Clark et al. 1989, Childress 1997
	Manele, HI	1.25	313	57		2	Grigg 1994
	Merritt Island, FL	39.6		51			Johnson et al. 199
	Red Hind Bank, USVI	41	60	61	4		Nemeth 2005
	Tortugas Bank, FL	566		52			Ault et al. 2006
	Western Sambo, FL	30		49	9		Cox & Hunt 2005
Venezuela	Los Roques Archipelago	4		156	6		Weil & Laughlin 1984, Robertson et al. 2005

^aThe 'outside' reserve at Sumilon in the Philippines refers to the area outside the reserve that received protection at various times (it is distinct from, but adjacent to, the Sumilon reserve)

LITERATURE CITED FOR TABLE S1

- Abesamis RA, Russ GR (2005) Density-dependent spillover from a marine reserve: long-term evidence. *Ecol Appl* 15: 1798–1812
- Abesamis RA, Alcalá AC, Russ GR (2006a) How much does the fishery at Apo Island benefit from spillover of adult fish from the adjacent marine reserve? *Fish Bull* 104:360–375
- Abesamis RA, Russ GR, Alcalá AC (2006b) Gradients of abundance of fish across no-take marine reserve boundaries: evidence from Philippine coral reefs. *Aquat Conserv* 16: 349–371
- Acosta CA, Robertson DN (2003) Comparative spatial ecology of fished spiny lobsters *Panulirus argus* and an unfished congener *P. guttatus* in an isolated marine reserve at Glover's Reef atoll, Belize. *Coral Reefs* 22:1–9
- Alcalá AC (1988) Effects of marine reserves on coral fish abundances and yields of Philippine coral reefs. *Ambio* 17:194–199
- Alcalá AC, Russ GR, Maypa AP, Calumpong HP (2005) A long-term, spatially replicated experimental test of the effect of marine reserves on local fish yields. *Can J Fish Aquat Sci* 62:98–108
- Ashworth JS, Ormond RFG (2005) Effects of fishing pressure and trophic group on abundance and spillover across boundaries of a no-take zone. *Biol Conserv* 121:333–344
- Ashworth JS, Ormond RFG, Sturrock HT (2004) Effects of reef-top gathering and fishing on invertebrate abundance across take and no-take zones. *J Exp Mar Biol Ecol* 303:221–242
- Ault JS, Smith SG, Bohnsack JA, Luo JG, Harper DE, McClellan DB (2006) Building sustainable fisheries in Florida's coral reef ecosystem: positive signs in the Dry Tortugas. *Bull Mar Sci* 78:633–654
- Babcock RC, Kelly S, Shears NT, Walker JW, Willis TJ (1999) Changes in community structure in temperate marine reserves. *Mar Ecol Prog Ser* 189:125–134
- Bell JD (1983) Effects of depth and marine reserve fishing restrictions on the structure of a rocky reef fish assemblage in the northwestern Mediterranean Sea. *J Appl Ecol* 20:357–369
- Benedetti-Cecchi L, Bertocci I, Micheli F, Maggi E, Fosella T, Vaselli S (2003) Implications of spatial heterogeneity for management of marine protected areas (MPAs): examples from assemblages of rocky coasts in the northwest Mediterranean. *Mar Environ Res* 55:429–458
- Bennett BA, Attwood CG (1991) Evidence for recovery of a surf-zone fish assemblage following the establishment of a marine reserve on the southern coast of South Africa. *Mar Ecol Prog Ser* 75:173–181
- Borja A, Muxika I, Bald J (2006) Protection of the goose barnacle *Pollicipes pollicipes*, Gmelin, 1790 population: the Gaztelugatxe Marine Reserve (Basque Country, northern Spain). *Sci Mar* 70:235–242
- Branch GM, Odendaal F (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. *Biol Conserv* 114:255–269
- Buxton CD (1993) Life history changes in exploited reef fishes on the east coast of South Africa. *Environ Biol Fishes* 36: 47–63
- Buxton CD, Smale MJ (1989) Abundance and distribution patterns of 3 temperate marine reef fish (Teleostei, Sparidae) in exploited and unexploited areas off the southern Cape coast. *J Appl Ecol* 26:441–451
- Carter J, Sedberry GR (1997) The design, function and use of marine fishery reserves as tools for the management and conservation of the Belize barrier reef. *Proc Eighth Int Coral Reef Symp, Balboa* 2:1911–1916
- Castilla JC, Bustamante RH (1989) Human exclusion from rocky intertidal of Las Cruces, central Chile: effects on *Durvillaea antarctica* (Phaeophyta, Durvilliales). *Mar Ecol Prog Ser* 50:203–214
- Ceccherelli G, Casu D, Pala D, Pinna S, Sechi N (2006) Evaluating the effects of protection on two benthic habitats at Tavolara-Punta Coda Cavallo MPA (north-east Sardinia, Italy). *Mar Environ Res* 61:171–185
- Chapman MR, Kramer DL (1999) Gradients in coral reef fish density and size across the Barbados Marine Reserve boundary: effects of reserve protection and habitat characteristics. *Mar Ecol Prog Ser* 181:81–96
- Chateau O, Wantiez L (2005) Comparison of coral reef fish communities between two fished and one protected reefs in New Caledonia South Lagoon Marine Park. *Cybium* 29:159–174
- Chiappone M, Sluka R, Sealey KS (2000) Groupers (Pisces: Serranidae) in fished and protected areas of the Florida Keys, Bahamas and northern Caribbean. *Mar Ecol Prog Ser* 198:261–272
- Childress MJ (1997) Marine reserves and their effects on lobster populations: report from a workshop. *Mar Freshw Res* 48:1111–1114

- Clark J, Causey B, Bohnsack JA (1989) Benefits from coral reef protection: Looe Key Reef, Florida. In: Magoon O, Converse H, Minor D, Tobin L, Clark D (eds) Coastal zone '89: Proc Sixth Symp Coastal Ocean Manage, Charleston, SC. American Society of Civil Engineers, New York, p 3076–3086
- Claudet J, Pelletier D, Jouvenel JY, Bachet F, Galzin R (2006) Assessing the effects of marine protected area (MPA) on a reef fish assemblage in a northwestern Mediterranean marine reserve: identifying community-based indicators. *Biol Conserv* 130:349–369
- Cole RG, Ayling TM, Creese RG (1990) Effects of marine reserve protection at Goat Island, northern New Zealand. *NZ J Mar Freshw Res* 24:197–210
- Cole RG, Villouta E, Davidson RJ (2000) Direct evidence of limited dispersal of the reef fish *Parapercis colias* (Pinguipedidae) within a marine reserve and adjacent fished areas. *Aquat Conserv* 10:421–436
- Cowley PD, Brouwer SL, Tilney RL (2002) The role of the Tsitsikamma National Park in the management of four shore-angling fish along the south-eastern Cape coast of South Africa. *South African J Mar Sci* 24:27–35
- Cox C, Hunt JH (2005) Change in size and abundance of Caribbean spiny lobsters *Panulirus argus* in a marine reserve in the Florida Keys National Marine Sanctuary, USA. *Mar Ecol Prog Ser* 294:227–239
- Craik G (1981) Underwater survey of coral trout *Plectropomus leopardus* (Serranidae) populations in the Carpricorn section of the Great Barrier Reef Marine Park. *Proc Fourth Int Coral Reef Symp, Manila* 1:53–58
- Davidson RJ (2001) Changes in population parameters and behaviour of blue cod (*Parapercis colias*; Pinguipedidae) in Long Island Kokomohua Marine Reserve, Marlborough Sounds, New Zealand. *Aquat Conserv* 11:417–435
- Davidson RJ, Villouta E, Cole RG, Barrier RGF (2002) Effects of marine reserve protection on spiny lobster (*Jasus edwardsii*) abundance and size at Tonga Island Marine Reserve, New Zealand. *Aquat Conserv* 12:213–227
- Davis GE (1977) Effects of recreational harvest on a spiny lobster, *Panulirus argus*, population. *Bull Mar Sci* 27:223–236
- Davis G (1989) Designated harvest refugia: the next stage of marine fishery management in California. *Calif Coop Ocean Fish Invest Rep* 30:53–58
- Denny CM, Willis TJ, Babcock RC (2004) Rapid recolonisation of snapper *Pagrus auratus*: Sparidae within an offshore island marine reserve after implementation of no-take status. *Mar Ecol Prog Ser* 272:183–190
- Duran LR, Castilla JC (1989) Variation and persistence of the middle rocky intertidal community of central Chile, with and without human harvesting. *Mar Biol* 103:555–562
- Duran LR, Oliva D (1987) Intensity of human predation on rocky shores at Las Cruces in central Chile. *Environ Conserv* 14:143–149
- Edgar GJ, Barrett NS (1999) Effects of the declaration of marine reserves on Tasmanian reef fishes, invertebrates and plants. *J Exp Mar Biol Ecol* 242:107–144
- Epstein N, Bak RPM, Rinkevich B (1999) Implementation of a small-scale 'no-use zone' policy in a reef ecosystem: Eilat's reef lagoon six years later. *Coral Reefs* 18:327–332
- Evans RD, Russ GR (2004) Larger biomass of targeted reef fish in no-take marine reserves on the Great Barrier Reef, Australia. *Aquat Conserv* 14:505–519
- Fanshawe S, Vanblaricom GR, Shelly AA (2003) Restored top carnivores as detrimentals to the performance of marine protected areas intended for fishery sustainability: a case study with red abalones and sea otters. *Conserv Biol* 17:273–283
- Ferraris J, Pelletier D, Kulbicki M, Chauvet C (2005) Assessing the impact of removing reserve status on the Abore Reef fish assemblage in New Caledonia. *Mar Ecol Prog Ser* 292:271–286
- Floeter S, Halpern BS, Ferreira C (2006) Effects of fishing and protection on Brazilian reef fishes. *Biol Conserv* 128:391–402
- Francour P (1991) The effect of protection level on a coastal fish community at Scandola, Corsica. *Rev Ecol Terre & Vie* 46:65–81
- Francour P (1994) Pluriannual analysis of the reserve effect on ichthyofauna in the Scandola Natural Reserve (Corsica, northwestern Mediterranean). *Oceanol Acta* 17:309–317
- Francour P (1996) L'Ichthofaune de l'herbier a *Posidonia oceanica* dans la reserve marine de Scandola (Corse, Mediterranee Nord-Occidentale): influence des mesures de protection. *J Res Oceanogr* 21:29–34
- Francour P (2000) Long term monitoring of *Posidonia oceanica* fish assemblages of the Scandola Marine Reserve (Corsica, northwestern Mediterranean). *Cybiurn* 24:85–95
- Galal N, Ormond RFG, Hassan O (2002) Effect of a network of no-take reserves in increasing catch per unit effort and stocks of exploited reef fish at Nabq, South Sinai, Egypt. *Mar Freshw Res* 53:199–205
- Garcia-Charton JA, Perez-Ruzafa A, Sanchez-Jerez P, Bayle-Sempere JT, Renones O, Moreno D (2004) Multi-scale spatial heterogeneity, habitat structure, and the effect of marine reserves on Western Mediterranean rocky reef fish assemblages. *Mar Biol* 144:161–182
- Garcia-Rubies A, Zabala M (1990) Effects of total fishing prohibition on the rocky fish assemblages of Medes Islands marine reserve (NW Mediterranean). *Sci Mar* 54:317–328
- Garla RC, Chapman DD, Shivji MS, Wetherbee BM, Amorim AF (2006) Habitat of juvenile Caribbean reef sharks, *Carcharhinus perezi*, at two oceanic insular marine protected areas in the southwestern Atlantic Ocean: Fernando de Noronha Archipelago and Atol das Rocas, Brazil. *Fish Res* 81:236–241
- Goñi R, Renones O, Quetglas A (2001) Dynamics of a protected Western Mediterranean population of the European spiny lobster *Palinurus elephas* (Fabricius, 1787) assessed by trap surveys. *Mar Freshw Res* 52:1577–1587
- Graham NAJ, Evans RD, Russ GR (2003) The effects of marine reserve protection on the trophic relationships of reef fishes on the Great Barrier Reef. *Environ Conserv* 30:200–208
- Grigg RW (1994) Effects of sewage discharge, fishing pressure and habitat complexity on coral ecosystems and reef fishes in Hawaii. *Mar Ecol Prog Ser* 103:25–34
- Guidetti P (2006) Marine reserves reestablish lost predatory interactions and cause community changes in rocky reefs. *Ecol Appl* 16:963–976
- Guidetti P, Bussotti S, Boero F (2005a) Evaluating the effects of protection on fish predators and sea urchins in shallow artificial rocky habitats: a case study in the northern Adriatic Sea. *Mar Environ Res* 59:333–348
- Guidetti P, Verginella L, Viva C, Odorico R, Boero F (2005b) Protection effects on fish assemblages, and comparison of two visual-census techniques in shallow artificial rocky habitats in the northern Adriatic Sea. *J Mar Biol Assoc UK* 85:247–255
- Harmelin JG, Bachet F, Garcia F (1995) Mediterranean marine reserves: fish indices as test of protection efficiency. *PSZN I: Mar Ecol* 16:233–250
- Hawkins JP, Roberts CM (2004) Effects of fishing on sex-changing Caribbean parrotfishes. *Biol Conserv* 115:213–226

- Hawkins JP, Roberts CM, Dytham C, Schelten C, Nugues MM (2006) Effects of habitat characteristics and sedimentation on performance of marine reserves in St. Lucia. *Biol Conserv* 127:487–499
- Hereu B, Zabala M, Linares C, Sala E (2005) The effects of predator abundance and habitat structural complexity on survival of juvenile sea urchins. *Mar Biol* 146:293–299
- Hockey PAR, Bosman AL (1986) Man as an intertidal predator in Transkei: disturbance, community convergence and management of a natural food resource. *Oikos* 46:3–14
- Jennings S, Marshall SS, Polunin NVC (1996) Seychelles' marine protected areas: comparative structure and status of reef fish communities. *Biol Conserv* 75:201–209
- Johnson D, Funicelli N, Bohnsack JA (1999) Effectiveness of an existing estuarine no-take fish sanctuary within the Kennedy Space Center, Florida. *N Am J Fish Manage* 19:436–453
- Jones GP, McCormick MI, Srinivasan M, Eagle JV (2004) Coral decline threatens fish biodiversity in marine reserves. *Proc Natl Acad Sci USA* 101:8251–8253
- Jouvenel JY, Pollard DA (2001) Some effects of marine reserve protection on the population structure of two spearfishing target fish species, *Dicentrarchus labrax* (Moronidae) and *Sparus aurata* (Sparidae), in shallow inshore waters, along a rocky coast in the northwestern Mediterranean Sea. *Aquat Conserv* 11:1–9
- Jouvenel JY, Bachet F, Harmelin JG, Bellan-Santini D (2004) Biological monitoring of a marine reserve ('Cote bleue' marine park, Marseilles Bay, Mediterranean Sea, France). *Rev Ecol Terre & Vie* 59:243–251
- Kaunda-Arara B, Rose GA (2004) Effects of marine reef national parks on fishery CPUE in coastal Kenya. *Biol Conserv* 118:1–13
- Keough MJ, Quinn GP (2000) Legislative vs. practical protection of an intertidal shoreline in southeastern Australia. *Ecol Appl* 10:871–881
- Koslow JA, Hanley F, Wicklund R (1988) Effects of fishing on reef fish communities at Pedro Bank and Port Royal Cays, Jamaica. *Mar Ecol Prog Ser* 43:201–212
- La Mesa G, Di Muccio S, Vacchi M (2006) Structure of a Mediterranean cryptobenthic fish community and its relationships with habitat characteristics. *Mar Biol* 149:149–167
- Langlois TJ, Anderson MJ, Babcock RC (2005) Reef-associated predators influence adjacent soft-sediment communities. *Ecology* 86:1508–1519
- Lasiak T (1993) Temporal and spatial variations in exploited and non-exploited populations of the intertidal limpet *Cellana capensis*. *J Molluscan Stud* 59:295–307
- Lasiak T (2006) Spatial variation in density and biomass of patellid limpets inside and outside a marine protected area. *J Molluscan Stud* 72:137–142
- Lecchini D, Lenfant P, Planes S (2002) Variation in abundance and population dynamics of the sea urchin *Paracentrotus lividus* on the Catalan coast (north-western Mediterranean Sea) in relation to habitat and marine reserve. *Vie Milieu* 52:111–118
- Letourneur Y (1996) Influence of establishing marine reserves on fish populations: the case of Mayotte Island (western Indian Ocean). *Ecoscience* 3:442–450
- Lincoln-Smith MP, Pitt KA, Bell JD, Mapstone BD (2006) Using impact assessment methods to determine the effects of a marine reserve on abundances and sizes of valuable tropical invertebrates. *Can J Fish Aquat Sci* 63:1251–1266
- Lipcius RN, Stockhausen WT, Eggleston DB (2001) Marine reserves for Caribbean spiny lobster: empirical evaluation and theoretical metapopulation recruitment dynamics. *Mar Freshw Res* 52:1589–1598
- Lloret J, Planes S (2003) Condition, feeding and reproductive potential of white seabream *Diplodus sargus* as indicators of habitat quality and the effect of reserve protection in the northwestern Mediterranean. *Mar Ecol Prog Ser* 248:197–208
- Loot G, Aldana M, Navarrete S (2005) Effects of human exclusion on parasitism in intertidal food webs of central Chile. *Conserv Biol* 19:203–212
- MacDiarmid AB, Breen P (1992) Spiny lobster population change in a marine reserve. In: Battershill CN (ed) *Proc Second Int Temp Reef Symp*, Auckland, 7–10 Jan 1992. NIWA Marine, Wellington, p 47–56
- Macpherson E, Garcia-Rubies A, Gordo A (2000) Direct estimation of natural mortality rates for littoral marine fishes using populational data from a marine reserve. *Mar Biol* 137:1067–1076
- Maliao RJ, Webb EL, Jensen KR (2004) A survey of stock of the donkey's ear abalone, *Haliotis asinina* L. in the Sagay Marine Reserve, Philippines: evaluating the effectiveness of marine protected area enforcement. *Fish Res* 66:343–353
- Manriquez PH, Castilla JC (2001) Significance of marine protected areas in central Chile as seeding grounds for the gastropod *Concholepas concholepas*. *Mar Ecol Prog Ser* 215:201–211
- Martell SJD, Walters CJ, Wallace SS (2000) The use of marine protected areas for conservation of lingcod (*Ophiodon elongatus*). *Bull Mar Sci* 66:729–743
- Mayfield S, Branch GM, Cockcroft AC (2005) Role and efficacy of marine protected areas for the South African rock lobster, *Jasus lalandii*. *Mar Freshw Res* 56:913–924
- McClanahan TR (1994) Kenyan coral reef lagoon fish: effects of fishing, substrate complexity, and sea urchins. *Coral Reefs* 13:231–241
- McClanahan TR, Kaunda-Arara B (1996) Fishery recovery in a coral reef marine park and its effect on the adjacent fishery. *Conserv Biol* 10:1187–1199
- McClanahan TR, Muthiga NA (1988) Changes in Kenyan coral reef community structure and function due to exploitation. *Hydrobiologia* 166:269–276
- McCormick MI, Choat JH (1987) Estimating total abundance of a large temperate reef fish using visual strip-transects. *Mar Biol* 96:469–478
- Micheli F, Benedetti-Cecchi L, Gambaccini S, Bertocci I, Borsini C, Osio GC, Roman F (2005) Cascading human impacts, marine protected areas, and the structure of Mediterranean reef assemblages. *Ecol Monogr* 75:81–102
- Milazzo M, Chemello R, Badalamenti F, Riggio S (2000) Molluscan assemblages associated with photophilic algae in the marine reserve of Ustica Island (Lower Tyrrhenian Sea, Italy). *Ital J Zool (Modena)* 67:287–295
- Millar RB, Willis TJ (1999) Estimating the relative density of snapper in and around a marine reserve using a log-linear mixed-effects model. *Aust NZ J Stat* 41:383–394
- Moreno CA, Lunecke KM, Lepez MI (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
- Mumby PJ, Dahlgren CP, Harborne AR, Kappel CV and others (2006) Fishing, trophic cascades, and the process of grazing on coral reefs. *Science* 311:98–101
- Narvarte M, Gonzalez R, Fernandez M (2006) Comparison of Tehuelche octopus (*Octopus tehuelchus*) abundance between an open-access fishing ground and a marine protected area: evidence from a direct development species. *Fish Res* 79:112–119

- Nemeth RS (2005) Population characteristics of a recovering US Virgin Islands red hind spawning aggregation following protection. *Mar Ecol Prog Ser* 286:81–97
- Oliva D, Castilla JC (1986) The effect of human exclusion on the population structure of key hole limpets *Fissurella crassa* and *Fissurella limbata* on the coast of central Chile. *PSZN I: Mar Ecol* 7:201–217
- Ortega S (1987) The effect of human predation on the size distribution of *Siphonaria gigas* (Mollusca, Pulmonata) on the Pacific coast of Costa Rica. *Veliger* 29:251–255
- Paddock MJ, Estes JA (2000) Kelp forest fish populations in marine reserves and adjacent exploited areas of central California. *Ecol Appl* 10:855–870
- Parnell PE, Lennert-Cody CE, Geelen L, Stanley LD, Dayton PK (2005) Effectiveness of a small marine reserve in southern California. *Mar Ecol Prog Ser* 296:39–52
- Pederson HG, Johnson CR (2006) Predation of the sea urchin *Heliocidaris erythrogramma* by rock lobsters (*Jasus edwardsii*) in no-take marine reserves. *J Exp Mar Biol Ecol* 336:120–134
- Pillans S, Pillans RD, Johnstone RW, Kraft PG, Haywood MDE, Possingham HP (2005) Effects of marine reserve protection on the mud crab *Scylla serrata* in a sex-biased fishery in subtropical Australia. *Mar Ecol Prog Ser* 295: 201–213
- Polunin NVC, Roberts CM (1993) Greater biomass and value of target coral-reef fishes in two small Caribbean marine reserves. *Mar Ecol Prog Ser* 100:167–176
- Rakitin A, Kramer DL (1996) Effect of a marine reserve on the distribution of coral reef fishes in Barbados. *Mar Ecol Prog Ser* 131:97–113
- Rice M, Hickox C, Zehra I (1989) Effects of intensive fishing effort on the population structure of Quahogs, *Mercenaria mercenaria* (Linnaeus 1758), in Narragansett Bay. *J Shellfish Res* 8:345–354
- Roberts CM, Hawkins JP (1997) How small can a marine reserve be and still be effective? *Coral Reefs* 16:150
- Roberts CM, Polunin N (1992) Effects of marine reserve protection on northern Red Sea fish populations. *Proc Seventh Int Coral Reef Symp* 2:969–977
- Roberts CM, Polunin NVC (1993) Marine reserves: simple solutions to managing complex fisheries. *Ambio* 22:363–368
- Roberts CM, Bohnsack JA, Gell F, Hawkins JP, Goodridge R (2001) Effects of marine reserves on adjacent fisheries. *Science* 294:1920–1923
- Robertson DR, Choat JH, Posada JM, Pitt J, Ackerman JL (2005) Ocean surgeonfish *Acanthurus bahianus*. II. Fishing effects on longevity, size and abundance? *Mar Ecol Prog Ser* 295:245–256
- Rogers-Bennett L, Haaker PL, Karpov KA, Kushner DJ (2002) Using spatially explicit data to evaluate marine protected areas for abalone in southern California. *Conserv Biol* 16:1308–1317
- Rowe S (2002) Population parameters of American lobster inside and outside no-take reserves in Bonavista Bay, Newfoundland. *Fish Res* 56:167–175
- Russ GR (1985) Effects of protective management on coral reef fishes in the central Philippines. *Proc Fifth Int Coral Reef Cong, Moorea* 4:219–224
- Russ GR, Alcala AC (1996) Marine reserves: rates and patterns of recovery and decline of large predatory fish. *Ecol Appl* 6:947–961
- Russ GR, Alcala AC (1998) Natural fishing experiments in marine reserves 1983–1993: community and trophic responses. *Coral Reefs* 17:383–397
- Russ GR, Alcala AC (2003) Marine reserves: rates and patterns of recovery and decline of predatory fish, 1983–2000. *Ecol Appl* 13:1553–1565
- Russ GR, Alcala AC, Maypa AP (2003) Spillover from marine reserves: the case of *Naso vlamingii* at Apo Island, the Philippines. *Mar Ecol Prog Ser* 264:15–20
- Russ GR, Alcala AC, Maypa AP, Calumpog HP, White AT (2004) Marine reserve benefits local fisheries. *Ecol Appl* 14:597–606
- Russ GR, Stockwell B, Alcala AC (2005) Inferring versus measuring rates of recovery in no-take marine reserves. *Mar Ecol Prog Ser* 292:1–12
- Sala E, Zabala M (1996) Fish predation and the structure of the sea urchin *Paracentrotus lividus* populations in the NW Mediterranean. *Mar Ecol Prog Ser* 140:71–81
- Schroeder DM, Love MS (2002) Recreational fishing and marine fish populations in California. *Calif Coop Ocean Fish Invest Rep* 43:182–190
- Shears NT, Babcock RC (2002) Marine reserves demonstrate top-down control of community structure on temperate reefs. *Oecologia* 132:131–142
- Shears NT, Babcock RC (2003) Continuing trophic cascade effects after 25 years of no-take marine reserve protection. *Mar Ecol Prog Ser* 246:1–16
- Shears NT, Grace RV, Usmar NR, Kerr V, Babcock RC (2006) Long-term trends in lobster populations in a partially protected vs. no-take marine park. *Biol Conserv* 132:222–231
- Siegfried WR, Hockey PAR, Crowe AA (1985) Exploitation and conservation of brown mussel stocks by coastal people of Transkei. *Environ Conserv* 12:303–307
- Sluka R, Chiappone M, Sullivan K, Wright R (1997) The benefits of a marine fishery reserve for Nassau Grouper *Epinephelus striatus* in the central Bahamas. *Proc Eighth Int Coral Reef Symp, Balboa* 2:1961–1964
- Stoner AW, Ray M (1996) Queen conch, *Strombus gigas*, in fished and unfished locations of the Bahamas: effects of a marine fishery reserve on adults, juveniles, and larval production. *Fish Bull* 94:551–565
- Tsounis G, Rossi S, Gili JM, Arntz W (2006) Population structure of an exploited benthic cnidarian: the case study of red coral (*Corallium rubrum* L.). *Mar Biol* 149:1059–1070
- Tunesi L, Molinari A, Salvati E (2006) Fish assemblage of the marine protected area of Cinque Terre (NW Mediterranean Sea): first characterization and assessment by visual census. *Chem Ecol* 22:245–253
- Tupper M, Juanes F (1999) Effects of a marine reserve on recruitment of grunts (Pisces: Haemulidae) at Barbados, West Indies. *Environ Biol Fishes* 55:53–63
- Tuya F, Garcia-Diez C, Espino F, Haroun RJ (2006) Assessment of the effectiveness of two marine reserves in the Canary Islands (eastern Atlantic). *Cienc Mar* 32:505–522
- Wallace SS (1999) Evaluating the effects of three forms of marine reserve on northern abalone populations in British Columbia, Canada. *Conserv Biol* 13:882–887
- Walmsley SF, White AT (2003) Influence of social, management and enforcement factors on the long-term ecological effects of marine sanctuaries. *Environ Conserv* 30: 388–407
- 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
- Watson M, Ormond RFG (1994) Effect of an artisanal fishery on the fish and urchin populations of a Kenyan coral reef. *Mar Ecol Prog Ser* 109:115–129
- Weil E, Laughlin R (1984) Biology, population dynamics, and reproduction of the queen conch *Strombus gigas* Linne in the archipelago de los Roques National Park. *J Shellfish Res* 4:45–62
- Westera M, Lavery P, Hyndes G (2003) Differences in recreationally targeted fishes between protected and fished

- areas of a coral reef marine park. *J Exp Mar Biol Ecol* 294:145–168
- White AT (1988) The effect of community-managed marine reserves in the Philippines on their associated coral reef fish populations. *Asian Fish Sci* 2:27–41
- Williams ID, Polunin NVC (2000) Differences between protected and unprotected reefs of the western Caribbean in attributes preferred by dive tourists. *Environ Conserv* 27: 382–391
- Williamson DH, Russ GR, Ayling AM (2004) No-take marine reserves increase abundance and biomass of reef fish on inshore fringing reefs of the Great Barrier Reef. *Environ Conserv* 31:149–159
- Willis TJ, Anderson MJ (2003) Structure of cryptic reef fish assemblages: relationships with habitat characteristics and predator density. *Mar Ecol Prog Ser* 257:209–221
- Willis TJ, Babcock RC (2000) A baited underwater video system for the determination of relative density of carnivorous reef fish. *Mar Freshw Res* 51:755–763
- Willis TJ, Millar RB (2005) Using marine reserves to estimate fishing mortality. *Ecol Lett* 8:47–52
- Willis TJ, Millar RB, Babcock RC (2000) Detection of spatial variability in relative density of fishes: comparison of visual census, angling, and baited underwater video. *Mar Ecol Prog Ser* 198:249–260
- Willis TJ, Millar RB, Babcock RC (2003) Protection of exploited fish in temperate regions: high density and biomass of snapper *Pagrus auratus* (Sparidae) in northern New Zealand marine reserves. *J Appl Ecol* 40:214–227
- Yoklavich M, Cailliet G, Lea RN, Greene HG, Starr R, De Marignac J, Field J (2002) Deepwater habitat and fish resources associated with the Big Creek Marine Ecological Reserve. *Calif Coop Ocean Fish Invest Rep* 43: 120–140
- Zeller DC, Russ GR (1998) Marine reserves: patterns of adult movement of the coral trout (*Plectropomus leopardus* (Serranidae)). *Can J Fish Aquat Sci* 55:917–924

Table S2. Average percent change calculated from reserve response ratios for invertebrate characteristics. N (in parentheses): number of reserves for which each biological variable was measured; B: biomass; D: density; S: organism size. There was not sufficient species richness data for analysis. Significance for 2-tailed *t*-tests, testing for mean log response ratios significantly different than zero, is indicated as follows: * $p \leq 0.05$; ** $p \leq 0.01$; *** $p \leq 0.001$

Characteristic	Categories	Category details	Percent change (N)		
			B	D	S
Adult mobility	Sessile	Attached to substrate	472(2)	370(35)	45(4)
	Limited mobility	e.g. limpets and other small gastropods, abalone, surf clams, nudibranchs, sea cucumbers, polychaetes	213(5)	252**(26)	35**(16)
		e.g. lobster, crabs, conch, octopus, urchins	850(9)	277*(35)	22*(19)
Target status	High		820*(12)	385***(58)	28(31)
	Low		24(1)	4(9)	0.3(1)
	Not targeted		33(4)	115(19)	20(3)
Trophic level	Herbivore		83(3)	135(33)	25**(22)
	Primary producer/ filter feeder	e.g. corals		110(23)	77(2)
	Filter feeder		142(5)	1150(17)	42(3)
	Detritivore		-36(2)	-26(3)	-11(1)
	Omnivore		-2(3)	65(5)	4(2)
Larval dispersal potential	Invertivore		1173**(10)	501***(26)	41*(12)
	Little/none	Direct developing/brooding species		3(3)	-3(2)
	Short distance	Indirect development with larval duration ≤ 4 d		200(10)	61(3)
	Longer distance	Indirect development with larval duration >4 d	738(13)	340***(50)	26***(31)

Table S3. Average percent change calculated from reserve response ratios for the algal functional groups. N: number of reserves for which each biological variable was measured. None of the mean log response ratios were significantly different than zero (2-tailed *t*-tests, $p \leq 0.05$)

Functional group	Biomass percent change	N	Density percent change	N
Crustose algae	121	1	-2	7
Filamentous algae	-96	1	33	4
Articulated calcareous algae	67	1	54	7
Corticated foliose algae	-27	1	25	8
Corticated macrophytes	-41	1	184	4
Leathery macrophytes	812	1	512	11

Table S4. Average percent change calculated from reserve response ratios for the invertebrate taxonomic classifications. N (in parentheses): number of reserves for which each biological variable was measured; B: biomass; D: density; S: organism size. There was not sufficient species richness data for analysis. Significance for 2-tailed *t*-tests, testing for mean log response ratios significantly different than zero, is indicated as follows: **p* ≤ 0.05; ***p* ≤ 0.01; ****p* ≤ 0.001

Phylum	Percent change (N)			Taxonomic group	Percent change (N)		
	B	D	S		B	D	S
Mollusca	240(5)	422***(29)	33***(18)	Gastropods	423(5)	301***(26)	31**(16)
				Bivalves	129(4)	1471(12)	64(2)
Echinodermata	-50(3)	198(19)	-0.1(7)	Cephalopods		3(3)	-7(1)
				Urchins	-50(3)	205(18)	2(6)
Arthropoda	889**(10)	323***(24)	33*(12)	Sea cucumbers		-26(3)	-11(1)
				Barnacles	194(1)	248(1)	-3(1)
Cnidaria		98(25)	77(2)	Crabs	77(1)	155*(6)	4(2)
				Hermit crabs	-41(2)	-39(2)	
Porifera		868(2)		Lobsters	1450***(6)	541***(21)	44*(9)
				Hard corals		120(22)	102(1)
Annelida		3(3)		Soft corals		-14(3)	52(1)
				Anthozoa (hard and soft corals)		-2(4)	
				Hydrozoa		-44(2)	
				Sponges		868(2)	
				Polychaetes		3(3)	