

Modelling the effects of establishing a marine reserve for mobile fish species

P. Apostolaki, E.J. Milner-Gulland, M.K. McAllister, and G.P. Kirkwood

Abstract: We present a model of the effects of a marine reserve on spawning stock biomass (SSB) and short- and long-term yield for a size-structured species that exhibits seasonal movements. The model considers the effects of protecting nursery and (or) spawning grounds under a range of fishing mortalities and fish mobility rates. We consider two extremes of effort redistribution following reserve establishment and analyze the effects of a reserve when the fishery targets either mature or immature fish. We apply the model to the Mediterranean hake (*Merluccius merluccius*) and show that a marine reserve could be highly beneficial for this species. We demonstrate benefits from reserves not just for overexploited stocks of low-mobility species, but also (to a lesser extent) for underexploited stocks and high-mobility species. Greatly increased resilience to overfishing is also found in the majority of cases. We show that a reserve provides benefits additional to those obtained from simple effort control. Benefits from reserves depend to a major extent on the amount of effort redistribution following reserve establishment and on fishing selectivity; hence, these factors should be key components of any evaluation of reserve effectiveness.

Résumé : On trouvera ici un modèle qui décrit les effets d'une réserve marine sur la biomasse du stock des reproducteurs et sur les rendements à court et à long termes chez une espèce à structure de taille définie qui fait des déplacements saisonniers. Le modèle examine les effets de la protection des zones d'alevinage et (ou) de fraye sur une gamme de mortalités dues à la pêche et de taux de mobilité des poissons. Nous considérons deux extrêmes dans la redistribution de l'effort de pêche à la suite de l'établissement d'une réserve et nous analysons les effets de la réserve quand la pêche cible les poissons immatures ou alors les poissons adultes. Nous appliquons le modèle au merlu commun (*Merluccius merluccius*) et démontrons qu'une réserve marine lui serait très bénéfique. Les bénéfices d'une réserve s'appliquent non seulement aux stocks surexploités d'espèces à mobilité réduite, mais aussi, bien que dans une plus faible mesure, aux stocks sous-exploités et aux espèces très mobiles. Dans la majorité des cas, il existe aussi une résilience fortement accrue à la surpêche. La réserve apporte des bénéfices additionnels à ceux que génère le simple contrôle de l'effort de pêche. Ces bénéfices dépendent en grande partie de l'importance de la redistribution de l'effort de pêche après l'établissement de la réserve et de la sélectivité de la pêche; ces facteurs devraient donc être les éléments essentiels de toute évaluation de l'efficacité d'une réserve.

[Traduit par la Rédaction]

Introduction

There has been much recent interest in the potential of marine reserves as a fishery management tool, based on the perception that conventional fishery management techniques have failed to prevent overexploitation of target species (FAO 1995; Beverton 1998; Buckworth 1998) and the depletion of nontarget species, habitat degradation, and associated disruption of the food chain (Roberts and Polunin 1993; Dayton et al. 1995; Pitcher and Pauly 1998). Marine reserves have been proposed as an easily enforced management method that could reduce the impacts of fishing on

marine populations and habitats and help managers to cope with the inherent irreducible uncertainty in stock assessments (e.g., Allison et al. 1998; Lauck et al. 1998; Roberts 1998). In this paper, we consider a marine reserve to be an area that is permanently closed to all fishing.

Compared to other methods, marine reserves have not been considered to be a widely applicable fishery management tool. However, they have long been used for particular problems; for example, the protection of river mouths for homing Atlantic and Pacific salmon; Mediterranean coastal area closures for the protection of immature fish; and protection of coral reefs. Increases in fish abundance and size in reserves have been widely reported (Mosqueira et al. 2000), although whether these benefits are exported to surrounding areas is less clear. Some of the reasons why marine reserves have not been more widely used include the uncertainties concerning the yield improvements that reserves can offer, issues concerning the placement and size of reserves, and opposition to prohibiting fishing in areas that are currently fished (Ballantine 1995; Sant 1996).

Given these uncertainties and the lack of empirical data, much recent modelling has focused on the effects of establishing a reserve on fishery yields and spawning stock biomass (SSB). So far, these studies have shown that yield

Received 27 February 2001. Accepted 8 February 2002.
Published on the NRC Research Press Web site at
<http://cjfas.nrc.ca> on 21 March 2002.
J16241

P. Apostolaki,¹ E.J. Milner-Gulland, M.K. McAllister, and G.P. Kirkwood. Renewable Resources Assessment Group, Department of Environmental Science and Technology, Imperial College of Science, Technology and Medicine, Royal School of Mines, Prince Consort Road, London SW7 2BP, U.K.

¹Corresponding author (e-mail: y.apostolaki@ic.ac.uk).

enhancement is possible only if the fishery is initially over-exploited, although the predicted degree of enhancement varies from minimal (e.g., Polacheck 1990; Die and Watson 1992) to considerable (Sladek Nowlis and Roberts 1999; Mangel 2000a, 2000b). In contrast, yields have been predicted to decline if a reserve is instituted for an under-exploited fishery. The effect of reserves on SSB has always been found to be positive.

The assumptions made about the biology of the target species, reserve size, and fisher behaviour are key to predicting the effectiveness of marine reserves. The early models tended to assume random movement and spawning throughout the area under study, and no population structure (Table 1). More recent models have increased realism by including population structure, directional movement of larvae or adults, and protection of key areas such as spawning grounds. However, a major gap in modelling is the interaction between spatial and temporal heterogeneities in fish abundance and fishing selectivity. This is important because many exploited fish species exhibit seasonal movement and have distinct spawning and (or) nursery grounds, combined with size-selective fishing. Here, we present a general model of the effects of a marine reserve on yield and SSB for such species. We also consider the effects of the extent of effort redistribution that occurs following the establishment of a marine reserve on its effectiveness, both in the short and long term. We apply the model to the Mediterranean hake (*Merluccius merluccius*).

Materials and methods

The general model

Population dynamics

We assume a size-structured population with overlapping generations to capture the effects of both size-related fishing selectivity and size-related fish movement. It is assumed that the area inhabited by the fish population is divided into two. One of the areas (area *a*) is a spawning and (or) nursery ground, and the marine reserve is created by closing this area to fishing. Model parameters are defined in Table 2. The first size category is recruits to the fishery, *R*, numbers of which depend on the number of eggs, *E*, according to the Beverton–Holt egg–recruit relationship (Beverton and Holt 1957),

$$(1) \quad R = \frac{E}{\alpha + \beta E}$$

where α and β are constants (see Appendix A).

The number of fish spawning in time period *t* depends on the number of mature fish in the spawning area, since it is assumed that fish spawn only in the spawning area. This number is calculated as

$$(2) \quad N_{sp,t} = \sum_{S \geq S_{mat}} \sum_{I \subseteq \text{spawn}} N_{I,S,t} Q_{S,t} (1 - e^{-(F_{I,S} + M_S)}) \frac{1}{F_{I,S} + M_S}$$

following Quinn and Deriso (1999), where *S* is a particular size class (mature fish only, $S > S_{mat}$), *I* is the area (the spawning area only, which is area *a* if it is assumed to be the

spawning area or area *b* otherwise), and $N_{I,S,t}$ is the number of fish in size class *S* and area *I* at the beginning of period *t*. $F_{I,S}$ is the fishing mortality rate per time period for fish in size class *S* and area *I*, M_S is natural mortality rate per time period for fish in size class *S*, and $Q_{S,t}$ is the proportion of mature fish (size class *S*) in the spawning area that spawn in time period *t*. A time period of 1.5 months has been used in the calculations.

We assume that all mature females spawn once each year. When spawning occurs in area *a* (hence fish must migrate into this area to spawn), we assume that *Q* varies with *S*, but not with *t*. We set Q_S to the value at which all the fish in each mature age class spawn once during a year. When spawning occurs in area *b*, fish do not migrate into a spawning area. In this case, we assume that *Q* varies only with *t*, but not with *S*. We vary Q_t over the eight time periods that make up a year such that the proportion of fish spawning in each period is the same as when fish must move to area *a* to spawn. This requires a reduction in Q_t to account for the fact that all mature fish are in area *b*.

The number of eggs spawned in time period *t*, E_t , is $f_S N_{sp,t}$, where f_S is the fecundity of fish in size class *S* (Table 3). The spawning stock biomass, SSB, is $\bar{W}_S N_{sp,t}$, where \bar{W}_S is the mean weight of fish in a size category. \bar{W}_S is determined as the mean of the weights corresponding to the minimum, maximum, and mean length of a fish in this size class using a weight–length relationship. Fish weight, *W*, is assumed to scale exponentially with length, *L* (Abella et al. 1995; Table 3).

The biomass of fish caught during time period *t*, Y_t , is the sum of the numbers of fish caught from each size category multiplied by the corresponding mean weights (Quinn and Deriso 1999),

$$(3) \quad Y_t = \sum_{S,I} \frac{F_{I,S}}{F_{I,S} + M_S} N_{I,S,t} (1 - e^{-(F_{I,S} + M_S)}) \bar{W}_S$$

The probability, $P_{S-1,S}$, of a fish in size class *S* – 1 growing to the next size class during a time period depends on the mean growth, $\bar{\Delta L}_{S-1}$, of fish in this size class:

$$(4) \quad P_{S-1,S} = \frac{\bar{\Delta L}_{S-1}}{L_{min,S} - L_{min,S-1}}$$

where $L_{min,S}$ denotes the minimum length of fish in category *S* and $L_{min,S-1}$ is the minimum length of fish in size category *S* – 1. The size intervals are chosen such that fish move at most one size class in a time period but do not remain in any size class (except the last) for a long period. The mean growth, $\bar{\Delta L}_{S-1}$, is calculated as the mean of the growth per time period of fish of the minimum, mean, and maximum size in the class. Growth declines with length such that fish belonging to the last size class barely increase in size.

Fish movement

Fish are distributed across the study area over time using movement coefficients. These coefficients describe the proportion of a given size class that moves from one area to another in each time period. Movement between areas *a* and *b* is seasonal and directional, comprising movement of recruits out of the nursery area and adults into and out of the spawning area. The model can be run with different patterns of

Table 1. A categorization of models of marine reserve effectiveness, showing the major assumptions made in each case.

Source	Model structure	<i>F</i> modified?	Movement	Other characteristics
Beverton and Holt (1957)	Age	Yes	Random	Per-recruit analysis
Polacheck (1990)	Age	Yes	Random	Per-recruit analysis
Mangel (2000a)	Age	N/A	Pelagic juvenile phase	Effects of reserve on catch variability
Mangel (2000b)	Age	No	Uniform distribution	Distinct spawning ground
Die and Watson (1992)	Age	N/A	Age- and area-dependent	Per recruit analysis, area-dependent recruitment
Guénette and Pitcher (1999)	Age	Yes	Area-dependent	Comparison of egg–recruit functions, stochastic recruitment
Sladek Nowlis and Roberts (1999)	Size	No	Larval dispersal	Short- and long-term effects, stochastic survivorship
Lauck et al. (1998)	Logistic	N/A	Uniform distribution	Stochastic harvesting
This paper	Size	Yes	Directed, seasonal & size dependent	Distinct spawning and nursery grounds, short- and long-term effects.

Note: *F* modified refers to whether the fishing effort is redistributed following reserve creation. N/A, not applicable.

Table 2. A list of the parameters used in the model.

Parameter	Symbol	Units
Age	<i>A</i>	year
Recruits to the fishery	<i>R</i>	number of individuals
Number of eggs	<i>E</i>	eggs × 10 ³
Constants	α, β	—
Number of fish	<i>N</i>	—
Size class	<i>S</i>	—
Area (divided into <i>a, b</i>)	<i>I</i>	—
Time period	<i>t</i>	1.5 months
Proportion of mature fish spawning	<i>Q</i>	—
Natural mortality rate for a given size class	<i>M</i>	year ⁻¹
Fishing mortality rate for a given size class and area	<i>F</i>	year ⁻¹
Fishing mortality multiplier	\hat{F}	—
Fecundity of an individual female	<i>f</i>	eggs × 10 ³
Fish weight	<i>W</i>	g
Fish length	<i>L</i>	cm
Biomass yield (of fish caught)	<i>Y</i>	g
Probability of moving into the next size category	<i>P</i>	—
Movement coefficient (between areas)	ϑ	<i>t</i> ⁻¹
Size of area <i>a</i> as a proportion of total study area	ρ	—
Steepness of the egg–recruit curve	<i>h</i>	—

Table 3. Values of the parameters used in the model.

Parameter	Symbol (units)	Value and function	Source
Growth model	<i>L</i> (cm)	$L = L_{\infty}(1 - e^{-kt})$ $L_{\infty} = 79.1$ cm, $k = 0.185$ year ⁻¹	Abella et al. (1995)
Fecundity (by size and age)	<i>f</i> (× 10 ³)	$\log_{10} f = 3.33 \log_{10} L - 3.52$ $\log_{10} f_A = 2.06 \log_{10} A - 0.4$	Papaconstantinou et al. (1986)
Fish weight	<i>W</i> (g)	$W = 0.0041 L^{3.192}$	Abella et al. (1995)
Constants in egg–recruit relationship (eq. 1)	α, β	$\alpha = 1512.04$ $\beta = 7.87 \times 10^{-7}$	Calculated from simulation
Steepness of egg–recruits function	<i>h</i>	0.7	—
Age at reproductive maturity	<i>A</i> _{mat}	4 years	Oliver and Massutí (1995)
Size class at reproductive maturity	<i>S</i> _{mat}	7	Recasens et al. (1998)
Area <i>a</i> as a proportion of the total area	—	0.35	—

Note: The model is parameterized for the Mediterranean hake (*Merluccius merluccius*) where data are available, otherwise, reasonable values and sensitivity analyses are used.

Table 4. Natural mortality rate (M) and fishing mortality rate (F) per size class for Mediterranean hake (*Merluccius merluccius*).

Size interval (cm)	M (year ⁻¹)	F (year ⁻¹) (i)	F (year ⁻¹) (ii)
7–8.5	2.6	0.35	0.05
8.5–11	2.1	1	0.1
11–16.5	1.55	1.4	0.1
16.5–22	1.1	0.73	0.1
22–28.5	0.8	0.37	0.3
28.5–36	0.65	0.2	0.5
36–43	0.52	0.15	0.7
43–50	0.43	0.15	0.8
50–55	0.4	0.2	0.8
55–60	0.4	0.2	0.8
60–65	0.4	0.2	0.8
65–70	0.4	0.2	0.8
70–75	0.4	0.2	0.8
75–79	0.4	0.2	0.8

Note: Three assumptions about fishing mortality are modelled: selectivity for small fish (i), no selection by size (fishing mortality constant at 0.5), and selectivity for larger fish (ii). The values of natural mortality and of fishing mortality (case i) are from Caddy and Abella (1999) up to 50 cm and are our assumptions from 50 cm onwards. Actual fishing mortalities on each size class (F_s) are calculated by multiplying these values by the fishing mortality multiplier, F .

movement and different locations for the spawning and nursery areas and can also be used to represent traditional closed areas (which are closed only for part of the year). In the realizations presented here, area a is assumed to be a nursery and (or) a spawning area. If it is a nursery area only, fish recruit into the population in the nursery area and are distributed across the study area in subsequent time periods, and all spawning is assumed to occur in area b . If area a is a spawning area only, then fish recruit in area b . We assume that in all cases, area a contains either all or none of the spawning or nursery ground; partially overlapping areas are not considered. We also assume that the whole area a is protected once a marine reserve is established. The model can easily be extended to the case where only a proportion of area a is protected. However, because the results obtained are intermediate between those obtained when area a is fully protected, or not protected, we do not present them here.

In the absence of fishing, the number of fish in area a in size class S in the beginning of period t is assumed to be (Hilborn 1990)

$$(5) \quad N_{a,S,t} = (N_{a,S-1,t-1} P_{S-1,S} e^{-M_{S-1}} + N_{a,S,t-1} P_{S,S} e^{-M_S})(1 - \vartheta_{a,b}) + (N_{b,S-1,t-1} P_{S-1,S} e^{-M_{S-1}} + N_{b,S,t-1} P_{S,S} e^{-M_S}) \vartheta_{b,a}$$

where $\vartheta_{b,a}$ and $\vartheta_{a,b}$ are movement coefficients (from area b to a and a to b , respectively). For ease of presentation, eq. 6 does not show the dependence of the movement coefficients on fish length and time period. The number of fish in a given size category and area is calculated, accounting for growth, movement, and mortality (Appendix B).

Fishing effort

When a marine reserve is instituted, an assumption has to be made concerning the redistribution of fishing effort into the reduced area that is now available. The usual assumption is that effort previously expended within the reserve relocates to the nonreserve area. In this case, and assuming that fishing mortality is proportional to fishing effort, fishing mortality in the remainder of the study area after the reserve is instituted (F^{mr} ; mr = marine reserve) increases to (Guénette and Pitcher 1999)

$$(6) \quad F_{I,S}^{\text{mr}} = F_{I,S} \frac{1}{(1 - \rho)}$$

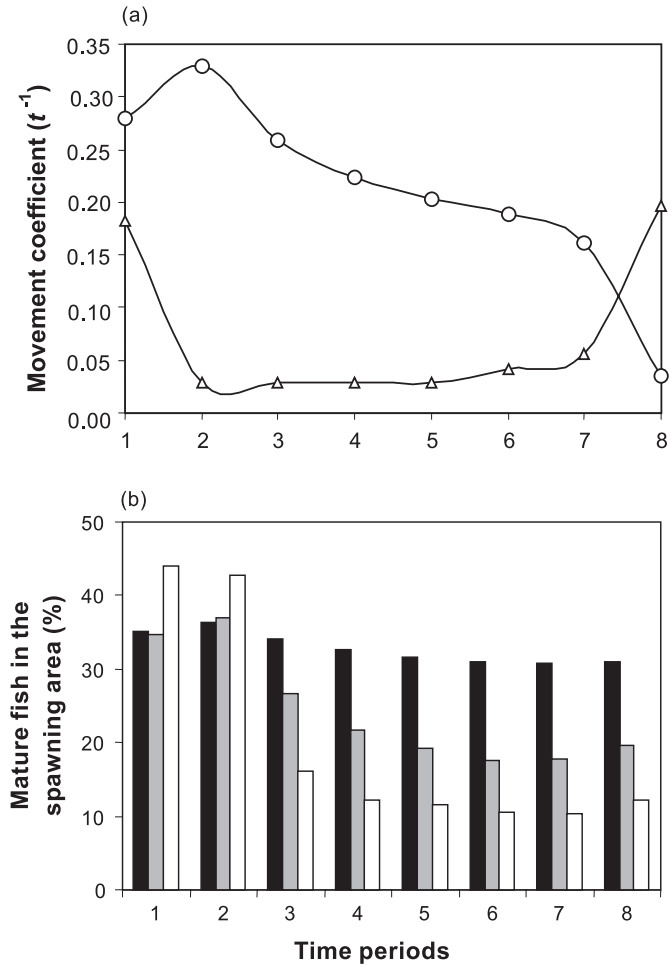
where F is fishing mortality prior to the reserve and ρ is the size of area a as a proportion of the total area. Hence, $1 - \rho$ is the proportion of the total area available to fishing. Equation 6 cannot realistically be used for all values of ρ , since for very large marine reserves, the exploited area becomes so small that it cannot sustain the fishing effort that operated prior to reserve establishment. Also, eq. 6 gives the fishing mortality needed to achieve catches equal to those before reserve establishment if fish are uniformly distributed. However, the distribution of fish in our model is not uniform because we have segregation of fish in different areas during different time periods, so the use of eq. 6 results in catches that are not exactly equal to pre-reserve levels. Therefore, we also investigate two cases in which effort limitation is instituted along with the marine reserve: either effort in the nonreserve area is held at the previous level (i.e., effort that was expended in the reserve is not redistributed), or F^{mr} is set at a value producing an initial annual catch that is the same as that immediately prior to the institution of the reserve, so that the reserve does not initially lead to a loss in catch. In practice, this last assumption gave results intermediate between full redistribution of effort and no redistribution, so the results are not presented.

The Mediterranean hake

Many Mediterranean fisheries are multispecies and multi-gear, characterized by heavy exploitation of demersal fish at small sizes (Caddy 1990; Papaconstantinou and Stergiou 1995). The variety of target species results in small individual catches, a considerable proportion of which are small fish (Caddy 1990). The preference for small fish can be attributed to the high value of fish of that size in many Mediterranean markets (Abella et al. 1997). Hake is one of the most commercially important of these species. It is caught mainly with bottom trawls, and to a lesser degree with gillnets and longlines. Each fishing technique exploits particular sections of the population; bottom trawls target recruits and juveniles, whereas adults are mainly caught with gillnets and longlines (Oliver and Massuti 1995). Immature fish make up the largest proportion of the catch and have the highest fishing mortality (Oliver and Massuti 1995; Abella et al. 1997; Caddy and Abella 1999).

Hake occur at depths from approximately 50 m to more than 700 m (Papaconstantinou and Stergiou 1995; Recasens et al. 1998). Mature hake move inshore to spawn and then return to deeper waters; immature fish remain for the first period of their lives in the nursery area and then exhibit sim-

Fig. 1. (a) Values of the movement coefficients that describe movement between area *a* and *b* for fish of size 55–60 cm and moderate mobility. $\vartheta_{a,b}$, movement from area *a* to area *b* (○); $\vartheta_{b,a}$, movement from area *b* to area *a* (△). (b) Number of mature fish in area *a* (when it is a spawning ground) expressed as a percentage of the total number of mature fish per time period (1.5 months) for the three types of movement. A full year is shown (8 time steps). High mobility is shown as open, moderate mobility as shaded, and low mobility as solid bars.



ilar migratory behaviour (Zupanovic and Jardas 1986; Recasens et al. 1998). In some cases, the spawning and nursery areas are known to overlap. Size at maturity varies regionally and by sex; the length at which 50% of the specimens examined have spawned at least once is 26–36 cm for males and 34–43 cm for females, depending on the location (Orsi Relini et al. 1989; Recasens et al. 1998). Spawning takes place all year, but is more intense during particular time periods, depending on the location; peak spawning has been reported either in autumn and early winter or in summer (Oliver and Massuti 1995; Papaconstantinou and Stergiou 1995; Recasens et al. 1998). Recruitment to the fishery occurs approximately six months after hatching, at a size of 6–9 cm (Orsi Relini et al. 1989; Papaconstantinou and Stergiou 1995). Myers et al. (1995) present data suggesting that recruitment in Mediterranean hake is independent of the number of eggs produced for a wide range

of egg values. Males grow more slowly and to a smaller maximum length than females, with size differentiation being more marked after male maturation (Oliver and Massuti 1995; Recasens et al. 1998).

The Mediterranean hake is an ideal species for evaluating the effectiveness of marine reserves for species that carry out directional migration. It uses specific nursery grounds, has seasonally defined periods of peak spawning and recruitment, and is heavily exploited. The segregation of immature fish into a restricted inshore area probably makes them an easy target and facilitates their intense exploitation (A.J. Abella, Agenzia Regionale per la Protezione Ambientale della Toscana, Via dell’Ambrogiana 2, 57127 Livorno, Italy, personal communication). Hence, marine reserves are a potentially useful management option for this species.

Model implementation

The parameter values used in the model were taken from the literature on the Mediterranean hake (Table 3). The values of *a* and β (eq. 1) were calculated for a given number of eggs, E_0 , and steepness, *h* (Appendix A). Two values of *h* were tested, 0.7 and 0.9. The latter was based on the results obtained by Myers et al. (1995) (i.e., stock–recruitment curve characterized by steepness which is close to 1); the former represents a greater level of dependence of *E* on SSB. Model results did not depend strongly on *h*, and results are presented only for *h* = 0.7; this value gives larger benefits from spawning stock protection.

Only females were modelled; a full model also including males was found to give very similar results. There were 14 size classes, with natural mortality rates for the majority of size classes taken from Caddy and Abella (1999); the values for the largest size classes were assumed (Table 4). A 1.5-month time step was used, such that each year consisted of eight time steps. Recruitment into the first size class occurs six months after hatching. The time step was chosen so that all fish in the first size class enter the second class after one time step, and to allow seasonality to be modelled.

We assumed that fish spawn only once per year, but that spawning can occur at any time throughout the year. The largest proportion of adults was assumed to enter the spawning area in autumn and winter and to leave in the spring and summer. Recruits were assumed to stay in the nursery area (when area *a* is a nursery area) for one time period and then follow the movement pattern into and out of area *a*, as described by the movement rates in Fig. 1. Slow-moving fish remained for longer in the spawning area than fast-moving fish. Because data on hake movement are not available, and to allow model results to be generalized, three sets of movement coefficients were examined, representing high, moderate, and low levels of mobility. The movement coefficient $\vartheta_{a,b}$ that characterizes fish of size 55–60 cm and describes moderate mobility is high for the first two time steps of the year and then decreases, while the value of $\vartheta_{b,a}$ is high in the first time period of the year, becomes smaller afterwards and increases again in the last time step of the year (Fig. 1a). Movement coefficients characterizing fish of other sizes are similar. Each set of movement coefficients results in a different distribution of fish in the study area (Fig. 1b).

Table 5. Results of the model under assumptions that best represent the situation for Mediterranean hake (*Merluccius merluccius*).

Redistribution	Exploitation	Change from nonreserve value (%)			Recovery time (years)
		SSB	Equilibrium yield	Year 1 yield	
Full	Under	+1	+38	+32	—
	MSY	+10	+42	+28	—
	Over	+16	+50	+24	—
None	Under	+26	+9	-11	6
	MSY	+54	+25	-13	4
	Over	+87	+47	-14	3

Note: Assumptions are that fish have moderate mobility (Fig. 1), there is selectivity for small fish (Table 4), and the marine reserve protects the nursery area. Results are presented as the long-run equilibrium spawning stock biomass (SSB) and yield as well as the yield in the first year after the reserve is instituted, all as percentages of the pre-reserve yield. We also show the number of years required for yield to recover to at least pre-reserve levels. Three levels of pre-reserve fishing mortality are shown (underexploited, $\hat{F} = 0.3$; maximum sustainable yield (MSY), $\hat{F} = 0.5$; and overexploited, $\hat{F} = 0.7$). Fishing effort from the reserve area is either fully redistributed to the rest of the fishing area (full) or not redistributed at all (none). For comparative purposes, the values in bold are for the situation shown in Fig. 2d.

The model was run under unexploited conditions until the population reached equilibrium. Starting from this point, the model was run for different levels of fishing pressure under a no-reserve regime, which allowed the maximum sustainable yield (MSY) fishing effort and the lowest fishing mortality resulting in fish extinction to be found. Three assumptions about fishing selectivity were modelled: selection for smaller size classes, which was based on estimated fishing mortalities for Mediterranean hake (Caddy and Abella 1999); no selection by size class; and selection for larger fish (Table 4). Fishing mortality by size class was obtained by multiplying the reference values given in Table 4 by a fishing mortality multiplier, \hat{F} .

Three values for \hat{F} were chosen, representing a fishery that was underexploited prior to reserve establishment, the MSY level, and an overexploited fishery. The institution of a marine reserve was assumed to occur after the fished population had reached equilibrium for a given value of \hat{F} , and was accompanied by a redistribution of fishing effort. After the institution of the reserve, no fishing took place in area *a*. The post-reserve value of \hat{F} depended on the assumption made about effort redistribution. A number of assumptions were also tested concerning fish movement patterns, spawning behaviour, and use of area *a*.

Results are presented in terms of biomass yield and SSB. To capture both short- and long-term effects of the reserve, the time required for yields to reach pre-reserve levels is presented. Another possible advantage of instituting a reserve is increased resilience to high fishing mortalities. Hence, we also present the fishing mortality at which population extinction would occur before and after reserve establishment.

Results

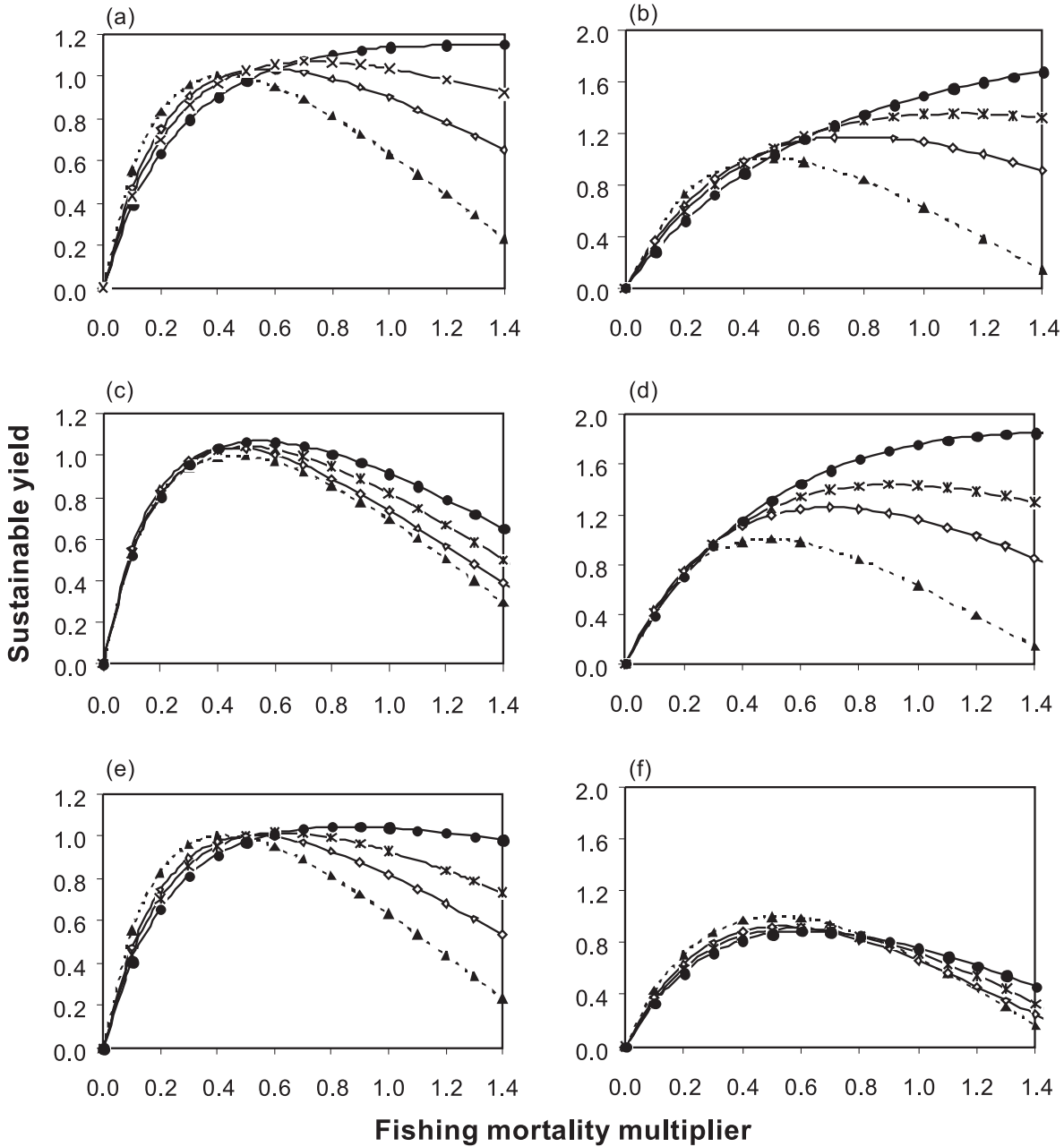
Under the movement and selectivity assumptions that best represent the situation for Mediterranean hake (moderate fish mobility, which results in movement patterns that are closest to available descriptions of hake movement, and selectivity for small fish), the institution of a marine reserve always has beneficial results. The reserve leads to increases in both SSB and long-term equilibrium yield (Table 5). Greatest long-term benefits from the reserve occur if the fishery is over-

exploited before its institution. Yield increases are obtained even in the first year after the reserve is instituted if effort is redistributed. If a more precautionary approach is taken, by not redistributing effort following reserve creation (instead keeping \hat{F} at the pre-reserve level in area *b*), short-term losses in yield are incurred. However, yields recover rapidly, particularly if the fishery was initially overexploited. The advantage of not redistributing effort is that SSB shows a marked increase, whereas long-term yields are still improved over the pre-reserve level.

The benefits obtained from a marine reserve depend on fish mobility and on the interaction between fishing selectivity and the placing of the reserve area (Fig. 2). As would be expected, the greatest benefits are obtained if the area protected is both a spawning and a nursery area (Figs. 2a, 2b). If the spawning and nursery areas are separate, benefits are highest when the area used by the size classes that are the main target of the fishery is protected. Hence, protecting the nursery area has greatest benefits if immature fish are targeted, whereas protecting the spawning area is most beneficial if mature fish are targeted (Figs. 2d and 2f, 2c and 2e). The more mobile the fish are, the lower are the yield improvements from the marine reserve. Nonetheless, under the assumptions in Fig. 2, the protection of a nursery area leads to long-term yield improvements at all fishing mortalities and mobilities, whatever the size selectivity of the fishery. On the other hand, if the spawning area is protected, yield improvements are obtained at higher fishing mortalities, but not for underexploited fisheries (Figs. 2e, 2f). Underexploited fisheries also do not show yield improvements if the area protected is both a spawning and a nursery area, despite the much higher yields obtained for overexploited fisheries (Figs. 2a, 2b).

Another potential benefit of marine reserves is increased resilience to high fishing mortalities (leading to a shift in \hat{F}_{MSY} to the right), and hence protection against over-exploitation and uncertainty in stock assessments. Our results suggest that the marine reserve gives a resilience benefit, such that the fishing mortality at which stock extinction is predicted (\hat{F}_{ext}) is much higher when a reserve is in place (Fig. 2). The fishing mortality on area *b* that is required to drive the stock to extinction when area *a* is pro-

Fig. 2. The sustainable yield from fishing with a marine reserve that protects the whole of area *a*, shown for a range of fishing mortalities. The sustainable yield per fishing mortality curves before the establishment of the reserve are also given for comparative purposes. The maximum sustainable yield (MSY) fishing mortality coefficients without a reserve can be found from these curves. Sustainable yield with and without a marine reserve is normalized to the MSY without a reserve in each case. It is assumed that there is no redistribution of effort from area *a* to *b* when the reserve is instituted. Broken line and solid triangle, no reserve; with reserve: open diamond, high mobility; ×, moderate mobility; solid circle, low mobility fish. Note the different scales on the y axis when immature fish are targeted (*b*, *d*, *f*) and mature fish are targeted (*a*, *c*, *e*). (*a*) Selectivity for mature fish; area *a* is a spawning and nursery area. (*b*) Selectivity for immature fish; area *a* is a spawning and nursery area. (*c*) Selectivity for mature fish; area *a* is a nursery area. (*d*) Selectivity for immature fish; area *a* is a nursery area. (*e*) Selectivity for mature fish; area *a* is a spawning area. (*f*) Selectivity for immature fish; area *a* is a spawning area.



tected is considerably higher than that required when the entire area is fished (Table 6); the gains are substantial when the area protected is biologically important (hence the benefits are much higher if the nursery ground is protected and immature fish are targeted in the fishery), and for less mo-

bile fish. If spawners get incidental protection because the nursery ground is also a spawning ground, the benefits are even more pronounced. \hat{F}_{ext} would be expected to be higher on the remaining area if a part of the area is not fished, although this may not constitute an overall benefit to the fish-

Table 6. The resilience of a fish population to overexploitation when protected by a marine reserve.

	Actual \hat{F}			Comparative \hat{F}		
	L	M	H	L	M	H
Spawning	33	20	13	-13	-20	-27
Nursery	300	107	53	160	33	0
Spawning & nursery	>500	213	73	>500	100	13

Note: Results are shown as the percent difference between the value of the fishing mortality multiplier causing extinction of the population when area *a* is fully protected as a marine reserve and when there is no reserve. The fishing mortality multiplier leading to extinction without a reserve is $\hat{F}_{\text{ext}} = 1.5$. It is assumed that fishermen are targeting small fish. Once the reserve is instituted, fishing mortality takes place only in area *b*. Results are shown for three levels of fish mobility (L, low; M, moderate; H, high). Area *a* is assumed to be either a spawning ground, a nursery ground, or both. Actual \hat{F} is based on the fishing mortality on area *b* that produces extinction; comparative \hat{F} is based on this value multiplied by the proportion of the total area that area *b* makes up, thus showing the effect on overall fishing effort of instituting a reserve.

ery if this fishing mortality corresponds to an overall fishing effort that is lower than that immediately prior to reserve establishment. But overall benefits can also be substantial, particularly when the fish are not mobile and the reserve protects both the spawning and nursery areas (Table 6).

As well as long-term benefits, an important consideration is whether a marine reserve can provide short-term benefits. This depends on the type of effort redistribution and fish mobility. The quantitative dependence of the short-term effects of reserve establishment on these factors is presented for a situation in which the nursery area is protected and there is no size selectivity (Table 7a). The general patterns shown here are similar to those found under other assumptions about selectivity and the status of area *a*. Long-term benefits (increases in equilibrium SSB and yield) are inversely related to fish mobility, whereas short-term benefits (yield in the first year after reserve creation and yield recovery rate) are positively related to mobility.

The type of effort redistribution also affects reserve effectiveness: full redistribution leads to SSB reductions compared with the situation before reserve establishment (except in some cases of lower mobility fish), whereas SSB is always increased by a reserve if effort is not redistributed. Conversely, full redistribution generally leads to yield increases in both the short and long terms, (except in the case of highly mobile overexploited stocks, for which the large reduction in SSB leads to long-term yield reductions). If effort is not redistributed, yield does increase in the long term (by very little if the fishery was previously underexploited), although reductions in yield are experienced in the short term.

A marine reserve without effort control (full redistribution) is beneficial in some cases, whereas a reserve with effort control is always beneficial in terms of SSB and long-term yield (Table 7a). However, some of that benefit is likely attributable to the effort control itself, rather than to the act of limiting access to a distinct area. For this reason, the effect of effort control alone, in the absence of a marine reserve, is also given (Table 7b). For comparability, fishing effort was reduced to the level that gives the same yield in the first year after control as is obtained when a reserve is instituted and effort is not redistributed. Effort control alone

produces an increase in SSB for both under- and over-exploited fisheries and in long-term yield for overexploited fisheries, although substantially less than when a marine reserve is also created. Hence, the marine reserve leads to a substantial improvement in fishery performance over effort control alone.

Discussion

Our study has evaluated a broad range of assumptions concerning fish mobility, the status of the area being protected (spawning ground and (or) nursery ground), effort redistribution, and fishing selectivity. Previous studies have shown that each of these factors separately could be significant for the effectiveness of a reserve (e.g., movement rate, Polacheck 1990; fishing effort control, Sladek Nowlis and Roberts 1999), but we have shown how these factors affect reserve effectiveness in combination, thereby moving towards an approach that combines realistic assumptions about both the biology of the target species and the response of the fishery to area closure. Previous studies of the effectiveness of marine reserves have generally concluded that they are beneficial only for overexploited fisheries (e.g., Guénette and Pitcher 1999; Sladek Nowlis and Roberts 1999). Those studies that have considered mobility have found yield improvements only for species that are not highly mobile, although Guénette and Pitcher (1999) noted that SSB and resilience of mobile species were improved by a reserve. Our results concur with those of some recent modelling studies regarding overexploited fisheries (Guénette and Pitcher 1999; Sladek Nowlis and Roberts 1999), but we have found that yield and SSB benefits can be obtained through the use of a marine reserve even for highly mobile fish and under-exploited fisheries. Thus, marine reserves could be used for the protection of a larger range of marine species than previously thought. However, our model showed that the establishment of a reserve is not always beneficial, and could lead to both yield and SSB reductions. To avoid this, it is important to designate reserves only in appropriate areas and to consider the regulatory measures needed in conjunction with the reserve (see Roberts and Hawkins 2000).

Generally there are trade-offs to be made between the short-term and long-term effects of a marine reserve. The short-term effects of reserve establishment are not usually considered in modelling studies (but see Sladek Nowlis and Roberts 1997); however, they are of crucial importance in practical implementation. Our study has shown that the short-term losses associated with reserve establishment are less severe for highly mobile fish. If effort from the reserve area is redistributed to the rest of the fishing area on establishment of a reserve, short-term losses can be minimized or avoided, although this can lead to a concomitant reduction in long-term benefits from the reserve both in terms of yield and SSB, and even to decreases in SSB. Although our study does not address the important and overlooked issues of the economic and social impacts of reserve establishment, it does address effort redistribution following reserve creation, albeit in a highly simplified manner. Changes in effort levels following the closure of a fished area can be due to the reactions of individual fishers or to management actions accompanying reserve creation. The results suggest that

Table 7. (a) The effects of the type of effort redistribution (full or none) and fish mobility on spawning stock biomass (SSB), equilibrium biomass yield, yield in the first year (Year 1), and the time taken for yield to recover to the pre-reserve level (time), shown for two levels of initial fishing mortality; an underexploited stock and an overexploited stock. (b) The effect of effort limitation without a marine reserve, with effort being reduced such that yields in the first year are the same as those obtained for a marine reserve with no effort redistribution.

(a) Effort redistribution.*									
Redistribution	Mobility	Underexploited				Overexploited			
		SSB	Equilibrium yield	Year 1	Time	SSB	Equilibrium yield	Year 1	Time
Full	Low	-5	+30	+32	—	+9	+39	+15	—
	Moderate	-14	+27	+40	—	-3	+6	+28	—
	High	-19	+23	+42	—	-46	-14	+32	—
None	Low	+19	+4	-12	5	+90	+49	-18	3
	Moderate	+12	+4	-6	6	+53	+34	-9	3
	High	+9	+3	-5	6	+39	+27	-6	3

(b) Effort limitation.									
Mobility	Underexploited				Overexploited				
	SSB	Equilibrium yield	Year 1	Time	SSB	Equilibrium yield	Year 1	Time	
Low	+8	-6	-12	∞	+50	+11	-18	6	
Moderate	+4	-3	-6	∞	+24	+7	-9	6	
High	+3	-2	-5	∞	+17	+6	-6	6	

*Results are presented as the percentage change compared with the equilibrium value before the institution of the reserve, except time, which is given in years. It is assumed that the reserve is protecting the nursery area. The effect of selectivity is removed from the results by assuming no selectivity by size.

consideration of the extent to which effort is redistributed following reserve creation will be a key determinant of management success, and thus should be a priority for future modelling work.

Another major benefit that has been suggested for marine reserves is improved resilience to overexploitation (e.g., Lauck et al. 1998). We have shown that this is indeed a benefit in most cases, particularly for less mobile fish, except when the area protected does not shelter the size classes primarily targeted by the fishery.

Our study has shown that reserves could be beneficial in the specific instance of Mediterranean hake, because there is a defined area in which the sought-after immature fish are mostly found. If this area also happens to coincide with the spawning ground, as is sometimes the case, benefits from a reserve can be greater still. These benefits are found for underexploited as well as overexploited fisheries. Benefits also depend on the assumptions made concerning effort redistribution; if effort is not redistributed, short-term yields are reduced but SSB is higher. It should be noted, however, that these conclusions are preliminary for Mediterranean hake, because of the uncertainty in parameter estimation (particularly with respect to movement rates), and because we have not considered sociopolitical barriers to reserve creation. Nevertheless, the use of area closures for the management of red mullet (*Mullus barbatus*) fisheries in the Mediterranean and the protection of part of the Gulf of Castellammare (Sicily), where many juvenile hake are caught (C. Pipitone, National Research Council, Istituto di ricerche sulle Risorse Marine e l'Ambiente, Laboratorio di Biologia Marina, Castellammare del Golfo, Italy, personal communication), have produced positive results, supporting our predictions (Garcia and Demetropoulos 1986; Caddy 1990; Pipitone et al. 2002).

The model investigates some of the potential benefits of

marine reserves for a single species. However, marine reserves also have broader benefits. The establishment of a reserve in an area offers protection to all species inhabiting the area (Allison et al. 1998) and could protect habitats from destructive fishing techniques (Roberts 1998). They also contribute to the protection and enhancement of biodiversity and could benefit tourism (Lauck et al. 1998; Roberts and Hawkins 2000).

We have shown here how important it is to account correctly for the biological characteristics of an exploited species and the dynamics of the fishery targeting it when considering the benefits of a marine reserve. By increasing model realism, we have shown that marine reserves that take spatial and temporal variation in fish population dynamics into account (e.g., by protecting nursery areas) could be beneficial even for underexploited stocks and for highly mobile species. The modelling framework presented here is likely to be useful for the many other species that, like hake, exhibit seasonal migrations and defined spawning and nursery areas. Our analysis suggests that reserves may well also be of value for these species. However, the theoretical models presented here now need to be tested by application to fisheries in practice.

Acknowledgements

We would like to thank A.J. Abella, J.F. Caddy, Callum Roberts, and two anonymous referees for the information and the valuable comments they provided, and R.I.C.C. Francis for his help with the construction of some of the equations used in the model. C. Cunningham and I. Mosquera are thanked for their comments on earlier versions of the manuscript. This work was partly funded by the Wildlife Conservation Society.

References

- Abella, A.J., Auteri, R., and Serena, F. 1995. Some aspects of growth and recruitment of hake in the Northern Tyrrhenian sea. *Rapport Commission International Mer Méditerranée*, **34**: 235.
- Abella, A.J., Caddy, J.F., and Serena, F. 1997. Does natural mortality decline with age? An alternative yield paradigm for juvenile fisheries, illustrated by the hake *M. merluccius* fishery in the Mediterranean. *Aquat. Living Resour.* **10**: 257–269.
- Allison, G.W., Lubchenco, J., and Carr, M.H. 1998. Marine reserves are necessary but not sufficient for marine conservation. *Ecol. Appl.* **8**(1)(Suppl.): S79–S92.
- Ballantine, W.J. 1995. The New Zealand experience with 'no-take' marine reserves. *In Review of the use of marine fishery reserves in the U.S. southeastern Atlantic. Edited by C. Roberts et al. NOAA Tech. Memo. NMFS-SEFSC-376.* pp. C15–C31.
- Beverton, R.J. 1998. Fish, fact and fantasy: a long view. *Rev. Fish Biol. Fish.* **8**: 229–249.
- Beverton, R.J., and Holt S.J. 1957. On the dynamics of exploited fish population. Her Majesty's Stationary Office, London.
- Buckworth, R.C. 1998. World fisheries are in crisis? We must respond. *In Reinventing fisheries management. Edited by T.J. Pitcher, P.J.B. Hart, and D. Pauly.* Fish and Fisheries Series 23. Chapman and Hall. pp. 3–14.
- Caddy, J.F. 1990. Options for the regulation of Mediterranean demersal fisheries. *Natural Resources Modeling*, **4**: 427–475.
- Caddy, J.F., and Abella, A.J. 1999. Reconstructing reciprocal M vectors from length cohort analysis (LCA) of commercial size frequencies of hake, and fine mesh trawl surveys over the same grounds. *Fish. Res.* **41**: 169–175.
- Dayton, P.K., Thrush, S.F., Agardy, M.T., and Hofman, R.J. 1995. Environmental effects of marine fishing. *Aquat. Conserv. Mar. Freshwater Ecosyst.* **5**: 205–32.
- Die, D.J., and Watson, R.A. 1992. A per-recruit simulation model for evaluating spatial closure in an Australian penaeid fishery. *Aquat. Living Resour.* **5**: 145–153.
- Food and Agriculture Organization (FAO). 1995. The state of the world fisheries and aquaculture. FAO Fisheries Department, Rome.
- Francis, R.I.C.C. 1992. Use of risk analysis to assess fishery management strategies: a case study using orange roughy (*Hoplostethus atlanticus*) on the Chatham Rise, New Zealand. *Can. J. Fish. Aquat. Sci.* **49**: 922–930.
- Garcia, S., and Demetropoulos, A. 1986. Management of Cyprus fisheries. FAO Fish. Rep. No. 253.
- Guénette, S., and Pitcher, T.J. 1999. An age-structured model showing the benefits of marine reserves in controlling overexploitation. *Fish. Res.* **39**: 295–303.
- Hilborn, R. 1990. Determination of fish movement patterns from tag recoveries using maximum likelihood estimators. *Can. J. Fish. Aquat. Sci.* **47**: 635–643.
- Lauck, T., Clark C.W., Mangel, M., and Munro, G.R. 1998. Implementing the precautionary principle in fisheries management through marine reserves. *Ecol. Appl.* **8**: S72–S78.
- Mangel, M. 2000a. On the fraction of habitat allocated to marine reserves. *Ecol. Lett.* **3**: 15–22.
- Mangel, M. 2000b. Trade-offs between fish habitat and fishing mortality and the role of reserves. *Bull. Mar. Sci.* **66**: 663–674.
- Mosqueira, I., Côté, I.M., Jennings, S., and Reynolds, J.D. 2000. Conservation benefits of marine reserves for fish populations. *Anim. Conserv.* **3**: 321–332.
- Myers, R.A., Bridson, J., and Barrowman, N.J. 1995. Summary of worldwide spawner and recruitment data. *Can. Tech. Rep. Fish. Aquat. Sci. No.* **2024**: 120–124.
- Oliver, P., and Massuti, E. 1995. Biology and fisheries of eastern Mediterranean hake (*M. merluccius*) *In Hake: fisheries, ecology and markets. Edited by J. Alheit and T.J. Pitcher.* Fish Fish. Ser. 15. Chapman and Hall, London. 181–202.
- Orsi Relini, L., Cappanera, M., and Fiorentino, F. 1989. Spatial-temporal distribution and growth of *M. merluccius* recruits in the Ligurian Sea. Observations on the 0 group. *Cybiurn*, **13**: 263–270.
- Papaconstantinou, C., and Stergiou, K.I. 1995. Biology and fisheries of eastern Mediterranean hake (*M. merluccius*) *In Hake: fisheries, ecology and markets. Edited by J. Alheit and T.J. Pitcher.* Fish Fish. Ser. 15. Chapman and Hall. pp. 149–180.
- Papaconstantinou, C., Petrakis, G., and Vassilopoulou, V. 1986. The fecundity of hake (*Merluccius merluccius*) and red Pandora (*Pagellus Erythrinus*) in Greek seas. *Acta Adriat.* **27**(1–2): 85–95.
- Pipitone, C., D'Anna, G., Badalamenti, F., Scotti, G., Coppola, M., Di Stefano, G., and Kienzle, M. 2002. Fishery reserves as a management tool: the case of the Gulf of Castellammare. *Fishery Exclusion Zones Internet Conference*, 21 January – 4 February 2002. http://www.valfez.org/internet_conf/ (accessed 27 January 2002).
- Pitcher, T.J., and Pauly, D. 1998. Rebuilding ecosystems, not sustainability, as the proper goal of fishery management. *In Reinventing fisheries management. Edited by T.J. Pitcher, P.J.B. Hart, and D. Pauly.* Fish Fish. Ser. 23. Chapman and Hall, London. pp. 311–325.
- Polacheck, T. 1990. Year around closed areas as a management tool. *Nat. Resour. Model.* **4**: 327–354.
- Quinn, T.J., and Deriso, R.B. 1999. Quantitative fish dynamics. Oxford University Press, New York.
- Recasens, L., Lombarte, A., Morales-Nin, B., and Torres, G.J. 1998. Spatio-temporal variation in the population structure of the European hake in the NW Mediterranean. *J. Fish Biol.* **53**: 387–401.
- Roberts, C.M. 1998. No-take marine reserves: unlocking the potential for fisheries. *Marine Environmental Management: Review of Events in 1997 and Future Trends*, **5**: 127–132.
- Roberts, C.M., and Hawkins, J.P. 2000. Fully-protected marine reserves: a guide. WWF Endangered Seas Campaign, 1250 24th Street NW, Washington, DC 20037, U.S.A., and Environment Department, University of York, York, YO10 5DD, U.K.
- Roberts, C.M., and Polunin, N.V.C. 1993. Marine reserves: simple solutions to managing complex fisheries? *Ambio*, **22**: 363–368.
- Sant, M. 1996. Environmental sustainability and the public: responses to a proposed marine reserve at Jervis Bay, New South Wales, Australia. *Ocean Coast. Manag.* **32**: 1–16.
- Sladek Nowlis, J., and Roberts, C.M. 1997. You can have your fish & eat it too: theoretical approaches to marine reserve design. *Proc. 8th Int. Coral Reef Symp. (Issue 2)*, 24–29 June 1996, Panama City. *Edited by W. Holland.* pp. 1907–1910.
- Sladek Nowlis, J., and Roberts, C.M. 1999. Predicted Fisheries Benefits and Optimal Marine Fishery Reserves Design. *Fish. Bull.* **97**: 604–616.
- Zupanovic, S., and Jardas, I. 1986. A contribution to the study of biology and population dynamics of the Adriatic hake, *M. merluccius*. *Acta Adriat.* **27**(1–2): 97–146.

Appendix A. Calculation of stock–recruitment parameters.

The values of α and β in eq. 1 depend on the steepness, h , of the egg–recruits curve and on the number of eggs, E_0 , produced under natural mortality

$$(A1.1) \quad a = \sum_{A \geq A_{\text{mat}}} n_{0,A} f_A \frac{(1-h)}{4h}$$

$$(A1.2) \quad \beta = \sum_{A \geq A_{\text{mat}}} n_{0,A} f_A \frac{(5h-1)}{4h \cdot E_0}$$

where A denotes the age of the fish, A_{mat} is the age at maturity of female fish, and f_A is fish fecundity at age (see Table 3 for the values of A_{mat} and f_A). The steepness, h , is equal to the fraction of the recruits under virgin conditions, R_0 (the recruitment corresponding to E_0), that are expected when the number of eggs is reduced to 20% of E_0 . The parameter $n_{0,A}$ is the exponential factor that determines the proportion of fish at age A that survive under virgin conditions (Francis 1992),

$$(A1.3) \quad n_{0,A} =$$

$$\begin{cases} e^{-\left(\sum_{j=1}^A M_j\right)} e^{\frac{1}{2}M_A} e^{-\frac{1}{2}M_{A=0.5}} & A < A_{\text{max}} \\ \frac{e^{-\left(\sum_{j=1}^{A_{\text{max}}-1} M_j\right)} e^{\frac{1}{2}M_{A_{\text{max}}-1}} e^{-\frac{1}{2}M_{A=0.5}}}{1 - e^{-M_{A_{\text{max}}}}} & A = A_{\text{max}} \end{cases}$$

The natural mortality at age, M_A , as well as the maximum age of fish, A_{max} , are necessary for the estimation of $n_{0,A}$. The expression for $n_{0,A_{\text{max}}}$ was derived assuming that M of fish at age $A_{\text{max}-1}$ or older remains constant. M of six-month-old fish, $M_{A=0.5}$, is needed, since recruitment is assumed to take place six months after spawning. Because this formulation was developed for age- rather than stage-structured models, we must assume that all spawning takes place in a single time period. Then, once the virgin biomass is found, the model is run without fishing until the equilibrium for the size-structured model is found.

Appendix B. Calculation of the number of fish in a given size category and area.

To calculate the number of fish in an area that belong to size category S at the beginning of time period t , it is necessary to account for fish that have grown from size category $S-1$ at the beginning of time period $t-1$ to size category S at the beginning of time period t , as well as fish that have remained in size category S between the two time periods. It is also necessary to account for fish that have remained in area a or b or moved into or out of each area between the two time periods. As an example, we show the calculation for the number of fish in area a that belong to size category S at the beginning of time period t .

First, consider the fish that have remained in area a . The number of these is given by

$$(A2.1) \quad N_{a \rightarrow a, S, t} = N_{a, S-1, t-1} e^{-(F_{a, S-1} + M_{S-1})} P_{S-1, S} (1 - \vartheta_{a, b, S-1, t-1}) + N_{a, S, t-1} e^{-(F_{a, S} + M_S)} P_{S, S} (1 - \vartheta_{a, b, S, t-1})$$

The number of fish that moved from area a to area b is given by

$$(A2.2) \quad N_{a \rightarrow b, S, t} = N_{a, S-1, t-1} e^{-(F_{a, S-1} + M_{S-1})} P_{S-1, S} \vartheta_{a, b, S-1, t-1} + N_{a, S, t-1} e^{-(F_{a, S} + M_S)} P_{S, S} \vartheta_{a, b, S, t-1}$$

The number of fish that moved from area b to area a is given by

$$(A2.3) \quad N_{b \rightarrow a, S, t} = N_{b, S-1, t-1} e^{-(F_{b, S-1} + M_{S-1})} P_{S-1, S} \vartheta_{b, a, S-1, t-1} + N_{b, S, t-1} e^{-(F_{b, S} + M_S)} P_{S, S} \vartheta_{b, a, S, t-1}$$

Thus, the number of fish in area a that belong to size category S at the beginning of time period t is given by

$$(A2.4) \quad N_{a, S-1, t-1} = N_{a \rightarrow a, S, t} + N_{b \rightarrow a, S, t} - N_{a \rightarrow b, S, t}$$

Similar formulas apply for calculating the numbers of fish in area b . When area a is a marine reserve, $F_{a, S} = 0$ for each size class, S , because fishing does not take place in the area.