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# Predicting indirect effects of fishing in Mediterranean rocky littoral communities using a dynamic simulation model ☆

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## Abstract

Modelling may significantly enhance our understanding of the potential impacts of fisheries at larger spatial scales and on groups that would otherwise be very difficult to study. An aggregated biomass-based simulation model of a Mediterranean infralittoral zone was developed and used to carry out fishing 'experiments' where fishing intensity and catch selection were varied. The model was constructed for the Bay of Calvi, Corsica, using the Ecopath with Ecosim software, and was composed of 27 compartments, including seabirds, 11 groups of fish, 12 groups of invertebrates, 2 primary producers, bacteria and detritus.

Several instances of indirect fishing effects ('trophic cascades' and 'keystone predation') have been proposed from anecdotal evidence in the western Mediterranean. Model outcomes provided little support for the widely accepted paradigm that fishing, by removing invertebrate-feeding fish, allows increases in the biomass of sea urchins and as a consequence the formation of overgrazed 'barrens' of bare substrate. Simulated harvesting of sea urchins by humans did, however, results in an increase of macroalgal biomass as reported previously. Intensified fishing pressure on 'macrocarnivorous' fish resulted in a 'release' of small fish species (e.g. blennies), and as a consequence a decline in the biomass of some small invertebrates on which they feed (e.g. amphipods). Increased fishing on large 'piscivores' resulted in increases in other small fish groups and consequential effects on other benthic invertebrate groups (e.g. polychaetes). Depletion of piscivorous fish resulted in a dramatic increase in the biomass of seabirds, which apparently compete with piscivores for small demersal and pelagic fish. An intensification of fishing pressure overall resulted in an increase in cephalopod biomass.

Responses of target species to increased fishing pressure were most marked within the first 5 years of the new fishing regime. Indirect responses exhibited varying degrees of inertia, and biomasses of many groups did not assume a new equilibrium within the first 20 years of the simulation.

The Mediterranean infralittoral rocky-bottom ecosystem was predicted to be relatively resilient to pulses of increased fishing and exhibited a high degree of detritus recycling. However, the speed and magnitude of ecosystem responses was shown to depend greatly on the extent of 'top-down' or 'bottom-up' control assumed for components within the system.
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## 1. Introduction

One of the most widely expressed concerns about intensive fishing is that it will lead to imbalances in ecosystem function with knock-on effects for community structure overall (Jennings and Kaiser, 1998; Pinnegar et al., 2000). The initiation of fishing or harvesting in a previously unfished system leads to

dramatic reductions in the abundance of target stocks (Sánchez Lizaso et al., 2000) and this may in-turn induce indirect trophic (food web) interactions, such as trophic cascade effects or 'keystone predation' (see definitions in Menge, 1995), whereby removal of a predatory species may result in a 'release' of its prey or competitors. This signal that may proliferate throughout food webs and descend four or more trophic levels in some instances (Pinnegar et al., 2000).

Human exploitation of inshore marine resources dates back thousands of years in the Mediterranean and most commercial fish stocks are considered to be greatly overexploited (Farrugio et al., 1993). It has been suggested that the increased prevalence of barrens of bare substrate and coralline algae in many parts of the western Mediterranean may be one symptom of this long-standing intensive use of the littoral zone (Sala et al., 1998a). Many studies have demonstrated that large piscivorous and invertebrate-feeding fish are more abundant within Mediterranean marine protected areas (MPAs) than outside them (reviewed in García Charton et al., 2000; Sánchez Lizaso et al., 2000) and this is often particularly so for the sparid fishes *Diplodus sargus* and *Diplodus vulgaris* (e.g. Bell and Harmelin-Vivien, 1983; Harmelin et al., 1995). These *Diplodus* species, along with the wrasse *Coris julis*, are considered to be major predators of sea urchins (Sala, 1997), and at unprotected sites where density of fish is low, urchin populations tend to be greatly increased (Sala and Zabala, 1996). When at high densities, sea urchins have been shown to remove large erect algae and induce formation of coralline barrens (Lawrence, 1975; Verlaque, 1987). The elimination of erect algae and the simplification of community structure associated with sea urchin overgrazing has been shown to result in a dramatic reduction in associated fauna (Vukovic, 1982). In some areas of the Mediterranean, sea urchins are considered a delicacy (Le Direach, 1987) and intense *Paracentrotus lividus* harvesting (commercial and recreational) has caused local depletion of urchins (Gras, 1987). Elsewhere, urchin harvesting has resulted in an increase in macroalgal biomass (e.g. Steneck et al., 1995).

Conspicuously, lower abundance and species richness of macroinvertebrates (mostly echinoderms and large molluscs) were observed within the Scandola MPA (Fig. 2) in Corsica (Boudouresque et al., 1992) where the abundance, biomass and diversity of predatory fishes were greater than outside this MPA (Francour, 1994). In contrast, within the integral (no-fishing) zone of the Ustica MPA (Fig. 2), abundance and species richness of small invertebrates (polychaetes and gastropods) were greater than outside it (Badalamenti et al., 1999; Chemello et al., 1999; Milazzo et al., 2000). This coincided with lower abundance of small microcarnivorous fish species (e.g. blenniids, gobiids, tripterygiids and juveniles of several taxonomic groups) and an increase of piscivorous and macrocarnivorous fish abundance (e.g. groupers) in the same area (Vacchi et al., 1998; La Mesa and Vacchi, 1999). Macpherson (1994) also observed fewer species and much lower abundance of small fish (blenniids) inside the Medes Marine Reserve (Fig. 2) than in sites outside, where potential predators were less abundant. Therefore, from anecdotal evidence it would seem that at least four distinct 'trophic cascades' have been documented for Mediterranean rocky littoral areas (Fig. 1).

Demonstrating indirect effects of fishing, such as trophic cascades, is difficult and has only been possible in shallow, hard-bottom communities that are amenable to investigation (see Pinnegar et al., 2000). The most conspicuous consumers, such as sea urchins and fish, typically tend to be studied, while other potentially important organisms, such as polychaetes and small crustaceans or molluscs, have been neglected. Most of the data used to support the notion of trophic cascades are inferential (Elner and Vadas, 1990; Sala et al., 1998a) or based on small-scale experiments that may not be applicable at larger spatial scales. The large-scale and long-term implications of small-scale observations remain essentially untested in the Mediterranean and the potential ecological effects of closing large areas to fishing are poorly understood (Sala et al., 1998a; Pinnegar et al., 2000).

There is little consensus concerning the conceptual and analytical tools that should be used to study trophic interactions in ecosystems (Walters et al., 1997). Modelling can increase understanding of fisheries and their potential influence on groups that are otherwise difficult to study. Construction, validation and application of models to projection of future stock levels are desirable for fisheries management. The last two decades have seen an explosive growth in the number and type of multispecies models directed at fisheries questions (reviewed in Hollowed
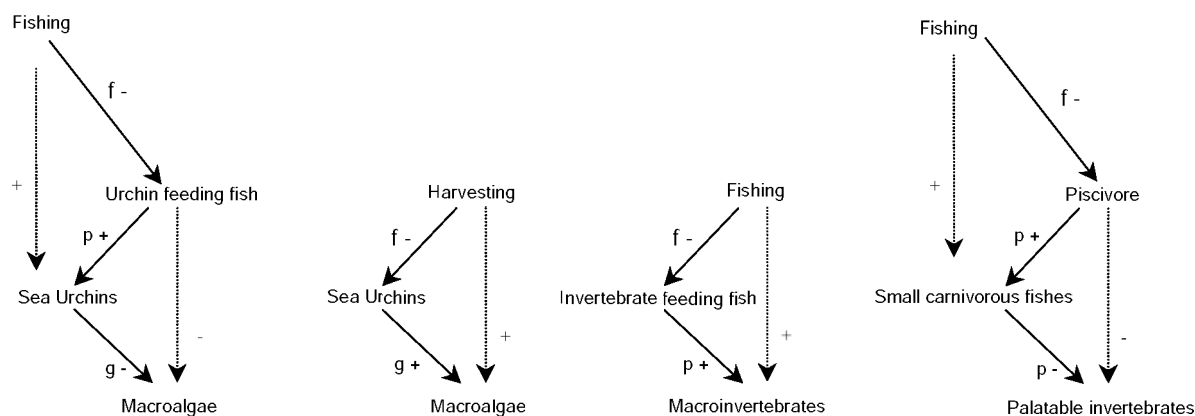
Fig. 1. Schematic diagrams of four fishery-mediated trophic cascade effects proposed from field studies in western Mediterranean rocky littoral communities; f: fishing/harvesting, g: grazing and p: predation. Direct interactions are denoted by solid arrows and indirect effects by dotted arrows.

et al., 2000; Whipple et al., 2000), each of which has benefits and limitations.

McClanahan and Sala (1997) constructed a biologically aggregated energy-based simulation model of a Mediterranean infralittoral rocky-bottom grazer community using Lotka–Volterra equations. This model yielded useful predictions of the effects of fishing, which generally agreed with patterns observed in the field. However, that model suffered several major limitations, chief among these being the low taxonomic differentiation (three fish groups, two invertebrate groups) and the complete exclusion of pathways associated with plankton and detritus. Planktivorous fish may represent as much as 32% of fish biomass and 18% of fisheries catches, and can be responsible for 40% of all fish throughput at some Mediterranean sites. Plankton and planktivorous fishes have been shown to be important prey for littoral predators and important producers of detritus (Pinnegar, 2000; Pinnegar and Polunin, 2000), which may be very important in governing a system's ability to recover from disturbances, such as fishing (Vasconcellos et al., 1997).

The mass-balance approach incorporated in the Ecopath software has been widely used for constructing food web models of marine ecosystems and to address issues of relevance to fisheries management (Pauly et al., 2000). The non-dynamic nature of Ecopath, however, greatly limits its predictive power and consequently its usefulness (McClanahan and Sala,

1997) but such limitations were overcome through introduction of the Ecosim module (Walters et al., 1997). Ecosim has been widely used to predict and evaluate ecosystem effects of fishing (e.g. Christensen, 1998; Trites et al., 1999a,b; Arreguin-Sanchez, 2000; Shannon et al., 2000; Stevens et al., 2000). In the present study of the Bay of Calvi, Corsica, Ecosim is used to see whether:

(a) the ecosystem was able to recover from pulses of increased fishing pressure;
(b) fishing resulted in the same cascades indicated by the anecdotal field evidence (Fig. 1);
(c) the predicted cascade effects were detectable over time scales which correspond with those indicated from field studies; and
(d) potential cascade effects might exist, other than those already documented from existing anecdotal field evidence.

## 2. Methods

### 2.1. The study area

An Ecopath steady-state model was constructed to represent the rocky sublittoral community of the Bay of Calvi, Corsica (Fig. 2), which has a total area of approximately 2200 ha (Dauby, 1989). Many aspects of the Bay's ecology and biology have been studied
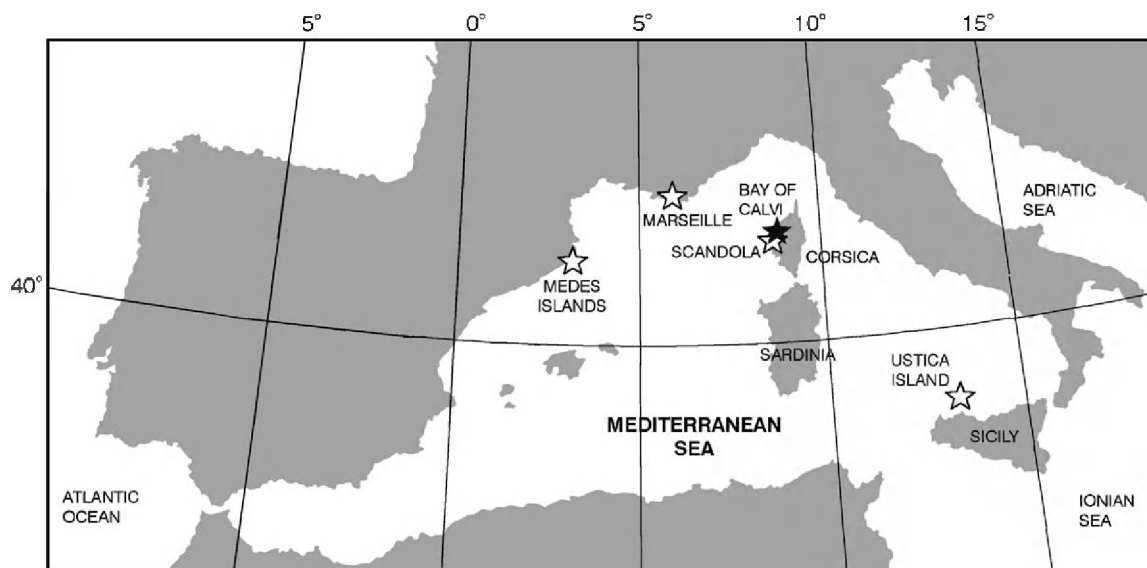
Fig. 2. Map of the western Mediterranean showing the site on which the model is based (Bay of Calvi, Corsica—filled star) and those locations from which anecdotal evidence for trophic cascade effects exist (open stars).

(Pinnegar, 2000), particularly in the western part, which is also known as the Bay of Revellata. The Bay of Revellata has approximately 7.8 km of shoreline, fringed by 53.1 ha of rocky sublittoral habitat, 179 ha of *Posidonia oceanica* seagrass meadow and 14 ha of sandy substrate (Sargian, 1997). Rocky communities generally exist to a depth of around 9 m and surface temperatures range from 13 °C in February to 26 °C in August (STARESO, unpublished data).

## 2.2. The Ecopath model

Originally proposed by Polovina (1984), Ecopath is a program for balancing steady-state ecosystem models and has been combined with routines for network analysis based on the approach of Ulanowicz (1986). Trophic interactions among the functional groups of the ecosystem can be described by a set of linear equations, the equation for each group ($i$) being:

production by ($i$) − predation on ($i$)

  − non-predation losses of ($i$) − export of ($i$) = 0

which may also be written as:

$$P_i = Y_i + B_i M2_i + E_i + P_i(1 - \mathrm{EE}_i) \qquad (1)$$

where $P_i$ is the total production of $i$; $Y$ is the total catch of $i$, $M2_i$ is the predation mortality rate for group $i$; $B$ is the biomass of the group, $E$ is the net migration rate (emigration–imegration) and $\mathrm{EE}_i$ is the ecotrophic efficiency of $i$ (the fraction of the production of $i$ that is consumed within the system, exported or harvested). Eq. (1) can also be expressed as:

$$B_i \left(\frac{P}{B}\right)_i \mathrm{EE}_i - \sum_{j=1}^{n} B_j \left(\frac{Q}{B}\right)_j \mathrm{DC}_{ji} - Y_i - E_i = 0$$

$$(2)$$

where $P/B_i$ is the production/biomass ratio, and $Q/B_j$ is the consumption/biomass ratio and $\mathrm{DC}_{ji}$ the fraction of the prey ($i$) in the average diet of predator $j$ (Christensen and Pauly, 1992).

This system of linear equations can be solved using standard matrix algebra (Christensen and Pauly, 1992), and although $\mathrm{Dc}_{ji}$, $Y_i$ and $E_i$ must always be entered, entry is optional for any one of the other four parameters ($B_i$, $P/B_i$, $Q/B_i$, $\mathrm{EE}_i$).

The Ecopath model presented here was developed using an alpha-version of the Ecopath 4 (Ecopath with Ecosim) software (Pinnegar, 2000). Flows within the model were given in g wet weight m$^{-2}$ per year (equivalent to t km$^{-2}$ per year) and consequently

stocks (biomasses) as g wet weight m$^{-2}$. Where available, published and unpublished sources concerning the Gulf of Calvi were used to generate input parameters; however, in some cases it was necessary to draw from the wider literature, from Corsica or elsewhere in the western Mediterranean and lastly from outside the Mediterranean. The 'pedigree' of input data was recorded, identifying whether it was taken from a model of a similar system, or based on a rough or precise estimate from local data (*sensu* Funtowicz and Ravetz, 1990), these values were then used to assess model quality (Pauly et al., 2000). Model quality ($P$) was estimated at 0.528 and the overall measure of fit $t^*$, which takes into account the number of living groups in the system (26) was estimated at 3.05.

Fish species were aggregated into 11 distinct functional groups (Appendix A) on the basis of Bray–Curtis similarity coefficients and hierarchical agglomerative clustering of published gut-contents data (Pinnegar, 2000). Invertebrates were grouped into 11 categories, based largely on published prey types of fish; these were usually taxonomic groupings (e.g. decapods, amphipods and polychaetes). However, there were also several aggregate groups, namely, herbivorous zooplankters, protozoans, macro-mero-holo plankton, suspension feeders, and 'other' crustaceans. Additional groups included seabirds, phytoplankton, bacteria, macroalgae and detritus (Table 1).

The 'cycling index', the fraction of the ecosystem's throughput that is recycled (Finn, 1976), the omnivory index and trophic level of each group were calculated using procedures outlined by Christensen and Pauly (1992, 1993).

## 2.3. The Ecosim model

Ecosim is a time-dynamic simulation model that takes the set of linear equations used to construct Ecopath models (Eq. (1)), and sets up a series of differential equations (Walters et al., 1997; Christensen and Walters, 2004) The Ecosim master equation takes the form:

$$\frac{dB_i}{dt} = g_i \sum_j Q_{ji} - \sum_j Q_{ij} + I_i - (M_i + F_i + e_i)B_i \tag{3}$$

where $dB_i/dt$ represents the growth rate during the time interval $dt$ of group ($i$) in terms of its biomass $B_i$, $g_i$

is the net growth efficiency (production/consumption ratio), $M_i$ is the non-predation ('other') natural mortality rate, $F_i$ is fishing mortality rate, $e_i$ is emigration rate, $I_i$ is immigration rate, and $e_i B_i - I_i$ is the net migration rate. The consumption rates $Q_{ji}$ are calculated based on the 'foraging arena' concept, where $B_i$'s are divided into vulnerable and invulnerable components (Walters et al., 1997), and it is the transfer rate ($v_{ij}$) between these two parameters that determines if control is top-down (i.e. Lotka–Volterra), bottom-up (i.e. donor-driven) or of an intermediate type.

The user-defined vulnerability ($v$) setting can range from 0 for total bottom-up control to 1 for complete top-down control. For the present simulations, a default value of $v = 0.5$ was used for all groups unless otherwise stated, and this represents mixed 'top-down' and 'bottom-up' control. $v$ is converted to $x_{ij}$ within Ecosim using the scaling equation:

$$x_{ij} = \exp 2((\exp v) - 1) \tag{4}$$

$x_{ij}$ is then multiplied by the instantaneous mortality rate of $i$ caused by $j$ in order to obtain $v_{ij}$:

$$v_{ij} = x_{ij} \frac{Q_{ij}}{B_{ij}} \tag{5}$$

Note that over the course of development, different versions of the Ecopath with Ecosim software have assumed different 'default' values for user-defined $v$.

## 2.4. Fisheries data

The Gulf of Calvi artisanal fisheries have been reviewed by Culioli (1986), Riutort (1989) and Anon. (1998). Culioli (1986) estimated that each fishing boat from the port of Calvi caught around 20.72 kg of fish per trip. Assuming that in 1998, seven boats operated out of Calvi (Anon., 1998), and that these made an average of 139 trips over the course of the year (based on values collated over 89 days by Culioli, 1986), then the annual catch was around 20.22 t. Riutort (1989) suggested that the Calvi fishing boats generally operate over distances less than 16 km, between Punta di Spano and Punta di Morsetta. Within this zone, there are approximately 33.8 km of coastline open to fishing (excluding the marine reserve at the tip of the Revellata peninsula and areas of sandy beach) of which the Bay of Revellata represents 21.1% (7.5 km).

Table 1
Input data and resulting parameters (biomass, $P/B$ ratio, $Q/B$ ratio, catch and ecotrophic efficiency EE) for the 27 groups of the Ecopath steady-state model of the Bay of Calvi, Corsica, developed by Pinnegar (2000)

| | Group | Tropic level | Biomass (g m$^{-2}$) | $P/B$ (per year) | $Q/B$ (per year) | EE | Catch (g m$^{-2}$ per year) | Flow to detritus (g m$^{-2}$ per year) | Omnivory index |
|---|---|---|---|---|---|---|---|---|---|
| 1 | Cephalopods | 3.6 | 6.678 | 0.891 | 5.176 | (0.946) | 0.000 | 7.235 | 0.037 |
| 2 | Seabirds | 4.3 | 0.009 | 5.400 | 80.000 | (0.000) | 0.000 | <0.001 | 0.615 |
| 3 | Piscivorous fish | 4.3 | 1.922 | 0.729 | 4.887 | (0.379) | 0.531 | <0.001 | 0.894 |
| 4 | Macrocarnivorous fish | 4.1 | 2.312 | 0.726 | 5.735 | (0.385) | 0.532 | <0.001 | 0.520 |
| 5 | IF1 | 3.3 | (12.385) | 0.514 | 6.251 | 0.950 | 0.192 | 8.989 | 0.244 |
| 6 | IF2 | 3.2 | 2.900 | 0.391 | 5.366 | (0.101) | 0.039 | 2.763 | 0.455 |
| 7 | IF3 | 3.5 | 7.472 | 0.756 | 7.149 | (0.312) | 0.122 | 9.871 | 0.437 |
| 8 | Sessile invertebrate feeders | 3.1 | 0.640 | 0.475 | 5.761 | (0.064) | 0.008 | 0.697 | 0.422 |
| 9 | IF4 | 2.9 | 0.036 | 1.828 | 7.377 | (0.988) | 0.065 | 0.031 | 0.361 |
| 10 | Omnivorous blennies | 2.8 | (0.617) | 0.605 | 13.171 | 0.950 | 0.000 | 0.929 | 0.344 |
| 11 | Herbivorous fish | 2.1 | 4.740 | 0.780 | 12.025 | (0.040) | 0.074 | 34.900 | 0.124 |
| 12 | Planktivorous fish | 3.5 | 15.401 | 0.937 | 10.284 | (0.169) | 0.354 | 29.729 | 0.548 |
| 13 | Mugilidae | 2.5 | 0.153 | 0.624 | 8.587 | (0.992) | 0.022 | 0.723 | 0.379 |
| 14 | Pelagic bacteria | 2.0 | (0.724) | 284.800 | 1898.730 | 0.950 | 0.000 | 1109.357 | 0.000 |
| 15 | Zooplankton | 2.5 | (0.2991) | 50.000 | 170.000 | 0.950 | 0.000 | 208.799 | 0.435 |
| 16 | Macroplankton | 3.3 | 0.745 | 25.000 | 70.000 | (0.611) | 0.000 | 14.031 | 0.794 |
| 17 | Pelagic protozoa | 2.4 | (1.219) | 150.000 | 300.000 | 0.990 | 0.000 | 149.969 | 0.279 |
| 18 | Phytoplankton | 1.0 | (4.570) | 112.650 | – | 0.950 | 0.000 | 25.741 | 0.000 |
| 19 | Suspension feeders | 2.5 | 70.000 | (4.412) | 6.531 | 0.950 | 0.000 | 106.878 | 0.462 |
| 20 | Echinoderms | 2.1 | 64.426 | (0.506) | 2.771 | 0.950 | 0.000 | 73.065 | 0.095 |
| 21 | 'Other' crustacea | 2.1 | 10.002 | 20.210 | 92.595 | (0.787) | 0.000 | 228.252 | 0.173 |
| 22 | Amphipods | 2.1 | (20.718) | 9.000 | 21.744 | 0.950 | 0.000 | 130.954 | 0.115 |
| 23 | Decapods | 3.0 | 24.630 | (3.064) | 18.890 | 0.950 | 0.000 | 96.826 | 0.405 |
| 24 | Polychaetes | 2.5 | 62.339 | 3.360 | 19.260 | (0.822) | 0.000 | 493.561 | 0.398 |
| 25 | Gastropods | 2.5 | (67.142) | 1.913 | 10.710 | 0.950 | 0.000 | 423.492 | 0.487 |
| 26 | Macroalgae | 1.0 | (899.286) | 1.573 | – | 0.950 | 0.000 | 70.729 | 0.000 |
| 27 | Detritus | 1.0 | 230.850 | – | – | (0.768) | 0.000 | – | 0.143 |

Values in parentheses are those calculated by Ecopath assuming mass-balance.

Consequently, we estimated that around 4.47 t of fish are removed from the Bay of Revellata each year.

Catch composition (% weight) was derived from Culioli (1986), and species were divided into those found only over rocks, those found over both rocks and *Posidonia* seagrass meadows, and those only found over *Posidonia* (Bell and Harmelin-Vivien, 1983; J.K. Pinnegar, personal observations). The catch associated with species found only over *Posidonia* was first subtracted from the total catch and then that associated with both habitats was divided in accordance with the relative abundance of the two habitats in the Bay of Revellata (1:3.4) in order to obtain a figure for the weight of fish caught only over rocky substratum. This was then divided by the total surface area of rocky substratum (53.1 ha) in order to calculate catch in $g m^{-2}$ per year. The composition and relative biomass of by-catch/reject species caught by the fishery (Riutort, 1989) were added to the estimates of total catch landed. The resulting total catch data were divided by the biomass of each group in order to obtain an estimate of fishery mortality ($F$).

### 2.5. Fishing scenarios

#### 2.5.1. Resilience to short-term disturbance
In the present study, four groups were considered 'wasp-waist' species (*sensu* Rice, 1995), namely, 'planktivorous fish' and 'invertebrate-feeding fish' groups 1–3 (trophic level 3.5, 3.3, 3.2 and 3.5, respectively). Simulations were conducted to establish the recovery time of the ecosystem after a 10-year pulse (five times the baseline) of increased fishing on each of these groups, where vulnerability ($v$) was set at 0.5 (equal top-down and bottom-up control). In separate simulations $v$ was set at 0.4 and 0.6.

#### 2.5.2. Response to different levels of fishing mortality
To test for possible 'top-down' effects of fishing, simulations were conducted in which catches of piscivorous, macrocarnivorous and invertebrate-feeding fish or echinoderms (primarily sea urchins) were individually altered from their steady-state settings and ranged from zero, representing the initiation of an MPA, to six times the steady-state value. Biomasses of each of the groups in the ecosystem were recorded after 40 years.

In order to obtain sensible harvesting scenarios for sea urchins, which are not commercially exploited in the Bay of Revellata, we used values from the Marseilles region (Fig. 2), where on average some 78,380 kg of urchins are collected from 50 km of rocky shoreline (~7.08 ha) each year (Le Direach, 1987). A harvest of ~22.1 g m$^{-2}$ was estimated for Marseilles and simulations in which catch was set at 0, 8, 16, 24 and 32 g m$^{-2}$ were conducted using the model presented here.

#### 2.5.3. Speed of biomass changes
The majority of MPAs in the Mediterranean are less than 15 years old (Badalamenti et al., 2000) and changes in the biomass of both target and non-target species were reported shortly after the establishment of many of these (Pipitone et al., 2000; Sanchez Lizaso et al., 2000). Thus, simulations were conducted to explore the time scale over which any predicted/modelled trophic cascades might occur. Catches of piscivorous, macrocarnivorous and invertebrate-feeding fishes or echinoderms were set at twice the steady-state values derived from the Ecopath model. Biomasses were recorded at 2-year intervals for a period of 20 years.

## 3. Results

### 3.1. The Ecopath model

The balanced Ecopath model (fully documented in Pinnegar, 2000) consisted of 27 compartments (Table 1) and a total biomass (excluding detritus) of 1284 g m$^{-2}$. The total fisheries catch amounted to 1.94 g m$^{-2}$ per year and operated at a mean trophic level of 3.77, with catches being highest on piscivorous, macrocarnivorous and planktivorous fish (Table 1). The amount of detritus in the ecosystem that was recycled, relative to the total system throughput (13,535 g m$^{-2}$ per year), i.e. Finn's Cycling Index (FCI), was estimated at 21.69%.

### 3.2. Resilience

Following a pulse of increased fishing at five times baseline fishing pressure for 10 years, and under a regime slightly dominated by bottom-up control ($v =$

Table 2
Maximum ecosystem response duration ($t$, the time in years it takes for all components to recover to within 1% of the original biomass) and magnitude ($m$, the greatest response relative to the steady-state value measured at year 20) following a pulse of increased fishing ($\times 5$ for 10 years) on 'wasp-waist' groups under differing vulnerability ($v$) scenarios

| Group | $F^a$ | $v = 0.4$ | | $v = 0.5$ | | $v = 0.6$ | |
|---|---|---|---|---|---|---|---|
| | | $t$ | $m$ | $t$ | $m$ | $t$ | $m$ |
| Planktivores | 0.023 | 9.75 | 0.17 | 22.67 | 0.23 | 57.25 | 0.29 |
| IF1 | 0.016 | 19.50 | 0.28 | 38.5 | 0.44 | >80 | 0.63 |
| IF2 | 0.013 | 14.58 | 0.26 | 20.92 | 0.31 | 38.67 | 0.36 |
| IF3 | 0.016 | 11.33 | 0.23 | 18.75 | 0.41 | 61.5 | 0.64 |

[a] $F$ is the baseline fishing mortality (per year) from the Ecopath steady-state model.

0.4), all components of the ecosystem recovered fully to within 1% of the starting value within 20 years of the disturbance (Table 2). Manipulation of fishing pressure on the invertebrate-feeding fish group IF1 resulted in the long-lasting responses (19.5 years) and manipulation of fishing on planktivorous fish revealed the most short-lived responses (9.8 years). Introducing top-down control into the simulation ($v = 0.6$), resulted in a response that endured for more than 80 years. The magnitude of the response measured at the end of the fishing pulse ($m$), was also very sensitive to changes in $v$; responses of greater magnitude were observed when top-down control was higher (Table 2).

## 3.3. Responses to differing fishing intensity

Increased fishing on the urchin-feeding IF2 group (*D. sargus, D. vulgaris*) resulted in a linear decline in the biomass of this group (Fig. 3a) such that at six times steady-state fishing pressure ($0.234 \, \text{g m}^{-2}$ per year), biomass was reduced by 44%. The indirect effect of this depletion was an increase in the biomass of echinoderms by 8.7% and a decrease in the biomass of macroalgae by 0.7% (Fig. 3a). Increased fishing on the urchin-feeding IF3 group of fish (*C. julis, Symphodus roissali, Aidablennius sphynx* and *Parablennius zvonimiri*) also led to a decline in the biomass of the target group (Fig. 3b), such that at six times steady-state fishing pressure ($0.732 \, \text{g m}^{-2}$ per year), biomass was reduced by 14.6%, but echinoderms increased by only 0.8% and macroalgae decreased by 1.7% (Fig. 3b).
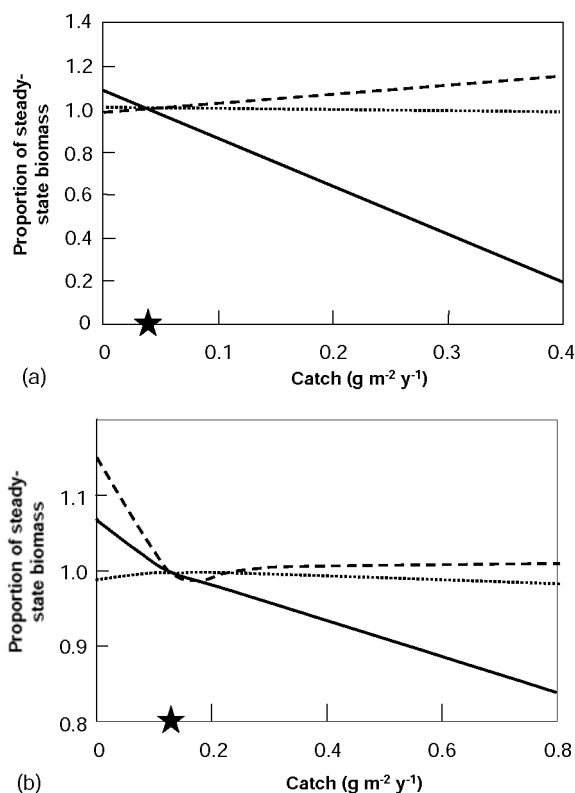


Fig. 3. Effects of simulated increases in fishing pressure on two groups (a) IF2 and (b) IF3 of invertebrate-feeding fishes and the consequential indirect effects on echinoderm (dashed line) and macroalgal (dotted line) biomasses. Star indicates steady-state fishing pressure.

Complete cessation of fishing on IF2 and IF3 led to a 7.7% increase in IF2 and a 6.4% increase in IF3, but mixed/variable impact on echinoderm and macroalgal biomass was predicted (Fig. 3a and b). A halt in fishing the IF2 group resulted in a 1.5% decline in echinoderm biomass and a 0.13% increase in macroalgal biomass, while cessation of fishing the IF3 group had greater impact, namely, a 15% increase in echinoderm biomass and a 1% decrease in macroalgal biomass.

Increased human harvesting of echinoderms resulted in an exponential decline in echinoderm biomass such that at high harvesting pressures, echinoderms were almost completely extirpated (Fig. 4a). Even low levels of harvesting resulted in considerable impact on echinoderm biomass, a harvest of only $5 \, \text{g m}^{-2}$ per year (equivalent to a harvesting
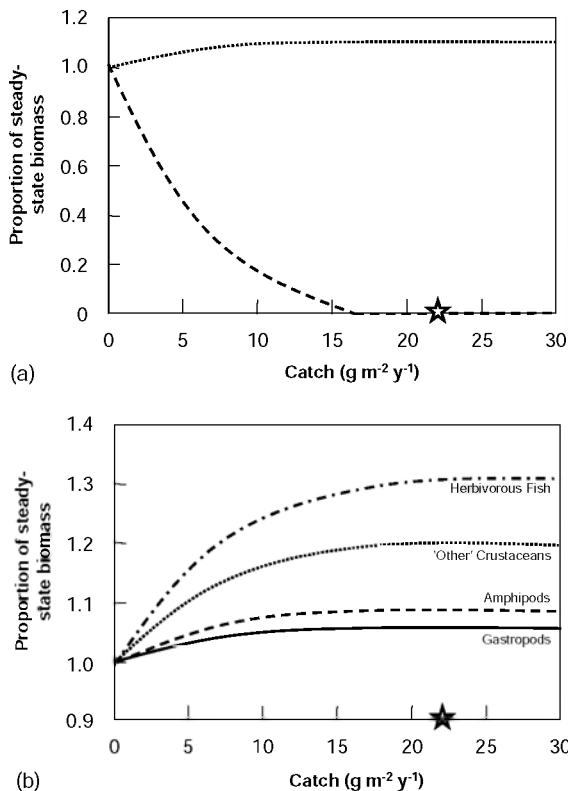
Fig. 4. (a) Effects of simulated increases in harvesting pressure on echinoderms (dashed line) and the consequential indirect effect on macroalgae (dotted line); and (b) indirect effects of harvesting echinoderms on other groups of herbivorous invertebrates and fish. Star indicates harvesting pressure on shores adjacent to Marseille.

mortality of 7.8%) resulted in a 48.5% decline in stock biomass. Direct harvesting of echinoderms also affected herbivorous fish and invertebrates (Fig. 4b).

Increased fishing pressure on the piscivorous fish group (including *Dentex dentex, Epinephelus marginatus, Muraena helena, Conger conger, Scorpaena scrofa* and *Serranus cabrilla*) led to an exponential reduction in the biomass of these species, such that at four times steady-state fishing pressure (Table 1), piscivorous fish were all but extirpated (Fig. 5a). This decline in the biomass of piscivores led to substantial increases in the biomass of macrocarnivorous and IF1 fish groups and decreases in the biomass of omnivorous blennies (Fig. 5b). The indirect effects of reduced piscivore biomass on benthic invertebrates varied according to taxon with increases
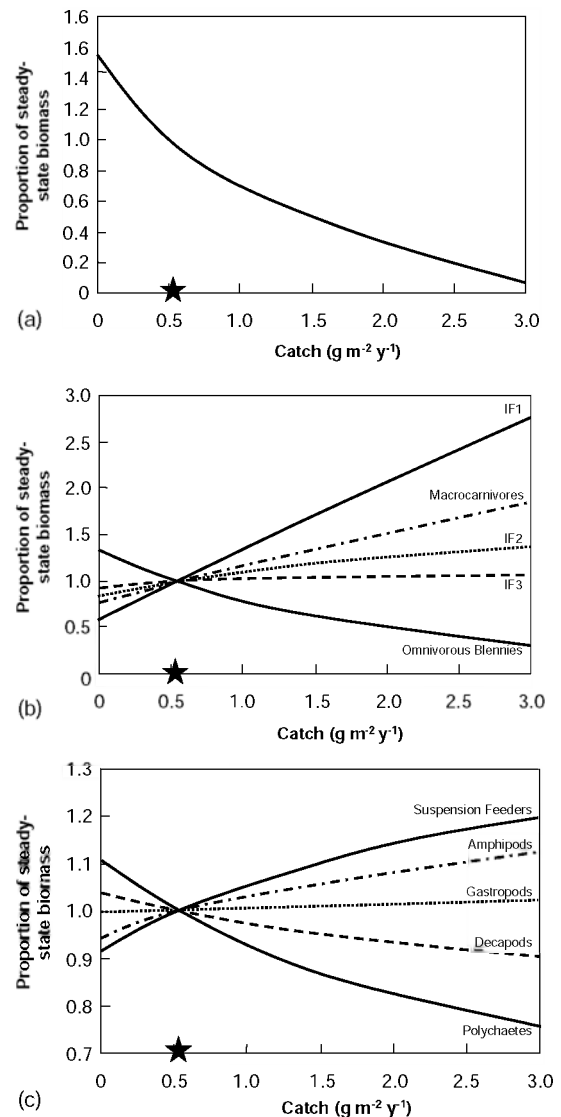


Fig. 5. (a) Direct effect of simulated increases in fishing pressure on large piscivorous fish; (b) indirect effects on small invertebrate-feeding fish groups; and (c) indirect effects on benthic invertebrates. Star indicates steady-state fishing pressure.

in the biomass of amphipods and suspension feeders, a decrease in the biomass of polychaetes and decapods, but very little change in the biomass of gastropod molluscs (Fig. 5c).

The macrocarnivorous fish (including *Scorpaena porcus, Scorpaena notata, Serranus scriba, Labrus* spp., *Apogon imberbis, Symphodus rostratus* and
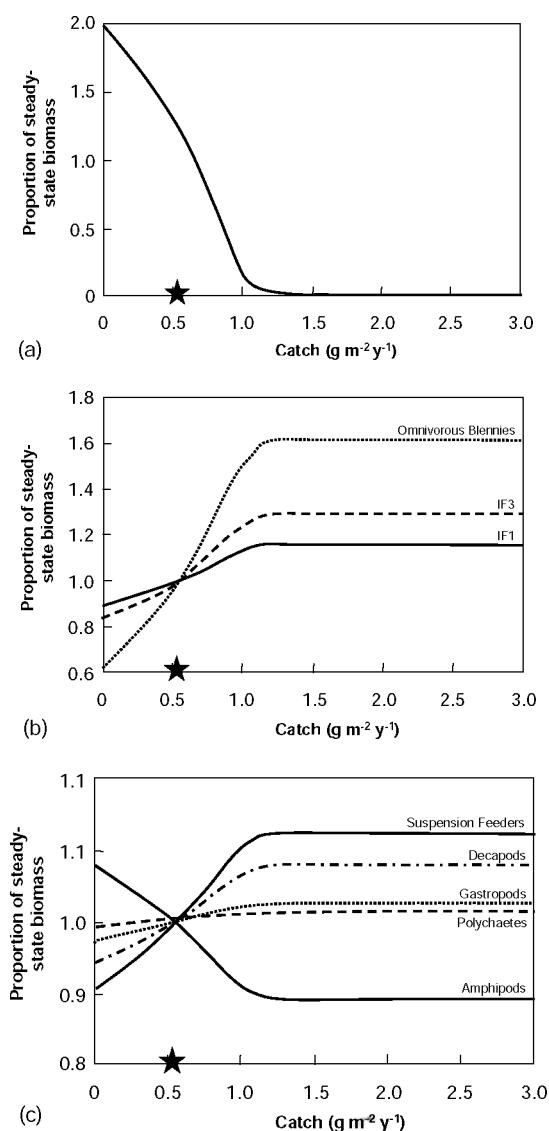
Fig. 6. (a) Direct effect of simulated increases in fishing pressure on macrocarnivorous fish; (b) indirect effects on small invertebrate-feeding fish groups; and (c) indirect effects on benthic invertebrates. Star indicates steady-state fishing pressure.

*Phycis blennoides*) declined markedly with increased fishing pressure. At three times steady-state fishing pressure ($1.596 \, \mathrm{g \, m^{-2}}$ per year), the macrocarnivorous fish had been extirpated (Fig. 6a). This reduction in predation pressure led to a substantial increase in the biomass of small fish (Fig. 6b) and a slight increase in the biomass of decapod crustaceans and suspension

feeders (Fig. 5c). These changes also coincided with a slight decline in the biomass of amphipods and an increase in that of gastropods and polychaetes (Fig. 6c). Complete cessation of fishing on macrocarnivorous fish species resulted in a recovery in biomass and a notable decrease in the biomass of small benthic fishes (Fig. 6b).

When fishing pressure was increased on all 10 exploited fish groups, the most heavily fished (piscivores and macrocarnivores) were rapidly depleted and then extirpated (Fig. 7a). Other target groups, however, including three invertebrate-feeding fish groups (IF1–3) and planktivores, experienced increases in biomass, and this was particularly so for IF1 (which includes *Symphodus tinca*, *Symphodus mediterraneus*, *Diplodus annularis*, *Mullus surmuletus*, *Gobius* spp., *Tripterygion* spp.) (Fig. 7a). The biomass of herbivorous fishes and the unfished omnivorous blennies was reduced by the increase in fishing pressure, whilst both Mugilidae and IF4 groups of fishes (of which *Sciaena umbra* was heavily fished) were particularly vulnerable and were rapidly extirpated (Fig. 7a).

Indirect effects of the increase in fishing pressure on invertebrates were equally as mixed as the effect on the different fish groups. The biomasses of gastropods, amphipods, decapods and macroalgae were little impacted by increases in overall fishing, whilst the biomass of echinoderms and polychaetes declined. The biomass of suspension feeders (sponges, bivalves, hydrozoans, bryozoans, sea anemones and tunicates) and 'other crustaceans' (isopods, ostracods, tanaids, cumaceans and caprellids) was enhanced (Fig. 7b).

### 3.4. Temporal dynamics

When fishing pressure was doubled on any particular group (piscivores, macrocarnivores, IF2 or IF3), the most rapid responses were among the target species (Fig. 8) and in each case the target group exhibited exponential decline, with much of the biomass change occurring within the first 5 years. Indirect responses of other groups in the system occurred over longer time scales, and with varying degrees of inertia, thus often displaying sigmoidal patterns (Fig. 8).

After fishing pressure on piscivores increased to $1.062 \, \mathrm{g \, m^{-2}}$ per year, their biomass declined by 52.7% within the first 5 years, but over the following 10 years, experienced a 22.5% recovery (Fig. 8a). By contrast,
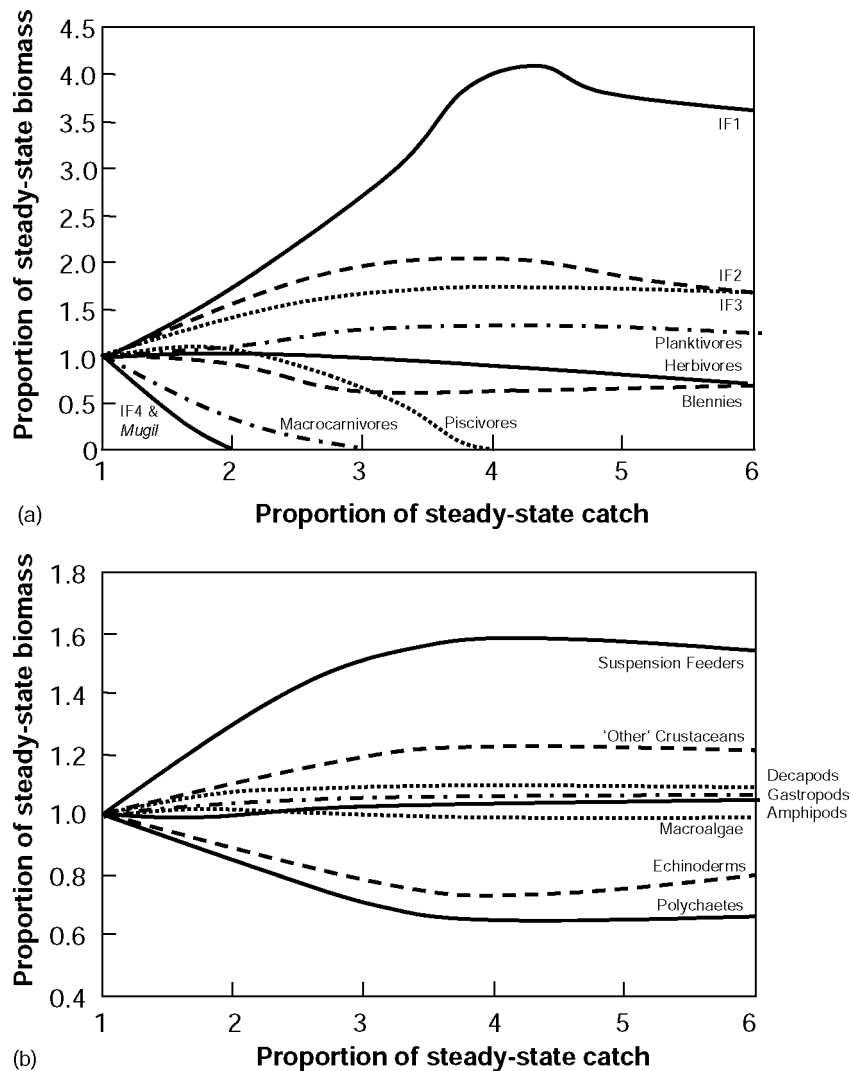
Fig. 7. (a) Effect of general increases in fishing pressure (all target species) on fish groups; and (b) indirect effects on benthic invertebrates.

the biomass of omnivorous blennies rose slightly for the first 4 years of increased fishing, but then rapidly declined over the following 10 years, as the biomass of macrocarnivorous and other fish groups began to accumulate (Fig. 8a). The IF1 group of fishes increased rapidly as the biomass of piscivores declined, while other fish and invertebrates tended to show more sustained responses (Fig. 8a). In most groups, there was little evidence that any new equilibrium had been reached within 20 years after the initiation of the new fishing regime.

When fishing on macrocarnivorous fish was doubled, their biomass decreased rapidly by 53.3% within the first 5 years, and continued to decline up to year 20. The most marked and rapid indirect response was experienced by the omnivorous blennies, and again, no groups reached a new equilibrium before year 20 (Fig. 8b).

When IF2 was more heavily fished (Fig. 8c), their biomass continued to decline up to year 20. The biomass of echinoderms, suspension feeders, macroalgae and IF3 fish in all cases increased very little.
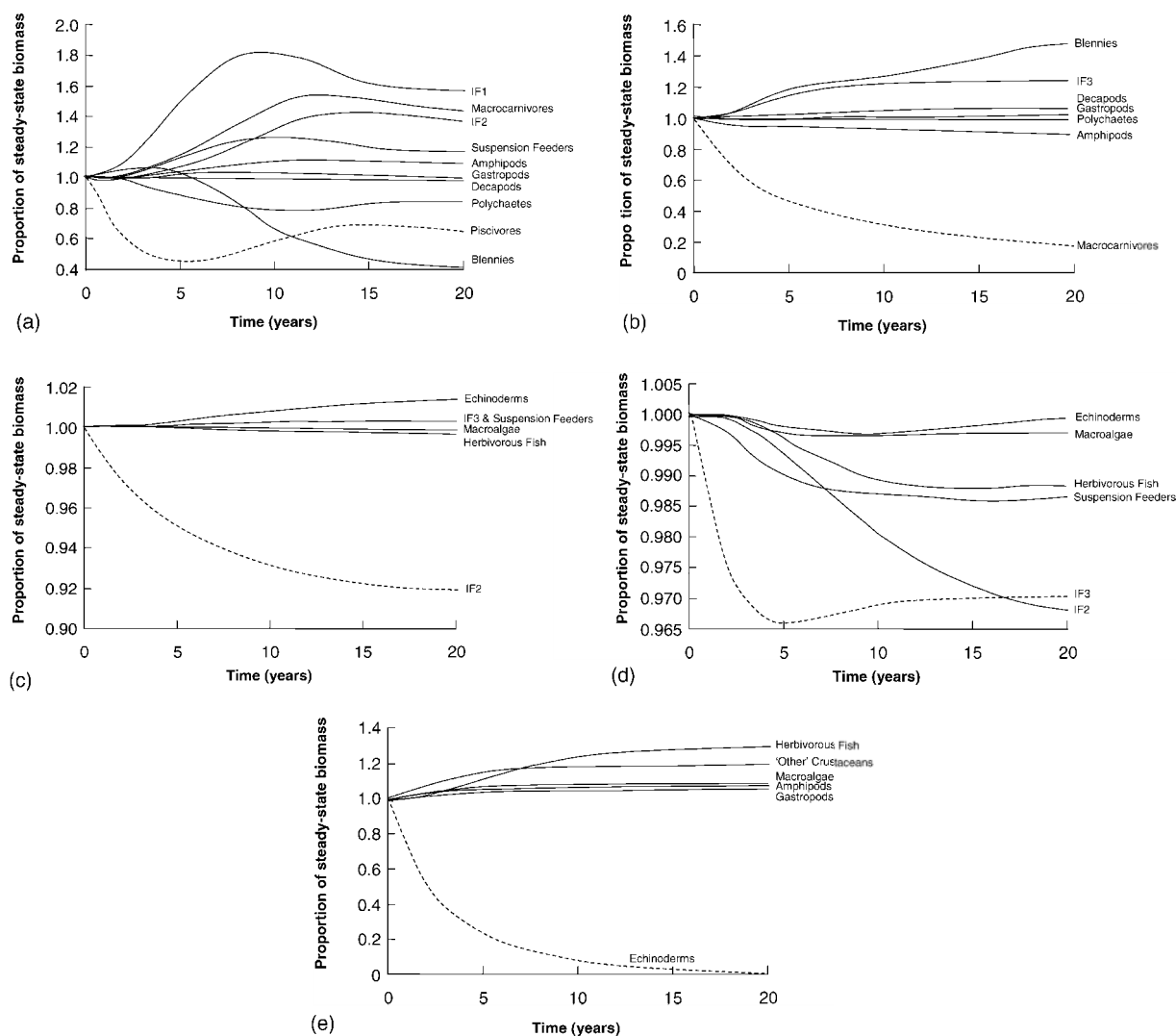
Fig. 8. Responses of system components to a doubling of fishing pressure on (a) piscivorous fish, (b) macrocarnivorous fish, (c) IF2 fish, (d) IF3 fish and (e) echinoderms. Direct responses of target/manipulated groups are indicated by dashed lines.

More intensive fishing on the IF3 fish led to an initially very rapid decline in their biomass, then a slight recovery, whereas the IF2 fish declined markedly and had not reached equilibrium by year 20. Macroalgae, echinoderms and herbivorous fish experienced slight declines in biomass over the first 5–10 years, but then reached new equilibria or, in the case of echinoderms, increased up to year 20 (Fig. 8d). Direct and indirect responses to complete cessation of fishing on any particular target group were numerically opposite those when fishing pressure was doubled.

When harvesting at a rate of $22.1 \, \mathrm{g \, m^{-2}}$ per year was initiated on echinoderms, there was very rapid decline in the biomass of this group by 75.6% within the first 5 years (Fig. 8e). This was followed by a continued but much slower decline up to year 20, when echinoderms were almost completely extirpated. In response, macroalgae experienced a gradual increase in biomass over the 20-year duration of the simulation, and herbivorous fish, after a period of inertia (~2 years), responded markedly, reaching a new asymptote around year 20 (Fig. 8e).
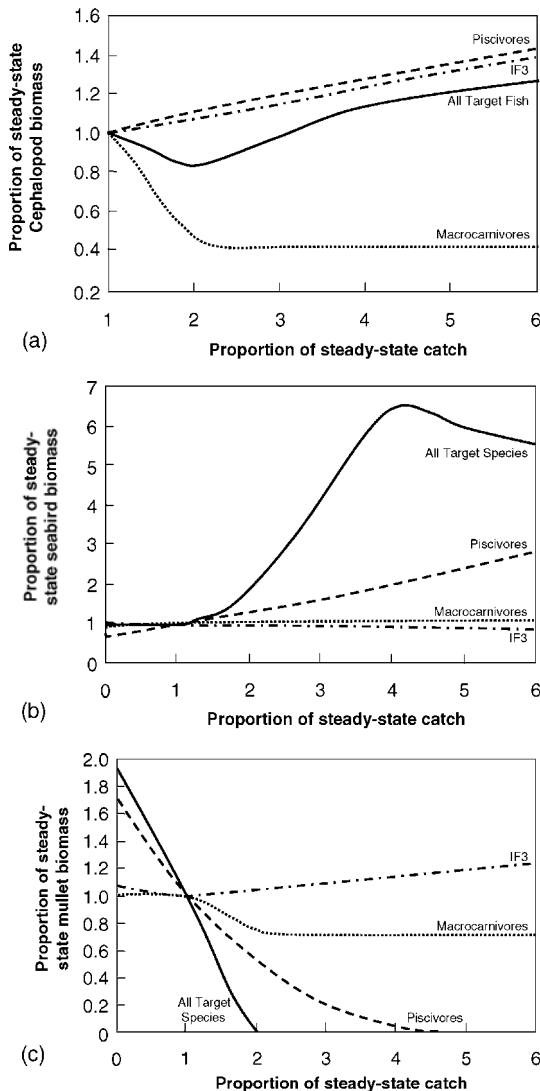
Fig. 9. (a) Indirect effect on cephalopod biomass of increasing fishing pressure; (b) indirect effects on seabirds of increasing fishing pressures, and (c) indirect effects of increasing fishing pressures on grey-mullets (Mugildae).

## 3.5. Other indirect effects of fishing

Increased fishing pressure on piscivores, all target species together and IF3 fish, resulted in increase in the biomass of cephalopods (Fig. 9a). However, an increase in fishing pressure on macrocarnivorous fish resulted in a negative impact on cephalopods. Increased fishing on piscivores or all target fishes to-

gether resulted in a marked increase in seabird biomass (Fig. 9b) and marked decline in the biomass of mullets (Mugilidae) (Fig. 9c), which as surface swimmers were heavily preyed upon by seabirds (especially the Osprey *Pandion haliaetus*).

## 4. Discussion

The relationship between stability and the structure of ecosystems has been widely discussed in the ecological literature (e.g. Odum, 1969; Holling, 1973; May, 1973; McCann et al., 1998; Johnson, 2000) and the time required for functional groups to return to baseline levels following a disturbance has been found to be closely correlated with the fraction of the ecosystem's throughput that is recycled (Vasconcellos et al., 1997). The capacity of an ecosystem to entrap, withhold and cycle nutrients increases with system 'maturity' (Odum, 1969), and Christensen and Pauly (1993) found a strong correlation between FCI and maturity rankings described by Christensen (1995). The FCI value reported here (21.69%) was relatively high, indicating a substantial degree of recycling. This value was higher than reported for tropical coral reef systems (Dalsgaard, 1995) and was roughly equivalent to values reported for Lake Turkana and the Mandinga Lagoon (Christensen and Pauly, 1993). Taken with the short recovery times that we report (Table 2), it would seem that the Mediterranean rocky littoral ecosystem is relatively resilient and 'mature' compared to many other coastal and shelf systems (Vasconcellos et al., 1997; Pauly et al., 2000).

Many of the existing Ecosim studies (e.g. Walters et al., 1997; Stevens et al., 2000; Shannon et al., 2000) indicate that the longevity and magnitude of predicted responses are very sensitive to the amount of 'top-down' or 'bottom-up' control assumed for components within the system ($v$). This was also the case in the present study, where higher values of $v$ resulted in more dramatic and longer term responses than lower values of $v$. With a predominance of top-down control ($v$ set at 0.6), most functional groups did not recover to 1% of their original biomass within 40 years, and recovery following a pulse of increased fishing on the IF1 group in particular, took more than 80 years. Clearly, had higher values of $v$ been used in all simulations, a greater number and more dramatic

examples of fishing-induced 'trophic cascades' would have been predicted, although Walters et al. (1997) suggested that strong top-down control might not be very common because of evolutionary constraints, such as the constant colonisation and vacation of evolutionary niches. Pinnegar et al. (2000) reviewed many examples of top-down trophic cascades in benthic marine systems, these often involved a rather limited range of prey organisms, particularly sea urchins or limpets, which have few specialist predators. Most predation by fishes is of a generalist nature, such that there is great overlap in diet, and great scope for prey species to replace one another in diets (Pinnegar et al., 2000). Natural ecosystems most likely exhibit a mixture of low $v$ and high $v$ linkages (rather than a uniform $v$ throughout) and weak trophic links may be important in promoting community persistence and stability (McCann et al., 1998; Polis, 1998).

The model of McClanahan and Sala (1997) emphasised strong top-down control, and thus supported the paradigm that fishing, by removing invertebrate-feeding fish, allows increases in the biomass of sea urchins and as a consequence the formation of over-grazed 'barrens' of bare substrate (e.g. Sala and Zabala, 1996). The Ecosim model presented here provides little support for this trophic cascade, and implies that some factor other than fishing may be responsible for the proliferation of coralline barrens in the western Mediterranean. The substantial decrease in the biomass of invertebrate-feeding fish groups IF2 and IF3, resulting from a sixfold increase in fishing pressure, led to only small increases in echinoderm abundance (8.7 and 0.8%, respectively) and suggests that predation could not alone cause the very high sea urchin densities observed at some unprotected Mediterranean sites (e.g. Sala and Zabala, 1996). In contradiction to their earlier work, Sala et al. (1998b) suggested that sea urchin populations in the Medes Islands (Spain), exhibited striking short-term fluctuations in abundance in both protected and unprotected sites, such that factors including recruitment variability may outweigh the effects of fish predation. In the north-western Atlantic, a large temperature anomaly may have led to intense sea urchin recruitment, the appearance of large adult populations 4–6 years later and proliferation of coralline barrens after 8 years (Hart and Scheibling, 1988), despite earlier contentions that this too had been related to a depletion of urchin predators. The present observation that direct harvesting of urchins can result in substantial macroalgal overgrowth, does suggest that urchin populations may be in some way involved in the mechanism responsible for corralline barren proliferation. Benedetti-Cecchi et al. (1998) have suggested that in Mediterranean areas where corralline barrens are common, recovery of fleshy algae may only occur when sea urchins are totally removed. Were harvesting to commence in a previously unfished area, at levels equivalent to those predicted for Marseilles, our model predicts that an 8.6% increase in macroalgal biomass would result.

On tropical coral reefs, increases in fishing effort may result in an exponential decline in the biomass of many predatory fish species, and even low levels of fishing pressure may have substantial impact on stocks (Jennings et al., 1995; Jennings and Polunin, 1997). In the present study, small departures of fishing pressure from steady-state conditions were also predicted to greatly affect the biomass of large piscivorous and macrocarnivorous fish species. However, the decrease in small invertebrate-feeding fish (blennies and IF3 species) observed within MPAs (Macpherson, 1994; Vacchi et al., 1998; La Mesa and Vacchi, 1999) did not result from the increase in large piscivorous fish (e.g. groupers), as supposed in Pinnegar et al. (2000). The phenomenon may be more related to the increased prevalence of smaller predators, such as scorpaenids and serranids (i.e. the 'macrocarnivores').

Increases in prey fish abundance as a result of predator depletion may not be as prevalent as previously thought (Jennings et al., 1995; Jennings and Polunin, 1997; Polunin and Jennings, 1998; Russ and Alcala, 1998a,b), although it has occasionally been observed for some grazing surgeonfish, diodontids, small-bodied wrasses and damselfish in coral reef systems (Roberts and Polunin, 1992; McClanahan, 1994). Mechanisms leading to the increase in small benthic invertebrates within MPAs, as observed in the field by Badalamenti et al. (1999), Chemello et al. (1999) and Milazzo et al. (2000), remain unclear. This is particularly so for gastropods, since none of the fishing scenarios in the present study revealed a higher gastropod biomass at low fishing pressures. Pinnegar et al. (2000) suggested that the increased abundances of polychaetes observed by Badalamenti et al. (1999) within an MPA might be related to the reduced prevalence of small blennies, but the present

model suggests that this is more likely to be related to the reduced abundance of other invertebrate-feeding fishes (IF1) and especially *M. surmuletus*, in which polychaetes may comprise 30% of the diet (Riutort, 1994). There have been several studies in the Mediterranean which have demonstrated that abundances of small invertebrates (e.g. polychaetes and gastropods) are influenced more by algal cover and structural complexity than any other factor (Abbiati et al., 1987; Giangrande, 1988; Chemello et al., 1997). This may be because structural complexity has an inhibitory effect on predatory success, by diminishing the predators movements and the visibility of prey (Orth et al., 1984).

Throughout the world, soft-bottom communities, where intensively fished, have exhibited increased dominance of cephalopods, particularly squid (Caddy, 1983; Gulland and Garcia, 1984; Pauly, 1985, 1988; Sissenwine, 1986; Pipitone et al., 2000). In the present study, this was found to be true when fishing pressure was increased on all target groups generally or on piscivores and IF3 fish individually. This may be partly due to a reduction in the prevalence of potential cephalopod predators, but it may also be related to increase in the availability in the present model of bivalve molluscs included among the suspension feeders, which together with decapods form the major prey of *Octopus vulgaris* (Ambrose and Nelson, 1983).

Western Mediterranean populations of many seabirds have experienced dramatic changes, with marked declines in populations of European Shag (*Phalacrocorax aristotelis*) and European Storm Petrel (*Hydrobates pelagicus*) (Thibault et al., 1996). In the present model, seabird biomass was dominated (81%) by that of *P. aristotelis* (the other 19% being Osprey *P. haliaetus*). Corsican populations of *P. aristotelis* are known to have declined markedly from 1977 to 1993, such that the Lavezzi and Cerbicale Islands, which previously accounted for 65% of the Corsican population, have lost nearly all of their breeding pairs (Thibault et al., 1996). Many factors, including fishing activities, the accidental introduction of predatory mammals and pollution/poisoning, have been considered responsible, although potential food-chain influences (bottom-up) have yet to be fully explored. In the Lavezzi Islands, Thibault et al. (1996) suggest that the decline in the European Shag

population may be related to the increased scarcity of small planktivorous fish, such as Atherininae and Ammodytidae. European Shag faecal pellets at the beginning of the 1980s, i.e. when their numbers were high, were composed mainly of the remains of these fish, but in recent years the latter are now nearly absent from pellets. In the present study, where fishing was increased on piscivorous fish, the main competitors of seabirds in the system, seabird biomass greatly increased (Fig. 9b). However, the indirect food-chain effects of fishing may be greatly outweighed by accidental mortality of seabirds in fishing nets or lines. In Corsica, accidental capture in fishing gear is thought to be the primary cause (60.3%) of European Shag mortality (Guyot, 1990).

### 4.1. Timing of responses

Most Mediterranean MPAs have been established only within the past 15 years (Badalamenti et al., 2000), a time period which the present study suggests is insufficient for a new equilibrium to be established. Consequently, differences observed in target or non-target populations between MPAs and unprotected sites (e.g. Sala and Zabala, 1996; Badalamenti et al., 1999; Milazzo et al., 2000) might represent only snapshots of a community that is in the process of much longer term changes. The model of McClanahan and Sala (1997) also predicted long-term successional dynamics, with some processes occurring only after 20 years of simulation. However, in the present study, responses of target species were predicted to occur very shortly after the initiation of a new fishing regime, and this has been borne out in Mediterranean field studies, such as that of Pipitone et al. (2000). Our results predict that effects, such as trophic cascades, are expected only after several years of the prevailing fishing regime, and even then they may be somewhat obscured by temporal dynamics of other processes, such as recruitment variability (Sala et al., 1998b). Harmelin et al. (1995) observed long-term and apparently rhythmic fluctuations in the fish assemblage of a Mediterranean MPA, while these fluctuations were largely masked by short-term variability outside it. The authors supposed that the greater fluctuations outside the reserve were most likely related to human activities. Francour (1994) also observed lower variability, diversity, density and biomass in protected sites

(Scandola Reserve, Corsica) compared with nearby fished areas, and attributed this to the control of natural recruitment fluctuations (mainly labrids) by high-level predators that were more abundant in the protected area.

## 5. Conclusions

The Ecosim approach can be a valuable tool for ecosystem-scale adaptive management experiments and in the present case, has helped to elucidate possible mechanisms underlying observations from the field. Our simulations have demonstrated that in general the ecosystem was able to recover from pulses of increased fishing pressure, although this recovery was reliant on the configuration of the model and particularly the value assumed for $v$. In many instances, the model did give predictions which were consistent with field data, whilst also highlighting the possibility of additional trophic cascades involving seabirds and cephalopods. It must be remembered, however, that in the present paper we have only examined the tip of a very large the 'iceberg', in the sense that we have evaluated the effects of particular combinations of Ecosim settings and possible Ecopath input parameters. There is a clear need for formal sensitivity analysis, in order to explore the multitude of possible permutations and possible 'parameter-space '. This being said, modelling may significantly enhance our understanding of the potential impact of fisheries at larger spatial scales and on groups that would otherwise be very difficult to study. The model developed in the present paper is the most comprehensive yet constructed for any system in the western Mediterranean. Predictions resulting from the present model may form the basis for hypotheses to be tested in the future.

## Acknowledgements

## Appendix A. Functional groupings of 34 species of rocky littoral fishes. Fishes aggregated on the basis of diet similarity using Bray–Curtis similarity indices, hierarchical agglomerative clustering and group-average linking (after Pinnegar, 2000)

**Piscivorous Fish**
*Dentex dentex*
*Serranus cabrilla*
*Scorpaena scrofa*
*Muraena helena*
*Conger conger*

**Macrocarnivorous Fish**
*Apogon imberbis*
*Labrus merula*
*Scorpaena porcus*
*Scorpaena notata*
*Serranus scriba*
*Symphodus rostratus*
*Phycis blennoides*

**Benthic Invert. Feeders (IF1)**
*Mullus surmuletus*
*Symphodus tinca*
*Symphodus mediterraneus*
*Diplodus annularis*
*Tripterygion* sp.
*Gobius* sp.

**Benthic Invert. Feeders (IF2)**
*Diplodus sargus*
*Diplodus vulgaris*

**Benthic Invert. Feeders (IF3)**
*Coris julis*
*Symphodus roissali*

*Aidablennius sphynx*
*Parablennius zvonmiri*

**Benthic Invert. Feeders (IF4)**
*Symphodus melanocercus*
*Sciaena umbra*

**Sessile Invert. Feeders**
*Diplodus puntazzo*

**Omnivorous Blennies**
*Lipophrys* sp.
*Parablennius rouxi/ P. incognitus*

**Herbivores**
*Sarpa salpa*
*Parablennius sanguinolentus*

**Zooplanktivores**
*Chromis chromis*
*Boops boops*
*Symphodus ocellatus*
*Atherina presbyter*
*Oblada melanura*
*Thalassoma pavo*

**Mugilidae**
*Mugil cephalus*
*Liza aurata*

# References

Abbiati, M., Bianchi, C.N., Castelli, A., 1987. Polychaete vertical zonation along a littoral cliff in the Western Mediterranean. Mar. Ecol. (Pubbl. Stn. Zool. Napoli I) 8, 33–48.

Anon., 1998. Evaluation de l' effort deployé par la peche professionnelle dans le périmètre du project Parc National Marin de Corse. Préfecture de Corse, Direction Régionale de l'Environment Mission Parc National Marin de Corse.

Ambrose, R.F., Nelson, B.V., 1983. Predation by *Octopus vulgaris* in the Mediterranean. Mar. Ecol. (Pubbl. Stn. Zool. Napoli I) 4, 251–261.

Arreguin-Sanchez, F., 2000. Octopus-red grouper interaction in the exploited ecosystem of the northern continental shelf of Yucatan, Mexico. Ecol. Model. 129, 119–129.

Badalamenti, F., Cantone, G., Domina, R., Di Pietro, N., Catalano, D., Mollica, E., D'Anna, G., 1999. Primi dati sulla fauna a policheti di substrato duro dell' infralitorale fotofilo superiore dell'Isola di Ustica. Biol. Mar. Mediterr. 6, 230–236.

Badalamenti, F., Ramos, A.A., Voultsiadou, E., Sanchez-Lizaso, J.L., D'Anna, G., Pipitone, C., Mas, J., Ruiz Fernandez, J.A., Whitmarsh, D., Riggio, S., 2000. Cultural and socio-economic impacts of Mediterranean marine protected areas. Environ. Conserv. 27, 110–125.

Bell, J.D., Harmelin-Vivien, M.L., 1983. Fish fauna of French Mediterranean *Posidonia oceanica* seagrass meadows. 2. Feeding habits. Tethys 11, 1–14.

Benedetti-Cecchi, L., Bulleri, F., Cinelli, F., 1998. Density dependent foraging of sea urchins in shallow subtidal reef on the west coast of Italy (western Mediterranean). Mar. Ecol. Prog. Ser. 163, 203–211.

Boudouresque, C.F., Caltagirone, A., Lefevre, J.R., Rico, V., Semroud, R., 1992. Macrozoobenthos in the Scandola Nature Reserve (Corsica, North-west Mediterranean): pluriannual analysis of the 'reserve effect'. MEDPAN News 3, 15–20.

Caddy, J.F., 1983. The cephalopods: factors relevant to their population dynamics and to the management of stocks. FAO Fish. Tech. Pap. 231, 416–452.

Chemello, R., Di Piazza, F., Dieli, T., Riggio, S., 1997. Strutta della malacocenosi associata ad alghe fotofile: effetti della profondità e della complessità d'habitat. Biol. Mar. Mediterr. 4, 167–168.

Chemello, R., Milazzo, M., Nasta, E., Riggio, S., 1999. Studio della malacofauna associata ad alghe fotofile nella riserva marina Isola di Ustica. Biol. Mar. Mediterr. 6, 247–249.

Christensen, V., 1995. Ecosystem maturity—towards quantification. Ecol. Model. 77, 3–32.

Christensen, V., 1998. Fishery-induced changes in a marine ecosystem: insight from models of the Gulf of Thailand. J. Fish Biol. 53 (Suppl. A), 128–142.

Christensen, V., Pauly, D., 1992. A Guide to the Ecopath Software System (version 2.1). ICLARM, Manila, 72 pp.

Christensen, V., Pauly, D., 1993. Flow characteristics of aquatic ecosystems. In: Christensen, V., Pauly, D. (Eds.), Trophic Models of Aquatic Ecosystems. ICLARM, Manila, pp. 338–352.

Christensen, V., Walters, C.J., 2004. Ecopath with Ecosim: methods, capabilities and limitations. Ecol. Model. 172, 109–139.

Culioli, M.J., 1986. Valorisation des ressources de la pêche cotière Corse: Estimation de la production en région de Calvi, étude des paramètres de croissance de cinq éspèces de poissons d'intérêt economique. Maitrise de Sciences et Techniques Thesis, Universite de Corse Pascal Paoli. 56 pp.

Dalsgaard, A.J.T., 1995 Modelling the Trophic Transfer of Beta Radioactivity in the Marine Food Web of Enewetak Atoll, Micronesia. M.Sc. Thesis, Fisheries Centre, University of Copenhagen, 125 pp.

Dauby, P., 1989. The stable carbon isotope ratios in benthic food webs of the Gulf of Calvi, Corsica. Cont. Shelf Res. 9, 181–195.

Elner, R.W., Vadas, S.R.L., 1990. Inference in ecology: the sea urchin phenomenon in the northwestern Atlantic. Am. Nat. 136, 108–125.

Farrugio, H., Olivier, P., Biagi, F., 1993. An overview of the history, knowledge, recent and future research trends in Mediterranean fisheries. Sci. Mar. 57, 105–119.

Finn, J.T., 1976. Measurements of ecosystem structure and function derived from analysis of flows. J. Theor. Biol. 56, 363–380.

Francour, P., 1994. Pluriannual analysis of the reserve effect on ichthyofauna in the Scandola Natural Reserve (Corsica, northwestern Mediterranean). Oceanol. Acta 17, 309–317.

Funtowicz, S.O., Ravetz, J.R., 1990. Uncertainty and Quality in Science for Policy. Kluwer, Dortrecht, 229 pp.

García Charton, J.A., Williams, I.D., Pérez Ruzafa, A., Milazzo, M., Chemello, R., Marcos, C., Kitsos, M.-S., Koukouras, A., Riggio, S., 2000. Evaluating the ecological effects of Mediterranean marine protected areas: habitat, scale and the natural variability of ecosystems. Environ. Conserv. 27, 159–178.

Giangrande, A., 1988. Polychaete zonation and its relation to algal distribution down a vertical cliff in the western Mediterranean (Italy): a structural analysis. J. Exp. Mar. Biol. Ecol. 122, 225–241.

Gras, G., 1987. Evolution des stocks de l'oursin comestible *Paracentrotus lividus* dans les quartier maritime de Marseille (France), soumis a une peche intensive, entre les campagnes 1984–1985 et 1986–1987. In: Boudouresque, C.F. (Ed.), Colloque International sur Paracentrotus lividus et les oursins comestibles. GIS Posidonie Publications, Marseille, pp. 363–370.

Gulland, J.A., Garcia, S., 1984. Observed patterns in multispecies fisheries. In: May, R.M. (Ed.), Exploitation of Marine Communities. Springer-Verlag, Berlin, pp. 155–190.

Guyot, I., 1990. Le Cormoran Huppé en Corse: biologie et interactions avec la pêche professionnelle. Trav. Sci. Parc. Nat. Rég. Nat. Corse 28, 1–40.

Harmelin, J.G., Bachet, F., Garcia, F., 1995. Mediterranean marine reserves: fish indices as tests of protection efficiency. Mar. Ecol. (Pubbl. Stn. Zool. Napoli I) 16, 233–250.

Hart, M.W., Scheibling, R.E., 1988. Heat waves, baby booms, and the destruction of kelp beds by sea urchins. Mar. Biol. 99, 167–176.

Holling, C.S., 1973. Resilience and stability of ecological systems. Ann. Rev. Ecol. Syst. 4, 1–23.

Hollowed, A.B., Bax, N., Beamish, R., Collie, J., Fogarty, M., Livingston, P., Pope, J., Rice, J.C., 2000. Are multispecies models an improvement on single-species models for measuring

fishing impacts on marine ecosystems? ICES J. Mar. Sci. 57, 707–719.

Jennings, S., Kaiser, M.J., 1998. The effects of fishing on marine ecosystems. Adv. Mar. Biol. 34, 201–352.

Jennings, S., Polunin, N.V.C., 1997. Impacts of predator depletion by fishing on the biomass and diversity of non-target reef fish communities. Coral Reefs 16, 71–82.

Jennings, S., Grandcourt, E.M., Polunin, N.V.C., 1995. The effects of fishing on the coral diversity, biomass and trophic structure of Seychelles' reef fish communities. Coral Reefs 14, 225–235.

Johnson, K.S., 2000. Trophic-dynamic considerations in relating species diversity to ecosystem resilience. Biol. Rev. 75, 347–376.

La Mesa, G., Vacchi, M., 1999. An analysis of the coastal fish assemblage of the Ustica Island Marine Reserve (Mediterranean Sea). Mar. Ecol. (Pubbl. Stn. Zool. Napoli I) 20, 147–165.

Lawrence, J.M., 1975. On the relationships between marine plants and sea urchins. Oceanogr. Mar. Biol. Ann. Rev. 13, 213–286.

Le Direach, J.P., 1987. La peche des oursins en Mediterranee: historique, techniques, legislation, production. In: Boudouresque, C.F. (Ed.), Colloque International sur Paracentrotus lividus et les oursins comestibles. GIS Posidonie Publications, Marseille, pp. 335–362.

Macpherson, E., 1994. Substrate utilisation in a Mediterranean littoral fish community. Mar. Ecol. Prog. Ser. 114, 211–218.

May, R.M., 1973. Stability and Complexity in Model Ecosystems. Princeton University Press, Princeton, NJ, 265 pp.

McCann, K., Hastings, A., Huxel, G.R., 1998. Weak trophic interactions and balance of nature. Nature 395, 794–798.

McClanahan, T.R., 1994. Kenyan coral reef lagoon fish: effects of fishing, substrate complexity, and sea urchins. Coral Reefs 13, 231–241.

McClanahan, T.R., Sala, E., 1997. A Mediterranean rocky-bottom ecosystem fisheries model. Ecol. Model. 104, 145–164.

Menge, B.A., 1995. Indirect effects in marine rocky intertidal interaction webs: patterns and importance. Ecol. Monogr. 65, 21–74.

Milazzo, M., Chemello, R., Riggio, S., 2000. Molluscan assemblages associated with photophilic algae in the marine reserve of Ustica Island (southern Tyrrhenian Sea, Italy). Ital. J. Zool. 67, 287–295.

Odum, E.P., 1969. The strategy of ecosystem development. Science 164, 262–270.

Orth, R.J., Heck Jr., K.L., Van Montfrans, J., 1984. Faunal communities in seagrass beds: a review of the influence of plant structure and prey characteristics on predator–prey relationships. Estuaries 7, 339–350.

Pauly, D., 1985. The population dynamics of short-lived species, with emphasis on squids. NAFO Sci. Counc. Stud. 9, 143–154.

Pauly, D., 1988. Fisheries research and the demersal fisheries of Southeast Asia. In: Gulland, J.A. (Ed.), Fish Population Dynamics. Wiley, Chichester, pp. 329–348.

Pauly, D., Christensen, V., Walters, C., 2000. Ecopath, Ecosim and Ecospace as tools for evaluating ecosystem impact of fisheries. ICES J. Mar. Sci. 57, 697–706.

Pinnegar, J.K., 2000. Planktivorous Fishes: Links Between the Mediterranean Littoral and Pelagic. Ph.D. Thesis, University of Newcastle, 213 pp.

Pinnegar, J.K., Polunin, N.V.C., 2000. Contributions of stable-isotope data to elucidating food webs of Mediterranean rocky littoral fishes. Oecologia 122, 399–409.

Pinnegar, J.K., Polunin, N.V.C., Francour, P., Badalamenti, F., Chemello, R., Harmelin-Vivien, M.-L., Hereu, B., Milazzo, M., Zabala, M., D'Anna, G., Pipitone, C., 2000. Trophic cascades in benthic marine ecosystems: lessons for fisheries and protected-area management. Environ. Conserv. 27, 179–200.

Pipitone, C., Badalamenti, F., D'Anna, G., Patti, B., 2000. Fish biomass increase after a four-year trawl ban in the Gulf of Castellamare (NW Sicily, Mediterranean Sea). Fish Res. (Amst.) 48, 23–30.

Polis, G., 1998. Stability is woven by complex webs. Nature 395, 744–745.

Polovina, J.J., 1984. Model of a coral reef ecosystem. Part I. The ECOPATH model and its application to French Frigate Shoals. Coral Reefs 3, 1–11.

Polunin, N.V.C., Jennings, S., 1998. Differential effects of small-scale fishing on predatory and prey fishes on Fijian reefs. In: Newbery, D.M., Prins, H.H.T., Brown, N.D. (Eds.), Dynamics of Tropical Communities. Blackwell Science, Oxford, pp. 95–124.

Rice, J., 1995. Food web theory, marine food webs, and what climate changes may do to northern marine fish populations. Can. Spec. Publ. Fish. Aquat. Sci. 121, 561–568.

Riutort, J.J., 1989. Première estimation des captures et de l'effort de pêche deployé par les 'petits metiers' sur le littoral nord-ouest de la Corse. Station de Recherches Sous-Marines et Oceanographiques (STARESO), Calvi.

Riutort, J.J., 1994. Le pêche en Corse: la rouget de roche, espèce cible. Contract Report CEE XIV-I/MED/91/006. Commission de Communautés Européenes, Direction Générale des Pêches, Brussels.

Roberts, C.M., Polunin, N.V.C., 1992. Effects of marine reserve protection on northern Red Sea fish populations. Proc. 7th Int. Coral Reef Symp. 2, 969–977.

Russ, G.R., Alcala, A.C., 1998a. Natural fishing experiments in marine reserves 1983–1993: community and trophic responses. Coral Reefs 17, 383–397.

Russ, G.R., Alcala, A.C., 1998b. Natural fishing experiments in marine reserves 1983–1993: roles of life history and fishing intensity in family responses. Coral Reefs 17, 399–416.

Sala, E., 1997. Fish predators and scavengers of the sea urchin Paracentrotus lividus in protected areas of the north-west Mediterranean Sea. Mar. Biol. 129, 531–539.

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.

Sala, E., Boudouresque, C.F., Harmelin-Vivien, M., 1998a. Fishing, trophic cascades, and the structure of algal assemblages: evaluation of an old but untested paradigm. Oikos 82, 425–439.

Sala, E., Ribes, M., Hereu, B., Zabala, M., Alva, M., Coma, R., Garrabou, J., 1998b. Temporal variability in abundance of the sea urchins Paracentrotus lividus and Arbacia lixula in the north-western Mediterranean: comparison between a marine reserve and an unprotected area. Mar. Ecol. Prog. Ser. 168, 135–145.

Sánchez Lizaso, J.L., Goñi, R., Reñones, O., García Charton, J.A., Galzin, R., Bayle, J.T., Sánchez Jerez, P., Pérez Ruzafa, A., Ramos, A.A., 2000. Density dependence in marine protected populations: a review. Environ. Conserv. 27, 144–158.

Sargian, P., 1997. Contribution a la cartographie de la bande rocheuse infralittorale et de l'herbier a *Posidonia oceanica* dans la Baie de la Revellata (Calvi). Maitrise Sciences et Techniques Thesis, Universite de Corse, 26 pp.

Shannon, L.J., Cury, P.M., Jarre, A., 2000. Modelling effects of fishing in the Southern Benguela ecosystem. ICES J. Mar. Sci. 57, 720–722.

Sissenwine, M.P., 1986. Perturbation of a predator-controlled continental shelf ecosystem. In: Sherman, K., Alexander, L.M. (Eds.), Variability and Management of Large Marine Ecosystems, vol. 99. AAAS Selected Symposia Series. Westview Press, Boulder, CO, USA, pp. 55–85.

Steneck, R.S., McNaught, D., Zimsen, S., 1995. Spatial and temporal patterns in sea urchin populations, herbivory and algal community structure in the Gulf of Maine. In: Proceedings of the 1994 Workshop on the Management and Biology of the Green Sea Urchin (*Strongylocentrotus droebachiensis*). Massachusetts Department of Natural Resources, pp. 34–73.

Stevens, J.D., Bonfil, R., Dulvy, N.K., Walker, P.A., 2000. The effects of fishing on sharks, rays and chimaeras (chondrichthyans), and the implications for marine ecosystems. ICES J. Mar. Sci. 57, 476–494.

Thibault, J.-C., Zotier, R., Guyot, I., Bretagnolle, V., 1996. Recent trends in breeding marine birds of the Mediterranean region with special reference to Corsica. Colonial Waterbirds 19 (1), 31–40 (special publication).

Trites, A.W., Livingston, P.A., Vasconcellos, M.C., Mackinson, S., Springer, A., Pauly, D., 1999a. Ecosystem Change and the Decline of Marine Mammals in the Eastern Bering Sea: Testing Ecosystem Shift and Commercial Whaling Hypotheses. University of British Columbia Fisheries Centre Reports 7, 106 pp.

Trites, A.W., Livingston, P.A., Vasconcellos, M.C., Mackinson, S., Springer, A., Pauly, D., 1999b. Ecosystem considerations and the limitations of Ecosim models in fisheries management: insights from the Bering Sea. In: Keller, S. (Ed.), Ecosystem Approaches for Fisheries Management. University of Alaska Sea Grant, Fairbanks, pp. 609–618.

Ulanowicz, R.E., 1986. Growth and Development: Ecosystems Phenomenology. Springer Verlag, New York, 203 pp.

Vacchi, M., Bussotti, S., Guidetti, P., La Mesa, G., 1998. Study of the coastal fish assemblage in the marine reserve of the Ustica Island (southern Tyrrhenian Sea). Ital. J. Zool. 65, 281–286.

Vasconcellos, M., Mackinson, S., Pauly, D., 1997. The stability of trophic mass-balance models of marine ecosystems: a comparative analysis. Ecol. Model. 100, 125–134.

Verlaque, M., 1987. Relations entre *Paracentrotus lividus* (Lamark) et le phytobenthos de Méditerranée occidentale. In: Boudouresque, C.F. (Ed.), Colloque Intérnationale sur Paracentrotus lividus et les Oursins Comestibles. GIS Posidonie Publications, Marseille, pp. 5–36.

Vukovic, A., 1982. Florofaunistic changes in the infralitoral zone after the sea urchin *Paracentrotus lividus* (L) population explosion. Acta Adriat. 23, 237–241.

Walters, C., Christensen, V., Pauly, D., 1997. Structuring dynamic models of exploited ecosystems from trophic mass-balance assessments. Rev. Fish Biol. Fish. 7, 139–172.

Whipple, S.J., Link, J.S., Garrison, L.P., Fogarty, M.J., 2000. Models of predation and fishing mortality in aquatic ecosystems. Fish Fish. 1, 22–40.