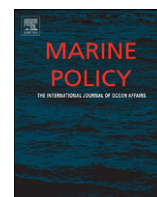




ELSEVIER

Contents lists available at [SciVerse ScienceDirect](http://SciVerse.Sciencedirect.com)

Marine Policy

journal homepage: www.elsevier.com/locate/marpol

The science of European marine reserves: Status, efficacy, and future needs

Phillip B. Fenberg^{a,*}, Jennifer E. Caselle^b, Joachim Claudet^{c,d}, Michaela Clemence^b, Steven D. Gaines^b, Jose Antonio García-Charton^e, Emanuel J. Gonçalves^f, Kirsten Grorud-Colvert^a, Paolo Guidetti^g, Stuart R. Jenkins^h, Peter J.S. Jonesⁱ, Sarah E. Lester^b, Rob McAllen^j, Even Moland^k, Serge Planes^{c,d}, Thomas K. Sørensen^l^a Oregon State University, Department of Zoology, Corvallis, OR 97331, USA^b University of California, Santa Barbara, Marine Science Institute, Santa Barbara, CA 93106, USA^c National Center for Scientific Research (CNRS), USR 3278 CNRS-EPHE CRIOBE, University of Perpignan, 66860 Perpignan Cedex, France^d Laboratoire d'Excellence "CORAIL", France^e University of Murcia, Department of Ecology and Hydrology, 30100 Murcia, Spain^f Eco-Ethology Research Unit, Instituto Superior de Psicologia Aplicada, 1149-041 Lisboa, Portugal^g University of Salento, Department of Biological and Environmental Sciences and Technology, 73100 Lecce, Italy^h School of Ocean Sciences, Bangor University, Menai Bridge, Anglesey LL59 5AB, United Kingdomⁱ Department of Geography, University College London, WC1E 6BT, United Kingdom^j School of Biological, Earth and Environmental Sciences, University College Cork, Ireland^k Institute of Marine Research, Flødevigen Marine Research Station, His, N-4817, Norway^l National Institute of Aquatic Resources, Technical University of Denmark, Charlottenlund, Denmark

ARTICLE INFO

Article history:

Received 8 November 2011

Received in revised form

17 February 2012

Accepted 18 February 2012

Keywords:

Marine protected areas

Marine reserves

Marine Strategy Framework Directive

Conservation

Spillover

Europe

ABSTRACT

The ecologically and socio-economically important marine ecosystems of Europe are facing severe threats from a variety of human impacts. To mitigate and potentially reverse some of these impacts, the European Union (EU) has mandated the implementation of the Marine Strategy Framework Directive (MSFD) in order to achieve *Good Environmental Status* (GES) in EU waters by 2020. The primary initiative for achieving GES is the implementation of coherent networks of marine protected areas (MPAs). Marine reserves are an important type of MPA in which no extraction is allowed, but their usefulness depends upon a number of ecological, management, and political factors. This paper provides a synthesis of the ecological effects of existing European marine reserves and the factors (social and ecological) underlying their effectiveness. Results show that existing European marine reserves foster significant positive increases in key biological variables (density, biomass, body size, and species richness) compared with areas receiving less protection, a pattern mirrored by marine reserves around the globe. For marine reserves to achieve their ecological and social goals, however, they must be designed, managed, and enforced properly. In addition, identifying whether protected areas are ecologically connected as a network, as well as where new MPAs should be established according to the MSFD, requires information on the connectivity of populations across large areas. The adoption of the MSFD demonstrates willingness to achieve the long-term protection of Europe's marine ecosystems, but whether the political will (local, regional, and continent wide) is strong enough to see its mandates through remains to be seen. Although the MSFD does not explicitly require marine reserves, an important step towards the protection of Europe's marine ecosystems is the establishment of marine reserves within wider-use MPAs as connected networks across large spatial scales.

© 2012 Elsevier Ltd. All rights reserved.

1. Introduction

Marine ecosystems around the globe increasingly face severe threats from a variety of human impacts, including over-harvesting,

habitat degradation, ocean acidification, and climate change [1–4]. These impacts can result in a multitude of biological and ecological changes, most notably reductions in numbers, biomass, body size of organisms, lower species diversity, and changes in life history and genetics [5–9]. Such changes can cascade through the food web to influence whole communities (via direct and indirect effects) [10] and alter ecosystem functioning and services, prompting the need for management approaches that mitigate and potentially reverse some of these effects [11–13].

* Corresponding author. Tel.: +1 541 207 8695; fax: +1 541 737 3360.

E-mail addresses: fenbergp@science.oregonstate.edu, pfenberg@gmail.com (P.B. Fenberg).

Europe is no exception to the global pattern of threatened marine ecosystems. European waters have a long history of human use, including thousands of years of fish and invertebrate harvesting [14–17]. This has resulted in depletions of fish stocks and habitat degradation [12,15,16,18,19], leading the governing bodies of the European Union (EU) to mandate ocean protection initiatives among member states. The most notable of these policy initiatives is the Marine Strategy Framework Directive (MSFD), adopted by the EU in 2008. The stated goal of the MSFD is for member states to use an ecosystem-based management approach in order to achieve *Good Environmental Status* (GES) of their waters by 2020 [20]. In order for member states to comply with the MSFD they must ensure that their biological and physical marine features adhere to the 11 qualitative descriptors of GES for the maintenance of biological diversity, habitat quality, and sustainable harvest levels of fish and shellfish stocks [20]. Member states must put in place measures to achieve GES, with the establishment of coherent networks of marine protected areas (MPAs) as the only mandated measure [20–22].

A key component for achieving a coherent network of MPAs will be the inclusion of the Natura 2000 protected areas network, which includes both terrestrial and marine protected areas aiming to safeguard European species and habitats (www.natura.org). The designation of these sites is based on criteria issued by the European Commission (EC) Habitat and EC Wild Bird Directives, including habitat representativeness and population size. Other drivers for the establishment of EU MPAs include international obligations such as those under the Convention on Biological Diversity. Regionally, the key drivers are The Convention for the Protection of the Marine Environment of the North-East Atlantic (OSPAR), Helsinki Commission (HELCOM) and Barcelona regional seas conventions. For example, the OSPAR Convention commits contracting parties to establish an ecologically coherent network of well-managed MPAs [23]. These initiatives will spur the creation of new MPAs by 2020, prompting a need for more knowledge about the factors influencing MPA success and the gaps in scientific information for existing EU MPAs.

Globally, MPAs, and in particular, marine reserves (a type of MPA in which all extraction is prohibited), have been shown to foster biological recovery over time, making them important tools

for ecosystem-based management [11,24,25]. In European waters, reserves are usually embedded as sub-units within MPAs with other protection levels. Although the MSFD does not explicitly require marine reserves, numerous studies, including recent global meta-analyses of reserve effects, show that, on average, biological measures such as population biomass and density, body size, and species richness all increase within reserve boundaries compared to areas receiving less protection [26–30]. Other types of MPAs can vary widely in their levels of allowable use, and thus, it is more difficult to make generalizations about the ecological outcome of protection. Reserves on the other hand, provide the highest level of area-based protection and therefore should indicate the upper range of ecological responses expected from MPAs [27,28,31].

Given the growing body of scientific evidence regarding the impacts of complete protection, marine reserves and/or MPAs that embed reserves may be an important component of the MSFD's ecosystem-based management approach. However, a detailed synthesis of the current status and effectiveness of these types of MPAs located throughout Europe is currently lacking. Such a synthesis is needed in order to establish how reserves may be utilized as an instrument to help achieve the goals of the MSFD and the extent to which new reserves are needed.

To better understand the effectiveness, strengths and limitations of existing marine reserves (including those embedded in MPAs), a European specific synthesis is provided for: (1) the status of marine protection in terms of geographic scope, numbers and size of reserves, (2) reserve effectiveness along ecological, economic, and social dimensions, (3) factors that underlie reserve effectiveness, such as enforcement, size, and age, and (4) future science needs for European reserves. Throughout the paper, the term “marine reserve” is used to refer to both MPAs that are entirely no-take and no-take areas embedded within broader MPAs.

2. The status of European marine reserves: geography, numbers and size

An extensive search of multiple sources was conducted (e.g. the primary literature, web based searches of government documents, and surveys of marine scientists and professionals) to determine the

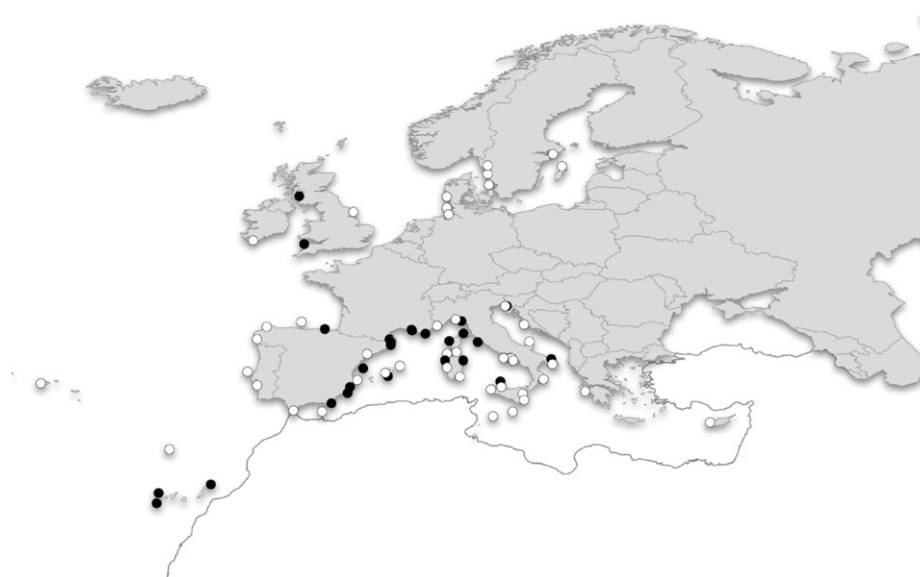


Fig. 1. Geographic distribution of European marine reserves as of 2011 ($n=74$). Most reserves ($n=50$, 68%) occur within the Mediterranean Sea, which range in size from 0.02 km^2 to 61.5 km^2 , covering a mean area of 4.9 km^2 and a median of 1.7 km^2 . Outside of the Mediterranean, reserves are much larger on average—with a mean size of 55 km^2 , but a median of 3.7 km^2 . The sizes of reserves outside of the Mediterranean range from 0.78 km^2 to 645 km^2 . The reserves marked by a black dot represent those that we included in the meta-analysis of reserves effects (see Section 3.1).

locations and sizes of the marine reserves in Europe (excluding overseas territories) as of 2011. This search revealed that presently, 74 marine reserves occur within the waters of 16 European countries (Fig. 1). These marine reserves, like many across the globe, are often nested within multi-use MPAs—generally taking the form of a no-take core surrounded by areas with lower levels of protection. This is a particularly common design for marine reserves in the Mediterranean. Of the total number of European reserves, 19 (26%) occur outside the Mediterranean Sea and 50 (68%) occur in the Mediterranean Sea (five reserves (6%) occur in the Azores, Madeira and Canary Islands; Fig. 1).

The overwhelming majority of European marine reserves are small; 92% of them cover an area less than 50 km². A total area of 1624 km² is covered by marine reserves in European waters, roughly two orders of magnitude lower than the area covered by European MPAs with lower levels of protection [\sim 124,000 km²; [32,33]]. In the Mediterranean for example, approximately 4% of the sea is protected by MPAs ($n=237$; \sim 97,000 km²), yet 90% of this area is the Pelagos Sanctuary (only designed to ensure protection for marine mammals and basically a 'paper park' with little to no enforcement), which covers the entirety of the Ligurian Sea [32,33]. Excluding the Pelagos Sanctuary, MPAs cover 0.4% of the total surface area of the Mediterranean, with the no-take portion consisting of only 242 km². Thus, while most European reserves occur in the Mediterranean, all together they comprise only a very small geographic area.

European waters outside the Mediterranean (excluding the Azores, Madeira, and Canary Islands) contain 799 MPAs, with varying levels of protection, covering approximately 27,000 km² [33]. This region contains 19 marine reserves, which cover approximately 1356 km². Thus, while the Mediterranean Sea contains the majority of marine reserves in Europe ($n=50$; 242 km²), they cover a much lower area (15% of the total surface area covered by all European reserves) compared to areas outside the Mediterranean. 74% of the area covered by reserves outside the Mediterranean is protected within two recently established Swedish reserves (Gotska Sandoen, covering 360 km² and Kattegat, covering 645 km²). It should be noted, however, that these two Swedish reserves are currently experimental and are due for evaluation in the near future. If these two reserves are removed, the total amount of area covered by non-Mediterranean marine reserves is similar to the area covered by reserves in the Mediterranean (377 km² compared to 242 km²). In the Azores, Madeira and Canary Islands, there are only five reserves, which occupy a total area of 28 km².

3. Are European marine reserves effective?

3.1. Ecological effectiveness: meta-analysis of European marine reserves

In order to determine whether existing European marine reserves foster positive biological effects on species and populations, a comprehensive search of the peer-reviewed literature was conducted to compile a dataset of studies that document biological effects of marine reserves within European waters (i.e. including member and non-member EU nations). Following the methods of Lester et al. [28], only studies in which data were available for individual no-take marine reserves and those which measured at least one of four biological variables (numerical density, biomass, individual organism size, and/or species richness) inside and outside the reserve were included.

For each study, quantitative data for the four biological variables described above were extracted from the text, tables, and figures. Using the extracted data, response ratios (inside

versus outside the reserve) were calculated for each study and for each biological variable. In many instances, data were extracted for multiple taxa in a given study. These ratios were averaged to determine the response ratio for all taxa combined for each study (regardless of commercial importance). In addition, some of the reserves in the dataset have been studied across numerous publications, in which case the average of the response ratios for each study were calculated as a single biological variable response per reserve. This was done rather than using the most recent study for a given reserve since studies often focus on different species and are conducted by different researchers. The response ratios were then converted to percentage increases or decreases ($[\text{response ratio} - 1] \times 100$) for presentation purposes, but log-transformed response ratios were used for all statistical analyses. This dataset is an update of the European reserves from a global meta-analysis published in 2009 [28].

The resulting combined dataset consists of 46 peer-reviewed publications published between 1983 and 2011 from 27 marine reserves located in four nations (United Kingdom, $n=2$; France, $n=6$; Italy, $n=8$; Spain, $n=11$; supplementary Table 1). Except for three reserves in the Canary Islands (Spain), one each in England, Scotland, and northern Spain, all reserves in our dataset are located in the Mediterranean Sea. There are 74 marine reserves that occur in Europe, but only about one-third have published data that met our criteria. Although there is a strong geographic bias, this reflects the overall distribution of European reserves (Fig. 1) and therefore should constitute a representative sample of the biological effects of existing reserves across Europe.

Analysis of the dataset reveals significant increases in all four of the biological variables examined (1-sample 2-tailed t -tests of log-transformed response ratios; $p < 0.004$ for biomass, density and species richness and $p = 0.04$ for organism size; Fig. 2). These results mirror those of the global dataset analysis from Lester et al. [28], with the largest increases occurring in biomass and density of organisms within reserves (238% and 116% respectively) followed by more moderate increases in individual size (13%) and species richness (19%). Medians between the global and Europe synthesis are strikingly similar, indicating that reserves in Europe are performing similarly to those around the world (Fig. 2).

The European reserve effects shown here are consistent with the findings of a previous meta-analysis of the biological effects of Mediterranean reserves, which revealed that fish density and richness not only increased compared to non-reserves, but that the larger and older reserves contain higher fish densities and species richness compared to those with younger and smaller no-take zones [26]. However, the analysis and literature search presented here reveals that small and newly established marine reserves can also foster significant biological effects over a short time span. This is perhaps best exemplified by the two recently established marine reserves in the United Kingdom. A 3.3 km² area of the coastal waters of Lundy Island, off southwest England, was established in 2003 as the first marine reserve in the UK. After only 18 months of full protection, researchers documented increases in size and numbers of the commercially important European lobster (*Homarus gammarus*); by 2007, legal-sized lobsters were 5 times more abundant and 9% larger within the reserve compared to fished areas nearby [34]. Likewise, the 2.67 km² Lamlash Bay marine reserve off the west coast of Scotland was only established in 2008, but dive surveys conducted in 2010 show that numbers of juvenile scallops (*Pecten maximus*) and the age, size, and biomass of adult scallops are significantly greater inside the reserve compared to adjacent areas that receive lower levels of protection [35].

The results suggest the importance of no-take protection, although conclusions are somewhat limited by the lack of comparable 'before' data. This is a general issue that should be

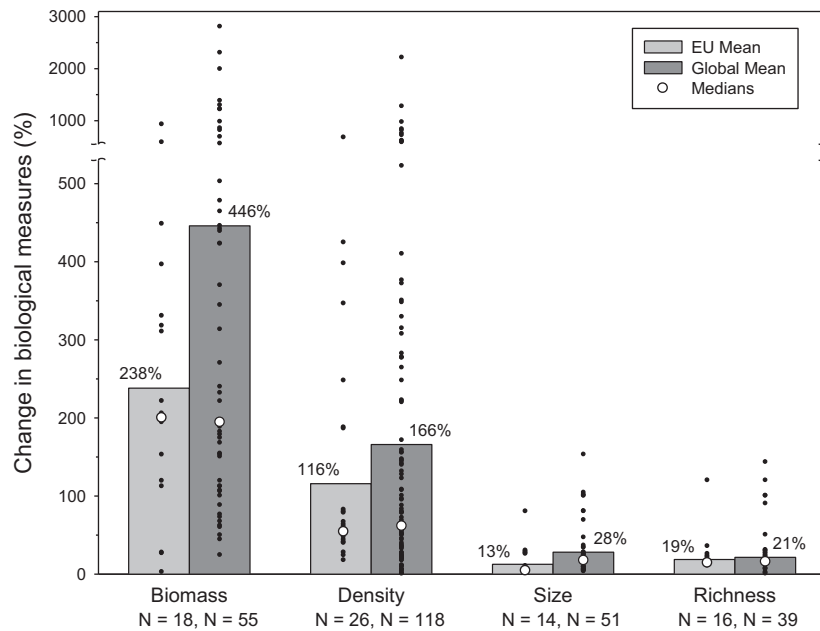


Fig. 2. Mean (bars) and median (o) percent change in biomass, density, organism size, and species richness calculated from response ratios for European reserves (light gray bars) and global reserves (dark gray bars). All four biological variables show statistically significant increases (1-sample 2-tailed *t*-tests) for the global dataset [28] and the European dataset ($p < 0.004$ for biomass, density and species richness and $p = 0.04$ for organism size; EU dataset). Dark circles represent individual reserve responses. *N*: number of reserves for which each biological variable was measured.

taken into consideration when interpreting reserve studies that employ the 'inside versus outside' comparative approach [36,37], the most commonly used method due to the general lack of data from reserves before full protection was initiated. This caveat aside, results are suggestive that European marine reserves of all sizes and ages are useful tools to help achieve GES and should be considered as an important component when establishing coherent networks of protected sites.

3.2. Evidence for indirect, ecosystem-wide effects of European marine reserves

Besides direct effects on the recovery of exploited species, marine reserves can have a wide variety of indirect effects, which lead both to declines in other species that coexist within marine reserves (e.g., prey species) [38] and also to the re-establishment of trophic relationships and community interactions typical of unfished conditions [39]. Understanding the variety and complexity of such indirect effects is necessary to predict how populations of non-target species, as well as ecological processes, will be affected by protection and to evaluate whether reserves are achieving their conservation goals. In some situations, the reduction in prey populations can have further indirect effects on lower trophic levels and result in a trophic cascade [40]. A top-down trophic cascade is capable of shaping the structure of entire communities whenever changes in predator density, size and behavior trigger a sequence of indirect effects throughout the food web. These cascading effects resulted in very different species assemblages and community structure between marine reserves and fished areas in some Mediterranean MPAs ([39,41] but see also [10] for a review), which can perpetuate a variety of other secondary or indirect effects at the population, community, and ecosystem-level. In the Mediterranean rocky reefs, for example, such indirect changes have taken the form of shifts from macroalgal forests to coralline barrens [41]. This shift in community structure is linked to predation rates on benthic invertebrates (especially sea urchins that are effective grazers of erected macroalgae); which were found at higher densities within marine

reserves that host more abundant and larger predators (fish like sea breams or large invertebrates like lobsters), compared to fished areas [39,41].

3.3. Evidence for the effects of European marine reserves outside their borders

In addition to the ecological benefits of marine reserves for species and populations within their boundaries, reserves can also increase the abundance and/or biomass of individuals in adjoining areas through spillover (i.e. the movement of adults from inside to outside the reserve; [42–46]). Net emigration of adult and juvenile individuals from reserves may result from density-dependent (e.g. enhanced intra- or inter-specific competition for food or shelter, increased predation) or density-independent (e.g. shifts in home ranges, ontogenetic migrations) processes [46,47]. When spillover occurs, fishing yield can be positively affected in adjacent areas [48–50].

Several methods have been used to detect the likely occurrence of spillover for European reserves and to measure its magnitude and effects, including: (i) measurement of gradients of abundance and/or biomass across the boundaries of reserves [51]; (ii) quantification of long-term responses in the abundance of species outside reserves [52]; and (iii) direct measurement of the mobility of individuals within and around reserves by tag-and-recapture and acoustic tracking studies [53,54].

Recent studies show that decreasing gradients of reef fish biomass from the boundaries of several Mediterranean reserves are common along with higher catches near reserve borders, indicating that spillover is likely occurring at short distances (hundreds to thousands of meters from the reserve [51,55–57]). Both the intensity of fishing pressure outside the studied reserves, the variability and the spatial continuity of coastal habitats may influence spillover effects. Further, combined experimental (i.e. sampling-directed) and commercial fishing data from lobster (*Palinurus elephas*) in a Mediterranean reserve (Columbretes Reserve) suggests that lobster export is sufficient to maintain stable catch rates up to 1500 m from the boundary [58]. However,

a significant non-linear decline of CPUE with distance from the center of the reserve suggests local depletion at the boundary due to a concentration of fishing effort (a phenomenon called 'fishing-the-line'; [59,60]). Increases in fishing yields at sites adjacent to reserves have been documented in other studies, suggesting a general pattern of spillover in the Mediterranean [61–63] and in northern waters [34].

The number of studies quantifying movement of individuals within and around European reserves has increased dramatically during the last decade. Ten years of tagging studies have demonstrated that lobsters continuously move away from the Columbretes reserve [58,64]. These studies estimated that approximately 7% of the lobster population protected in this reserve migrated annually to the adjacent fished grounds, with an annual spillover contribution to the commercial catch (by weight) of 31–43%. In contrast, acoustic tracking of both fish and decapod species within reserves showed high site fidelity [53,65–70]. Such studies show that some individuals are highly sedentary, while others show more mobility (e.g. [71]) indicating that more research efforts are needed to understand movement patterns of key coastal species.

In addition to spillover of adults, it has been hypothesized that reserves can act as a source of larvae due to increased density and fecundity (as a consequence of the recovery of larger size classes) of protected populations, thus replenishing unprotected areas by dispersal of eggs and larvae [72]. The few studies performed to date around Mediterranean reserves provide ambiguous evidence about their potential to supply recruits to exploited populations in the surrounding areas [73–77]. This limited evidence is not surprising given that empirical and theoretical results show the difficulty of detecting larval export from reserves in the field [78]. The magnitude and extent of larval export will likely depend on local oceanographic conditions and the biological characteristics of fish and invertebrate species.

4. Factors underlying the effectiveness of existing reserves

The average magnitude of ecological effects in reserves reported above may be poor predictors for any single reserve as the response to protection may vary greatly, from local to regional scales. A wide array of factors may influence biological response to protection, including: the time since reserve establishment and/or the implementation of enforcement, the reserve size, the life-history and ecological traits of the protected species, habitat diversity and complexity, and the socio-cultural context in which the reserve is established.

Direct effects of marine reserves, especially increases in commercial fish density, biomass, individual size and/or occurrence, typically require time to accrue [17,26,29,38]. In some cases, changes can be rapid (within 3 years, e.g. [79]), but often (e.g. for long-lived, slow-growing fishes, like groupers) the effects may take years, decades or even longer to accumulate [17,80]. Thus, judgment of the effectiveness of existing reserves will depend to a large extent on the time since reserve establishment in relation to the life history of species and the pattern of direct and indirect species interactions.

The effectiveness of marine reserves is also linked to their design. Although small reserves can be effective [81], increasing the size of a reserve increases the ratio of commercial fish density within the reserve relative to outside, whereas the size of a partially protected buffer zone may have the opposite effect [26,82]. Theoretical studies suggest that large reserves should be more effective for conservation than small reserves [83–86]. However, many syntheses and meta-analyses have failed to find support for this hypothesis of reserve size-dependency, although this may be an artifact of study design and the relatively small

range of reserve sizes examined [28,29,81,87,88] and exceptions do exist [26,82].

The life history and ecological traits of the protected species can also influence the effectiveness of reserves [29,38,82]. Recent work suggests that the effectiveness of European reserves increases as the maximum body size of the targeted species increased and that it is greater for non-schooling species [82]. Non-target species usually respond less strongly to protection [28], and when they do (in the case of unexploited benthic-pelagic species), they may exhibit the opposite response: their densities are sometimes lower inside reserves, suggesting an indirect response due to the increased density of their predators [39]. In addition, contrary to previous theoretical findings, mobile species with presumably wide home ranges can also benefit from protection. The effect of protection was found to be at least as strong for mobile species as it was for sedentary ones [82].

At a regional to local scale, heterogeneous reserve responses can be attributed in part to socio-cultural factors [89]. It has been clearly demonstrated, both theoretically [90] and empirically [91], that enforcement and compliance are fundamental aspects of effective reserves. Looking at the number of reserves established in Europe, especially in the Mediterranean region [32], one might have the impression of a huge investment in conservation and management policies. However, many of the reserves are established 'on paper' only [91]; in such cases, we should not expect any ecological or socio-economical effects. Even worse, establishing 'paper parks' often creates social friction without producing any benefits; increasing the risk that public opinion may dismiss marine reserves and MPAs as effective tools. Numerous studies from European coastal waters indicate that without enforcement and social compliance, reserves fail to achieve their goals [91–93]. Indeed, it is becoming widely recognized that conservation of natural heritage, proper management of natural resources and eventual recovery after impact require proper surveillance and rules enforcement [94].

The ecological effectiveness of reserves can also depend on human activities that occur outside the reserves, even when they are prohibited within the reserve. For example, overfishing of the spawning stock biomass in the surrounding fishing grounds may limit adult immigration or larval dispersal into the reserve, leading to smaller effects when stocks are more severely overfished (e.g. [95]). On the other hand, stressors occurring outside reserve borders including severe overfishing can also lead to dramatic increases when calculating response ratios from inside–outside comparisons. For example, when looking only at relative differences between control and protected locations, one reserve could appear more effective than another simply because the surrounding fishing grounds are more intensively fished. Quantifying the actual fishing pressure outside a reserve, the potential spillover across reserve boundaries, as well as human behavior in control areas (e.g. displacement effects, [61,96]) is therefore essential for an appropriate assessment of reserve effectiveness [97].

5. Effectively connected networks

The EU target of achieving both marine biodiversity conservation and socio-economic benefits requires a coherent framework to enhance and preserve fully functional marine ecosystems. Effectively connected networks of MPAs are integral to fulfilling these targets and, in particular, to achieving GES as specified by the MSFD. Assessments of whether protected sites are ecologically connected are key for determining whether existing reserves and other MPAs are functioning as effective ecological networks and not merely as a collection of unconnected sites.

To develop effective ecological networks of representative MPAs, designation of MPAs should take into account strict ecological criteria (for a full list of these criteria, see [32]). Such networks of ecologically connected and effective MPAs could provide better fishery outcomes by protecting areas that are sources of larvae, and offer a better compromise between human use and conservation than single large areas. For example, an existing collection of marine reserves in the northwestern Mediterranean Sea is considered to be an integral part of marine policy goals to meet international conservation targets. Even though these Mediterranean reserves are in relatively close proximity to each other, data have shown no evidence of a distance effect on the ecological effectiveness across these well-enforced sites; thus, they may not constitute an effectively connected network [26]. To evaluate connectivity across these reserves, studies utilizing genetic analyses, oceanographic modeling, and fish otolith microchemistry should assess spatial scales of connectivity among populations (see e.g. [98]).

Similarly, when accounting for fish habitat use across life stages, the Natura 2000 MPA network in the Baltic Sea was inadequate for protecting conservation features and allowing for connectivity across protected areas [99]. According to the IUCN-Marine MPA network definition, sites in the Mediterranean and Baltic Seas may not be considered ecologically effective networks since these collections of marine reserves do not exceed the ecological outcomes of individual or multiple, unconnected reserves. Unconnected marine reserves may be unable to meet the MSFD or other management goals of fully protecting populations of marine life [100].

A properly designed MPA network should achieve the goals of protecting a connected set of sites and species, covering an appropriate geographical gradient and considering the needs of managed fisheries in the surrounding waters. Yet the design, implementation, and management of cohesive MPA networks in the EU is not without its challenges. Multi-national coastlines lead to jurisdictional complexities for establishing and managing a network of marine reserves along appropriate ecological spatial scales. Particularly challenging are the EU's deep sea and open ocean habitats, where scientific knowledge is scarce and the uses and influences of fisheries are powerful. The distribution of these habitats is unbalanced between member states (the vast majority of the EU's deep sea areas are under the jurisdiction of a few countries), and, in spite of recent advances in the designation of high seas MPAs under the OSPAR convention, there is no framework for implementing coherent networks. Additionally, across the region, major gaps in ecological information exist, most notably the absence of coherent and comprehensive habitat and species distribution maps across EU waters and the frequent lack of comprehensive monitoring of socio-economic data for existing MPAs [101,102]. When metrics such as fishermen behavior and capacity for tourism were considered in the Mediterranean, sites that were high priority for protection based on both social and ecological factors seldom overlapped with sites recommended for protection as part of Natura 2000 or proposed by fishermen [103]. Clearly, practical advice about setting management goals and evaluating and monitoring effects of marine reserve networks is critical for identifying the key elements of a successful management plan for connected and ecologically coherent networks throughout European waters.

6. What is needed to improve marine protection in Europe?

At present, the processes leading to implementation of marine protection at relevant spatial scales in Europe are in the planning stages. However, a number of initiatives do exist across the wider

region and both interest and resources are being invested in marine spatial planning processes. In contrast to the plethora of planning initiatives is the lack of efforts to experimentally evaluate marine protection in the region, especially in northern parts of Europe (with Sweden being the exception, see Section 2). In this context, we describe science gaps that may be impeding the adoption of marine reserves as management tools in Europe, either as stand-alone protection or within MPAs of varying protection levels.

6.1. Population structure and connectivity

Recent work has shown that temperate coastal demersal species such as the Atlantic cod (*Gadus morhua*) are structured into local populations on limited spatial scales [104]. Management tailored to such population structure will need to be informed by species- and area-specific data on realized larval dispersal [105,106], good quality indicators such as retention mechanisms and behavior of coastal water masses [107], with knowledge regarding the spatial metapopulation structure of target species. However, information regarding population structure and connectivity for most commercial and non-commercial marine species is currently lacking and there is a need for research in Europe as well as globally. Through advances in a number of scientific frontiers such as population genetics, fish otolith microchemistry, transgenerational isotope labeling and numerical circulation modeling [106,108,109], scientists are poised to achieve more management-relevant knowledge. Most importantly, improved information on population structure and connectivity will improve our ability to design a coherent network of marine reserves [110,111].

Equally relevant is research into temporal patterns in space use, habitat use and home range behavior in key species aimed at informing marine reserve design (e.g. [67,68,71,112]). Although such knowledge is currently lacking for most marine species, it is crucial in forecasting potential impacts of marine reserves in nearby exploited areas. Also, larval behavior and, in particular, swimming abilities, habitat choice, vertical migrations and micro-patterns of distribution are essential to understand population dynamics of marine populations and may directly influence reserve design and location of reserve networks [113]. Studies aimed at linking population genetics and local adaptations in harvested species are another important emerging field (e.g. [114]). Such studies are essential to inform marine reserve design and to define the role of marine reserves in countering maladaptive fisheries-induced evolutionary changes in traits such as age and size at maturation.

6.2. Large-scale experimental evaluation of no-take marine reserves

Major interregional studies are urgently needed to move the discussion from 'what may or may not have an effect in European waters' to what has been demonstrated to work or fail in the field. Some good information is readily available from research conducted in southern Europe [26,39,115]. However, information regarding effects of protection is sparse for species and areas in northern Europe (but see: [34,35]). This can only be remedied by rigorous, medium- to long-term scientific experiments. To achieve the MSFD target, a replicated before-after control-impact (BACI) or at least after control-impact (ACI) studies across the wider region, designed to test marine protection at spatial scales that are relevant to fisheries management, would be particularly useful [36]. The recently initiated Joint Programming Initiative for Healthy and Productive Seas and Oceans (JPI Oceans, www.jpi-oceans.eu), aimed at tackling challenges that cannot be solved

solely on the national level, could be a framework for launching such a large-scale coordinated effort.

7. Socio-economics and politics

Marine reserves represent a wide spectrum of both costs and benefits to society, and their establishment can have negative and positive effects on communities that are dependent on the areas in which they are located. Within Europe, the economic drivers pushing marine reserve establishment vary greatly. Marine reserves in northern parts of Europe are often driven by a combination of existence value and overarching policy obligations relating to ecosystem-based marine management and species/habitat protection [116]. While reserve development in southern Europe is also driven by protection of biodiversity, more direct recreational uses such as diving and associated economic benefits due to the warmer, less turbid waters and well developed sea-based tourism are also key factors [117,118]. In some aspects, the socio-economic aspect of southern European reserves may be more easily compared with those of the tropics, where marine reserves provide valuable economic benefits from tourism to local communities and businesses [116]. However, many of the reserves in other parts of the world, for example, Southeast Asia, are also established with an objective of ensuring food security for adjacent communities, which can hardly be considered a main driver anywhere in Europe.

Marine reserves may be perceived as a threat to the livelihoods and way of life of those who will no longer be permitted to carry out their usual activities in these areas [21], and substantial economic impacts on local communities are a realistic threat related to reserve establishment in Europe and elsewhere. However, effective reserve networks can be designed to reach conservation targets while avoiding user conflicts by having collaborative and effective discussions amongst biologists and fisheries stakeholders. Much can be learned in Europe from this process. A recent study based on interviews of UK fishermen on the topic of reserves supports the conclusion that despite the fact that the majority of the representatives objected to the concept, there is potential for pragmatic and constructive participation of fishermen in reserve planning, including the use of experiential knowledge of the ecosystems in planning processes [21].

Many coastal EU Member States are currently facing the challenge of developing management plans for marine Natura 2000 sites as well as strategies for the MSFD. Given sufficient time, marine reserves have great potential to answer some of the questions that currently haunt these political processes, e.g., by providing reference areas that aid the assessment of impacts from fisheries and other activities on marine ecosystems. For instance, the effects of fishing on sandbanks have been the topic of discussion in Europe for decades, creating obstacles for the consensual development of fisheries management planning for protected sites that include such habitats. In all such cases, however, solid monitoring strategies are essential if marine reserves are to provide maximum benefits to society and information for management that might outweigh any costs from reserve establishment. Monitoring strategies must be able to separate the effects of fishing and other anthropogenic activities from those caused by environmental factors such as natural disturbance and climate change [37,97,119].

7.1. Political will

While a sound scientific evidence-base for marine reserves is important to improve their effectiveness, science also needs to be complemented, and ultimately implemented, through political

will [120]. There will always be a degree of uncertainty concerning the scientific basis for designing effective marine reserve networks due to the complexity, variability and interconnectedness of marine ecosystems, which makes it very difficult to prove cause–effect relationships [121]. Some stakeholders can highlight such uncertainties as a reason for maintaining the *status quo*, though proponents of marine reserves would counter that such designations actually provide insurance against uncertainty [122]. In addition, extractive stakeholders who can have shorter-term and individualistic priorities may resist and disregard marine reserve restrictions that are aimed at achieving broad long-term societal objectives. Without the political will to evaluate the wider fisheries benefits and ecosystem restoration potential of marine reserves, including promoting cross-sectoral cooperation, it is unlikely that we will move beyond the current very low number and coverage of such designations in the EU [123].

It is unclear whether the political will to designate and enforce MPAs will cascade downwards from the European Commission in Brussels and/or be generated at a national and local level. Regardless of origin of political will, it must be strong enough to overcome resistance from both extractive users and the politicians and regulators with vested interests in extractive uses. In this respect, it is important to note that while the Habitats/Birds Directives and MSFD may require and provide for multiple-use MPAs, and their implementation may be supported through the reformed Common Fisheries Policy, none of these policies require marine reserves. It would therefore seem that the political will for marine reserves must come from national and local levels, including building support for marine reserves from local stakeholders through collaborative initiatives [115]. Whether such a less centralized approach is sufficient remains to be seen.

8. Conclusions

There is growing evidence demonstrating the utility of European marine reserves to preserve the biodiversity of local ecosystems within their borders. Existing marine reserves in Europe show significant positive increases in key biological variables and re-establish trophic interactions typical of unfished ecosystems when compared with areas receiving less protection (including other types of MPAs)—and are beginning to affect areas outside reserve borders through adult spillover. The ecosystem-based management approach of the MSFD aims to ensure the long-term health of Europe's marine ecosystems and given the evidence presented in this paper, marine reserves may be an integral tool in achieving its stated goals. However, the usefulness of marine reserves, both ecologically and socio-economically, depends upon a number of factors, including reserve design and time since establishment, the life history and ecology of protected species, and effective management (i.e. enforcement). Moreover, establishing whether protected areas are connected as a network, as new MPAs are to be arranged according to the MSFD, requires information on the meta-population connectivity of species across large areas—which is not known for the vast majority of species in Europe or across the globe.

In order to partially overcome these obstacles, large-scale experimental evaluations of reserves (e.g. replicated BACI and ACI studies) should be designed to test protection throughout the region at spatial scales that are relevant for fisheries management and wider ecosystem protection. This type of study would require establishment of marine reserves that span a large geographic area, including both northern and southern regions. However, in order for such a network of reserves to be established, the political will must first be established and acted upon. The adoption of the MSFD demonstrates willingness to achieve the

long-term protection of Europe's marine ecosystems, but whether the political will (local, regional, and continent wide) is strong enough to see its mandates through, remains to be seen. Although the MSFD does not explicitly require marine reserves, an important step towards the protection of Europe's marine ecosystems will be set in place if properly designed and managed marine reserves are established within wider-use MPAs as connected networks across large spatial scales.

Acknowledgments

This publication stemmed from a workshop supported with funding from Natural England held in London in November 2010 for the Science of Marine Reserves Project The Partnership for Interdisciplinary Studies of Coastal Oceans (PISCO). This is publication no. 413 from PISCO, a long-term ecological consortium, which is partially funded by the David and Lucile Packard Foundation and the Gordon and Betty Moore Foundation. The views expressed in this paper are solely those of the authors and do not necessarily represent those of the funding organizations.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.marpol.2012.02.021.

References

- [1] Doney SC, Fabry VJ, Feely RA, Kleypas JA. Ocean acidification: the other CO₂ problem. *Ann Rev Mar Sci* 2009;1:169–92.
- [2] Halpern BS, Walbridge S, Selkoe KA, Kappel CV, Micheli F, D'Agrosa C, et al. A global map of human impact on marine ecosystems. *Science* 2008;319:948–952.
- [3] Jackson JBC, Kirby MX, Berger WH, Bjorndal KA, Botsford LW, Bourque BJ, et al. Historical overfishing and the recent collapse of coastal ecosystems. *Science* 2001;293:629–38.
- [4] Turner SJ, Thrush SF, Hewitt JE, Cummings VJ, Funnell G. Fishing impacts and the degradation or loss of habitat structure. *Fish Manage Ecol* 1999;6:401–20.
- [5] Fenberg PB, Roy K. Ecological and evolutionary consequences of size-selective harvesting: how much do we know? *Mol Ecol* 2008;17:209–20.
- [6] Grift RE, Rijnsdorp AD, Barot S, Heino M, Dieckmann U. Fisheries-induced trends in reaction norms for maturation in North Sea plaice. *Mar Ecol Prog Ser* 2003;257:247–57.
- [7] Jennings S, Kaiser MJ. The effects of fishing on marine ecosystems. *Adv Mar Biol* 1998;34:201–12.
- [8] Olsen EM, Heino M, Lilly GR, Morgan MJ, Brattey J, Ernande B, et al. Maturation trends indicative of rapid evolution preceded the collapse of northern cod. *Nature* 2004;428:932–5.
- [9] Wilson SK, Fisher R, Pratchett MS, Graham NAJ, Dulvy NK, Turner RA, et al. Habitat degradation and fishing effects on the size structure of coral reef fish communities. *Ecol Appl* 2010;20:442–51.
- [10] Pinnegar JK, Polunin NVC, Francour P, Badalamenti F, Chemello R, Harmelin-Vivien ML, et al. Trophic cascades in benthic marine ecosystems: lessons for fisheries and protected-area management. *Environ Conserv* 2000;27:179–200.
- [11] Lubchenco J, Palumbi SR, Gaines SD, Andelman S. Plugging a hole in the ocean: the emerging science of marine reserves. *Ecol Appl* 2003;13:53–7.
- [12] Barbier EB, Hacker SD, Kennedy C, Koch EW, Stier AC, Silliman BR. The value of estuarine and coastal ecosystem services. *Ecol Monogr* 2011;81:169–93.
- [13] Fox HE, Mascia MB, Basurto X, Costa A, Glew L, Heinemann D, et al. Reexamining the science of marine protected areas: linking knowledge to action. *Conserv Lett* 2011;5:1–10.
- [14] Bailey G, Barrett J, Craig O, Milner N. Historical ecology of the North Sea Basin. In: Erlandson J, Rick T, editors. *Human impacts on ancient marine ecosystems*. University of California Press; 2008.
- [15] Lotze HK. Rise and fall of fishing and marine resource use in the Wadden Sea, southern North Sea. *Fish Res* 2007;87:208–18.
- [16] Morales-Muñiz A, Roselló-Izquierdo E. Twenty thousand years of fishing in the Strait. In: Erlandson J, Rick T, editors. *Human impacts on ancient marine ecosystems*. University of California Press; 2008.
- [17] Guidetti P, Micheli F. Ancient art serving marine conservation. *Front Ecol Environ* 2011;9:374–5.
- [18] Airoidi L, Beck MW. Loss, status and trends for coastal marine habitats of Europe. *Oceanogr Mar Biol* 2007;45:345–405.
- [19] ICES. Environmental status of the European seas. 2003.
- [20] European Commission. On criteria and methodological standards on good environmental status of marine waters. Official Journal of the European Union 2010.
- [21] Jones PJS, Carpenter A. Crossing the divide: the challenges of designing an ecologically coherent and representative network of MPAs for the UK. *Mar Policy* 2009;33:737–43.
- [22] Rätz H-J, Dörner H, Scott R, Barbas T. Complementary roles of European and national institutions under the Common Fisheries Policy and the Marine Strategy Framework Directive. *Mar Policy* 2010;34:1028–35.
- [23] OSPAR. Guidance on developing an ecologically coherent network of OSPAR Marine Protected Areas. OSPAR Commission London, 2006.
- [24] Halpern BS, Lester SE, McLeod KL. Placing marine protected areas onto the ecosystem-based management seascape. *Proc Natl Acad Sci USA* 2010;107:18312–18317.
- [25] Katsanevakis S, Stelzenmüller V, South A, Sørensen TK, Jones PJS, Kerr S, et al. Ecosystem-based marine spatial management: review of concepts, policies, tools, and critical issues. *Ocean Coast Manage* 2011;54:807–20.
- [26] Claudet J, Osenberg CW, Benedetti-Cecchi L, Domenici P, García-Chartron J-A, Pérez-Ruzafa A, et al. Marine reserves: size and age do matter. *Ecol Lett* 2008;11:481–9.
- [27] Lester SE, Halpern BS. Biological responses in marine no-take reserves versus partially protected areas. *Mar Ecol Prog Ser* 2008;367:49–56.
- [28] Lester SE, Halpern BS, Grorud-Colvert K, Lubchenco J, Ruttenberg BI, Gaines SD, et al. Biological effects within no-take marine reserves: a global synthesis. *Mar Ecol Prog Ser* 2009;384:33–46.
- [29] Molloy PP, McLean IB, Côté IM. Effects of marine reserve age on fish populations: a global meta-analysis. *J Appl Ecol* 2009;46:743–51.
- [30] Di Franco A, Bussotti S, Navone A, Panzalis P, Guidetti P. Evaluating effects of total and partial restrictions to fishing on Mediterranean rocky-reef fish assemblages. *Mar Ecol Prog Ser* 2009;387:275–85.
- [31] Mora C, Andrefouet S, Costello MJ, Kranenburg C, Rollo A, Veron J, et al. Coral reefs and the global network of marine protected areas. *Science* 2006;312:1750–1.
- [32] Abdulla A, Gomei M, Maison E, Pianté C. Status of marine protected areas in the Mediterranean Sea. In: IUCN, editor. *Malaga and WWF. France* 2008. p. 152.
- [33] Spalding MD, Fish L, Wood LJ. Toward representative protection of the world's coasts and oceans-progress, gaps, and opportunities. *Conserv Lett* 2008;1:217–26.
- [34] Hoskin MG, Coleman RA, von Carlshausen E, Davis CM. Variable population responses by large decapod crustaceans to the establishment of a temperate marine no-take zone. *Can J Fish Aquat Sci* 2011;68:185–200.
- [35] Howarth LM, Wood HL, Turner AP, Beukers-Stewart BD. Complex habitat boosts scallop recruitment in a fully protected marine reserve. *Mar Biol* 2011;158:1767–80.
- [36] Guidetti P. The importance of experimental design in detecting the effects of protection measures on fish in Mediterranean MPAs. *Aquat Conserv-Mar Freshw Ecosyst* 2002;12:619–34.
- [37] Osenberg CW, Shima JS, Miller SL, Stier AC. Assessing effects of marine protected areas: confounding in space and possible solutions. In: Claudet J, editor. *Marine protected areas—a multidisciplinary approach*. Cambridge, UK: Cambridge University Press – Ecology, Biodiversity and Conservation Series; 2011.
- [38] Micheli F, Halpern BS, Botsford LW, Warner RR. Trajectories and correlates of community change in no-take marine reserves. *Ecol Appl* 2004;14:1709–1723.
- [39] Guidetti P. Marine reserves reestablish lost predatory interactions and cause community changes in rocky reefs. *Ecol Appl* 2006;16:963–76.
- [40] Witman JD, Dayton PK. Rocky subtidal communities. *Mar Community Ecol* 2001:339–66.
- [41] Sala E, Boudouresque CF, Harmelin-Vivien M. Fishing, trophic cascades, and the structure of algal assemblages: evaluation of an old but untested paradigm. *Oikos* 1998;82:425–39.
- [42] Gell FR, Roberts CM. Benefits beyond boundaries: the fishery effects of marine reserves. *Trends Ecol Evol* 2003;18:448–55.
- [43] Halpern BS, Lester SE, Kellner JB. Spillover from marine reserves and the replenishment of fished stocks. *Environ Conserv* 2010;36:268–76.
- [44] Roberts CM, Bohnsack JA, Gell F, Hawkins JP, Goodridge R. Effects of marine reserves on adjacent fisheries. *Science* 2001;294:1920–3.
- [45] Russ GR, Alcala AC. Do marine reserves export adult fish biomass? Evidence from Apo Island, central Philippines. *Mar Ecol Prog Ser* 1996;132:1–9.
- [46] Grüss A, Kaplan DM, Guenette S, Roberts CM, Botsford LW. Consequences of adult and juvenile movement for marine protected areas. *Biol Conserv* 2011;144:692–702.
- [47] Sánchez Lizaso JL, Goñi R, Reñones O, García-Chartron JA, Galzin R, Bayle JT, et al. Density dependence in marine protected populations: a review. *Environ Conserv* 2000;27:144–58.
- [48] Abesamis RA, Russ GR. Density-dependent spillover from a marine reserve: long-term evidence. *Ecol Appl* 2005;15:1798–812.
- [49] McClanahan TR, Mangi S. Spillover of exploitable fishes from a marine park and its effect on the adjacent fishery. *Ecol Appl* 2000;10:1792–805.
- [50] Murawski SA, Wigley SE, Fogarty MJ, Rago PJ, Mountain DG. Effort distribution and catch patterns adjacent to temperate MPAs. *ICES J Mar Sci* 2005;62:1150–67.

- [51] Harmelin-Vivien M, Le Direach L, Bayle-Sempere J, Charbonnel E, Antonio García-Charton J, Ody D, et al. Gradients of abundance and biomass across reserve boundaries in six Mediterranean marine protected areas: evidence of fish spillover? *Biol Conserv* 2008;141:1829–39.
- [52] Vandepierre F, Higgins RM, Sánchez-Meca J, Maynou F, Goñi R, Martín-Sosa P, et al. Effects of no-take area size and age of marine protected areas on fisheries yields: a meta-analytical approach. *Fish Fish* 2011;4:412–26.
- [53] Afonso P, Fontes J, Holland KN, Santos RS. Social status determines behaviour and habitat usage in a temperate parrotfish: implications for marine reserve design. *Mar Ecol Prog Ser* 2008;359:215–27.
- [54] Follasa MC, Cuccu D, Cannas R, Sabatini A, Deiana AM, Cau A. Movement patterns of the spiny lobster *Palinurus elephas* (Fabricius, 1787) from a central western Mediterranean protected area. *Sci Mar* 2009;73:499–506.
- [55] Forcada A, Bayle-Sempere JT, Valle C, Sánchez-Jerez P. Habitat continuity effects on gradients of fish biomass across marine protected area boundaries. *Mar Environ Res* 2008;66:536–47.
- [56] Forcada A, Valle C, Bonhomme P, Criquet G, Cadiou G, Lenfant P, et al. Effects of habitat on spillover from marine protected areas to artisanal fisheries. *Mar Ecol Prog Ser* 2009;379:197–211.
- [57] Guidetti P. Potential of marine reserves to cause community-wide changes beyond their boundaries. *Conserv Biol* 2007;21:540–5.
- [58] Goñi R, Quetzglas A, Reñones O. Spillover of spiny lobsters *Palinurus elephas* from a marine reserve to an adjoining fishery. *Mar Ecol Prog Ser* 2006;308:207–219.
- [59] Goñi R, Adlerstein S, Alvarez-Berastegui D, Forcada A, Reñones O, Criquet G, et al. Spillover from six western Mediterranean marine protected areas: evidence from artisanal fisheries. *Mar Ecol Prog Ser* 2008;366:159–74.
- [60] Kellner JB, Tetreault I, Gaines SD, Nisbet RM. Fishing the line near marine reserves in single and multispecies fisheries. *Ecol Appl* 2007;17:1039–54.
- [61] Stelzenmüller V, Maynou F, Bernard G, Cadiou G, Camilleri M, Crech'riou R, et al. Spatial assessment of fishing effort around European marine reserves: implications for successful fisheries management. *Mar Pollut Bull* 2008;56:2018–26.
- [62] Esparza O. Estudio de la pesca artesanal en el entorno de la reserva marina de Cabo de Palos – Islas Hormigas: Estrategias de pesca, efecto de la protección y propuestas para la gestión. University of Murcia, 2010.
- [63] Stobart B, Warwick R, Gonzalez C, Mallol S, Díaz D, Reñones O, et al. Long-term and spillover effects of a marine protected area on an exploited fish community. *Mar Ecol Prog Ser* 2009;384:47–60.
- [64] Goñi R, Hilborn R, Díaz D, Mallol S, Adlerstein S. Net contribution of spillover from a marine reserve to fishery catches. *Mar Ecol Prog Ser* 2010;400:233–43.
- [65] Jadot C, Donnay A, Acolas ML, Cornet Y, Anras MLB. Activity patterns, home-range size, and habitat utilization of *Sarpa salpa* (Teleostei: Sparidae) in the Mediterranean Sea. *ICES J Mar Sci* 2006;63:128–39.
- [66] Lembo G, Spedicato MT, Okland F, Carbonara P, Fleming IA, McKinley RS, et al. A wireless communication system for determining site fidelity of juvenile dusky groupers *Epinephelus marginatus* (Lowe, 1834) using coded acoustic transmitters. *Hydrobiologia* 2002;483:249–57.
- [67] Moland E, Olsen EM, Andvord K, Knutsen JA, Stenseth NC. Home range of European lobster (*Homarus gammarus*) in a marine reserve: implications for future reserve design. *Can J Fish Aquat Sci* 2011;68:1197–210.
- [68] Moland E, Olsen EM, Knutsen H, Knutsen JA, Enersen SE, Andre C, et al. Activity patterns of wild European lobster *Homarus gammarus* in coastal marine reserves: implications for future reserve design. *Mar Ecol Prog Ser* 2011;429:197–207.
- [69] Pastor J, Verdoit-Jarraya M, Astruch P, Dalias N, Pasqual J-SN, Saragoni G, et al. Acoustic telemetry survey of the dusky grouper (*Epinephelus marginatus*) in the Marine Reserve of Cerbère-Banyuls: informations on the territoriality of this emblematic species. *C R Biol* 2009;332:732–40.
- [70] Spedicato MT, Carbonara P, Lembo G. Insight into the homing behaviour of the dusky grouper (*Epinephelus marginatus* Lowe, 1834) around the island of Ustica, Italy. In: Spedicato MT LGMG (editor). Aquatic telemetry: advances and applications. Proceedings of the Fifth Conference on Fish Telemetry held in Europe. Ustica, Italy, 2005. p. 103–9.
- [71] March D, Palmer M, Alos J, Grau A, Cardona F. Short-term residence, home range size and diel patterns of the painted comber *Serranus scriba* in a temperate marine reserve. *Mar Ecol Prog Ser* 2010;400:195–206.
- [72] Planes S, Galzin R, Rubies AG, Goñi R, Harmelin JG, Le Direach L, et al. Effects of marine protected areas on recruitment processes with special reference to Mediterranean littoral ecosystems. *Environ Conserv* 2000;27:126–43.
- [73] Crech'riou R, Alemany F, Roussel E, Chassanite A, Marinaro JY, Mader J, et al. Fisheries replenishment of early life taxa: potential export of fish eggs and larvae from a temperate marine protected area. *Fish Oceanogr* 2010;19:135–50.
- [74] Lawson J. Export and spatial-temporal variation in the community structure of ichthyoplankton surrounding Marine Protected Areas in the Mediterranean. University College of Dublin; 2006.
- [75] López-Sanz A, Stelzenmüller V, Maynou F, Sabatés A. The influence of environmental characteristics on fish larvae spatial patterns related to a marine protected area: The Medes islands (NW Mediterranean). *Estuar Coast Shelf Sci* 2011;92:521–33.
- [76] O'Leary C. Spatial distribution and export of ichthyoplankton from Mediterranean Marine Protected Areas. University College of Dublin; 2006.
- [77] Sabatés A, Zabala M, García-Rubies A. Larval fish communities in the Medes Islands Marine Reserve (North-west Mediterranean). *J Plankton Res* 2003;25:1035–46.
- [78] Pelc RA, Warner RR, Gaines SD, Paris CB. Detecting larval export from marine reserves. *Proc Natl Acad Sci USA* 2010;107:18266–71.
- [79] Claudet J, Pelletier D, Jouvenel JY, Bacht F, Galzin R. Assessing the effects of marine protected area (MPA) on a reef fish assemblage in a northwestern Mediterranean marine reserve: identifying community-based indicators. *Biol Conserv* 2006;130:349–69.
- [80] Russ GR, Alcalá AC. Marine reserves: long-term protection is required for full recovery of predatory fish populations. *Oecologia* 2004;138:622–7.
- [81] Halpern BS. The impact of marine reserves: do reserves work and does reserve size matter? *Ecol Appl* 2003;13:S117–37.
- [82] Claudet J, Osenberg CW, Domenici P, Badalamenti F, Milazzo M, Falcon JM, et al. Marine reserves: fish life history and ecological traits matter. *Ecol Appl* 2010;20:830–9.
- [83] Botsford LW, Hastings A, Gaines SD. Dependence of sustainability on the configuration of marine reserves and larval dispersal distance. *Ecol Lett* 2001;4:144–50.
- [84] Botsford LW, Micheli F, Hastings A. Principles for the design of marine reserves. *Ecol Appl* 2003;13:S25–31.
- [85] Hastings A, Botsford LW. Comparing designs of marine reserves for fisheries and for biodiversity. *Ecol Appl* 2003;13:S65–70.
- [86] Roberts CM, Branch G, Bustamante RH, Castilla JC, Dugan J, Halpern BS, et al. Application of ecological criteria in selecting marine reserves and developing reserve networks. *Ecol Appl* 2003;13:S215–28.
- [87] Côté IM, Mosqueira I, Reynolds JD. Effects of marine reserve characteristics on the protection of fish populations: a meta-analysis. *J Fish Biol* 2001;59:178–89.
- [88] Guidetti P, Sala E. Community-wide effects of marine reserves in the Mediterranean Sea. *Mar Ecol Prog Ser* 2007;335:43–56.
- [89] Lundquist CJ, Granek EF. Strategies for successful marine conservation: integrating socioeconomic, political, and scientific factors. *Conserv Biol* 2005;19:1771–8.
- [90] Byers JE, Noonburg EG. Poaching, enforcement, and the efficacy of marine reserves. *Ecol Appl* 2007;17:1851–6.
- [91] Guidetti P, Milazzo M, Bussotti S, Molinari A, Murenu M, Pais A, et al. Italian marine reserve effectiveness: does enforcement matter? *Biol Conserv* 2008;141:699–709.
- [92] Ceccherelli G, Pais A, Pinna S, Sechi N, Chessa LA. Human impact on *Paracentrotus lividus*: the result of harvest restrictions and accessibility of locations. *Mar Biol* 2011;158:845–52.
- [93] Martins GM, Jenkins SR, Hawkins SJ, Neto AI, Medeiros AR, Thompson RC. Illegal harvesting affects the success of fishing closure areas. *J Mar Biol Assoc UK* 2011;91:929–37.
- [94] Haisfield KM, Fox HE, Yen S, Mangubhai S, Mous PJ. An ounce of prevention: cost-effectiveness of coral reef rehabilitation relative to enforcement. *Conserv Lett* 2010;3:243–50.
- [95] Lloret J, Zaragoza N, Caballero D, Font T, Casadevall M, Riera V. Spearfishing pressure on fish communities in rocky coastal habitats in a Mediterranean marine protected area. *Fish Res* 2008;94:84–91.
- [96] Mascia MB, Brosius JP, Dobson TA, Forbes BC, Horowitz L, McKean MA, et al. Conservation and the social sciences. *Conserv Biol* 2003;17:649–50.
- [97] Claudet J, Guidetti P. Fishermen contribute to protection of marine reserves. *Nature* 2010;464:673.
- [98] Schunter C, Carreras-Carbonell J, Macpherson E, Tintoré J, Vidal-Vijande E, Pascual A, et al. Matching genetics with oceanography: directional gene flow in a Mediterranean fish species. *Mol Ecol* 2011;20:5167–81.
- [99] Sundblad G, Bergstrom U, Sandstrom A. Ecological coherence of marine protected area networks: a spatial assessment using species distribution models. *J Appl Ecol* 2011;48:112–20.
- [100] Grorud-Colvert K, Claudet J, Carr M, Caselle J, Day J, Friedlander A, et al. The ecology of marine reserve networks: challenges and opportunities for design and monitoring. In: Claudet J, editor. Marine protected areas—a multidisciplinary approach. Cambridge, UK: Cambridge University Press - Ecology, Biodiversity and Conservation Series; 2011.
- [101] García-Charton JA, Pérez-Ruzafa A, Marcos C, Claudet J, Badalamenti F, Benedetti-Cecchi L, et al. Effectiveness of European Atlanto-Mediterranean MPAs: do they accomplish the expected effects on populations, communities and ecosystems? *J Nat Conserv* 2008;16:193–221.
- [102] Smith RJ, Eastwood PD, Ota Y, Rogers SI. Developing best practice for using Marxan to locate Marine Protected Areas in European waters. *ICES J Mar Sci* 2009;66:188–94.
- [103] Giakoumi S, Grantham HS, Kokkoris GD, Possingham HP. Designing a network of marine reserves in the Mediterranean Sea with limited socioeconomic data. *Biol Conserv* 2011;144:753–63.
- [104] Knutsen H, Jorde PE, Andre C, Stenseth NC. Fine-scaled geographical population structuring in a highly mobile marine species: the Atlantic cod. *Mol Ecol* 2003;12:385–94.
- [105] Christie MR, Tissot BN, Albins MA, Beets JP, Jia YL, Ortiz DM, et al. Larval connectivity in an effective network of marine protected areas. *PLoS One* 2010;5.
- [106] Planes S, Jones GP, Thorrold SR. Larval dispersal connects fish populations in a network of marine protected areas. *Proc Natl Acad Sci USA* 2009;106:5693–7.
- [107] Ciannelli L, Knutsen H, Olsen EM, Espeland SH, Asplin L, Jelmer A, et al. Small-scale genetic structure in a marine population in relation to water circulation and egg characteristics. *Ecology* 2010;91:2918–30.
- [108] Almamy GR, Berumen ML, Thorrold SR, Planes S, Jones GP. Local replenishment of coral reef fish populations in a marine reserve. *Science* 2007;316:742–744.
- [109] Cowen RK, Paris CB, Srinivasan A. Scaling of connectivity in marine populations. *Science* 2006;311:522–7.

- [110] Costello C, Rassweiler A, Siegel D, De Leo G, Micheli F, Rosenberg A. The value of spatial information in MPA network design. *Proc Natl Acad Sci USA* 2010;107:18294–9.
- [111] Gaines SD, White C, Carr MH, Palumbi SR. Designing marine reserve networks for both conservation and fisheries management. *Proc Natl Acad Sci USA* 2010;107:18286–93.
- [112] March D, Alos J, Grau A, Palmer M. Short-term residence and movement patterns of the annular seabream *Diplodus annularis* in a temperate marine reserve. *Estuar Coast Shelf Sci* 2011;92:581–7.
- [113] Leis JM. Behaviour as input for modelling dispersal of fish larvae: behaviour, biogeography, hydrodynamics, ontogeny, physiology and phylogeny meet hydrography. *Mar Ecol Prog Ser* 2007;347:185–93.
- [114] Olsen EM, Knutsen H, Gjosaeter J, Jorde PE, Knutsen JA, Stenseth NC. Small-scale biocomplexity in coastal Atlantic cod supporting a Darwinian perspective on fisheries management. *Evol Appl* 2008;1:524–33.
- [115] Guidetti P, Claudet J. Comanagement practices enhance fisheries in marine protected areas. *Conserv Biol* 2010;24:312–8.
- [116] Sørensen TK, Thomsen LN. A comparison of frameworks and objectives for implementation of marine protected areas in Northern Europe and in Southeast Asia. *Aquat Ecosyst Health Manage* 2009;12:258–63.
- [117] Alban F, Appéré G, Boncoeur J. Economic analysis of marine protected areas: a literature review. EMPAFISH Project Booklet 2006;3.
- [118] Roncin N, Alban F, Charbonnel E, Crec'hriou R, Modino RD, Culioli JM, et al. Uses of ecosystem services provided by MPAs: how much do they impact the local economy? A southern Europe perspective *J Nat Conserv* 2008;16:256–70.
- [119] García-Charton JA, Pérez-Ruzafa A. Ecological heterogeneity and the evaluation of the effects of marine reserves. *Fish Res* 1999;42:1–20.
- [120] Jones PJS, Qiu W, De Santo EM. Governing Marine Protected Areas—Getting the Balance Right. Technical Report, United Nations Environment Programme 2011. <www.mpag.info>.
- [121] Jones PJS. Marine protected area strategies: issues, divergences and the search for middle ground. *Rev Fish Biol Fish* 2001;11:197–216.
- [122] Jones PJS. Point-of-view: arguments for conventional fisheries management and against no-take marine protected areas: only half of the story? *Rev Fish Biol Fish* 2007;17:31–43.
- [123] Jones PJS. Collective action problems posed by no-take zones. *Mar Policy* 2006;30:143–56.