DTU Library

Using marine reserves to manage impact of bottom trawl fisheries requires consideration of benthic food-web interactions

van Denderen, Pieter Daniël; Rijnsdorp, Adriaan D.; van Kooten, Tobias

Published in:
Ecological Applications

Link to article, DOI:
10.1002/eap.1360

Publication date:
2016

Document Version
Peer reviewed version

Running head: Side-effects of trawling influence MPAs

Using marine reserves to manage impact of bottom trawl fisheries requires consideration of benthic food-web interactions

P. Daniël van Denderen[1,2,3], Adriaan D. Rijnsdorp[1,2] and Tobias van Kooten[1]

[1]Wageningen Institute for Marine Resources and Ecosystem Studies (IMARES), P.O. Box 68, 1970 AB IJmuiden, the Netherlands

[2]Aquaculture and Fisheries, Wageningen University, P.O. Box 338, 6700 AH Wageningen, the Netherlands

[3]Present address: National Institute of Aquatic Resources, Technical University of Denmark, Charlottenlund Castle, DK-2920 Charlottenlund, Denmark

Email: pdvd@aqua.dtu.dk

Abstract

Marine protected areas (MPAs) are widely used to protect exploited fish species as well as to conserve marine habitats and their biodiversity. They have become a popular management tool also for bottom trawl fisheries, a common fishing technique on continental shelves worldwide. The effects of bottom trawling go far beyond the impact on target species, as trawls also affect other components of the benthic ecosystem and the seabed itself. This means that for bottom trawl fisheries, MPAs can potentially be used not only to conserve target species but also to reduce impact of these side-effects of the fishery. However, predicting the protective effects of MPAs is complicated because the side-effects of trawling potentially alter the food-web interactions between target and non-target species. These changes in predatory and competitive interactions among fish and benthic invertebrates may have important ramifications for MPAs as tools to manage or mitigate the effects of bottom trawling. Yet, in current theory regarding the functioning of MPAs in relation to bottom trawl fisheries, such predatory and competitive interactions between species are generally not taken into account. In this paper, we discuss how food-web interactions that are potentially affected by bottom trawling may alter the effectiveness of MPAs to protect (i) biodiversity and marine habitats, (ii) fish populations, (iii) fisheries yield and (iv) trophic structure of the community. We make the case that in order to be applicable for bottom trawl fisheries, guidelines for the implementation of MPAs must consider their potential food-web effects, at the risk of failing management.

Key words

Benthic ecosystem, bottom trawl fisheries, demersal fish, ecosystem-based fisheries management, food webs, marine reserves

Introduction

Marine protected areas (MPAs, areas closed to fishing and other anthropogenic activities), are a popular management tool to protect exploited fish species and to conserve marine habitats and biodiversity (Gell and Roberts 2003, Lubchenco et al. 2003). The basic principle is that closing an area to fishing activities creates a safe haven for the species and habitats affected by the fisheries and promotes the recovery of the natural marine ecosystem. The increased survival of the target species may enhance its density inside the MPA and also outside through net export of eggs, larvae and/or adults (Rowley 1994).

A large number of empirical studies have shown the potential of MPAs to lead to an increase in density, biomass and individual size of target species (Halpern 2003, Lester et al. 2009, Sciberras et al. 2013) and an increase in species diversity, ecosystem structure and functioning (Babcock et al. 1999, Halpern 2003). How and when such effects of MPAs occur has also extensively been explored in modelling studies (for reviews see Guénette et al. 1998, Gerber et al. 2003, Baskett et al. 2007, Pelletier et al. 2008). However, the majority of these modelling studies focused on the effects of MPAs on the direct relationship between the fishery and the target stock and ignored the possible side-effects of fishing (Fig. 1).

Such side-effects are most prominent in bottom trawl fishing, which is an important fishing technique used in shelf areas worldwide. It is well established that the impact of bottom trawls goes far beyond the direct effect on its target species, as trawls cause mortality through bycatch and gear-induced physical damage on non-target organisms (Alverson et al. 1994, Kaiser et al. 2006). These effects may change the structure and functioning of the benthic community (Kaiser et al. 2000, Tillin et al. 2006). Bottom trawls may also disturb seabed habitat (Dayton et al. 1995, Puig et al. 2012) and perturb biogeochemical processes (Grant et al. 1997, Pilskaln et al. 1998). The side-effects of trawling may indirectly affect the target fish through the effect on their food, further complicating the relationship between trawling intensity, yield and the target fish stock (Hiddink et al. 2011, van Denderen et al. 2013, Johnson et al. 2015).

In this paper, we discuss how food-web interactions that are potentially affected by (side-effects of) bottom trawling can alter the effectivity of MPAs. This complex interplay between bottom trawls, target fish and their benthic food is ignored in current guidelines for the implementation of MPAs (Botsford et al. 2003, Halpern and Warner 2003, Roberts et al. 2003). We show how these interactions may potentially limit the effectiveness of MPAs by changing the recovery potential of previously trawled habitat and by influencing the protection of fish populations, fisheries yield and the trophic structure of the community. We conclude that acknowledging the impact of bottom trawling, through the food web, on the effectiveness of MPAs as a fisheries management and conservation tool is essential for their successful application. We then discuss future lines of investigation needed to derive guidelines for the implementation of MPAs that do incorporate the side-effects of bottom trawling.

Side-effects of bottom trawl fisheries

Bottom trawling, where a net or other collection device is dragged over the seabed, is the dominant technology used to catch demersal fish and benthic invertebrates (hereafter benthos). It is estimated that 23% of global fisheries or 20 million megagrams of seafood annually, comes from bottom trawling (FAO 2009). Bottom trawls generally catch substantial amounts of bycatch, of undersized fish and non-target species, which are discarded (Alverson et al. 1994). In some fisheries, the discarded bycatch approaches or exceeds the marketable fraction of the catch (Kelleher 2005). In addition, bottom trawls can damage seabed habitats (Watling and Norse 1998, Puig et al. 2012) and impose mortality on benthos (Collie et al. 2000, Kaiser et al. 2006).

Bottom trawls cause a decline of large, sessile and low productive benthos as these are most vulnerable to the direct passing of the trawl gears and have slowest recovery rates (Kaiser et al. 2006). Short-lived, opportunistic benthos and mobile scavengers/predators are generally less vulnerable or able to recover more rapidly, and such species usually dominate areas that are trawled frequently (Tillin et al. 2006, van Denderen et al. 2015a). Intensively trawled areas are generally less species-rich (Collie et al. 1997, Thrush et al. 1998, Hiddink et al. 2006, Hinz et al. 2009, van Denderen et al. 2014) and altered in their functional composition by a reduced abundance of suspension-feeding organisms (Tillin et al. 2006, de Juan et al. 2007)

Both the short-term effects of trawling, by discarding and mechanically damaging benthic organisms, and its effect on species composition lead to the question how trawling influences the food availability for the target fish. Discarded and mechanically damaged benthos form a potential food source for scavenging invertebrates and fish (Kaiser and Spencer 1994, Groenewold and Fonds 2000) and it has been suggested that this is an important part of the diet of some fish (Shephard et al. 2014). Benthivorous fish also respond to trawl-induced shifts in benthic species composition with changes in their diet compared with untrawled sites (Smith et al. 2013, Johnson et al. 2015) and historic times (Rijnsdorp and Vingerhoed 2001). Such changes may affect fish growth rates and body condition. A number of studies have reported positive and negative relationships between trawling intensity and the growth rates of target species (Millner and Whiting 1996, Rijnsdorp and van Leeuwen 1996, Shephard et al. 2010) and no or negative relationships between trawling intensity and fish condition (Hiddink et al. 2011). From theory, it is expected that trawling will increase food availability for target fish (and hence the productivity of the species), when the most profitable food source for fish is relatively resistant to trawling and benefits from reduced competition for space and/or resource with more susceptible benthos. Conversely, negative effects on the food availability may be expected when the more susceptible benthos is the most profitable prey (van Denderen et al. 2013).

There is limited empirical evidence of trawl-induced cultivation of food for fish based on the benthic response to trawling. Most studies reporting trawl-induced shifts in species composition refer to relative shifts; some (groups of) species are less affected by the trawls and as such increase proportionally in response to trawling. Still, some species' traits, belonging to opportunistic benthos, have been positively associated with trawl disturbance (van Denderen et al. 2015a) and it should also be noted that studies testing species-specific responses over a trawl disturbance gradient often find increases of some species, even with a reduction in total benthic biomass or production (e.g. Hinz et al. 2008, Hinz et al. 2009, Johnson et al. 2015). Despite these results, most studies support the finding that trawling may lead to trawl-induced depletion of food for target fish in chronically fished areas, as a result of direct trawl mortality on fish prey and declines in benthic production (e.g. Jennings et al. 2001, Queirós et al. 2006). Since suspension-feeding organisms are particularly negatively affected by trawling, such declines can become even larger as this functional group plays an important role in transporting food from the water column to the seabed and, as such, regulating benthic production (Gili and Coma 1998). Similarly, trawl-induced declines of other (groups of) benthic organisms that facilitate benthos could also lead to lower benthic production and depletion of food for target fish (e.g. declines of important habitat facilitators).

Finally, bottom trawls disturb biogeochemical processes on the seafloor by mixing the sediment and perturbing the (an)aerobic zone and by resuspension of nutrients and organic material into the water column (Riemann and Hoffmann 1991, Grant et al. 1997, Pilskaln et al. 1998). Nutrient resuspension has been suggested to change phytoplankton community composition and primary production (Riemann and Hoffmann 1991, Pilskaln et al. 1998). Resuspension of organic material by trawling has been shown to reduce organic matter in frequently trawled sediments (Pusceddu et al. 2014), while it has also supplied food to suspension-feeding organisms (Grant et al. 1997). The effects of sediment resuspension by trawls also include the smothering of benthic animals (Jones 1992) and the clogging of the feeding organs of suspension-feeding organisms (Rhoads, 1974), potentially affecting their growth.

The use of MPAs for (bottom trawl) fishing

Four general reasons can be distinguished for establishing MPAs for (bottom trawl) fishing. MPAs may be used for the protection of (i) biodiversity and marine habitats, (ii) fish populations, (iii) fisheries yield and, (iv) trophic structure of the community (for overview see Fig. 2).

MPAs established for biodiversity and habitat conservation are either meant to protect existing natural values or to allow for recovery of such values after they have been lost. The former are generally located in ecological hotspots that have a high diversity and contain (endemic) populations and/or habitat structures that are vulnerable to fisheries (Roberts et al. 2003). When an MPA is established in order to rebuild lost natural values, it is important to determine the potential for recovery. Recovery of some types of habitats, in particular those with complex structural properties (macrophytes, corals, sponge fields), may take decades or even centuries, while others may recover more quickly (Roberts and Hirshfield 2004, Kaiser et al. 2006). In addition to the growth rates of the species involved, an important determinant of the potential (and speed) of recovery is whether the area can be recolonized by species that have disappeared. This is determined by its connectivity to other areas in which the species still occurs (Shanks et al. 2003, D'Aloia et al. 2015).

The use of MPAs to protect fish populations has been most successful for fish with limited mobility. These species are often dependent on specific habitat-structures, such as reefs. For these species, it has been shown that MPAs often increased their density, biomass and individual size (Halpern 2003, Lester et al. 2009, Sciberras et al. 2013). In some areas, this also led to higher abundance of fish and marketable catch around the border of MPAs (McClanahan and Mangi 2000, Vandeperre et al. 2011). Protection of fish by MPAs is generally considered to be less effective for species with high mobility (Horwood et al. 1998, Gerber et al. 2003, Kaiser 2005, Grüss et al. 2011). These species are often less dependent on specific habitats and move considerable distances within a year (Shipp 2003, Kaiser 2005). Protection of certain life-stages is proposed as a more adequate option than implementing large MPAs for mobile species (Grüss et al. 2011). This may work when populations are regulated by processes in the protected life-stage (St. Mary et al. 2000, van de Wolfshaar et al. 2011).

The use of MPAs to protect fisheries yield has been studied in a wide variety of modelling studies. These generally conclude that MPAs will reduce yield whenever fishing mortality is below that which maximizes yield (for review see Gerber et al. 2003). This has been suggested as an important drawback to use MPAs in fisheries management compared to regular catch restrictions (Hilborn et al. 2006). Theoretical work by Hastings and Botsford (1999) has partially addressed this concern and illustrated that MPAs can produce equivalent yields compared to traditional quota-based management. Most of the above work is however based on non-spatial or highly simplified spatial models. Recently, spatially explicit models, with the inclusion of population structure, density-dependent processes and/or environmental stochasticity, have been used to show that a carefully designed network of MPAs can increase fisheries yields even when fish stocks are not overharvested (for review see Gaines et al. 2010). Obtaining such positive effects of MPAs on fisheries yield requires a detailed understanding of the behavior of the fishery and its target stocks (Rassweiler et al. 2012).

Finally, MPAs are also used to allow the trophic structure of the community to recover. Fishing changes the size structure of the fish community by reducing the abundance of large fish, mainly high trophic level species, limiting the predation mortality on the smaller prey species (Daan et al. 2005, Andersen and Pedersen 2010). Top-down control may be reinforced inside MPAs due to an increase of the predatory species that are now protected from the fisheries (for review see Pinnegar et al. 2000, Baskett et al. 2007).

Indirect food-web effects of trawling and their implication for MPAs

The indirect food-web effects of bottom trawl fisheries may affect the processes that determine MPA functioning (Fig. 2). We discuss how the incorporation of these food-web effects may (i) change the recovery potential of previously trawled habitat, (ii) affect changes in trophic structure and (iii) influence protection of fish populations and fisheries yield.

Biotic interaction may change recovery potential of trawled habitat

Soft-bottom habitats that have been impacted by trawls are often dominated by opportunistic and fast-growing species (Kaiser et al. 2006). An MPA may potentially shift the system back towards a community with slow-growing species that are less resilient to the impact of trawling. Whether this occurs depends strongly on the successful colonization of sensitive species in the MPA. This success depends on whether larvae can reach, settle and survive in the area.

Settlement of the sensitive species can be prevented by changes to the habitat after bottom trawling (Piersma et al. 2001) and by the biotic interactions present as a result of bottom trawling. The latter may occur when the opportunistic benthic residents remain the dominant species through direct feeding on the arriving larvae (by predators or deposit feeders), the smothering of the larvae (by bioturbators), filtering them from the water column as prey (by suspension feeders) or by denying them space to settle (tube-builders) (Woodin 1976, Hunt and Scheibling 1997). There is some evidence that such effects are strong enough to delay the recovery of sensitive species. This is best observed in defaunation experiments that show reduced colonization, and potentially coexistence, in areas that are occupied by a resident community, compared with an area that is empty (Lu and Wu 2000, Montserrat et al. 2008). Settlement success may also be reduced by resident species that can modify seabed sediment, making it less suitable for other organisms (van Nes et al. 2007). Such interactions indicate clearly that modification of the benthic ecosystem composition, as a result of the side-effects of bottom trawling, can reduce the recovery potential of an area after it has been designated an MPA and trawling has ceased. It is theoretically possible, if the resident community formed under the effects of trawling is stable enough that trawling induces an alternative stable state (ASS). The existence of an ASS would strongly reduce the value of MPAs as a recovery tool for the benthic ecosystem, but we are not aware of empirical support for trawling-induced ASSs. For other fisheries, large ecosystem shifts have already been suggested from which recovery to the pre-fished state is very difficult (Scheffer et al. 2001, Jensen et al. 2012).

Larvae of sensitive species that manage to settle in the MPA have to survive and grow. This may be limited through competition for food with the resident community, reducing food intake of the settled larvae and eventually causing starvation. Survival and growth may also be limited as a result of increased predation of both fish and benthic invertebrate predators that also benefit from the establishment of an MPA, as it is also a safe haven for these species. Fish and benthic invertebrate predation has been shown to limit survival of newly arrived benthic larvae (Hunt and Scheibling 1997) and an increase in these predatory species may induce stronger predation mortality on larval prey.

Trawl effects on both fish and benthos may affect trophic structure

It is often suggested that top-down control may be reinforced inside MPAs, due to an increase of the predatory species that are targeted by the fisheries (Pinnegar et al. 2000). In the case of benthivorous fish and their prey, this expectation is complicated by the fact that both are affected by bottom trawl fisheries. At low trawl intensity, fish density is relatively unaffected, and so, as a consequence, is the predation mortality on benthic prey. At high trawling intensity, fish density and the importance of fish predation is reduced, but mortality induced by trawls on the prey is high. Hence, for benthos, direct mortality of trawling replaces predation mortality as fish abundance is reduced at high trawling intensity. The relative change in these two sources of mortality per unit trawling intensity determines whether the benthos will increase (reduced trawl mortality) or decrease (increased predation mortality) inside MPAs (van Denderen et al. 2013, Johnson et al. 2015). This means that benthos vulnerable to trawl impact, which is not a preferred prey for fish, will likely benefit from MPAs, whereas benthos species that are less vulnerable to trawl impact or preferred prey for fish, may respond differently to MPA establishment.

There are a variety of studies that have shown top-down effects of benthivorous fish (and benthic invertebrate predators) on abundance of their benthic prey (Wilson 1991, Baum and Worm 2009). Top-down effects of fish on benthos are studied predominantly in systems that are not intensively bottom trawled (but see Heath 2005), as in many of the areas fished by bottom trawls it is notoriously difficult to carry out (experimental) studies of the subtle relationships between target fish and benthic prey.

Even with limited predation mortality on benthos, reduced trawling mortality inside MPAs does not necessarily increase benthic biomass, because increased abundance of resistant benthos may compensate for the decline of the more sensitive species in a trawled habitat. Although establishment of an MPA may reverse this shift (if these sensitive species can settle and grow in the area), it will primarily change species composition towards more sensitive benthos. Benthic biomass inside MPAs may increase when trawling impact was high and biomass compensation by resistant benthos limited. Benthic biomass may also increase when the sensitive species are more efficient in capturing food, enhancing the total carrying capacity of the area, or facilitate other benthos by providing resources or shelter, possibly reducing natural disturbance and predation (Thrush et al. 1992, Stachowicz 2001, Lohrer et al. 2013).

Biotic interactions influence protection of target fish and fisheries yield

Shifts in benthos species composition in response to changed trawling intensity may affect fish food availability, fish production and fisheries yield (Duplisea et al. 2002, Hiddink et al. 2008, van Denderen et al. 2013). The net effect on fish abundance and yield depends on how the prey species of the target fish are affected by trawling (Fig. 1).

When bottom trawling reduces benthic prey abundance, MPAs may increase food production for fish and hence support higher fish production than the surrounding trawled area. This mechanism further amplifies the expected build-up of fish biomass inside the MPA due to reduced mortality. The increased food production for fish results in higher fisheries yields if fish spill over into surrounding areas. If this increased fish food production in absence of trawling is strong enough, it may be expected that fisheries yields with an MPA are higher than those under maximum sustainable yield with traditional quota-based management, but only if the increased fish production and spillover more than compensates for the loss of fishing grounds. Contrastingly, when less sensitive species are a particularly good food source for fish, trawling can actually enhance food production for fish and fisheries yield (van Denderen et al. 2013). This implies that an MPA may become less attractive for fish and may reduce the overall productivity of the target fish species and hence fisheries yield in the area.

The asymmetry in food availability between MPA and fished area will affect how fish forage and migrate between these different areas. Mobile fish search for food in a larger area than fish that have high site fidelity and it may be expected that these mobile fish profit more easily from local changes in benthic prey in response to trawling and establishment of MPAs.

In addition to changes in food availability, fish migration may also be affected by (side-)effects of trawling that induce behavioral differences in fish between the trawled area and the MPA. Such effects may be expected when areas differ in density/type of prey and hence predator foraging behavior (Johnson et al. 2015), habitat structure (Kaiser et al. 1999) or density of conspecifics. Ultimately, movement of fish will depend on how fish species select their habitat (e.g. based on specific structures or energetic profitability of prey) and how fish interact with their prey (Grüss et al. 2011). Such findings show that MPAs may become suitable habitats for some fish species, while they reduce suitable habitat for others.

The overall productivity of the target fish species and hence the fisheries yield may also be affected by trawling-induced resuspension of nutrients and organic material. This has the potential to change both primary and secondary production (see also *side-effects of bottom trawl fisheries*) and as such also the productivity of benthic prey. How establishment of an MPA will affect food production for fish will depend on how the resuspended material (indirectly) contributes to the productivity of benthic prey.

Future directions to provide the scientific basis for the use of MPAs

MPAs protect a habitat from anthropogenic impacts and this has made them a promising management tool for bottom trawl fisheries, which affect many components of the benthic ecosystem in direct and indirect ways. It is clear from a large number of studies that the establishment of MPAs can enhance recovery of benthic habitats, communities and trawled fish populations inside the MPA and, in some cases, outside the protected area (e.g. Murawski et al. 2000, Blyth et al. 2004, Blyth-Skyrme et al. 2006, Duineveld et al. 2007). However, in this paper, we have argued that an MPA may not always positively affect all ecosystem components on which trawling has an impact, due to the food-web interactions between target and non-target species. The success of an MPA in achieving the underlying management objectives is a balance between the direct benefit (less mortality on fish and/or benthos) and the indirect food-web effects (e.g. less fish prey or more predation mortality).

These indirect food-web effects are generally ignored in studies that examine, both theoretically and empirically, the potential of MPAs for the management of bottom trawl fisheries and the conditions necessary for their successful application. In this work, we have shown how these food-web interactions may potentially limit the effectiveness of MPAs by changing the recovery potential of previously trawled habitat and by influencing the protection of fish populations, fisheries yield and the trophic structure of the community. This implies that the current guidelines regarding the functioning, design and implementation of MPAs must be extended to include food-web interactions, in order to provide the scientific basis for the application of MPAs in the sustainable management of exploited fish stocks and to protect marine habitats and their biodiversity from effects of bottom trawl fisheries. We discuss below what type of studies are needed to derive guidelines for the implementation of MPAs that incorporate the indirect food-web effects of bottom trawling.

Examining bottom trawl fishing disturbance at different spatial scales

Bottom trawl fishing can be described, dependent on the spatial scale examined, as a disturbance event or a continuous process affecting populations and communities. At small spatial scales, scales at which benthic organisms live, bottom trawling is a disturbance event caused by an individual tow that modifies seabed sediment and kills benthic organisms in the trawl path. This temporarily attracts both fish and benthic scavengers that benefit from these food subsidies (Kaiser and Spencer 1994, Groenewold and Fonds 2000). After such an event, the disturbed area has time to recover until the next event (van Denderen et al. 2015b) and an important determinant of the potential (and speed) of recovery is whether the area can be recolonized by species that have disappeared. This is determined by its connectivity to other areas in which the species still occurs (Thrush et al. 2013, Lambert et al. 2014). Studying these trawling effects leads to an understanding of the local population dynamics. However, they do not necessarily show the population response to trawling, e.g. the local food subsidies for both fish and benthic scavengers will not automatically increase their population sizes. To examine the consequences at the scale of the population, studies need to embed these local patch dynamics into an interconnected mosaic of patches. Alternatively, trawl impact may be described as a continuous mortality, produced by the fishing fleet, which affects part of the benthic and fish populations.

This implies that in order to determine the effectivity of MPAs to manage impacts of bottom trawl fishing there is a need to understand trawl impact at these different spatial scales and to examine the linkages between these scales. For some utilizations of MPAs, e.g. the recovery of disturbed habitat, an understanding of the local patch dynamics seems to be most important to determine MPA efficacy, while other usages of MPAs, e.g. the protection of fish populations or fisheries yield, need an approach that focusses on population dynamics.

Deriving a mechanistic understanding of the benthic system

Some of the indirect food-web effects of bottom trawling discussed in this work are only based on modelling studies, in particular obtained from van Denderen et al. (2013), but see also Duplisea et al. (2002) and Hiddink et al. (2008). These studies used a simplified benthic food-web model, with little biological differentiation and without considering individual-level processes, such as growth explicitly. The problem is that very little empirical data is available on the importance of different biotic processes (*i.e.* competition, predation and facilitation) in structuring benthic community dynamics. A review of the importance of predation and competition concluded that more experimental studies were needed to derive a unified theory of marine soft-sediment communities already two decades ago (Wilson 1991), but relatively few studies have examined these effects further in recent years. The importance of facilitation is even less studied, although it has been suggested as highly important for benthic community dynamics (Thrush et al. 1992, Lohrer et al. 2013). Hence, it remains unclear to what extent the dynamics of the simplified food-web models used, match real benthic systems. Additionally, the role of benthivorous fish targeted by the fishery on benthos and its response to changes in benthic prey could be further clarified by studying its feeding ecology and foraging behavior (e.g. Smith et al. 2013, Johnson et al. 2015). Ultimately, the above shows that a mechanistic understanding of the benthic system requires experimental set-ups in the field (e.g. caging experiments and recovery studies), in mesocosms (e.g. controlled impact studies, see Ingels et al. 2014) and in the laboratory (e.g. fish behavioral studies). Such studies will provide the scientific basis for the application of MPAs in the sustainable management of exploited fish stocks and to protect marine habitats and their biodiversity from bottom trawl fisheries.

Acknowledgements

We thank two anonymous reviewers for comments on an earlier version of this manuscript. This research was partially supported through the policy support research program (BO) of the Dutch Ministry of Economic Affairs to TvK. and the European Union FP7 project BENTHIS (312088) to ADR. and TvK. The article does not necessarily reflect the views of the European Commission and does not anticipate the Commission's future policy in this area. PDvD. conducted part of this work within the Centre for Ocean Life, a VKR center of excellence supported by the Villum foundation, while he received funding from the People Programme (Marie Curie Actions) of the European Union's Seventh Framework Programme (FP7/2007-2013) under REA grant agreement n° 609405 (COFUNDPostdocDTU).

References

Alverson, D. L., M. H. Freeberg, J. G. Pope, and S. A. Murawski. 1994. A global assessment of fisheries bycatch and discards. FAO Fisheries Technical Paper No. 339. Rome, FAO. Rome.

Andersen, K. H., and M. Pedersen. 2010. Damped trophic cascades driven by fishing in model marine ecosystems. Proceedings of the Royal Society B: Biological Sciences 277:795-802.

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

Baskett, M. L., F. Micheli, and S. A. Levin. 2007. Designing marine reserves for interacting species: insights from theory. Biological Conservation 137:163-179.

Baum, J. K., and B. Worm. 2009. Cascading top-down effects of changing oceanic predator abundances. Journal of Animal Ecology 78:699-714.

Blyth, R. E., M. J. Kaiser, G. Edwards-Jones, and P. J. B. Hart. 2004. Implications of a zoned fishery management system for marine benthic communities. Journal of Applied Ecology 41:951-961.

Blyth-Skyrme, R. E., M. J. Kaiser, J. G. Hiddink, G. Edwards-Jones, and P. J. B. Hart. 2006. Conservation benefits of temperate marine protected areas: variation among fish species. Conservation Biology 20:811-820.

Botsford, L. W., F. Micheli, and A. Hastings. 2003. Principles for the design of marine reserves. Ecological Applications 13:25-31.

Collie, J. S., G. A. Escanero, and P. C. Valentine. 1997. Effects of bottom fishing on the benthic megafauna of Georges Bank. Marine Ecology Progress Series 155:159-172.

Collie, J. S., S. J. Hall, M. J. Kaiser and I. R. Poiner. 2000. A quantitative analysis of fishing impacts on shelf-sea benthos. Journal of Animal Ecology 69:785-798.

Daan, N., H. Gislason, J. G. Pope, and J. C. Rice. 2005. Changes in the North Sea fish community: evidence of indirect effects of fishing? ICES Journal of Marine Science 62:177-188.

D'aloia, C. C., S. M. Bogdanowicz, R. K. Francis, J. E. Majoris, R. G. Harrison, and P. M. Buston. 2015. Patterns, causes, and consequences of marine larval dispersal. Proceedings of the National Academy of Sciences 112:139450-13945.

Dayton, P. K., S. F. Thrush, M. T. Agardy, and R. J. Hofman. 1995. Environmental effects of marine fishing. Aquatic Conservation: Marine and Freshwater Ecosystems 5:205-232.

de Juan, S., S. F. Thrush, and M. Demestre. 2007. Functional changes as indicators of trawling disturbance on a benthic community located in a fishing ground (NW Mediterranean Sea). Marine Ecology Progress Series 334:117-129.

Duineveld, G. C. A., M. J. N. Bergman, and M. S. S. Lavaleye. 2007. Effects of an area closed to fisheries on the composition of the benthic fauna in the southern North Sea. ICES Journal of Marine Science 64:899-908.

Duplisea, D. E., S. Jennings, K. J. Warr, and T. A. Dinmore. 2002. A size-based model of the impacts of bottom trawling on benthic community structure. Canadian Journal of Fisheries and Aquatic Sciences 59:1785-1795.

FAO. 2009. The state of world fisheries and aquaculture - 2008 (Sofia). Rome.

Gaines, S. D., C. White, M. H. Carr, and S. R. Palumbi. 2010. Designing marine reserve networks for both conservation and fisheries management. Proceedings of the National Academy of Sciences 107:18286-18293.

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

Gerber, L., L. Botsford, A. Hastings, H. Possingham, S. Gaines, S. Palumbi, and S. Andelman. 2003. Population models for marine reserve design: a retrospective and prospective synthesis. Ecological Applications 13:47-64.

Gili, J. M. and R. Coma. 1998. Benthic suspension feeders: their paramount role in littoral marine food webs. Trends in Ecology and Evolution 13:316-321.

Grant, J., P. Cranford, and C. Emerson. 1997. Sediment resuspension rates, organic matter quality and food utilization by sea scallops (*Placopecten magellanicus*) on Georges Bank. Journal of Marine Research 55:965-994.

Groenewold, S., and M. Fonds. 2000. Effects on benthic scavengers of discards and damaged benthos produced by the beam-trawl fishery in the southern North Sea. ICES Journal of Marine Science 57:1395-1406.

Grüss, A., D. M. Kaplan, S. Guénette, C. M. Roberts, and L. W. Botsford. 2011. Consequences of adult and juvenile movement for marine protected areas. Biological Conservation 144:692-702.

Guénette, S., T. Lauck, and C. Clark. 1998. Marine reserves: from Beverton and Holt to the present. Reviews in Fish Biology and Fisheries 8:251-272.

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

Halpern, B. S., and R. R. Warner. 2003. Matching marine reserve design to reserve objectives. Proceedings of the Royal Society B: Biological Sciences 270:1871-1878.

Hastings, A., and L. W. Botsford. 1999. Equivalence in yield from marine reserves and traditional fisheries management. Science 284:1537-1538.

Heath, M. R. 2005. Changes in the structure and function of the North Sea fish foodweb, 1973–2000, and the impacts of fishing and climate. ICES Journal of Marine Science 62:847-868.

Hiddink, J. G., S. Jennings, M. J. Kaiser, A. M. Queiros, D. E. Duplisea and G. J. Piet. 2006. Cumulative impacts of seabed trawl disturbance on benthic biomass, production, and species richness in different habitats. Canadian Journal of Fisheries and Aquatic Sciences 63:721-736.

Hiddink, J. G., A. F. Johnson, R. Kingham, and H. Hinz. 2011. Could our fisheries be more productive? Indirect negative effects of bottom trawl fisheries on fish condition. Journal of Applied Ecology 48:1441-1449.

Hiddink, J. G., A. D. Rijnsdorp, and G. Piet. 2008. Can bottom trawling disturbance increase food production for a commercial fish species? Canadian Journal of Fisheries and Aquatic Sciences 65:1393-1401.

Hilborn, R., F. Micheli, and G. A. De Leo. 2006. Integrating marine protected areas with catch regulation. Canadian Journal of Fisheries and Aquatic Sciences 63:642-649.

Hinz, H., J. G. Hiddink, J. Forde, and M. J. Kaiser. 2008. Large-scale responses of nematode communities to chronic otter-trawl disturbance. Canadian Journal of Fisheries and Aquatic Sciences 65:723-732.

Hinz, H., V. Prieto, and M. J. Kaiser. 2009. Trawl disturbance on benthic communities: chronic effects and experimental predictions. Ecological Applications 19:761-773.

Horwood, J. W., J. H. Nichols, and S. Milligan. 1998. Evaluation of closed areas for fish stock conservation. Journal of Applied Ecology 35:893-903.

Hunt, H. L., and R. E. Scheibling. 1997. Role of early post-settlement mortality in recruitment of benthic marine invertebrates. Marine Ecology Progress Series 155:269-301.

Ingels, J., S. L. Dashfield, P. J. Somerfield, S. Widdicombe, and M. C. Austen. 2014. Interactions between multiple large macrofauna species and nematode communities -

mechanisms for indirect impacts of trawling disturbance. Journal of Experimental Marine Biology and Ecology 456:41-49.

Jennings, S., T. A. Dinmore, D. E. Duplisea, K. J. Warr, and J. E. Lancaster. 2001. Trawling disturbance can modify benthic production processes. Journal of Animal Ecology 70:459-475.

Jensen, O., T. Branch, and R. Hilborn. 2012. Marine fisheries as ecological experiments. Theoretical Ecology 5:3-22.

Johnson, A. F., G. Gorelli, S. R. Jenkins, J. G. Hiddink, and H. Hinz. 2015. Effects of bottom trawling on fish foraging and feeding. Proceedings of the Royal Society B: Biological Sciences 282:20142336.

Jones, J. B. 1992. Environmental impact of trawling on the seabed: a review. New Zealand Journal of Marine and Freshwater Research 26:59-67.

Kaiser, M. J. 2005. Are marine protected areas a red herring or fisheries panacea? Canadian Journal of Fisheries and Aquatic Sciences 62:1194-1199.

Kaiser, M. J., K. R. Clarke, H. Hinz, M. C. V. Austen, P. J. Somerfield, and I. Karakassis. 2006. Global analysis of response and recovery of benthic biota to fishing. Marine Ecology Progress Series 311:1-14.

Kaiser, M. J., K. Ramsay, C. A. Richardson, F. E. Spence, and A. R. Brand. 2000. Chronic fishing disturbance has changed shelf sea benthic community structure. Journal of Animal Ecology 69:494-503.

Kaiser, M. J., S. I. Rogers, and J. R. Ellis. 1999. Importance of benthic habitat complexity for demersal fish assemblages. Pages 212-223 *in* L. Benaka, editor. Fish habitat: essential fish habitat and restoration. American Fisheries Society Symposium, Bethesda, Maryland.

Kaiser, M. J., and B. E. Spencer. 1994. Fish scavenging behaviour in recently trawled areas. Marine Ecology Progress Series 112:41-49.

Kelleher, K. 2005. Discards in the world's marine fisheries. An update. FAO Fisheries Technical Paper No. 470. Rome, FAO.

Lambert, G. I., S. Jennings, M. J. Kaiser, T. W. Davies, and J. G. Hiddink. 2014. Quantifying recovery rates and resilience of seabed habitats impacted by bottom fishing. Journal of Applied Ecology 51:1326–1336.

Lester, S. E., B. S. Halpern, K. Grorud-Colvert, J. Lubchenco, B. I. Ruttenberg, S. D. Gaines, S. Airame, and R. R. Warner. 2009. Biological effects within no-take marine reserves: a global synthesis. Marine Ecology Progress Series 384:33-46.

Lohrer, A. M., I. F. Rodil, M. Townsend, L. D. Chiaroni, J. E. Hewitt, and S. F. Thrush. 2013. Biogenic habitat transitions influence facilitation in a marine soft-sediment ecosystem. Ecology 94:136-145.

Lu, L., and R. S. S. Wu. 2000. An experimental study on recolonization and succession of marine macrobenthos in defaunated sediment. Marine Biology 136:291-302.

Lubchenco, J., S. R. Palumbi, S. D. Gaines, and S. Andelman. 2003. Plugging a hole in the ocean: the emerging science of marine reserves. Ecological Applications 13:S3-S7.

McClanahan, T. R., and S. Mangi. 2000. Spillover of exploitable fishes from a marine park and its effect on the adjacent fishery. Ecological Applications 10:1792-1805.

Millner, R. S., and C. L. Whiting. 1996. Long-term changes in growth and population abundance of sole in the North Sea from 1940 to the present. ICES Journal of Marine Science 53:1185-1195.

Montserrat, F., C. Van Colen, S. Degraer, T. Ysebaert, and P. Herman. 2008. Benthic community-mediated sediment dynamics. Marine Ecology Progress Series 372:43-59.

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

Pelletier, D., J. Claudet, J. Ferraris, L. Benedetti-Cecchi, and J. A. Garcìa-Charton. 2008. Models and indicators for assessing conservation and fisheries-related effects of marine protected areas. Canadian Journal of Fisheries and Aquatic Sciences 65:765-779.

Piersma, T., A. Koolhaas, A. Dekinga, J. J. Beukema, R. Dekker, and K. Essink. 2001. Long-term indirect effects of mechanical cockle-dredging on intertidal bivalve stocks in the Wadden Sea. Journal of Applied Ecology 38:976-990.

Pilskaln, C. H., J. H. Churchill, and L. M. Mayer. 1998. Resuspension of sediment by bottom trawling in the Gulf of Maine and potential geochemical consequences. Conservation Biology 12:1223-1229.

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

Puig, P., M. Canals, J. B. Company, J. Martin, D. Amblas, G. Lastras, A. Palanques, and A. M. Calafat. 2012. Ploughing the deep sea floor. Nature 489:286-289.

Pusceddu, A., S. Bianchelli, J. Martín, P. Puig, A. Palanques, P. Masqué, and R. Danovaro. 2014. Chronic and intensive bottom trawling impairs deep-sea biodiversity and ecosystem functioning. Proceedings of the National Academy of Sciences 111:8861-8866.

Queirós, A. M., J. G. Hiddink, M. J. Kaiser, and H. Hinz. 2006. Effects of chronic bottom trawling disturbance on benthic biomass, production and size spectra in different habitats. Journal of Experimental Marine Biology and Ecology 335:91-103.

Rassweiler, A., C. Costello, and D. A. Siegel. 2012. Marine protected areas and the value of spatially optimized fishery management. Proceedings of the National Academy of Sciences 109:11884-11889.

Rhoads, D. C. 1974. Organisms-sediment relations on the muddy sea floor. Oceanography and Marine Biology Annual Review 12:263-300.

Riemann, B., and E. Hoffmann. 1991. Ecological consequences of dredging and bottom trawling in the Limfjord, Denmark. Marine Ecology Progress Series 69:171-178.

Rijnsdorp, A. D., and P. I. van Leeuwen. 1996. Changes in growth of North Sea plaice since 1950 in relation to density, eutrophication, beam-trawl effort, and temperature. ICES Journal of Marine Science 53:1199-1213.

Rijnsdorp, A. D., and B. Vingerhoed. 2001. Feeding of plaice *Pleuronectes platessa* (L.) and sole *Solea solea* (L.) in relation to the effects of bottom trawling. Journal of Sea Research 45:219-229.

Roberts, C. M., S. Andelman, G. Branch, R. H. Bustamante, J. Carlos Castilla, J. Dugan, B. S. Halpern, K. D. Lafferty, H. Leslie, J. Lubchenco, D. McArdle, H. P. Possingham, M. Ruckelshaus, and R. R. Warner. 2003. Ecological criteria for evaluating candidate sites for marine reserves. Ecological Applications 13:199-214.

Roberts, S., and M. Hirshfield. 2004. Deep-sea corals: out of sight, but no longer out of mind. Frontiers in Ecology and the Environment 2:123-130.

Rowley, R. J. 1994. Marine reserves in fisheries management. Aquatic Conservation: Marine and Freshwater Ecosystems 4:233-254.

Scheffer, M., S. Carpenter, J. A. Foley, C. Folke, and B. Walker. 2001. Catastrophic shifts in ecosystems. Nature 413:591-596.

Sciberras, M., S. Jenkins, M. Kaiser, S. Hawkins, and A. Pullin. 2013. Evaluating the biological effectiveness of fully and partially protected marine areas. Environmental Evidence 2:4.

Shanks, A. L., B. A. Grantham, and M. H. Carr. 2003. Propagule dispersal distance and the size and spacing of marine reserves. Ecological Applications 13:S159-S169.

Shephard, S., D. Brophy, and D. Reid. 2010. Can bottom trawling indirectly diminish carrying capacity in a marine ecosystem? Marine Biology 157:2375-2381.

Shephard, S., C. Minto, M. Zölck, S. Jennings, D. Brophy, and D. Reid. 2014. Scavenging on trawled seabeds can modify trophic size structure of bottom-dwelling fish. ICES Journal of Marine Science 71:398-405.

Shipp, R. L. 2003. A perspective on marine reserves as a fishery management tool. Fisheries 28:10-21.

Smith, B. E., J. S. Collie, and N. L. Lengyel. 2013. Effects of chronic bottom fishing on the benthic epifauna and diets of demersal fishes on northern Georges Bank. Marine Ecology Progress Series 472:199-217.

St. Mary, C. M., C. W. Osenberg, T. K. Frazer, and W. J. Lindberg. 2000. Stage structure, density dependence and the efficacy of marine reserves. Bulletin of Marine Science 66:675-690.

Stachowicz, J. J. 2001. Mutualism, facilitation, and the structure of ecological communities. Bioscience 51:235-246.

Thrush, S. F., J. E. Hewitt, V. J. Cummings, P. K. Dayton, M. Cryer, S. J. Turner, G. A. Funnell, R. G. Budd, C. J. Milburn, and M. R. Wilkinson. 1998. Disturbance of the marine benthic habitat by commercial fishing: impacts at the scale of the fishery. Ecological Applications 8:866-879.

Thrush, S. F., J. E. Hewitt, A. M. Lohrer, and L. D. Chiaroni. 2013. When small changes matter: the role of cross-scale interactions between habitat and ecological connectivity in recovery. Ecological Applications 23:226-238.

Thrush, S. F., R. D. Pridmore, J. E. Hewitt, and V. J. Cummings. 1992. Adult infauna as facilitators of colonization on intertidal sandflats. Journal of Experimental Marine Biology and Ecology 159:253-265.

Tillin, H. M., J. G. Hiddink, S. Jennings, and M. J. Kaiser. 2006. Chronic bottom trawling alters the functional composition of benthic invertebrate communities on a sea-basin scale. Marine Ecology Progress Series 318:31-45.

van de Wolfshaar, K. E., R. HilleRisLambers, and A. Gårdmark. 2011. Effect of habitat productivity and exploitation on populations with complex life cycles. Marine Ecology Progress Series 438:175-184.

van Denderen, P. D., S. G. Bolam, J. G. Hiddink, S. Jennings, A. Kenny, A. D. Rijnsdorp, and T. van Kooten 2015a. Similar effects of bottom trawling and natural disturbance on composition and function of benthic communities across habitats. Marine Ecology Progress Series 541:31-43.

van Denderen, P. D., N. T. Hintzen, A. D. Rijnsdorp, P. Ruardij, and T. van Kooten. 2014. Habitat-specific effects of fishing disturbance on benthic species richness in marine soft sediments. Ecosystems 17:1216-1226.

van Denderen, P. D., N. T. Hintzen, T. van Kooten, and A. D. Rijnsdorp. 2015b. Temporal aggregation of bottom trawling and its implication for the impact on the benthic ecosystem. ICES Journal of Marine Science 72:952-961.

van Denderen, P. D., T. van Kooten, and A. D. Rijnsdorp. 2013. When does fishing lead to more fish? Community consequences of bottom trawl fisheries in demersal food webs. Proceedings of the Royal Society B: Biological Sciences 280:20131883.

van Nes, E. H., T. P. F. Amaro, M. Scheffer, and G. Duineveld. 2007. Possible mechanisms for a marine benthic regime shift in the North Sea. Marine Ecology Progress Series 330:39 - 47.

Vandeperre, F., R. M. Higgins, J. Sánchez-Meca, F. Maynou, R. Goñi, P. Martín-Sosa, A. Pérez-Ruzafa, P. Afonso, I. Bertocci, R. Crec'hriou, G. D'Anna, M. Dimech, C. Dorta, O. Esparza, J. M. Falcón, A. Forcada, I. Guala, L. Le Direach, C. Marcos, C. Ojeda-Martínez, C. Pipitone, P. J. Schembri, V. Stelzenmüller, B. Stobart, and R. S. Santos. 2011. Effects of no-take area size and age of marine protected areas on fisheries yields: a meta-analytical approach. Fish and Fisheries 12:412-426.

Watling, L., and E. A. Norse. 1998. Disturbance of the seabed by mobile fishing gear: a comparison to forest clearcutting. Conservation Biology 12:1180-1197.

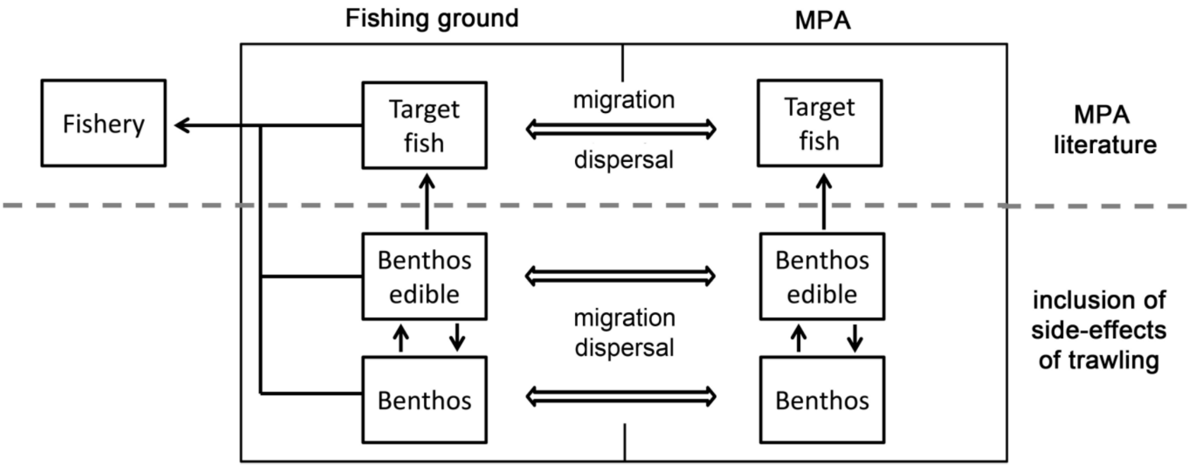
Wilson, W. H. 1991. Competition and predation in marine soft-sediment communities. Annual Review of Ecology and Systematics 21:221-241.

Woodin, S. A. 1976. Adult-larval interactions in dense infaunal assemblages - patterns of abundance. Journal of Marine Research 34:25-41.

Figure legends

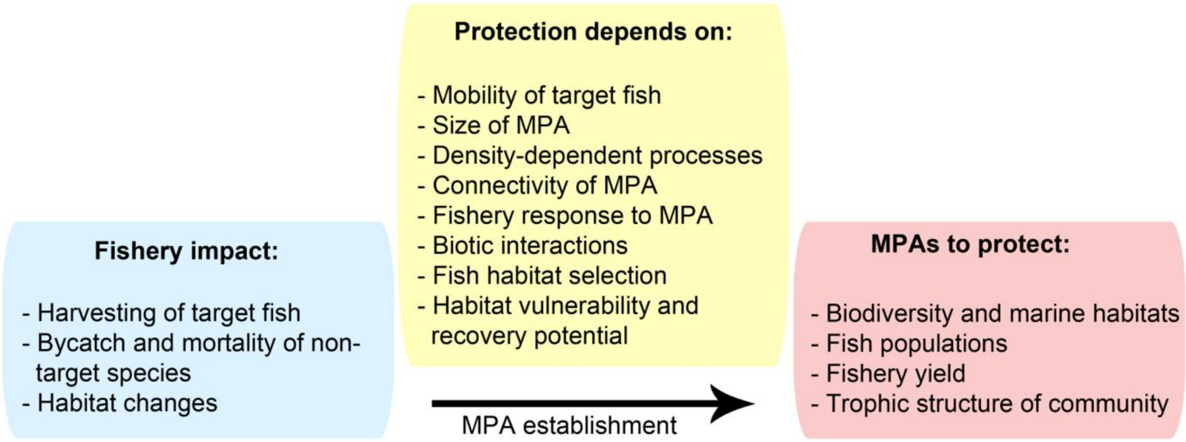
Figure 1. The interplay between bottom trawling and target fish and benthos in a fishing ground and an MPA. Fish and benthos migrate (as adults) or disperse (as eggs or larvae) between the different areas. All components above the dashed line have generally been studied to develop MPA theory.

Figure 2. Overview of the role of MPAs to conserve different ecosystem indicators from the adverse effects of fishing. The box in the middle shows the processes that determine (often in interaction with each other) whether MPAs can induce benefits to (some of) the ecosystem indicators.


Fishing ground
MPA
Fishery
Target fish
migration
dispersal
Target fish
MPA literature
Benthos edible
migration dispersal
Benthos edible
inclusion of side-effects of trawling
Benthos
Benthos

652

653


Protection depends on:
- Mobility of target fish
- Size of MPA
- Density-dependent processes
- Connectivity of MPA
- Fishery response to MPA
- Biotic interactions
- Fish habitat selection
- Habitat vulnerability and recovery potential
Fishery impact:
- Harvesting of target fish
- Bycatch and mortality of non-target species
- Habitat changes
MPAs to protect:
- Biodiversity and marine habitats
- Fish populations
- Fishery yield
- Trophic structure of community
MPA establishment

654