



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

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1 Running head: Side-effects of trawling influence MPAs

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

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15 **Abstract**

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

35 **Key words**

36 Benthic ecosystem, bottom trawl fisheries, demersal fish, ecosystem-based fisheries

37 management, food webs, marine reserves

38 **Introduction**

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

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

54 Such side-effects are most prominent in bottom trawl fishing, which is an important fishing  
55 technique used in shelf areas worldwide. It is well established that the impact of bottom  
56 trawls goes far beyond the direct effect on its target species, as trawls cause mortality through  
57 bycatch and gear-induced physical damage on non-target organisms (Alverson et al. 1994,  
58 Kaiser et al. 2006). These effects may change the structure and functioning of the benthic  
59 community (Kaiser et al. 2000, Tillin et al. 2006). Bottom trawls may also disturb seabed  
60 habitat (Dayton et al. 1995, Puig et al. 2012) and perturb biogeochemical processes (Grant et  
61 al. 1997, Pilskaln et al. 1998). The side-effects of trawling may indirectly affect the target

62 fish through the effect on their food, further complicating the relationship between trawling  
63 intensity, yield and the target fish stock (Hiddink et al. 2011, van Denderen et al. 2013,  
64 Johnson et al. 2015).

65 In this paper, we discuss how food-web interactions that are potentially affected by (side-  
66 effects of) bottom trawling can alter the effectivity of MPAs. This complex interplay between  
67 bottom trawls, target fish and their benthic food is ignored in current guidelines for the  
68 implementation of MPAs (Botsford et al. 2003, Halpern and Warner 2003, Roberts et al.  
69 2003). We show how these interactions may potentially limit the effectiveness of MPAs by  
70 changing the recovery potential of previously trawled habitat and by influencing the  
71 protection of fish populations, fisheries yield and the trophic structure of the community. We  
72 conclude that acknowledging the impact of bottom trawling, through the food web, on the  
73 effectiveness of MPAs as a fisheries management and conservation tool is essential for their  
74 successful application. We then discuss future lines of investigation needed to derive  
75 guidelines for the implementation of MPAs that do incorporate the side-effects of bottom  
76 trawling.

77 **Side-effects of bottom trawl fisheries**

78 Bottom trawling, where a net or other collection device is dragged over the seabed, is the  
79 dominant technology used to catch demersal fish and benthic invertebrates (hereafter  
80 benthos). It is estimated that 23% of global fisheries or 20 million megagrams of seafood  
81 annually, comes from bottom trawling (FAO 2009). Bottom trawls generally catch substantial  
82 amounts of bycatch, of undersized fish and non-target species, which are discarded (Alverson  
83 et al. 1994). In some fisheries, the discarded bycatch approaches or exceeds the marketable  
84 fraction of the catch (Kelleher 2005). In addition, bottom trawls can damage seabed habitats  
85 (Watling and Norse 1998, Puig et al. 2012) and impose mortality on benthos (Collie et al.  
86 2000, Kaiser et al. 2006).

87 Bottom trawls cause a decline of large, sessile and low productive benthos as these are most  
88 vulnerable to the direct passing of the trawl gears and have slowest recovery rates (Kaiser et  
89 al. 2006). Short-lived, opportunistic benthos and mobile scavengers/predators are generally  
90 less vulnerable or able to recover more rapidly, and such species usually dominate areas that  
91 are trawled frequently (Tillin et al. 2006, van Denderen et al. 2015a). Intensively trawled  
92 areas are generally less species-rich (Collie et al. 1997, Thrush et al. 1998, Hiddink et al.  
93 2006, Hinz et al. 2009, van Denderen et al. 2014) and altered in their functional composition  
94 by a reduced abundance of suspension-feeding organisms (Tillin et al. 2006, de Juan et al.  
95 2007)

96 Both the short-term effects of trawling, by discarding and mechanically damaging benthic  
97 organisms, and its effect on species composition lead to the question how trawling influences  
98 the food availability for the target fish. Discarded and mechanically damaged benthos form a  
99 potential food source for scavenging invertebrates and fish (Kaiser and Spencer 1994,  
100 Groenewold and Fonds 2000) and it has been suggested that this is an important part of the

101 diet of some fish (Shephard et al. 2014). Benthivorous fish also respond to trawl-induced  
102 shifts in benthic species composition with changes in their diet compared with untrawled sites  
103 (Smith et al. 2013, Johnson et al. 2015) and historic times (Rijnsdorp and Vingerhoed 2001).  
104 Such changes may affect fish growth rates and body condition. A number of studies have  
105 reported positive and negative relationships between trawling intensity and the growth rates  
106 of target species (Millner and Whiting 1996, Rijnsdorp and van Leeuwen 1996, Shephard et  
107 al. 2010) and no or negative relationships between trawling intensity and fish condition  
108 (Hiddink et al. 2011). From theory, it is expected that trawling will increase food availability  
109 for target fish (and hence the productivity of the species), when the most profitable food  
110 source for fish is relatively resistant to trawling and benefits from reduced competition for  
111 space and/or resource with more susceptible benthos. Conversely, negative effects on the  
112 food availability may be expected when the more susceptible benthos is the most profitable  
113 prey (van Denderen et al. 2013).

114 There is limited empirical evidence of trawl-induced cultivation of food for fish based on the  
115 benthic response to trawling. Most studies reporting trawl-induced shifts in species  
116 composition refer to relative shifts; some (groups of) species are less affected by the trawls  
117 and as such increase proportionally in response to trawling. Still, some species' traits,  
118 belonging to opportunistic benthos, have been positively associated with trawl disturbance  
119 (van Denderen et al. 2015a) and it should also be noted that studies testing species-specific  
120 responses over a trawl disturbance gradient often find increases of some species, even with a  
121 reduction in total benthic biomass or production (e.g. Hinz et al. 2008, Hinz et al. 2009,  
122 Johnson et al. 2015). Despite these results, most studies support the finding that trawling may  
123 lead to trawl-induced depletion of food for target fish in chronically fished areas, as a result  
124 of direct trawl mortality on fish prey and declines in benthic production (e.g. Jennings et al.  
125 2001, Queirós et al. 2006). Since suspension-feeding organisms are particularly negatively



126 affected by trawling, such declines can become even larger as this functional group plays an  
127 important role in transporting food from the water column to the seabed and, as such,  
128 regulating benthic production (Gili and Coma 1998). Similarly, trawl-induced declines of  
129 other (groups of) benthic organisms that facilitate benthos could also lead to lower benthic  
130 production and depletion of food for target fish (e.g. declines of important habitat  
131 facilitators).

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

143 **The use of MPAs for (bottom trawl) fishing**

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

148 MPAs established for biodiversity and habitat conservation are either meant to protect  
149 existing natural values or to allow for recovery of such values after they have been lost. The  
150 former are generally located in ecological hotspots that have a high diversity and contain  
151 (endemic) populations and/or habitat structures that are vulnerable to fisheries (Roberts et al.  
152 2003). When an MPA is established in order to rebuild lost natural values, it is important to  
153 determine the potential for recovery. Recovery of some types of habitats, in particular those  
154 with complex structural properties (macrophytes, corals, sponge fields), may take decades or  
155 even centuries, while others may recover more quickly (Roberts and Hirshfield 2004, Kaiser  
156 et al. 2006). In addition to the growth rates of the species involved, an important determinant  
157 of the potential (and speed) of recovery is whether the area can be recolonized by species that  
158 have disappeared. This is determined by its connectivity to other areas in which the species  
159 still occurs (Shanks et al. 2003, D'Aloia et al. 2015).

160 The use of MPAs to protect fish populations has been most successful for fish with limited  
161 mobility. These species are often dependent on specific habitat-structures, such as reefs. For  
162 these species, it has been shown that MPAs often increased their density, biomass and  
163 individual size (Halpern 2003, Lester et al. 2009, Sciberras et al. 2013). In some areas, this  
164 also led to higher abundance of fish and marketable catch around the border of MPAs  
165 (McClanahan and Mangi 2000, Vandeperre et al. 2011). Protection of fish by MPAs is  
166 generally considered to be less effective for species with high mobility (Horwood et al. 1998,

167 Gerber et al. 2003, Kaiser 2005, Grüss et al. 2011). These species are often less dependent on  
168 specific habitats and move considerable distances within a year (Shipp 2003, Kaiser 2005).  
169 Protection of certain life-stages is proposed as a more adequate option than implementing  
170 large MPAs for mobile species (Grüss et al. 2011). This may work when populations are  
171 regulated by processes in the protected life-stage (St. Mary et al. 2000, van de Wolfshaar et  
172 al. 2011).

173 The use of MPAs to protect fisheries yield has been studied in a wide variety of modelling  
174 studies. These generally conclude that MPAs will reduce yield whenever fishing mortality is  
175 below that which maximizes yield (for review see Gerber et al. 2003). This has been  
176 suggested as an important drawback to use MPAs in fisheries management compared to  
177 regular catch restrictions (Hilborn et al. 2006). Theoretical work by Hastings and Botsford  
178 (1999) has partially addressed this concern and illustrated that MPAs can produce equivalent  
179 yields compared to traditional quota-based management. Most of the above work is however  
180 based on non-spatial or highly simplified spatial models. Recently, spatially explicit models,  
181 with the inclusion of population structure, density-dependent processes and/or environmental  
182 stochasticity, have been used to show that a carefully designed network of MPAs can  
183 increase fisheries yields even when fish stocks are not overharvested (for review see Gaines  
184 et al. 2010). Obtaining such positive effects of MPAs on fisheries yield requires a detailed  
185 understanding of the behavior of the fishery and its target stocks (Rassweiler et al. 2012).

186 Finally, MPAs are also used to allow the trophic structure of the community to recover.  
187 Fishing changes the size structure of the fish community by reducing the abundance of large  
188 fish, mainly high trophic level species, limiting the predation mortality on the smaller prey  
189 species (Daan et al. 2005, Andersen and Pedersen 2010). Top-down control may be

190 reinforced inside MPAs due to an increase of the predatory species that are now protected  
191 from the fisheries (for review see Pinnegar et al. 2000, Baskett et al. 2007).

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

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

197 ***Biotic interaction may change recovery potential of trawled habitat***

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

204 Settlement of the sensitive species can be prevented by changes to the habitat after bottom  
205 trawling (Piersma et al. 2001) and by the biotic interactions present as a result of bottom  
206 trawling. The latter may occur when the opportunistic benthic residents remain the dominant  
207 species through direct feeding on the arriving larvae (by predators or deposit feeders), the  
208 smothering of the larvae (by bioturbators), filtering them from the water column as prey (by  
209 suspension feeders) or by denying them space to settle (tube-builders) (Woodin 1976, Hunt  
210 and Scheibling 1997). There is some evidence that such effects are strong enough to delay the  
211 recovery of sensitive species. This is best observed in defaunation experiments that show  
212 reduced colonization, and potentially coexistence, in areas that are occupied by a resident  
213 community, compared with an area that is empty (Lu and Wu 2000, Montserrat et al. 2008).  
214 Settlement success may also be reduced by resident species that can modify seabed sediment,  
215 making it less suitable for other organisms (van Nes et al. 2007). Such interactions indicate

216 clearly that modification of the benthic ecosystem composition, as a result of the side-effects  
217 of bottom trawling, can reduce the recovery potential of an area after it has been designated  
218 an MPA and trawling has ceased. It is theoretically possible, if the resident community  
219 formed under the effects of trawling is stable enough that trawling induces an alternative  
220 stable state (ASS). The existence of an ASS would strongly reduce the value of MPAs as a  
221 recovery tool for the benthic ecosystem, but we are not aware of empirical support for  
222 trawling-induced ASSs. For other fisheries, large ecosystem shifts have already been  
223 suggested from which recovery to the pre-fished state is very difficult (Scheffer et al. 2001,  
224 Jensen et al. 2012).

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

### 233 *Trawl effects on both fish and benthos may affect trophic structure*

234 It is often suggested that top-down control may be reinforced inside MPAs, due to an increase  
235 of the predatory species that are targeted by the fisheries (Pinnegar et al. 2000). In the case of  
236 benthivorous fish and their prey, this expectation is complicated by the fact that both are  
237 affected by bottom trawl fisheries. At low trawl intensity, fish density is relatively unaffected,  
238 and so, as a consequence, is the predation mortality on benthic prey. At high trawling  
239 intensity, fish density and the importance of fish predation is reduced, but mortality induced

240 by trawls on the prey is high. Hence, for benthos, direct mortality of trawling replaces  
241 predation mortality as fish abundance is reduced at high trawling intensity. The relative  
242 change in these two sources of mortality per unit trawling intensity determines whether the  
243 benthos will increase (reduced trawl mortality) or decrease (increased predation mortality)  
244 inside MPAs (van Denderen et al. 2013, Johnson et al. 2015). This means that benthos  
245 vulnerable to trawl impact, which is not a preferred prey for fish, will likely benefit from  
246 MPAs, whereas benthos species that are less vulnerable to trawl impact or preferred prey for  
247 fish, may respond differently to MPA establishment.

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

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

263 reducing natural disturbance and predation (Thrush et al. 1992, Stachowicz 2001, Lohrer et  
264 al. 2013).

265 ***Biotic interactions influence protection of target fish and fisheries yield***

266 Shifts in benthos species composition in response to changed trawling intensity may affect  
267 fish food availability, fish production and fisheries yield (Duplisea et al. 2002, Hiddink et al.  
268 2008, van Denderen et al. 2013). The net effect on fish abundance and yield depends on how  
269 the prey species of the target fish are affected by trawling (Fig. 1).

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

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



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

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

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

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

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

325 *Examining bottom trawl fishing disturbance at different spatial scales*

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

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

349 ***Deriving a mechanistic understanding of the benthic system***

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

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382 **References**

- 383 Alverson, D. L., M. H. Freeberg, J. G. Pope, and S. A. Murawski. 1994. A global assessment  
384 of fisheries bycatch and discards. FAO Fisheries Technical Paper No. 339. Rome,  
385 FAO. Rome.
- 386 Andersen, K. H., and M. Pedersen. 2010. Damped trophic cascades driven by fishing in  
387 model marine ecosystems. *Proceedings of the Royal Society B: Biological Sciences*  
388 *277:795-802.*
- 389 Babcock, R. C., S. Kelly, N. T. Shears, J. W. Walker, and T. J. Willis. 1999. Changes in  
390 community structure in temperate marine reserves. *Marine Ecology Progress Series*  
391 *189:125-134.*
- 392 Baskett, M. L., F. Micheli, and S. A. Levin. 2007. Designing marine reserves for interacting  
393 species: insights from theory. *Biological Conservation* *137:163-179.*
- 394 Baum, J. K., and B. Worm. 2009. Cascading top-down effects of changing oceanic predator  
395 abundances. *Journal of Animal Ecology* *78:699-714.*
- 396 Blyth, R. E., M. J. Kaiser, G. Edwards-Jones, and P. J. B. Hart. 2004. Implications of a zoned  
397 fishery management system for marine benthic communities. *Journal of Applied*  
398 *Ecology* *41:951-961.*
- 399 Blyth-Skyrme, R. E., M. J. Kaiser, J. G. Hiddink, G. Edwards-Jones, and P. J. B. Hart. 2006.  
400 Conservation benefits of temperate marine protected areas: variation among fish  
401 species. *Conservation Biology* *20:811-820.*
- 402 Botsford, L. W., F. Micheli, and A. Hastings. 2003. Principles for the design of marine  
403 reserves. *Ecological Applications* *13:25-31.*
- 404 Collie, J. S., G. A. Escanero, and P. C. Valentine. 1997. Effects of bottom fishing on the  
405 benthic megafauna of Georges Bank. *Marine Ecology Progress Series* *155:159-172.*

406

- 407 Collie, J. S., S. J. Hall, M. J. Kaiser and I. R. Poiner. 2000. A quantitative analysis of fishing  
408 impacts on shelf-sea benthos. *Journal of Animal Ecology* 69:785-798.
- 409 Daan, N., H. Gislason, J. G. Pope, and J. C. Rice. 2005. Changes in the North Sea fish  
410 community: evidence of indirect effects of fishing? *ICES Journal of Marine Science*  
411 62:177-188.
- 412 D'aloia, C. C., S. M. Bogdanowicz, R. K. Francis, J. E. Majoris, R. G. Harrison, and P. M.  
413 Buston. 2015. Patterns, causes, and consequences of marine larval dispersal.  
414 *Proceedings of the National Academy of Sciences* 112:139450-13945.
- 415 Dayton, P. K., S. F. Thrush, M. T. Agardy, and R. J. Hofman. 1995. Environmental effects of  
416 marine fishing. *Aquatic Conservation: Marine and Freshwater Ecosystems* 5:205-232.
- 417 de Juan, S., S. F. Thrush, and M. Demestre. 2007. Functional changes as indicators of  
418 trawling disturbance on a benthic community located in a fishing ground (NW  
419 Mediterranean Sea). *Marine Ecology Progress Series* 334:117-129.
- 420 Duineveld, G. C. A., M. J. N. Bergman, and M. S. S. Lavaleye. 2007. Effects of an area  
421 closed to fisheries on the composition of the benthic fauna in the southern North Sea.  
422 *ICES Journal of Marine Science* 64:899-908.
- 423 Duplisea, D. E., S. Jennings, K. J. Warr, and T. A. Dinmore. 2002. A size-based model of the  
424 impacts of bottom trawling on benthic community structure. *Canadian Journal of*  
425 *Fisheries and Aquatic Sciences* 59:1785-1795.
- 426 FAO. 2009. *The state of world fisheries and aquaculture - 2008* (Sofia). Rome.
- 427 Gaines, S. D., C. White, M. H. Carr, and S. R. Palumbi. 2010. Designing marine reserve  
428 networks for both conservation and fisheries management. *Proceedings of the*  
429 *National Academy of Sciences* 107:18286-18293.
- 430 Gell, F. R., and C. M. Roberts. 2003. Benefits beyond boundaries: the fishery effects of  
431 marine reserves. *Trends in Ecology and Evolution* 18:448-455.

- 432 Gerber, L., L. Botsford, A. Hastings, H. Possingham, S. Gaines, S. Palumbi, and S.  
433 Andelman. 2003. Population models for marine reserve design: a retrospective and  
434 prospective synthesis. *Ecological Applications* 13:47-64.
- 435 Gili, J. M. and R. Coma. 1998. Benthic suspension feeders: their paramount role in littoral  
436 marine food webs. *Trends in Ecology and Evolution* 13:316-321.
- 437 Grant, J., P. Cranford, and C. Emerson. 1997. Sediment resuspension rates, organic matter  
438 quality and food utilization by sea scallops (*Placopecten magellanicus*) on Georges  
439 Bank. *Journal of Marine Research* 55:965-994.
- 440 Groenewold, S., and M. Fonds. 2000. Effects on benthic scavengers of discards and damaged  
441 benthos produced by the beam-trawl fishery in the southern North Sea. *ICES Journal*  
442 *of Marine Science* 57:1395-1406.
- 443 Grüss, A., D. M. Kaplan, S. Guénette, C. M. Roberts, and L. W. Botsford. 2011.  
444 Consequences of adult and juvenile movement for marine protected areas. *Biological*  
445 *Conservation* 144:692-702.
- 446 Guénette, S., T. Lauck, and C. Clark. 1998. Marine reserves: from Beverton and Holt to the  
447 present. *Reviews in Fish Biology and Fisheries* 8:251-272.
- 448 Halpern, B. S. 2003. The impact of marine reserves: do reserves work and does reserve size  
449 matter? *Ecological Applications* 13:117-137.
- 450 Halpern, B. S., and R. R. Warner. 2003. Matching marine reserve design to reserve  
451 objectives. *Proceedings of the Royal Society B: Biological Sciences* 270:1871-1878.
- 452 Hastings, A., and L. W. Botsford. 1999. Equivalence in yield from marine reserves and  
453 traditional fisheries management. *Science* 284:1537-1538.
- 454 Heath, M. R. 2005. Changes in the structure and function of the North Sea fish foodweb,  
455 1973–2000, and the impacts of fishing and climate. *ICES Journal of Marine Science*  
456 62:847-868.



- 457 Hiddink, J. G., S. Jennings, M. J. Kaiser, A. M. Queiros, D. E. Duplisea and G. J. Piet. 2006.  
458 Cumulative impacts of seabed trawl disturbance on benthic biomass, production, and  
459 species richness in different habitats. *Canadian Journal of Fisheries and Aquatic*  
460 *Sciences* 63:721-736.
- 461 Hiddink, J. G., A. F. Johnson, R. Kingham, and H. Hinz. 2011. Could our fisheries be more  
462 productive? Indirect negative effects of bottom trawl fisheries on fish condition.  
463 *Journal of Applied Ecology* 48:1441-1449.
- 464 Hiddink, J. G., A. D. Rijnsdorp, and G. Piet. 2008. Can bottom trawling disturbance increase  
465 food production for a commercial fish species? *Canadian Journal of Fisheries and*  
466 *Aquatic Sciences* 65:1393-1401.
- 467 Hilborn, R., F. Micheli, and G. A. De Leo. 2006. Integrating marine protected areas with  
468 catch regulation. *Canadian Journal of Fisheries and Aquatic Sciences* 63:642-649.
- 469 Hinz, H., J. G. Hiddink, J. Forde, and M. J. Kaiser. 2008. Large-scale responses of nematode  
470 communities to chronic otter-trawl disturbance. *Canadian Journal of Fisheries and*  
471 *Aquatic Sciences* 65:723-732.
- 472 Hinz, H., V. Prieto, and M. J. Kaiser. 2009. Trawl disturbance on benthic communities:  
473 chronic effects and experimental predictions. *Ecological Applications* 19:761-773.
- 474 Horwood, J. W., J. H. Nichols, and S. Milligan. 1998. Evaluation of closed areas for fish  
475 stock conservation. *Journal of Applied Ecology* 35:893-903.
- 476 Hunt, H. L., and R. E. Scheibling. 1997. Role of early post-settlement mortality in  
477 recruitment of benthic marine invertebrates. *Marine Ecology Progress Series* 155:269-  
478 301.
- 479 Ingels, J., S. L. Dashfield, P. J. Somerfield, S. Widdicombe, and M. C. Austen. 2014.  
480 Interactions between multiple large macrofauna species and nematode communities -

- 481 mechanisms for indirect impacts of trawling disturbance. *Journal of Experimental*  
482 *Marine Biology and Ecology* 456:41-49.
- 483 Jennings, S., T. A. Dinmore, D. E. Duplisea, K. J. Warr, and J. E. Lancaster. 2001. Trawling  
484 disturbance can modify benthic production processes. *Journal of Animal Ecology*  
485 70:459-475.
- 486 Jensen, O., T. Branch, and R. Hilborn. 2012. Marine fisheries as ecological experiments.  
487 *Theoretical Ecology* 5:3-22.
- 488 Johnson, A. F., G. Gorelli, S. R. Jenkins, J. G. Hiddink, and H. Hinz. 2015. Effects of bottom  
489 trawling on fish foraging and feeding. *Proceedings of the Royal Society B: Biological*  
490 *Sciences* 282:20142336.
- 491 Jones, J. B. 1992. Environmental impact of trawling on the seabed: a review. *New Zealand*  
492 *Journal of Marine and Freshwater Research* 26:59-67.
- 493 Kaiser, M. J. 2005. Are marine protected areas a red herring or fisheries panacea? *Canadian*  
494 *Journal of Fisheries and Aquatic Sciences* 62:1194-1199.
- 495 Kaiser, M. J., K. R. Clarke, H. Hinz, M. C. V. Austen, P. J. Somerfield, and I. Karakassis.  
496 2006. Global analysis of response and recovery of benthic biota to fishing. *Marine*  
497 *Ecology Progress Series* 311:1-14.
- 498 Kaiser, M. J., K. Ramsay, C. A. Richardson, F. E. Spence, and A. R. Brand. 2000. Chronic  
499 fishing disturbance has changed shelf sea benthic community structure. *Journal of*  
500 *Animal Ecology* 69:494-503.
- 501 Kaiser, M. J., S. I. Rogers, and J. R. Ellis. 1999. Importance of benthic habitat complexity for  
502 demersal fish assemblages. Pages 212-223 *in* L. Benaka, editor. *Fish habitat: essential*  
503 *fish habitat and restoration*. American Fisheries Society Symposium, Bethesda,  
504 Maryland.

- 505 Kaiser, M. J., and B. E. Spencer. 1994. Fish scavenging behaviour in recently trawled areas.  
506 Marine Ecology Progress Series 112:41-49.
- 507 Kelleher, K. 2005. Discards in the world's marine fisheries. An update. FAO Fisheries  
508 Technical Paper No. 470. Rome, FAO.
- 509 Lambert, G. I., S. Jennings, M. J. Kaiser, T. W. Davies, and J. G. Hiddink. 2014. Quantifying  
510 recovery rates and resilience of seabed habitats impacted by bottom fishing. Journal  
511 of Applied Ecology 51:1326–1336.
- 512 Lester, S. E., B. S. Halpern, K. Grorud-Colvert, J. Lubchenco, B. I. Ruttenberg, S. D. Gaines,  
513 S. Airame, and R. R. Warner. 2009. Biological effects within no-take marine reserves:  
514 a global synthesis. Marine Ecology Progress Series 384:33-46.
- 515 Lohrer, A. M., I. F. Rodil, M. Townsend, L. D. Chiaroni, J. E. Hewitt, and S. F. Thrush.  
516 2013. Biogenic habitat transitions influence facilitation in a marine soft-sediment  
517 ecosystem. Ecology 94:136-145.
- 518 Lu, L., and R. S. S. Wu. 2000. An experimental study on recolonization and succession of  
519 marine macrobenthos in defaunated sediment. Marine Biology 136:291-302.
- 520 Lubchenco, J., S. R. Palumbi, S. D. Gaines, and S. Andelman. 2003. Plugging a hole in the  
521 ocean: the emerging science of marine reserves. Ecological Applications 13:S3-S7.
- 522 McClanahan, T. R., and S. Mangi. 2000. Spillover of exploitable fishes from a marine park  
523 and its effect on the adjacent fishery. Ecological Applications 10:1792-1805.
- 524 Millner, R. S., and C. L. Whiting. 1996. Long-term changes in growth and population  
525 abundance of sole in the North Sea from 1940 to the present. ICES Journal of Marine  
526 Science 53:1185-1195.
- 527 Montserrat, F., C. Van Colen, S. Degraer, T. Ysebaert, and P. Herman. 2008. Benthic  
528 community-mediated sediment dynamics. Marine Ecology Progress Series 372:43-59.

- 529 Murawski, S. A., R. Brown, H. L. Lai, P. J. Rago, and L. Hendrickson. 2000. Large-scale  
530 closed areas as a fishery-management tool in temperate marine systems: the Georges  
531 Bank experience. *Bulletin of Marine Science* 66:775-798.
- 532 Pelletier, D., J. Claudet, J. Ferraris, L. Benedetti-Cecchi, and J. A. Garcia-Charton. 2008.  
533 Models and indicators for assessing conservation and fisheries-related effects of  
534 marine protected areas. *Canadian Journal of Fisheries and Aquatic Sciences* 65:765-  
535 779.
- 536 Piersma, T., A. Koolhaas, A. Dekinga, J. J. Beukema, R. Dekker, and K. Essink. 2001. Long-  
537 term indirect effects of mechanical cockle-dredging on intertidal bivalve stocks in the  
538 Wadden Sea. *Journal of Applied Ecology* 38:976-990.
- 539 Pilskaln, C. H., J. H. Churchill, and L. M. Mayer. 1998. Resuspension of sediment by bottom  
540 trawling in the Gulf of Maine and potential geochemical consequences. *Conservation*  
541 *Biology* 12:1223-1229.
- 542 Pinnegar, J. K., N. V. C. Polunin, P. Francour, F. Badalamenti, R. Chemello, M.-L.  
543 Harmelin-Vivien, B. Hereu, M. Milazzo, M. Zabala, G. D'Anna, and C. Pipitone.  
544 2000. Trophic cascades in benthic marine ecosystems: lessons for fisheries and  
545 protected-area management. *Environmental Conservation* 27:179-200.
- 546 Puig, P., M. Canals, J. B. Company, J. Martin, D. Amblas, G. Lastras, A. Palanques, and A.  
547 M. Calafat. 2012. Ploughing the deep sea floor. *Nature* 489:286-289.
- 548 Pusceddu, A., S. Bianchelli, J. Martín, P. Puig, A. Palanques, P. Masqué, and R. Danovaro.  
549 2014. Chronic and intensive bottom trawling impairs deep-sea biodiversity and  
550 ecosystem functioning. *Proceedings of the National Academy of Sciences* 111:8861-  
551 8866.

- 552 Queirós, A. M., J. G. Hiddink, M. J. Kaiser, and H. Hinz. 2006. Effects of chronic bottom  
553 trawling disturbance on benthic biomass, production and size spectra in different  
554 habitats. *Journal of Experimental Marine Biology and Ecology* 335:91-103.
- 555 Rassweiler, A., C. Costello, and D. A. Siegel. 2012. Marine protected areas and the value of  
556 spatially optimized fishery management. *Proceedings of the National Academy of*  
557 *Sciences* 109:11884-11889.
- 558 Rhoads, D. C. 1974. Organisms-sediment relations on the muddy sea floor. *Oceanography*  
559 *and Marine Biology Annual Review* 12:263-300.
- 560 Riemann, B., and E. Hoffmann. 1991. Ecological consequences of dredging and bottom  
561 trawling in the Limfjord, Denmark. *Marine Ecology Progress Series* 69:171-178.
- 562 Rijnsdorp, A. D., and P. I. van Leeuwen. 1996. Changes in growth of North Sea plaice since  
563 1950 in relation to density, eutrophication, beam-trawl effort, and temperature. *ICES*  
564 *Journal of Marine Science* 53:1199-1213.
- 565 Rijnsdorp, A. D., and B. Vingerhoed. 2001. Feeding of plaice *Pleuronectes platessa* (L.) and  
566 sole *Solea solea* (L.) in relation to the effects of bottom trawling. *Journal of Sea*  
567 *Research* 45:219-229.
- 568 Roberts, C. M., S. Andelman, G. Branch, R. H. Bustamante, J. Carlos Castilla, J. Dugan, B.  
569 S. Halpern, K. D. Lafferty, H. Leslie, J. Lubchenco, D. McArdle, H. P. Possingham,  
570 M. Ruckelshaus, and R. R. Warner. 2003. Ecological criteria for evaluating candidate  
571 sites for marine reserves. *Ecological Applications* 13:199-214.
- 572 Roberts, S., and M. Hirshfield. 2004. Deep-sea corals: out of sight, but no longer out of mind.  
573 *Frontiers in Ecology and the Environment* 2:123-130.
- 574 Rowley, R. J. 1994. Marine reserves in fisheries management. *Aquatic Conservation: Marine*  
575 *and Freshwater Ecosystems* 4:233-254.

- 576 Scheffer, M., S. Carpenter, J. A. Foley, C. Folke, and B. Walker. 2001. Catastrophic shifts in  
577 ecosystems. *Nature* 413:591-596.
- 578 Sciberras, M., S. Jenkins, M. Kaiser, S. Hawkins, and A. Pullin. 2013. Evaluating the  
579 biological effectiveness of fully and partially protected marine areas. *Environmental*  
580 *Evidence* 2:4.
- 581 Shanks, A. L., B. A. Grantham, and M. H. Carr. 2003. Propagule dispersal distance and the  
582 size and spacing of marine reserves. *Ecological Applications* 13:S159-S169.
- 583 Shephard, S., D. Brophy, and D. Reid. 2010. Can bottom trawling indirectly diminish  
584 carrying capacity in a marine ecosystem? *Marine Biology* 157:2375-2381.
- 585 Shephard, S., C. Minto, M. Zölck, S. Jennings, D. Brophy, and D. Reid. 2014. Scavenging on  
586 trawled seabeds can modify trophic size structure of bottom-dwelling fish. *ICES*  
587 *Journal of Marine Science* 71:398-405.
- 588 Shipp, R. L. 2003. A perspective on marine reserves as a fishery management tool. *Fisheries*  
589 28:10-21.
- 590 Smith, B. E., J. S. Collie, and N. L. Lengyel. 2013. Effects of chronic bottom fishing on the  
591 benthic epifauna and diets of demersal fishes on northern Georges Bank. *Marine*  
592 *Ecology Progress Series* 472:199-217.
- 593 St. Mary, C. M., C. W. Osenberg, T. K. Frazer, and W. J. Lindberg. 2000. Stage structure,  
594 density dependence and the efficacy of marine reserves. *Bulletin of Marine Science*  
595 66:675-690.
- 596 Stachowicz, J. J. 2001. Mutualism, facilitation, and the structure of ecological communities.  
597 *Bioscience* 51:235-246.
- 598 Thrush, S. F., J. E. Hewitt, V. J. Cummings, P. K. Dayton, M. Cryer, S. J. Turner, G. A.  
599 Funnell, R. G. Budd, C. J. Milburn, and M. R. Wilkinson. 1998. Disturbance of the

- 600 marine benthic habitat by commercial fishing: impacts at the scale of the fishery.  
601 *Ecological Applications* 8:866-879.
- 602 Thrush, S. F., J. E. Hewitt, A. M. Lohrer, and L. D. Chiaroni. 2013. When small changes  
603 matter: the role of cross-scale interactions between habitat and ecological connectivity  
604 in recovery. *Ecological Applications* 23:226-238.
- 605 Thrush, S. F., R. D. Pridmore, J. E. Hewitt, and V. J. Cummings. 1992. Adult infauna as  
606 facilitators of colonization on intertidal sandflats. *Journal of Experimental Marine  
607 Biology and Ecology* 159:253-265.
- 608 Tillin, H. M., J. G. Hiddink, S. Jennings, and M. J. Kaiser. 2006. Chronic bottom trawling  
609 alters the functional composition of benthic invertebrate communities on a sea-basin  
610 scale. *Marine Ecology Progress Series* 318:31-45.
- 611 van de Wolfshaar, K. E., R. HilleRisLambers, and A. Gårdmark. 2011. Effect of habitat  
612 productivity and exploitation on populations with complex life cycles. *Marine  
613 Ecology Progress Series* 438:175-184.
- 614 van Denderen, P. D., S. G. Bolam, J. G. Hiddink, S. Jennings, A. Kenny, A. D. Rijnsdorp,  
615 and T. van Kooten 2015a. Similar effects of bottom trawling and natural disturbance  
616 on composition and function of benthic communities across habitats. *Marine Ecology  
617 Progress Series* 541:31-43.
- 618 van Denderen, P. D., N. T. Hintzen, A. D. Rijnsdorp, P. Ruardij, and T. van Kooten. 2014.  
619 Habitat-specific effects of fishing disturbance on benthic species richness in marine  
620 soft sediments. *Ecosystems* 17:1216-1226.
- 621 van Denderen, P. D., N. T. Hintzen, T. van Kooten, and A. D. Rijnsdorp. 2015b. Temporal  
622 aggregation of bottom trawling and its implication for the impact on the benthic  
623 ecosystem. *ICES Journal of Marine Science* 72:952-961.

- 624 van Denderen, P. D., T. van Kooten, and A. D. Rijnsdorp. 2013. When does fishing lead to  
625 more fish? Community consequences of bottom trawl fisheries in demersal food  
626 webs. *Proceedings of the Royal Society B: Biological Sciences* 280:20131883.
- 627 van Nes, E. H., T. P. F. Amaro, M. Scheffer, and G. Duineveld. 2007. Possible mechanisms  
628 for a marine benthic regime shift in the North Sea. *Marine Ecology Progress Series*  
629 330:39 - 47.
- 630 Vandeperre, F., R. M. Higgins, J. Sánchez-Meca, F. Maynou, R. Goñi, P. Martín-Sosa, A.  
631 Pérez-Ruzafa, P. Afonso, I. Bertocci, R. Crec'hriou, G. D'Anna, M. Dimech, C.  
632 Dorta, O. Esparza, J. M. Falcón, A. Forcada, I. Guala, L. Le Direach, C. Marcos, C.  
633 Ojeda-Martínez, C. Pipitone, P. J. Schembri, V. Stelzenmüller, B. Stobart, and R. S.  
634 Santos. 2011. Effects of no-take area size and age of marine protected areas on  
635 fisheries yields: a meta-analytical approach. *Fish and Fisheries* 12:412-426.
- 636 Watling, L., and E. A. Norse. 1998. Disturbance of the seabed by mobile fishing gear: a  
637 comparison to forest clearcutting. *Conservation Biology* 12:1180-1197.
- 638 Wilson, W. H. 1991. Competition and predation in marine soft-sediment communities.  
639 *Annual Review of Ecology and Systematics* 21:221-241.
- 640 Woodin, S. A. 1976. Adult-larval interactions in dense infaunal assemblages - patterns of  
641 abundance. *Journal of Marine Research* 34:25-41.

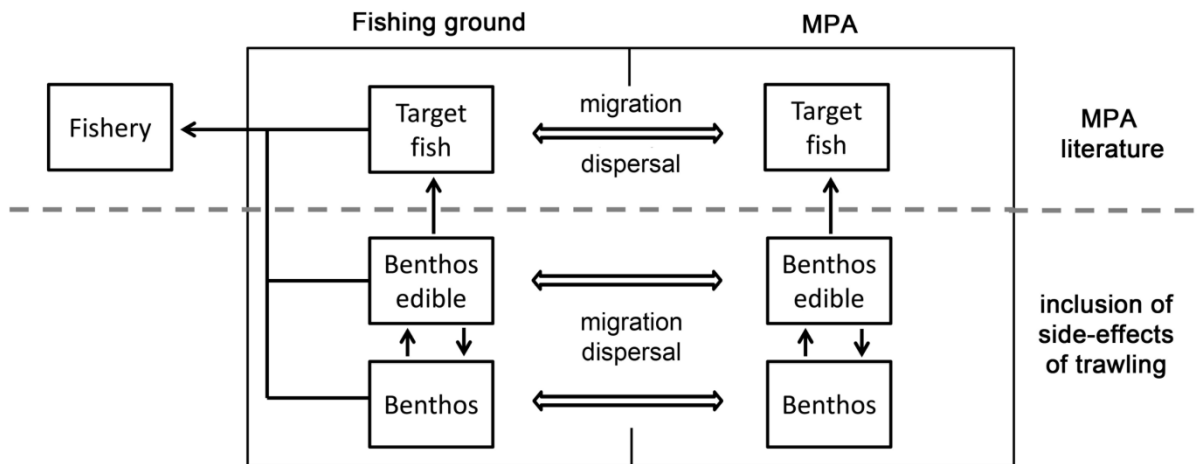


642 **Figure legends**

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

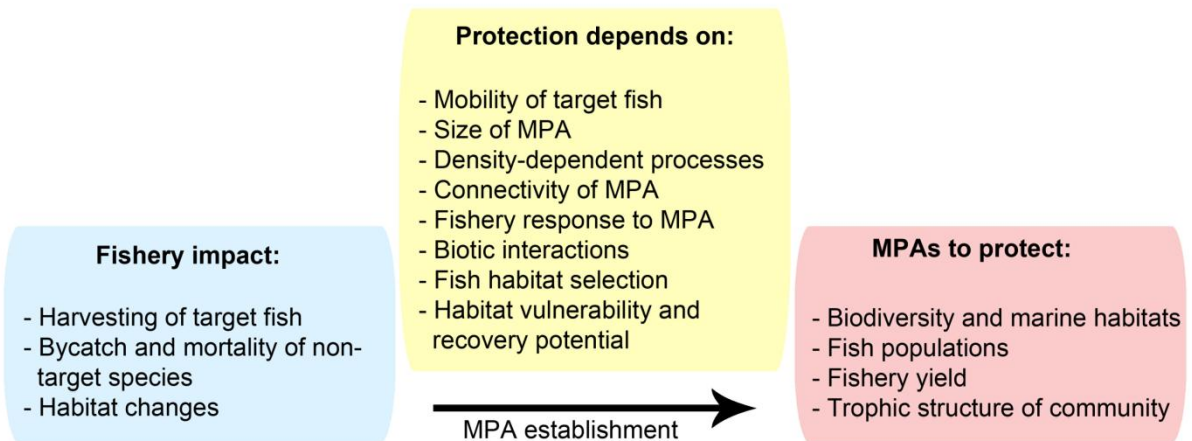
647 Figure 2. Overview of the role of MPAs to conserve different ecosystem indicators from the  
648 adverse effects of fishing. The box in the middle shows the processes that determine (often in  
649 interaction with each other) whether MPAs can induce benefits to (some of) the ecosystem  
650 indicators.

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