Contrasting consequences of species removal from higher and lower trophic levels in marine ecosystems

Daan van de Geer, 1607103 Supervisor: BDHK Eriksson

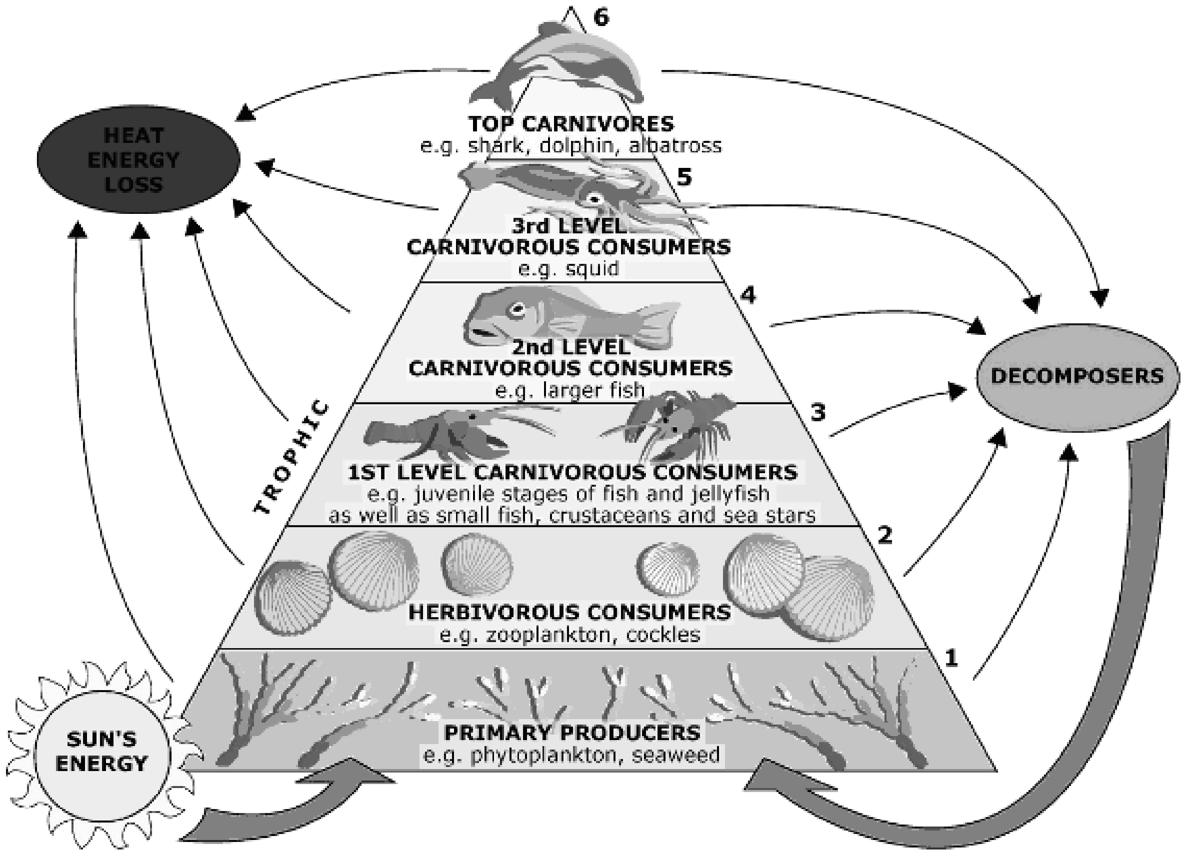

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Fig. 1 – Trophic levels with energy flow in a generic marine ecosystem.

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Summary

Industrial fishing can have a profound impact on food webs present in the system by altering the balance between species. The change in abundance of species and competitive interactions can sometimes have further consequences than the species directly affected. The effects depend, among other things, on the trophic position of the target species. In this report I compare food web consequences between removal of upper level predators and lower level filter feeding bivalves, which have radically different functions in their respective food webs.

Effects of removing predators from a food web depend on the predator diversity and niche overlap in prey consumption. When predator diversity is high, there is a greater chance that the loss of a specific predator can be overcome when other predator species feed on the same prey. If predators show very distinct niches, food webs may be far stronger affected, since their specific prey can flourish. It can also be so that predators don’t have a strong effect on their prey, which would produce very small effects in the food web. Lastly, an omnivorous predator can alter its diet when their regular prey becomes scarce. This predator would then switch to the lower trophic levels, stabilizing the food web by controlling the trophic cascades. Interestingly, in some cases predator removal led to higher predation pressure. This is thought to result from the lowered competition between predators.

Removal of filter feeding bivalves has very different consequences. Studies show that bivalve communities can sustain great stress, where a large drop in population size does not necessarily have to mean the end for the species in that area. However, when repopulation is made impossible, such as storms and dredging removing the finer silt needed for younger individuals, the population drop can be quite significant. When the direct predators find less prey, they look around for similar bivalves, competing directly with species that are otherwise not competed with.

Where removal of higher trophic levels results in varying new balances in the food web, removal of lower trophic levels often leads to severe damage to an ecosystem. These effects don’t limit themselves to the food web, but also impact the physical properties of the system. Removal of bivalves can severely affect the ability of the system to hold together sediment, for example.

Fisheries must take into consideration that continued fishing pressure will result in weaker and weaker ecosystems, where every subsequent action will have a higher chance of completely disrupting it.

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Introduction

In today's world, fishing pressure has a significant influence on ecosystem functioning. With technological advancements providing access to areas previously blocked by either distance or depth problems, almost every ecosystem now feels effects such as declining size of targeted species and altered balance in the system due to species loss (Pauly et al., 2005). The fishing gear used (trawling nets, floating nets, hooks, dredging) has a varying impact on the surrounding environment as well: trawling nets and cockle dredgers not only scrape the bottom for the target species, but in doing so overturn the entire top layer of sediment, destroying many delicate plants and sedimentary animals. While floating nets and other gears such as long line gears can also catch other animals, they do nowhere near as much physical damage as the trawling or dredging does (Alverson et al., 1994 (page 30, 31)).

Effects of fisheries on food-web structure depend on target species. Simple food web studies show that removing top-predators may induce trophic cascades, where taking away the top predator relieve pressure on their prey - medium sized predators - which in turn increases pressure on herbivores and so on (figure 1)(Frank et al., 2005). This mechanism was first mentioned in the Green World Hypothesis (Hairston et al., 1960) and was later named a trophic cascade (Paine, 1980). However, most foods-webs are more complicated: roles of species can differ quite greatly from earlier expectations (Polis and Strong, 1996).

Consequences of predator removal depend on the way the different predators interact. Niche complementarity means that every predator feeds on a certain prey and there is no real overlap in prey between different predator species. This would show as a degradation in predation pressure directly proportional to the individual predation pressure of the species removed (Loreau and Hector, 2001). A positive selection effect, on the other hand, means that there is a lot of overlap in prey preference. The result is that the overall predation pressure is identical to the highest predation pressure coming from one of the predator species (Loreau, 2000).

Effects of fisheries directed at filter feeders lower in the food web are poorly understood. Bivalves are prey both for marine invertebrates, fish and birds, and many bivalves are ecosystem engineers that determine sediment characteristics and landscape heterogeneity (Eriksson et al. 2010). Many of the commercially exploited bivalves also form reefs that provide substrate for a number of associated organisms. This suggest that exploitation of bivalves may even have a wider and more far reaching food web effects than fisheries on top-predator fish.

In this report I review differences in impacts on the ecosystem depending on fisheries directed at higher trophic level predators (e.g. killifish *Fundulus heteroclitus* or shrimp *Penaeus aztecus*) or fisheries directed at bivalve filter feeders, which are low trophic level species (the cockle *Cerastoderma edule*). My expectations are that the effects will be stronger when fisheries target higher trophic level predators, because predators have a more varied diet than bivalves and their range of influence should therefore be larger. The cockle has a less varied diet, eating particulate matter suspended in the water column. Even though the cockle has important functional roles (creating a more stable sediment, food source for birds etc.), they also share these traits with many other molluscs, like the mussel or oyster. Thus, I expect a bigger impact on systems where higher trophic levels are removed than systems where cockles are taken away, unless the cockle systems contain no other filter feeding species with similar functions.

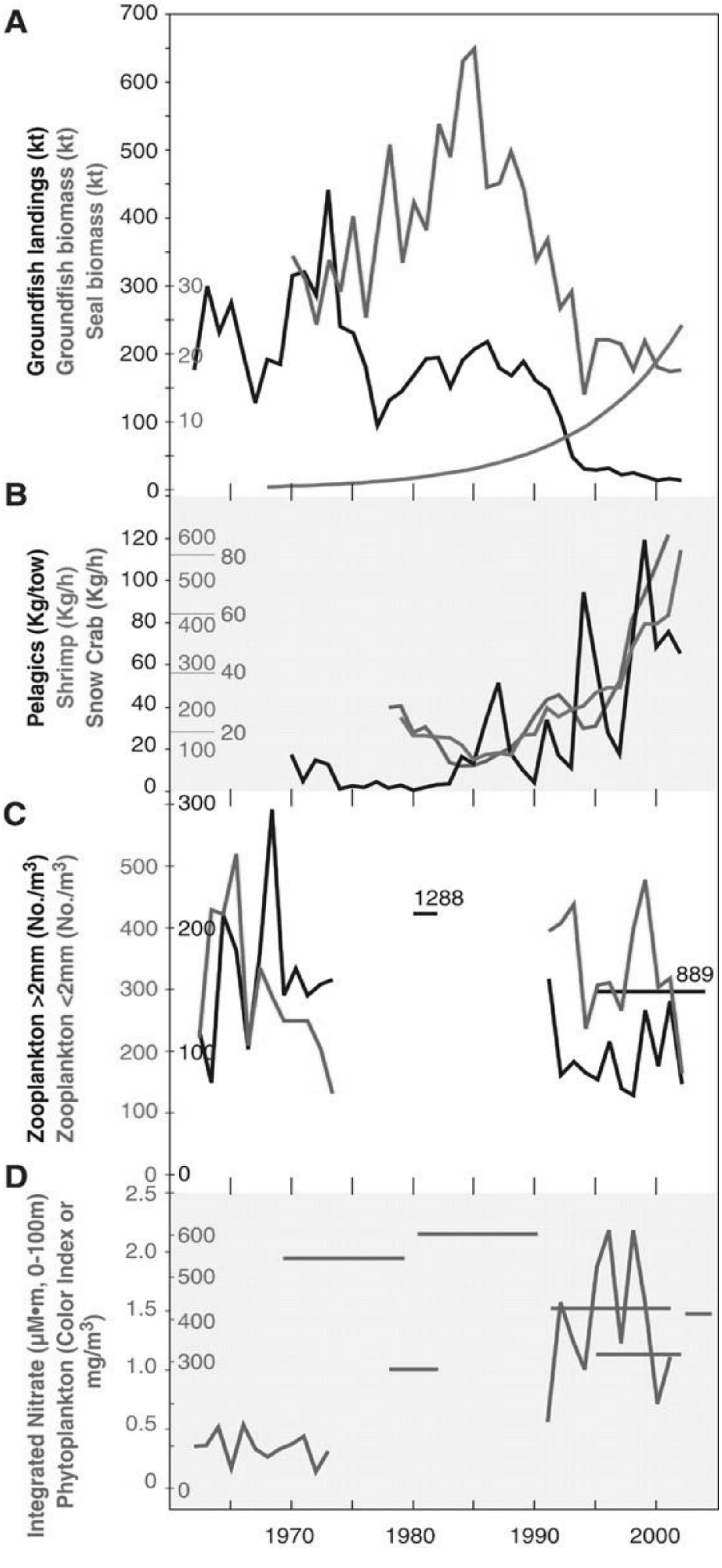

Fig. 2. Illustration of a trophic cascade on the eastern Scotian Shelf across four levels and nutrients (Frank et al. 2005). (**A**) Commercial landings of benthic fish species, fishery-independent survey estimates of benthic fish, and population biomass estimates of grey seals. (**B**) The forage base of benthic fish species (and seals), including small pelagic fish species and benthic macroinvertebrates. (**C**) Large (>2 mm) zooplankton, combined abundance of copepodite and adult stages of *Calanus finmarchicus, C. glacialis*, and *C. hyperboreous*; small zooplankton, represented by the combined abundance of Calanoid copepods (28 species) other than *Calanus* sp. with body lengths < 2 mm, and large *Calanus* sp. (average number per m^3) from two ancillary sampling programs shown as horizontal lines. (**D**) Phytoplankton color, 0 to 50 m average in situ chlorophyll (mg chlorophyll/m^3), shown as horizontal lines, and 0 to 100 m integrated, dissolved nitrate.

Effects of removing higher trophic level predators

As mentioned before, the effects of predator removal depend greatly on the functional role and identity of both the predators taken away and the ones remaining in the system. Bruno & O'Connor (2005) investigated the effects of predator diversity in a rocky shore ecosystem in the South Atlantic Bight by altering the composition of shrimp, blennies, killifish, crabs and pinfish. They performed the experiment in outdoor flow-through seawater mesocosms while observing changes in both the herbivore and algal level. It was clear that there was a significant predation pressure on the herbivores, which both increased richness and evenness in the algal community. However, when omnivores remained in the system, these predators would switch to an algal diet when prey became scarce. This would short-circuit the cascade by also decreasing the algal biomass. Monocultures induced a strong trophic cascade in the system while increasing diversity decreased algal biomass. This could be attributed to emerging interspecific interactions between the predators, alleviating the predation pressure on herbivores. Higher predator density did not significantly decrease herbivore abundance, but did increase algal biomass. This suggests the increased predation pressure, while not actually catching more prey, caused prey to devote less time to grazing and more time to evading predators.

When looking at specific predator diet preferences, Bruno & O'Connor (2007) found more evidence that functional role of the predator determines the strength and extent of the cascade. The experimental circumstances were the same as the 2005 study, but this time the predators were divided into three main groups: fish, crabs and shrimp. While the expectations were that each group would show a specific preference for prey, and would show complementary effect on herbivore abundance and diversity, they found that only fish impacted the herbivores significantly. Shrimp would only show a small impact when the researchers corrected for biomass. Crabs showed no effect. Interestingly, while fish impacted the herbivore species strongly, the algal biomass did not increase at all. This might mean that herbivores normally interact in ways that restrict time spent on foraging.

An experiment looking more closely at crabs was done by Griffin et al. (2008) in the United Kingdom with samples taken from the southwest intertidal rocky shores. This experiment was also done in flow-through, open air mesocosms. What they found was that each crab species they observed had a specific preference for prey. Because of this, prey capture was higher in mixed cultures than in monocultures which suggests good circumstances for a trophic cascade. However, prey density loss was only significant at higher densities. This suggests that crabs, although they are predators, play a relatively low (to non-existent) role in causing trophic cascades.

All studies on top down effects showed a cascading effect to some extent, while each had slightly differing end results: One showed a pretty standard decline in prey consistent with a regular trophic cascade, while the others showed relatively unexpected results. One showed no decrease in herbivores but still showed a strong increase in algal biomass and the other decreased herbivore abundance but did not increase algal biomass. In the first case the prey interactions with each other provide an explanation, where the increased predation pressure reduced energy available for foraging. The second case can be explained by predator functional roles, where one predator species apparently can switch diet to algae when the regular prey becomes unavailable.

Effects of removing lower trophic level filter feeders

Removing species on lower trophic levels, such as filter feeding cockles, is thought to impact mostly the direct predators. However, Beukema & Cadée (1996) have found that the effects ripple through to other predators as well, predators that don’t feed on cockles. The data was taken from 15 sampling locations on Balgzand, belonging to the catchment area of the Marsdiep, the westernmost inlet of the Wadden Sea. The samples taken were part of a larger sampling project dating from 1970.

After a large decrease in cockle and mussel populations, due to lowered recruitment, high mortality and unlimited fishing, fisheries started fishing in other areas. This depleted populations otherwise only predated upon by predator birds such as oystercatchers and eiders. When the oystercatchers experienced starvation due to the exceptionally low amount of their usual prey (cockle) present in the system, they changed their diet to other species such as clam. This chased eiders from their own natural feeding grounds, causing them to experience starvation as well. However, because eiders did not have a viable alternative food source to fall back on, they experienced a far greater drop in numbers than the oystercatchers. Interestingly, following the large influx of new recruits in the winter of 1991 the population sprung back quite quickly. This suggests a strong flexibility in the system.

However, this flexibility is dependent on rather important properties of the system. Piersma et al. (2001) examined the results of bivalve fishing in a different way. Samples were taken from cockle beds on the small uninhabited island of Griend in the western Wadden Sea from 1988 until 1994. The conclusions were that the most profound effect cockle dredging has on an ecosystem is not noticed in the food web, but rather in the environment. Cockle dredging does not only remove the cockles from the sediment, but takes the entire top layer with it. This removes the fine silt needed for the settlement of new recruits and prevents the population from recovering, especially when the fine silt is not allowed to settle back (such as during storms and high tide).

What we see in these two cases is a possibility of a widespread effect of removing only one or two species from a lower level in the food web. However, this effect only lasts when, in addition to removal of the species, the recruitment of young bivalves is prevented as well. This suggests that, as long as there remains a suitable settling ground, a very small remainder of bivalves can repopulate a rather large area.

Some sense in the chaos (Discussion)

Top down effects of predator removal are mainly dependent on diversity and the functional role of the predators present in the system (Loreau 2000, Loreasu & Hector 2001. For example, if omnivorous predators remain present in the system, effects on primary producers are smaller, because they can switch diet when their regular prey becomes scarce (Bruno & O’Connor 2005). Notably, removing predators generated a *higher* predation pressure in some cases (Bruno & O’Connor 2005). This is probably because predators don’t spend all of their time hunting for food, rather, the bulk of their time is spent interacting with other predators: establishing territory, fighting over food and other predator-predator interactions. These activities will take less time when there are fewer predators present in the ecosystem, freeing time for foraging. The review shows clearly that effects of predator removal are highly varied. It will therefore be very hard to predict the consequences of removing a certain predator from a system. Consequences will depend on many factors such as complexity of the food web, niche overlapping and density.

Bottom up effects of bivalve removal depend mostly on the way bivalves are removed from the system: when given the chance, bivalve communities will spring back in very short times indeed (Beukema & Cadée 1996). When resettlement is impaired by changes to the sediment due to the fishing technique being used the recovery will be much harder. This is complicated by the fact that most bivalves serve as ecosystem engineers by holding the silt together, and thereby facilitate their own settlement. Thus, removing the bivalves themselves may be enough to prevent resettlement.

When predators are removed from a system in which other predators live as well, I expect the remaining predators to be able to devote more time to hunting for food. In a way, the other predators benefit from the removal of competition from the food web. The balance will change, but the main effects are found downwards in the food web. When cockles are removed from the system, not only will there be impact downwards (on the phytoplankton normally filtered by the cockles) but also upwards on the predators. These predators usually don’t feed solely on cockles, and will shift their attention to species otherwise not used to such strong predation pressure. They not only affect their predators negatively, but also other species on the same level in the food web. This ripple effect has been seen before in other systems (Dunne 2002) and can be quite extensive.

The potential effects of filter feeder removal from an area are much greater (sediment destruction, great mortality in predators, ripple effect) than the change in balance caused by a different predation pressure when removing predators. Even though there have been cases where an entire system completely collapses (Pace et al. 1999), I believe the habitat destruction caused by the dredging when fishing for filter feeders constitutes a bigger risk of ecosystem collapse.

Any help for fisheries?

For a long time ecosystem regulation was viewed as some sort of function of primary producers. With the realisation that predation pressure and its consequences formed a strong influence as well, many models and approaches to conservation and fishing changed to incorporate the new insights. Unfortunately consequences of species removal, whether primary producers/consumers or predators, are very hard to predict. Effects depend on ecological role of the removed species, the role of the remaining species and the complexity of the system, to name a few. One thing is for sure: with the removal of species from a system that system will become simpler, and the simpler the system, the stronger the effect of further species removal will be. Fisheries around the world will have to take into account that, when they severely influence an ecosystem by altering the balance in top predators, their next actions will have bigger effects than firstly assessed.

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