Coastal habitat support to fish and fisheries on the Swedish west coast

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Abstract
Swedish coastal habitats provide significant support to the total marine finfish landings in Sweden. The fisheries are dependent on habitat quantity and quality because the fish species being caught are ecologically linked to the habitat and/or because the habitat is used as a location for harvest. Unfortunately, coastal areas are exposed to a variety of threats due to high population densities and high fishing pressure, which have resulted in habitat fragmentation and degradation. In this study, we use an interdisciplinary approach where ecological data on habitat structure and fish populations are combined with results from economic valuation case studies to assess and describe effects of habitat disturbance on the Swedish west coast. The focus is on three major habitats (soft sediment bottoms, seagrass beds and rocky bottoms with macroalgae), five fish species (cod, plaice, eel, mackerel and sea trout) and three types of fisheries (commercial, subsistence and recreational fisheries). We have shown that there exists a strong link between the major coastal habitats, the fish utilizing these habitats and the fisheries on the Swedish west coast. Cod, plaice and eel showed a high to medium association to one or several of the major habitats in the coastal zone. Cod and plaice were highly important in off-shore fisheries whereas eel was a significantly important fish species in coastal fisheries. Conversely, mackerel and sea-trout showed a medium to low dependence on coastal habitats, but were highly important in recreational fisheries. The results have important implications for coastal zone management, since they show both ecologically and economically how coastal habitats support fisheries.

Keywords: fisheries, habitat dependence, environmental valuation methods, habitat change, coastal zone management, ecosystem services

1. Introduction

Although those world's continental shelves that are shallower than 200 meters only cover 7 percent of the ocean surface, they support over 90 percent of the global fish catches [1]. Furthermore, around 40 percent of the world's population now live within 100 km of the coast (88 percent in Sweden) [2], and the impact of human activities in the coastal zone is substantial. Human activities have resulted in habitat fragmentation (e.g. through inshore boating and fishing), habitat alteration (e.g. due to increased nitrogen load), habitat destruction (for example by

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moorings and constructions of quays) and pollution (e.g. by the use of anti-fouling paints, oil spill and insufficient combustion).

Major coastal ecosystem changes have occurred on the Swedish west coast, mainly due to increased nutrient loading. For example, the areal extension of seagrass meadows has been reduced by 60 percent during the last two decades [3]. Furthermore, the coverage of green algal mats (i.e. *Ulva* spp. and *Cladophora* spp.) in shallow bays has increased from 3 percent to around 40 percent over two decades in several areas on the Swedish west coast [4]. Coastal marine ecosystems are, consequently, extremely exposed to a variety of threats, stressing the importance of evaluating potential impacts of these negative factors on the generation of ecosystem goods and services to society [5, 6].

Fish and shellfish resources are the best studied and perhaps the most important provisional service supported by marine ecosystems. Many fisheries species are dependent on a number of shallow coastal habitats during one or several parts of their life cycle [7]. Particularly, many species occur in the coastal waters during their juvenile life stages, as the waters offer nursery areas [8, 9] which provide protection against predation and generous food conditions [10, 11]. Certain fish species may be dependent on one single habitat, constituting a bottleneck, which determines the fisheries' recruitment success as concerns that species. Other species may, on the contrary, be less habitat specific, potentially utilizing alternative habitats in case of habitat degradation or loss. An identification of Essential Fish Habitats (EFHs), defined as "those waters and substrate necessary for fish for spawning, feeding or growth to maturity" [12], is thus a key component in habitat and biodiversity conservation as well as in fisheries management.

It has been estimated that Swedish coastal habitats (seagrass beds, macroalgae, blue mussel beds and unvegetated soft bottoms) provide significant support to total marine finfish landings. Species utilizing coastal ecosystems as nursery, feeding or breeding grounds comprise 77 percent by weight and 80 percent by revenues of commercial landings, and 77 percent by weight of recreational landings [13]. This suggests that an alteration in the properties of these habitats could have a great impact on commercial and recreational fisheries. Fisheries might depend on habitat quantity and quality because (i) the fish species being caught are ecologically linked to the habitat [14, 15] and/or (ii) the habitat is used as a location for harvest. If there is enough detailed knowledge of these dependencies, the economic effects (benefits and costs) of habitat change could be quantified by applying environmental valuation methods, and thereby they could be included in evaluations of activities and policies causing habitat change.

However, knowledge detailed enough to allow such economic valuation is scarce. A review by Ledoux and Turner (2002) [16] of economic studies valuing ocean and coastal resources indicates that most valuation efforts have concerned recreational benefits, while studies based on the consequences of specific habitat change are few. This paper contributes to filling this gap by showing how coastal habitats support fish populations and fisheries on the Swedish west coast. After a brief description of the studied system, we identify and evaluate the ecological links between the major habitats and fish species occupying the coastal habitats, and the link to different types of fisheries. We also assess and describe effects of habitat disturbance which are then used as a basis for economic valuation of habitat change. Finally, implications of the results for coastal management are discussed. The study hinges on a successful interdisciplinary approach, where ecological data on habitat structure and fish populations are combined with actual economic valuation case studies.

2. The studied system

Coastal habitats included in this investigation are distributed within the depth range 0-10 m on the Swedish west coast and extend from the Norwegian border in the north (59° N, 11° E) to Öresund (55° N, 12° E) in the south (Fig. 1). The coastline can broadly be divided into three major habitat types: soft sediment bottoms, seagrass beds (*Zostera marina*) and rocky bottoms with macroalgae. A detailed description of the areal extensions of these major habitats is given in [17]. The total areal extension within the 0-10 m depth interval was 939 km^2, of which soft bottoms, rocky bottoms and seagrass beds contribute 54 percent, 26 percent and 20 percent, respectively (Table 1).

The vegetation community on rocky bottoms is mainly dominated by brown algae (*Laminaria* sp. and *Fucus* sp.) and filamentous red and brown algae [18, 19]. Seagrass beds are generally found on soft sediment bottoms at between 1-5 m depth [20]. Soft bottoms have sediment structures varying from sand to sandy-silt and silt [21], and are in this study defined as sediment bottoms free of vegetation. The macrofauna associated with the coastal habitats constitutes a major food source for the fish communities present in these areas. The number of species of associated macrofauna was similar in the three habitats, whereas density and biomass vary considerably among the major habitat types. Generally, both density and biomass were higher in the two vegetated habitats as compared to the bare sediment (Table 1).

Rocky bottoms displayed the largest diversity of fish (42 species) followed by seagrass beds (33 species) and soft bottoms (25 species) (Table 1). Density of fish was around 1 individual per m^2 in rocky habitats and seagrass beds, which was about four times higher as compared to the fish density on soft sediment bottoms free of vegetation. Biomass of fish, however, was similar (around 5 g wet weight m^{-2}) on soft bottoms and in seagrass beds, but was four times higher on rocky bottoms. However, restricting the comparison to commercially important species, seagrass beds and soft bottoms had a 20 percent higher fish biomass as compared to rocky bottoms.

The impact of human activities in the coastal zone has in some areas on the Swedish west coast resulted in an alteration and degradation of the shallow habitats, suppressing the fish populations that are present. This has been shown for cod and plaice [14, 22]. The eel stock has also declined in recent years, but the reasons for this decline remain unclear, although different hypotheses are discussed in the literature. These include the exploitation of glass eel in estuaries, increased predation, barriers to upstream migration, exploitation of yellow and silver eel, impediments to downstream migration and habitat loss [23].

3. Links between habitats, fish species and fisheries

The link between a fish population and the coastal zone can be strong, and the degree of dependence for a fish species is often determined by how habitat-specific it is. Specific requirements for feeding, shelter or spawning often determine the dependence on a habitat. In the following subsections, we evaluate the degree of habitat dependence and the utilization of five commercial fish species which are typically dominant among fish communities occupying the coastal habitats on the Swedish west coast. Critical factors taken into consideration when determining habitat dependence include: (i) the habitats' function as feeding ground, (ii) the shelter function, (iii) the possibility for the fish species to utilize alternative habitats, and (iv) the presence of juvenile and/or adult stages. These factors, which are key components for identification of Essential Fish Habitats (EFHs), are then summarized to assess the strength of habitat dependence for individual fish species. Additionally, we performed an examination of the significance of each fish species in four important fisheries on the Swedish west coast. From these analyses, we then describe the strengths of the links between coastal habitats and the various fisheries supported by these fish species (Fig. 2).

3.1. Cod (Gadus morhua)

Cod is an important species in off-shore commercial trawl fishery as well as in coastal commercial gillnet fishery [24] (Fig. 2). Historically, cod has also been the main target species in subsistence and recreational fishery but due to stock, the catches of cod have decreased dramatically in these fisheries over the last two decades [25].

This species is believed to have a complex population structure with a mixture of ocean-spawning and stationary coastal populations [26]. Larvae from off-shore stocks may settle in various types of habitats, both on bottoms off-shore and in the coastal zone where they mix with recruits from local populations. In coastal areas, larvae mainly settle in shallow water (< 10 m) and the highest concentrations of first-year juveniles have been found in vegetated habitats; that is, rocky shore with algae and seagrass beds on soft sediment bottoms [14, 27]. The vegetated habitats are important nursery grounds that offer rich food resources in combination with protection against predation for young juveniles [28]. Older juveniles (1-2 years old) extend their distribution among coastal habitats to also include sediment bottoms without vegetation, which are used as feeding grounds during the night [29]. Juvenile cod that occupy vegetated rocky bottoms take 87 percent of their food from fauna directly associated with the habitat, while the corresponding figure from soft bottoms (including seagrass) is 41 percent [19]. Thus, juvenile cod display a strong dependence on vegetated coastal habitats that offer both protection and food (Fig. 2). Habitat dependence for older juveniles is moderate for sediment bottom, and mainly involves feeding. Although some minor local populations exist in the coastal archipelago, maturing cod mainly leave the costal areas for spawning in off-shore waters [30]. Adult cod may later return to the Skagerrak coast to use these highly productive areas as feeding grounds [31].

3.2. Plaice (Pleuronectes platessa)

Plaice is mainly harvested in commercial off-shore fishery (Fig. 2), where it is caught in mixed trawl fishery together with other demersal species such as gadoids and Norway lobsters. Coastal commercial, recreational and subsistence fishery for plaice is limited, and mainly associated with gillnet fishery [24].

After spawning off-shore, plaice larvae drift towards coastal areas during the spring, where they settle on shallow sediment bottoms [32]. Juvenile plaice are strongly habitat-specific in early benthic stages [33], and in the Skagerrak-Kattegat area, first-year juveniles are restricted to sandy-silt bottoms free of vegetation with a depth of less than 3 m [34, 35]. The strong link to this specific habitat during the recruitment implies that shallow nursery grounds may act as a bottleneck for the population. During the second year, juveniles stay on sediment bottoms within the depth range 0-10 m, and 92 percent of the consumed food derive from the benthic habitat [19]. Older plaice gradually move to deeper waters off-shore where the spawning and feeding grounds are located. Thus, habitat dependence for plaice is strong for sediment bottoms free of vegetation, low for seagrass and non-existing for rocky habitats (Fig. 2). Obviously, there is one major strong link between coastal plaice nursery habitats (sandy-silt sediment) and commercial off-shore fishery. The recruitment of plaice has been shown to be negatively affected by the increasing coverage of green algal mats in these habitats [22].

3.3. Eel (Anguilla anguilla)

Eel are caught in fyke-nets or eel-pots in shallow (<10 m) vegetated habitats (seagrass beds and rocky bottoms), and are of major importance in commercial coastal fishery [36] (Fig. 2). Eel is not harvested off-shore, but is of some importance in subsistence and recreational fishery [24].

The European eel is recruited to coastal areas by larval transport from the Sargasso Sea. In the Skagerrak-Kattegat area, larvae settle in vegetated shallow habitats, and juveniles as well as adults live stationary [technical term?] in seagrass beds and algae covered rocky habitats [36]. Eel is strongly linked to vegetated costal habitats both during juvenile and adult stages and adult eel may remain in the coastal zone for many years. They hibernate within the sediment of seagrass beds and are considered as highly dependent on this habitat. Habitat dependence for rocky and sediment bottoms is ranked as medium and low, respectively. However, adult eel may also migrate into fresh water systems or to the brackish Baltic Sea [37]. As almost all harvest of eel takes place in the vegetated costal habitats; the link between these areas and the fishery is strong.

3.4. Mackerel (Scomber scombrus)

After the decline in the cod stock, mackerel has become the most popular target fish in the recreational fishery on the Swedish west coast (Fig. 2). Mackerel is also an important complement in commercial fishery [24].

Spawning as well as nursery areas for mackerel are situated in off-shore pelagic environments in the North Sea and the North Atlantic [38]. Young mackerel make seasonal feeding migrations during the summer (May to September) into the Skagerrak-Kattegat, where they utilize the rich food supply of shallow coastal habitats. Mackerel is ranked as number 3 and 10 in terms of biomass among the fish community in seagrass beds and algae covered rocky habitats, respectively [27]. However, as only between 4 and 11 percent of the consumed food derive from soft and rocky bottom habitats [19], the link to benthic habitats in terms of feeding is not strong for mackerel. The habitat dependence for mackerel is considered as moderate for sediment bottoms and seagrass and low for rocky bottoms (Fig. 2). As mackerel live and are fished in alternative habitats in coastal waters, the links between benthic habitats and fishery are considered as moderate, but they might be stronger for recreational fishery.

3.5. Sea trout (Salmo trutta)

Sea trout is mainly caught in recreational fishery (Fig. 2), but has some minor importance in subsistence fishery [24].

The spawning of sea trout takes place in fresh water streams, where also the juveniles live for one to two years. When reaching maturity, they migrate to the marine environment and the adult trout stay close to the coast during the rest of their life, only interrupted by spawning migrations into fresh water during the autumn each year [39]. Trout have the second highest biomass among coastal fish species on soft sediment bottoms, including seagrass, and the fifth highest biomass in algae covered rocky habitats [27]. For trout occupying these habitats, the diet consists to 45 percent and 32 percent, respectively, of food items associated with the benthic habitat on rocky and soft bottoms [19]. The coastal zone is only used by adults and habitat dependence for trout is considered as moderate for sediment bottoms and seagrass and low for rocky habitats (Fig. 2). Harvest mainly takes place in shallow waters, and the link between habitat and fishery is considered to be moderate.

4. Valuation of changes in coastal fish habitats

Knowledge of links between habitats, fish species and fisheries as described above is necessary for an analysis of the benefits and costs of changes in habitat quantity and quality. Following welfare economics, benefits and costs are defined as variations in producer and consumer well-being, which are measured as changes in producer surplus (also referred to as profits below) and consumer surplus, respectively [40]. Valuing a modification in habitat properties economically for fisheries is thus about finding out how such an alteration influences these surpluses in different types of fisheries. Relating this to the fisheries identified above (Fig. 2), producer surplus change is likely to be applied to catching fish for sale (i.e. off-shore and coastal commercial fisheries), and consumer surplus change to recreational fisheries, which is mainly about fishing for the individual's own enjoyment and consumption. Subsistence fisheries are less unambiguous in this sense, since they might include significant elements of catching fish both for sale and for one's own enjoyment and consumption.

Given that enough information is available on how habitats support fish populations and thereby fisheries, producer surplus change caused by habitat alterations might be estimated using a production function approach [41, 42]. This involves a quantitative study on how a shift in habitat properties influences production in fisheries (i.e. catches), including how fishery firms respond to this shift by varying other inputs for their production such as labor and fuel. The presence of such a response explains why changes in producer surplus cannot, in general, be measured by changes in revenues. As for estimating consumer surplus change, the non-market nature of how habitat alterations influence recreational fisheries suggests the use of either (1) revealed preferences methods such as the travel cost method or (2) stated preferences methods such as the contingent valuation method and choice experiments [40, 43].

Below we use three cases related to the fish species above for illustrating the economic significance of habitat modifications: (1) the impact of alterations in quality of shallow soft sediment bottoms without vegetation on Danish commercial off-shore plaice fisheries; (2) the impact of degradation in quality and loss of seagrass bed areas on Swedish commercial coastal eel fisheries; and (3) the benefits to the general public of a recovery of the cod stock at the Swedish west coast. Note that the first case refers to plaice fisheries being dependent on an ecological link between plaice and soft sediment bottoms. The second case is about fishermen's use of seagrass beds as a location for harvesting eel. These two cases make use of different types of knowledge related to habitats: the first case requires scientific knowledge of how vegetation-free soft sediment bottoms support plaice populations and the second case is based on fishermen's knowledge of seagrass beds as locations for harvest.

4.1. Plaice

By combining an ecological model on how plaice recruitment is affected by an increase in filamentous green algal mats on shallow soft sediment bottoms along the Swedish west coast [22], with an economic model of Danish off-shore plaice fishery in the Kattegat and the Skagerrak, Paulsen [44] estimates how profits in this fishery are affected by different degrees of algae coverage of these nurseries. This is done in two steps: (1) the fishery model is used for estimating that a 1-million increase in the number of plaice recruits implies an increase in profits amounting to a present value of about DKK 450 million over a 55-year time horizon and a 1 percent discount rate, and (2) the ecological model is used for predicting the consequences on recruitment of different degrees of algae coverage.[5] As an example, Paulsen [44] shows that given an average of 30 percent of the nursery grounds being covered by algal mats, a 1 km^2 increase in the availability of vegetation-free bottoms would give an increase in profits amounting to a present value of about DKK 250-300 million. As another example, the present 30-50 percent algae coverage is likely to cause a 30-40 percent reduction in plaice recruitment [22], which is estimated to result in a profit loss of about DKK 7600-12500 million, once more expressed as a present value over a 55-year time horizon. Hence, the combination of ecological and economic models shows how habitat modification, plaice population dynamics and fisheries can be analyzed coherently. However, Paulsen [44] emphasizes that if the economic models are used for policy purposes, uncertainties might motivate a 50 percent reduction of the monetary estimates.

4.2. Eel

There are about 100 fishermen active in eel fishery on the Swedish west coast [45]. In 2005, all these fishermen were approached by a mail survey to collect information enabling an economic valuation of the impact of the loss of seagrass beds on eel fisheries [46]. The data collected allowed an analysis of the link between eel catch and habitats as locations for harvest. A regression model of determinants of eel catch, basically including variables representing effort (number of days at sea, number of gears in seagrass beds, on rocky bottoms and other habitats), showed a significant importance of seagrass beds as locations for eel harvest.

Therefore, it is not surprising that fishermen reported negative economic effects when directly asked about the consequences of the loss of seagrass beds on the Swedish west coast. According to their responses, this loss has resulted in, on average, a reduction in catch of around 480 kg per year; an increase in working hours of around 1.6 hours per day; and additional costs (e.g. higher fuel consumption) of around SEK 6500 per year (Table 2).[6] Extrapolating to the whole population of eel fishermen on the Swedish west coast, this indicates a loss of catch of approximately 46 tons of eel per year and more than 22 300 additional working hours. Using the fishermen's estimate of their own net salary (on average, SEK 136 per working hour) and a price of eel amounting to SEK 60 per kg [24], the total economic loss derived from the habitat deterioration would be equal to the cost of extra working hours, plus the value of the catch lost plus the additional costs. For the whole population of eel fishermen on the Swedish west coast, the economic loss derived from the decrease in the availability of seagrass beds for fishing would then be equal to SEK 6.4 million per year. Further, the fishermen were also asked to assess the impact of other environmental disturbances. Table 2 shows that the negative effect of the loss of seagrass beds is comparable to other important disturbances affecting the eel fishery.

[5] On 1 January 2007, DKK 1 was equal to USD 0.177.
[6] On 1 January 2007, SEK 1 was equal to USD 0.146.

4.3. Cod

Cod shows high ecological dependence on both rocky vegetated habitats and seagrass beds. Findings by Pihl et al. [14] suggest that the loss of seagrass beds in the Swedish Skagerrak archipelago over the last two decades could have resulted in a reduction in cod recruitment of 6.3 million juvenile cod each year (6 700 ind. km^{-2} per yr). The significance of this reduction is illustrated by the fact that the total annual recruitment of one-year old cod in the whole Skagerrak and North Sea is estimated to about 250 million (420 ind. km^{-2} per yr) as a geometric mean for the period of 2001-2003 [24]. Thus, the loss of seagrass habitats on the Swedish Skagerrak coast corresponds to approximately 3 percent of total annual cod recruitment in the entire North Sea and Skagerrak system. This suggests that habitat alterations must be considered together with overfishing to explain the dramatic decrease in the cod stock. The associated economic loss of the joint effect of habitat modifications and overfishing can be illustrated by estimates of the benefits of a cod stock recovery. This issue has been subject to stated preferences studies in the Swedish counties of Halland and Västra Götaland [47]. The results are likely to mainly reflect the importance of cod in recreational fisheries and indicate that the benefits of a policy that would result in a cod stock recovery at the Swedish west coast to the level of 1974 amounts to SEK 230-1300 per adult individual, which corresponds to SEK 254-1430 million if aggregated to the whole adult population in the two counties.

5. Discussion

In this paper, we have described the distribution of five important fish species (plaice, cod, eel, mackerel and sea trout) in coastal habitats, their habitat dependence and links to the fisheries on the Swedish west coast. The distribution pattern and habitat dependence varied among fish species. For example, plaice showed a strong affinity with shallow soft bottoms and juveniles are not able to utilize any alternative habitats for feeding, shelter or as a nursery. Plaice is almost exclusively caught in commercial fishery and thus, the link between the sediment bottoms and the fishery is considered to be especially strong.

Cod showed a less specific pattern in habitat utilization as compared to plaice, but a similarly high importance in commercial fishery. Cod is also able to utilize off-shore habitats as e.g. nursery and feeding grounds and the link between coastal habitats and fisheries is considered as of intermediate importance. Eel mainly exist in seagrass beds and on rocky bottoms, and these habitats provide shelter from predation and rich food conditions, both for adults and juveniles. Moreover, seagrass beds are the preferred location for harvest, according to the eel fishermen, and the link between this habitat and catches was found to be significant in the econometric study. It is important to emphasize that eel fishery is also an important source of income and around 50 percent of the fishermen in Skagerrak and Kattegat are to some extent dependent on eel fishery [24].

In conclusion, vegetated nursery habitats for cod and soft sediment nursery for plaice have strong links to commercial fishery. However, direct comparisons between the two species should not be made as cod also grow up in alternative habitats off-shore, whereas plaice are restricted to shallow coastal nurseries. Vegetated habitats, mainly seagrass beds, are strongly linked to commercial coastal eel fishery as eel both occupy and are fished in these areas. By the same argument, soft sediment bottoms and seagrass beds are mainly linked to recreational fishery for mackerel and sea trout.

The economic effects of coastal habitat degradations were illustrated with three case studies representing different degrees of habitat dependence/distribution conditions for fish: in the case of plaice, the habitat appears to be an ecological bottleneck; in the eel case, the habitat is essential as a location for harvest and in the case of cod; we illustrate difficulties in valuing habitat changes when the habitat dependence and association of a fish species are less obvious. The remaining two fish species, mackerel and sea trout, are common species in coastal habitats, but the bottleneck is in the fresh water system for sea trout and off-shore for mackerel. For these species, there are no known responses to habitat modifications in the coastal zone on which to build an economic analysis. However, this study illustrates their link to the coastal habitats and the importance of these fish species in subsistence- and recreational fisheries on the Swedish west coast.

Our study shows the importance of a combined interdisciplinary analysis in order to more specifically assess what economic values, besides ecological functions and services, are being lost in case of a habitat alteration. An adequate understanding of the ecological links between fish species and habitats is essential in an economic valuation exercise, which is well illustrated by the plaice case. The valuation cases also illustrate the considerable and diverse types of data required for carrying out this type of interdisciplinary research. Besides the need for detailed natural scientific data and ecological knowledge, surveys are generally needed in such research for estimating recreational values associated with fisheries. This might also be true for assessing profits in commercial fisheries since official fishery statistics might not contain enough details regarding, for example, the costs in fisheries or how fishermen are using different habitats for harvest. The latter was illustrated by the eel case, where a survey was used to collect fishermen's knowledge. This sort of knowledge has shown to be useful and, in some cases, almost constitutes an unexplored source of data [48]. The need for very diverse data makes it likely that a cost-effective data collection can only occur if the ecological and economic research efforts are coordinated at an early stage of the research. Such coordination also greatly facilitates the identification of crucial data gaps.

This study also illustrates the importance of considering habitat alterations in coastal zone management. Both plaice and eel fisheries are likely to be negatively affected by eutrophication due to their dependence on shallow soft bottoms free from vegetation and seagrass beds, respectively. This should be taken into account when deciding on efforts for reducing nutrient loads to the coastal zone. Further, the eel case illustrates that from an economic point of view, habitat loss could be equally important as damage caused by seals and cormorants, although the latter damage might be more conspicuous and might therefore generally receive more attention in fishery policies. In the case of cod, an economic loss of the joint effect of habitat modifications, fish habitat dependence and overfishing was illustrated by estimates of the benefits of a cod stock recovery on the Swedish west coast. Franzén et al. [49] showed that these benefits are sufficiently large to cover the costs of at least a 4½-year bilateral Danish-Swedish commercial cod fishery moratorium in the Kattegat and the Skagerrak Sea. Average estimates of benefits and costs suggest that a 21-year moratorium is economically motivated. While this indicates that catch restrictions might be a first-best measure for urgent action, the cod's habitat dependence suggests habitat restoration and protection as complementary measures.

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References

[1] Pauly D, Christensen V, Guenette S, Pitcher TJ, Sumaila UR, Walters CJ, Watson R, Zeller D. Towards sustainability in world fisheries. Nature 2002;418(6898):689-95.
[2] Earth Trends; World Resources Institute, 2006.
[3] Baden S, Gullström M, Lundén B, Pihl L, Rosenberg R. Vanishing Seagrass (*Zostera marina*, L.) in Swedish Coastal Waters. AMBIO 2003;32(5):374-77.
[4] Pihl L, Isaksson I, Wennhage H, Moksnes P-O. Recent increase of filamentous algae in shallow Swedish bays: Effects on the community structure of epibenthic fauna and fish. Netherlands journal of aquatic ecology 1995;29(3-4):349-58.
[5] Millennium Ecosystem Assessment. Ecosystems and Human Well-Being: Synthesis. Island Press, Washington, DC, 2005.
[6] Rönnbäck P, Kautsky NP, Pihl L, Troell M, Söderqvist T, Wennhage H. Ecosystem goods and services from Swedish coastal habitats- identification, valuation and implications of ecosystem shifts. Ambio 2007;*In press*.
[7] Gillanders BM, Able KW, Brown JA, Eggleston DB, Sheridan PF. Evidence of connectivity between juvenile and adult habitats for mobile marine fauna: an important component of nurseries. Marine Ecology-Progress Series 2003;247:281-95.
[8] Beck MW, Heck J, K.L., Able KW, Childers DL, Eggleston DB, Gillanders BM, Halpern B, Hays CG, Hoshino K, Minello TJ, Orth RJ, Sheridan PF, Weinstein MP. The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates. Bioscience 2001;51(8):633-41.
[9] Gibson RN. Impact of habitat quality and quantity in the recruitment of juvenile flatfishes. Netherlands journal of Sea Research 1994;32(2):191-206.
[10] Carr MH. Effects of makroalgal dynamics on recruitment of a temperate reef fish. Ecology 1994;75(5):1320-33.
[11] Choat JH, Ayling AM. The relationship between habitat structure and fish faunas on New Zealand reefs. Journal of Experimental Marine Biology and Ecology 1987;110(3):257-84.
[12] Benaka LR. Fish habitat: Essential fish habitat and rehabilitation. American Fisheries Society Symposium 1999;22.

[13] Rönnbäck P, Kautsky N, Pihl L, Troell M, Söderqvist T, Wennhage H. Ecosystem goods and services from Swedish coastal habitats- identification, valuation and implications of ecosystem shifts. Ambio 2006;*Submitted*.
[14] Pihl L, Baden S, Kautsky N, Ronnback P, Soderqvist T, Troell M, Wennhage H. Shift in fish assemblage structure due to loss of seagrass *Zostera marina* habitats in Sweden. Estuarine Coastal and Shelf Science 2006;67(1-2):123-32.
[15] Wennhage H, Pihl L, Stål J. Distribution and quality of plaice (*Pleuronectes platessa*) nursery grounds on the Swedish west coast. Journal of Sea Research 2006;, doi.org/10.1016/j.seares.2006.08.008.
[16] Ledoux L, Turner RK. Valuing ocean and coastal resources: a review of practical examples and issues for further action. Ocean and Coastal Management 2002;45(583-616).
[17] Stål J, Pihl L. Quantitative assessment of the areal extension of shallow fish habitats on the Swedish west coast. Ices Journal of Marine Science 2006;*Submitted*.
[18] Stål J. Motile epibenthic fauna in shallow subtidal rocky habitats on the Swedish west coast: changes in assemblage structure with season and depth. Marine biology research 2006;Submitted.
[19] Stål J, Pihl L, Wennhage H. Food utilisation by coastal fish assemblages in rocky and soft bottoms on the Swedish west coast: Inference for identification of essential fish habitats. Estuarine, Coastal and Shelf Science 2007;71(3-4):593-607.
[20] Baden S, Boström C. The leaf canopy of seagrass beds: fauna community structure and functional in a salinity gradient along the Swedish coast. In: Ecological comparisons of sedimentary shores: ecological studies 151, Reise, K. (ed) Springer Verlag 2001:213-36.
[21] Pihl L. Exposure, Vegetation and Sediment as Primary Factors for Mobile Epibenthic Faunal Community Structure and Production in Shallow Marine Soft Bottom Areas. Netherlands Journal of Sea Research 1986;20(1):75-83.
[22] Pihl L, Modin J, Wennhage H. Relating plaice (*Pleuronectes platessa*) recruitment to deteriorating habitat quality: effects of macroalgal blooms in coastal nursery grounds. Canadian Journal of Fisheries and Aquatic Sciences 2005;62(5):1184-93.
[23] Dekker W. Slipping through our hands – Population dynamics of the European eel. Ph.D thesis. 2004;University of Amsterdam:186pp.
[24] Swedish Board of Fisheries. Fakta om svenskt fiske [Facts about Swedish fisheries]. Fiskeriverket, Göteborg. [In Swedish] 2006.
[25] Svedäng H, Bardon G. Spatial and temporal aspects of the decline in cod (*Gadus morhua* L.) abundance in the Kattegat and eastern Skagerrak. Ices Journal of Marine Science 2003;60(1):32-37.
[26] Knutsen H, Andre C, Jorde PE, Skogen MD, Thuroczy E, Stenseth NC. Transport of North Sea cod larvae into the Skagerrak coastal populations. Proceedings of the Royal Society of London Series B-Biological Sciences 2004;271(1546):1337-44.
[27] Pihl L, Wennhage H. Structure and diversity of fish assemblages on rocky and soft bottom shores on the Swedish West Coast. Journal of Fish Biology 2002;61 (supplement A):148-66.
[28] Borg Å, Pihl L, Wennhage H. Habitat choice by juvenile cod (*Gadus morhua* L.) on sandy soft bottoms with different vegetation types. Helgolander Meeresuntersuchungen 1997;51(2):197-212.
[29] Pihl L, Rosenberg, R. Production, abundance and biomass of mobile epibenthic marine fauna in shallow waters, western Sweden. Journal of Experimental Marine Biology and Ecology 1982;57:273-301.
[30] Pihl L, Ulmestrand M. Migration Pattern of Juvenile Cod (*Gadus morhua*) on the Swedish West Coast. Ices Journal of Marine Science 1993;50(1):63-70.
[31] Svedäng H, Righton D, Jonsson P. Return migrations of Atlantic cod (*Gadus morhua* L.) to the North Sea evidenced by archival tagging of cod off the eastern Skagerrak coast. ICES. CM 2006/Q:06: 1-30. 2006.
[32] van der Veer HW. Immigration, settlement and density-dependent mortality of a larval and early post-larval 0-group plaice (*Pleuronectes platessa*) population in the western Wadden Sea. Mar. Ecol. Prog. Ser 1986(29): 223-36.

[33] Gibson RN, Robb L. Sediment selection in juvenile plaice and its behavioural basis. Journal of Fish Biology 2000;56(5):1258-75.
[34] Wennhage H, Pihl L. Substratum Selection by Juvenile Plaice (*Pleuronectes platessa* L) - Impact of Benthic Microalgae and Filamentous Macroalgae. Netherlands Journal of Sea Research 1994;32(3-4):343-51.
[35] Pihl L. Abundance biomass and production of juvenile flatfish in southeastern Kattegat. Netherlands Journal of Sea Research 1989(24):69-81.
[36] Svedäng H. Vital population statistics of the exploited eel stock on the Swedish west coast. Fisheries Research 1999;40(3):251-65.
[37] Tzeng WN, Wang CH, Wickstrom H, Reizenstein M. Occurrence of the semi-catadromous European eel *Anguilla anguilla* in the Baltic Sea. Marine Biology 2000;137(1):93-98.
[38] Borja A, Uriarte A, Egana J. Environmental factors and recruitment of mackerel, *Scomber scombrus* L. 1758, along the north-east Atlantic coasts of Europe. Fisheries Oceanography 2002;11(2):116-27.
[39] Bohlin T, Pettersson J, Degerman E. Population density of migratory and resident brown trout (*Salmo trutta*) in relation to altitude: evidence for a migration cost. Journal of Animal Ecology 2001;70(1):112-21.
[40] Freeman AM. The measurment of environmental and resource values: Theory and methods (Second edition), Resources for the future, Washington, DC. 2003.
[41] Barbier EB. Valuing the environment as input: review of applications to mangrove-fishery linkages. Ecological Economics 2000;35:47-61.
[42] Knowler DJ, MacGregor BW, Bradford MJ, Peterman RM. Valuing freshwater salmon habitat on the west coast of Canada. Journal of Environmental Management 2003;69(3):261-73.
[43] Söderqvist T, Eggert H, Olsson B, Soutukorva A. Economic valuation for sustainable development in the Swedish coastal zone. Ambio 2005;34(2):169-75.
[44] Paulsen S. Valuation of coastal habitats sustaining plaice fisheries. Manuscript, Beijer International Institute of Ecological Economics, Stockholm, and Department of Economics, Swedish University of Agricultural Sciences, Uppsala. 2007.
[45] Swedish Board of Fisheries. Sälskador i ålfisket längs den svenska västkusten [Damages from seals to eel fisheries at the Swedish west coast]. Finfo 2003:9, ISSN 1404-8590, Fiskeriverket, Göteborg. [In Swedish with summary in English]. 2003.
[46] Paulsen S. Economic impacts of coastal habitat change on eel fisheries: A fishermen's knowledge based survey. Manuscript., Beijer International Institute of Ecological Economics, Stockholm, and Department of Economics, Swedish University of Agricultural Sciences, Uppsala. 2007.
[47] Olsson B. Two essays on valuation of marine resources: applications to Sweden. Licentiate of Philosophy Thesis, Department of Economics, Göteborg University. 2004.
[48] Neis B, Schneider DC, L. F, Haedrich RL, Fischer J, Hutchings JA. Fisheries assessment: what can be learned from interviewing resource users? Canadian Journal of Fisheries and Aquatic Sciences 1999;56:1949-63.
[49] Franzén F, Soutukorva Å, Söderqvist T. Skagerraks miljö i samhällsekonomisk belysning. Report, Forum Skagerrak II. [In Swedish with summary in English.] 2006.

Figure 1.

Figure 2: Relative degree of dependence for five common fish species on three major shallow (0-10m) habitats in the coastal zone of the Skagerrak-Kattegat area, and the importance of the fish species in four types of fisheries. The link between fisheries and habitats is indicated with a bar. Circle size and bar thickness indicate high, medium and low dependence or importance, and ns = not significant. R=rocky vegetated habitats, S = Soft sediment without vegetation, Z = Zostera marina beds. CF = commercial fishery, SF =subsistence fishery, RF = recreational fishery.

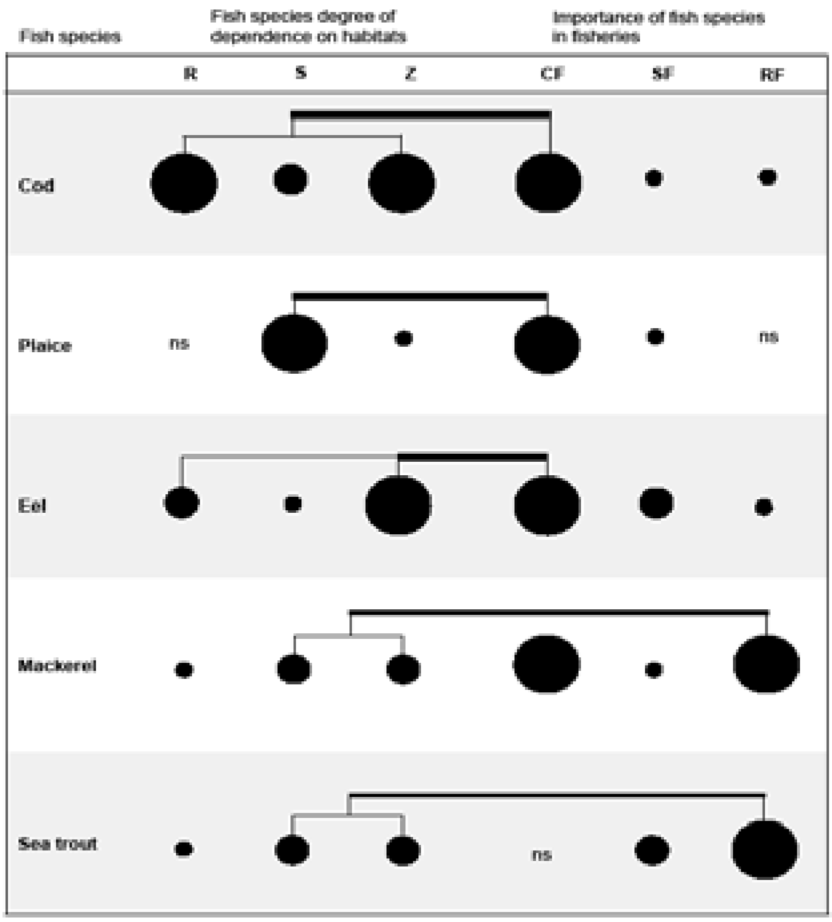

Table 1. Summary of major ecosystem structuring factors in coastal habitats on the Swedish west coast.

Habitats	**Sediment**	**Seagrass**		**Rocky algae**	**Total**	**References**
Areal distribution km^2 (%)	506 (54%)	187 (20%)		246 (26%)	939	Stål & Pihl 2007
Vegetation (g/m^2)	0	250-500		1900		Baden & Pihl 1984; Stål 2007
	Infauna	Infauna	Epifauna	Epifauna		
Macrofauna						
Number of species	101	72	43	127		Möller 1986; Baden 1990; Stål et al. 2007
Density (ind/m^2)	3500	10800	8000	14000		Möller 1986; Baden 1990; Stål et al. 2007
Biomass (g/m^2)	47	24	43	104		Möller 1986; Baden 1990; Stål et al. 2007
Fish						
Number of species	25	33		42		Stål et al 2007
Density (ind/m^2)	0.23	1.2		0.98		Stål et al 2007; Pihl et al 2006
Biomass (g/m^2)	4.4	5.5		23.2		Stål et al 2007; Pihl et al 2006

Table 2. Average negative impact of different factors affecting eel fisheries on the Swedish West Coast.

	Decrease in catch (kg/year)	Extra working hours (hours/day)	Extra costs (SEK/year)
Decrease in seagrass bed areas	480	1.6	6500
Fouling of gears (e.g. algae and other organisms)	80	1.0	1760
Seals	700	1.7	19500
Cormorants	500	1.2	9150
Crabs in the gears	180	1,0	3500