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When resilience is undesirable: Regime shifts and ecosystem service generation in Swedish coastal soft bottom habitats

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ABSTRACT

Recent findings from both terrestrial and aquatic systems suggest that ecosystems can undergo regime shifts where they suddenly change from one state into another. This can have important implications for formulation of management strategies, as undesired system characteristics (from a human perspective) with high resistance to restoration efforts may develop. This paper analyses ecological and economic consequences from increased filamentous algae cover on shallow soft bottoms along the Swedish West Coast. It is suggested that this emergent widespread phenomenon represents a regime shift caused by long-term increase in coastal nutrient conditions. A successive increase in the sediment nutrient pool has undermined the resilience of these shallow systems. After a regime shift, self-generation evolves as an emergent property keeping the system locked in a high-density algae state. The structural and functional characteristics of the new system state differ significantly from the original state, resulting in less valuable ecosystem goods and services being generated to the society. These include reduced capacity for mitigating further coastal eutrophication, reduced habitat quality for commercial fishery species and the loss of aesthetic and recreational values.

INTRODUCTION

Approximately 20% of the world's population live within 30 km of the coast (Gommes et al. 1998) and many coastal marine ecosystems worldwide are subject to heavy and increasing pressure from a variety of activities (e.g. industries, agriculture, settlements, fisheries, aquaculture, etc.). Nutrient discharge may have profound environmental consequences as it generally stimulates primary production and increases the trophic state of coastal ecosystems. Since the 1970's there has been a doubling of nutrient input (nitrogen) to Scandinavian waters (Skagerrak, Kattegat and the Baltic Sea), resulting in eutrophication effects along the Swedish coast (Richardsson and Heilman 1995, Lindahl et al. 2003). Eutrophication, here defined as an increase in the rate of supply of organic matter to an ecosystem (Nixon 1995), has the potential to impact negatively on ecosystem structure and function. Increased occurrence of filamentous algae on shallow soft bottoms along the Swedish West Coast, suggested to represent a symptom of large-scale eutrophication (Valiela et al., 1997, Pihl et al. 1999, Österling and Pihl 2001), is a phenomenon first reported in the late 1970s and has since escalated (Afzelius 1978, Wennberg 1987, Pihl et al. 1995, Pihl et al. 1999). Thus, soft bottoms with no or only patchy macrophyte vegetation are increasingly being transformed into systems dominated by filamentous algae. This new emergent "state" of a shallow coastal system has in Sweden proven to be resistant to restoration efforts (Harlén and Zackrisson 2001).

Recent findings within ecological research indicate that ecosystems can undergo relatively quick, large-scale shifts to drastically different states (Nystrom et al. 2000, Scheffer et al. 2001, Dent et al. 2002, Petraitis and Dudgeon 2004, Folke et al. in press). Even though examples of such regime shifts increasingly are discussed in the literature, still relatively few studies identify possible shifts between alternative states and analyse the consequences of such shifts within the resilience framework and its consequences for ecosystem services (see Folke et al. 2002, Folke et al. in press). The main aim of this paper is to analyse how the generation of ecosystem goods and services differ between the two possible alternative states of Swedish shallow soft bottom coastal habitats. Further aims are to describe structural and functional changes, identify main system drivers and discuss inherent self-generating properties from a resilience perspective.

RESILIENCE AND ALTERNATIVE STATES

Resilience is the ability of a social-ecological system to undergo, absorb and respond to change and disturbance, while maintaining its functions and controls (Carpenter et al. 2001). The definition of resilience includes three equally important aspects: (1) the ability of the system to resist a disturbance so that it is not overwhelmed, but instead retains its functions; (2) capability of the system for self-organization (endogenous reorganization); and (3) the ability to learn from and incorporate disturbances (mechanisms for adaptive capacity) (Carpenter 2001). Loss of resilience is not necessarily a *noticeable* gradual degradation, but can be a sudden shift triggered by a stochastic event or when a threshold is suddenly reached. Until then the system may not give any indication of vulnerability, particularly if we monitor the flows of ecosystem goods and services. Since the theory of multiple states was developed (May 1977), examples of alternative states have been appearing in the literature (see Table 1 for some examples from marine ecosystems). The new emergent properties

after a system shift can from a societal perspective either be positive or negative. From a management perspective one must be clear about which system is desired, i.e. what ecosystem goods and services are preferred and valued by society. To be able to take pro-action it is important to identify the drivers that shape the system and its resilience, i.e. what disturbances or changes the system encounters and what management institutions that are important. As Carpenter et al. (2001) phrased it: “*one must specify the resilience of what to what*”. Not only may the new system state be undesirable from a societal perspective, but the possibilities to transfer the system back to a previous state may also be either very costly or even impossible (i.e. a highly resilient “new state”). Since first described in mid 1970s (Holling 1973), work on resilience has moved from dealing with solely ecological systems to analyzing the interaction between social and ecological systems. Resilience has been used as a metaphor and framework to discuss paths to reach sustainable development, as a characteristic of dynamic systems and as an operational indicator of ecosystem states. Identification of operational indicators has been identified as a key research priority to make resilience more applicable from a management perspective. Attempts are being made to quantify the concept of resilience with operational indicators relevant for the system under study (Carpenter et al. 2001). Dynamic processes through which a system has evolved and the thresholds initiating change needs to be understood, and slow variables needs to be discerned from the fast.

COASTAL EUTROPHICATION-SWEDISH WEST COAST

In marine systems nitrogen is generally considered as a limiting factor for algal growth (Nixon 1995). Swedish coastal waters have received increasing amounts of nitrogen over the last decades from several sources such as direct point discharges (sewage and industries), land run-off and atmospheric deposition, leading to a generally higher trophic state. Nitrogen loading to the Skagerrak and Kattegat on the Swedish West Coast has increased about four times since 1930 and has doubled after 1970 (Rosenberg et al. 1990, Aure 1996, Rosenberg et al. 1996). Phytoplankton production in coastal waters has also doubled, from around $100 \text{ g C m}^{-2} \text{ y}^{-1}$ in the 1950's and 1960's, to $200 \text{ g C m}^{-2} \text{ y}^{-1}$ during the period 1980 to 2000 (Richardsson and Heilman 1995, Lindahl et al. 2003). Over the same time period coastal sedimentation has increased about five times, from 30 to $140 \text{ g C m}^{-2} \text{ y}^{-1}$ (Lindahl et al. 2003). Indications of eutrophication in these waters have been observed, for example as increased frequencies of algal blooms and reductions of oxygen in bottom waters (Baden et al. 1990). Swedish coastal waters have small tidal amplitudes, generally less than 20 cm, which creates only weak tidal currents. Thus the water exchange is mainly dependant on residual currents and on irregular changes in water level of up to 1.5 m caused by storms and fluctuations in atmospheric pressure. These conditions make the Swedish coastal zone and especially the inner archipelago sensitive to increased nutrient loading, as nutrients may not so easily be flushed out of the system.

An increased supply of nutrients to the coastal ecosystem may have strong effects on the structure and function of the assemblages of benthic vegetation. It often implies a shift in species composition from late successional perennial algae to fast growing annual species. Filamentous green algae such as species of *Cladophora* and *Enteromorpha* have a high surface area to volume and are characterised by fast growth rates and high nutrient uptake (Wallentinus 1984). Such ephemeral algae are commonly observed in areas with elevated nutrient supply where they occur as

epiphytes on other vegetation or forming mats covering the sediment (Pihl et al. 1996, 1999). The occurrence of such dense algal cover in coastal shallow waters is an increasing worldwide phenomenon (Hodking and Birch 1986, Valiela et al. 1997). The first documentation of a shift in algal composition from the Swedish West Coast is from the late 1970s and early 1980s. On some shallow rocky sites *Fucus vesiculosus* and *Fucus serratus* dominated from 1965 to the end of 1970's, when they gradually were replaced by species such as *Cladophora flexuosa*, *Cladophora glomerata*, *Enteromorpha linza* and *Enteromorpha simplex* (Wennberg 1987). In another study, investigating soft-bottom systems, the average cover of green algal mats in ten shallow (0-1 m) soft bottom bays increased from < 3 % during the period 1976 to 1978, to 40 % in the years 1992-1994 (Fig. 1) (Pihl et al. 1995). From 1994 to 1996, the distribution of algal mats was monitored by aerial photography in shallow (0-1 m) soft bottom areas along 200 km of the Swedish Skagerrak Coast. Average cover of green algal mats, estimated on six occasions during summer peak, ranged from 30 to 50 % of the total shallow soft bottom habitat in the archipelago (Pihl et al. 1999).

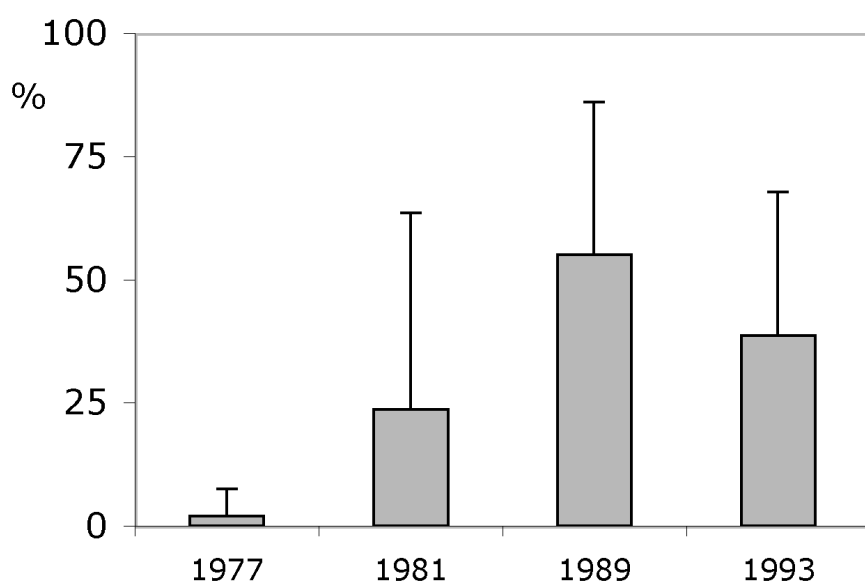


Figure1.
Percentage cover (mean and SD) of filamentous green algae in ten shallow (0-1 m) soft bottom bays on the Swedish West coast during four sampling period from 1976 to 1994 (Based on data from Pihl et al. 1995)

COASTAL SHALLOW SOFT BOTTOM ECOSYSTEM

Soft bottom sediments dominate the shallow part (0-1 m) of the coastal zone along the Swedish West Coast (Pihl and Rosenberg 1982). In most regions sediment with a sandy or sandy-silt structure contribute to more than 70 % of the bottom area within this depth interval (Pihl unpubl. data). Such habitats have usually no vegetation, but in

some areas a patchy coverage of the macrophytes *Zostera marina* and *Ruppia sp.* or macroalgae as *Fucus spp.* exists. *Z. marina* meadows are otherwise usually found in deeper areas (1-8 m) (Baden and Pihl 1984, Baden and Boström 2001).

The shallow soft bottom habitat constitutes a key coastal ecosystem, because of its wide distribution and its role in sustaining important ecological functions. Soft sediment bottoms are characterized by a high infauna and epibenthic fauna production (Pihl and Rosenberg 1982, Möller et al. 1985) and play an important role as nursing and feeding habitat for many commercial fish species (Pihl and Wennhage 2002). The main energy source for the shallow soft bottom system is the phytoplankton primary production imported from the pelagic system outside the littoral zone (Möller et al. 1985). Suspended phytoplankton is utilized by filter-feeders or after deposition on the sediment surface phytoplankton are eaten by deposit-feeders. In addition to this, micro-phytobenthic plankton attached to sediment particles makes significant contribution to the primary production of the shallow system (Sundbäck et al. 1990). In this way, secondary benthic fauna production can exceed primary production within the shallow system. Mainly depending on hydrodynamic conditions different functional groups dominate the benthic fauna assemblages. In exposed and semi-exposed sites benthic filter-feeders, as the bivalves *Mya arenaria* and *Cerastoderma edule*, constitute an important functional group (Möller 1986). The benthic filter-feeders capture and transfer energy from the pelagic system to other benthic and epibenthic organisms, including fish (Cloern 1982, Officer et al. 1982, Loo and Rosenberg 1989). In more sheltered areas surface deposit feeders, for example the crustacean *Corophium volutator*, may constitute the more important functional group due to higher sedimentation of organic matter in such areas (Möller and Rosenberg 1982).

The high food production and reduced predation pressure from larger fish make the shallow soft bottom ideal nursery grounds for fish (Zijstra 1972, Gibson 1994). Flatfishes, such as plaice, flounder, sole, turbot and brill, settle as larvae on sandy beaches and stay as juveniles for several months in shallow (< 3m) waters (Pihl 1989). Growth and survival of the juvenile flatfishes are significantly higher on the shallow soft bottoms compared to other alternative habitats, and such areas are therefore considered as “essential” in the life cycle of these species (Gibson 1994). Juvenile gadoids (codfish) and clupeids (herring) use the shallow habitats as feeding grounds, and perform seasonal or diurnal foraging migrations utilizing the rich production of the sandy beaches (Pihl and Wennhage 2002, Wennhage and Pihl 2002). The shallow sediment habitat thereby constitutes an important link in the recruitment process of many fish species.

Shallow soft bottoms also play an important role in the carbon and nutrient dynamic of coastal systems. Particulate organic material and plankton organisms in the surface water, is trapped and can accumulate temporarily in shallow soft bottom sediment during the summer. Some of this carbon is available for consumption by benthic meio- and macrofauna in the system, and can either be burrowed in the sediment or transferred out of the system via migration of mobile species or predatory fish. Möller et al. (1985) estimated that 50-75 % of the production of benthic fauna is consumed by epibenthic predators during most years, and that approximately 90 % of the production of these predators may be exported to deeper waters during late autumn. Micro-organisms in the sediments also take part in the transfer process by mineralization of organic matter. Thus, the shallow sediment system may function as

an important intermediate pathway to transfer energy from lower trophic levels in the pelagic system to those further up in the food web via transformations in the benthic system, but may also function as a sink for carbon and nutrients through sedimentation or transfer to the atmosphere.

ALTERNATIVE SYSTEM STATE- NET CHANGES IN ECOSYSTEM GOODS AND SERVICES

The supply from nature of ecosystem goods and services has usually been taken for granted and this has in many places resulted in poor management of underlying structures and processes that facilitate its generation. Researchers have just begun to identify the goods and services that society depends upon, and most studies have either focused on systematic typology (e.g. de Groot et al. 2002) or large spatial scales (Costanza et al. 1997, Daily 1997). Detailed studies at the ecosystem scale are few, and for coastal areas most studies are concerned with tropical systems such as mangroves and coral reefs (Ewel et al. 1998, Moberg and Rönnbäck 2001). Consequently, there is a need for studies that identify the generation of goods and services also from temperate coastal ecosystems. See Ledoux and Turner (2002) for a review of earlier attempts to value some goods and services in economic terms.

The formation of algal mats on unvegetated shallow soft bottoms implies considerable changes in ecosystem structure and functions, many of which are important for the generation of ecosystem goods and services. We will concentrate our analysis to the net effect on three groups of ecosystem services: (1) mitigation of eutrophication; (2) seafood production; and (3) aesthetic and recreational values (Table 2).

Mitigation of eutrophication

Bays with recurrent algal mats on the Swedish west coast have on average three times higher organic carbon and nitrogen sediment content compared to algae free bays (Pihl et al. 1999, Svensson and Pihl 2001). Besides localised effects from increased nutrient load to coastal environments, this can also be explained by increased sedimentation due to reduced water circulation caused by algal mats, and by the algae also acting as mechanical filters for organic matter in the water column. Further, parts of the algal mats decompose during the productive season and as much as 50% of the annual production can be incorporated in the sediment when dead algae accumulate on the bottom (Owens and Stewart 1983, Thiel and Watling 1998). The initial net result is enhanced accumulation of organic matter, which through a number of feedback mechanisms changes nutrient dynamic of the sediment. The organic enrichment may for example lead to higher oxygen consumption that, together with the reduced water exchange, will result in decreased oxygen levels in both the water column and the sediment. The reduced oxygenation of the sediment causes the redox-cline to move towards the sediment surface, and the volume and surface area of the sediment available for efficient mineralization will be reduced. This is mainly due to lower decomposition rates during anaerobic compared to aerobic conditions (Hansen and Blackburn 1991, Kristensen et al. 1995, Kristensen and Holmer 2001). The quality of the important ecosystem service of transferring organic particles to inorganic matter is thus severely reduced.

The reduction of oxygen in bottom water over the sediments under algal mats will also affect benthic infauna. Recent field investigations, comparing shallow soft bottom bays with and without macroalgal mat cover, have shown that the number of

species, density and biomass of benthic macrofauna are 40-50% lower under developed algal mats (Svensson et al. 2000). The changed structure and reduction of infauna under algal mats is not only an effect of deteriorating oxygen conditions, but may also be a consequence of algae filtering out settling larva, thus, preventing new faunal recruitment to the sediment (Olofsson 1980). The shift in species composition of the infauna in response to algal mats often results in dominance of tolerant opportunistic species (Norkko and Bonsdorff 1996 a, b). Such species shifts usually involve a change among functional groups. Suspension feeders and surface deposit feeders are drastically reduced in sediments under algal mats, whereas burrowing deposit feeders and predators remain more or less unaffected compared to natural sediments without algae (Fig. 2) (Österling and Pihl 2001). The functional groups of suspension feeders and surface deposit feeders are generally dependent on a good water circulation for feeding and are less tolerant to low oxygen levels. The loss of suspension and surface deposit feeder will dramatically decrease the capacity of the benthic system to absorb and transfer organic matter to higher trophic level such as fish harvested by humans (Cloern 1982, Officer et al. 1982). Further, deep-burrowing fauna are also important for sediment mineralization (Thrush and Dayton 2002) and their function may also be impaired from lower oxygen concentrations. The overall reduced efficiency of this ecosystem service will lead to an increased net accumulation of organic matter, with the potential of becoming a nutrient source in shallow coastal systems.

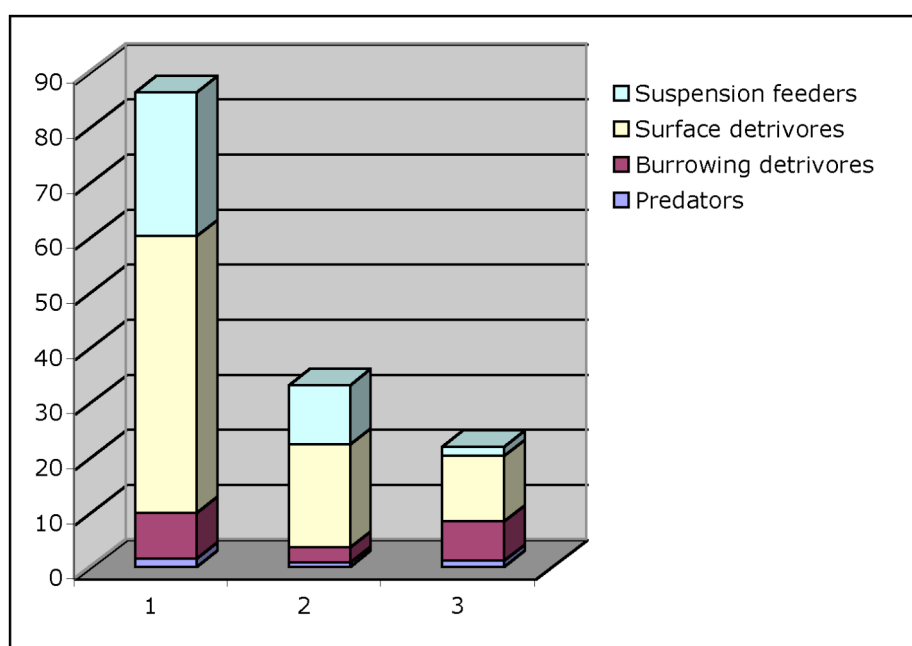


Figure 2.

Shift in species composition, i.e. functional groups, of infauna density (per 0.01 m²) in response to algal mats cover. Treatment 1= no algal mats; Treatment 2= 480 g m⁻² of algae in net-bags placed somewhat above the sediment; Treatment 3= 480 g m⁻² of algae in cages on the sediment. Treatment 2 simulates moderate algae cover as water exchange is facilitated. (based on data from Österling and Pihl, 2001).

Apart from the self-evident eutrophication problem in the local environment, organic enrichment may also create negative impacts at the regional scale when algal mats are transported to deeper bottoms. Such transfer can occur continuously by water currents

during the summer, but is especially evident in connection with autumn storm events. Deeper coastal areas are sensitive to increased levels of sedimentation since the decomposition of organic matter commonly results in oxygen deficiency in the bottom water and sediments (reviewed in Diaz & Rosenberg 1995). Several fjord system on the Swedish west coast show a significant negative trend in oxygen concentration in the bottom water over the last decades (Rosenberg 1990), which is believed to be caused by sedimentation of excess micro- and macroalgal blooms. There is, however, a need for studies looking at such inter-linkage in more detail.

Denitrification is another ecosystem service that is affected by algal mats. The reduced oxygenation of the sediment-water interface beneath algal mats has the potential to reduce the capacity of the denitrification process, i.e., the removal of dissolved inorganic nitrogen from the system. It has been shown, that in sediments enriched with algae the denitrification rate is reduced by one order of magnitude (Hansen and Blackburn 1991, Tuominen et al. 1999). The importance of infauna activity for loosening the sediment and thereby increasing denitrification processes is well documented (Hansen and Kristensen 1997, Berg et al. 2001, Gilbert et al. 2002). Furthermore, increased faunal activity can also increase DIN fluxes from the sediment (Christensen et al. 2000, Emmerson and Raffaelli 2000, Berg et al. 2002, Sundbäck et al. 2003). The presence of the amphipod *Corophium volutator*, common in shallow soft bottom sediments increased denitrification rates by a factor 3-5 (Pelegrí et al., 1994). However, the processes affecting nitrification and denitrification in shallow soft sediments are many and complex. Micro-phytobenthos (MPB) plays an important role for nutrient dynamics in shallow areas (Sundbäck et al. 1990, Havens et al. 2001) and the direct and indirect interaction between MPB and macroalgae will influence the denitrification processes. As previously described theories and some studies investigating the effects from macroalgae occurrence upon shallow sediment nitrogen dynamics indicate that macroalgae mats reduce denitrification. However, some studies imply that there is no clear-cut answer to how denitrification is affected by algal mats (Sundbäck and Miles, 2002, Sundbäck et al. 2003, Dalsgaard, 2003) indicating the need for future research. For example, the shading and competition for nitrate and ammonium with MPB may under some circumstances be significant but the competition will depend on both the placing of the algae cover (on water surface or sediment surface) as well as on the degree of shade-adapted MPB communities (Sundbäck and Miles, in press). The reduced infauna beneath algal mats can lower the denitrification rate by two mechanisms. The first is the reduction of sediment surfaces suitable for the denitrification process, and the second is increased MPB activity from decreased sediment stirring. Shallow soft sediments function as sinks for nutrients, but under anoxic conditions (resulting from development of macroalgae mats) these sediments can instead become sources and leach N and P to the water column (Tyler et al. 2003). It is important to remember that even if both macroalgae and MPB are sinks for nitrogen the nutrients still remain in the ecosystem (but transformed). Denitrification rates are between 0.060 to 1 m mol m⁻² h⁻¹ (7- 123 kg m⁻² yr⁻¹) in shallow sandy soft bottom habitats on the Swedish west coast (Sundbäck and Miles 2000, 2002), values being in the lower range reported from other shallow-water coastal sediments in temperate areas (Cabrita and Brotas 2000).

It should be emphasized that the reduction of denitrification as an ecosystem service have the potential to create negative impacts across the local, regional and international scale as dissolved inorganic nutrients can be transported over large

distances. The reduced capacity to remove dissolved nitrogen in Swedish coastal waters is linked to coastal eutrophication problems in neighbouring waters, although the relative importance may vary. The economic value of reduced marine eutrophication in Swedish coastal waters and in the Baltic Sea has been estimated in several studies. Frykblom et al. (2004) report that the benefits of a one-metre improvement in summer Secchi depth in the Stockholm archipelago amount to SEK 60-500 million yr⁻¹ (1 SEK is equivalent to around 0.13 USD). Further, a reduction of the nitrogen load to the coast of at least 2,725 tons yr⁻¹ is likely to be required for accomplishing this improvement (Scharin 2003). As a consequence, as far as the denitrification service in these coastal waters can help to reduce these nutrients, this would on average be worth about SEK 20,000-180,000 t⁻¹ reduced N. Similar computations for the case of the Laholm Bay at the Swedish West Coast and the whole Baltic Sea suggest SEK 40,000 t⁻¹ and SEK 20,000 t⁻¹, respectively (Frykblom 1998, Gren et al. 1997, Hökby and Söderqvist 2003). While these figures are highly uncertain because of particularities of the valuation methods used (e.g. the treatment of non-response to questionnaire surveys) and the difficulty to find out dose-response relationships between nutrient loads and eutrophication effects, they still suggest that the denitrification service of coastal habitats possess a substantial economic value. One might also get indications on the economic value of the denitrification service through the costs of replacing it by conventional sewage treatment or the avoidance costs that society is prepared to expend for any given nutrient reduction. For example, Gren et al. (2000) report that the costs of removing nitrogen in conventional Swedish sewage treatment plants are about SEK 30,000 t⁻¹ removed N, and that new treatment technology may reduce this cost to about SEK 20,000 t⁻¹. Such cost estimates should be compared to benefit estimates such as those mentioned above rather than being used as estimates of economic value. Attempts to still carry out a cost-based valuation rely on substitutability between the denitrification service and man-made alternatives, identification of cost-effective man-made alternatives and presence of a willingness of citizens' to pay the costs (Freeman 2003, Sundberg 2004).

Seafood production

Marine shallow soft bottoms are essential habitats for many crustaceans and fish species (Sogard and Able 1991). A shift from bare sand to sediment covered by algae will alter the quality and function of these habitats as nursery and feeding grounds for commercial fishery species such as flatfish, gadoids, clupeids and salmonids (see previous section). Generally, macro-vegetation such as kelp and seagrass are known to have positive effects on both abundance and diversity of fish assemblages in the coastal zone (Adams 1976, Carr 1989). However, in areas where the benthic vegetation, or as in this study a vegetation free bottom, becomes dominated by filamentous green algae, the number of fish species and fish biomass decrease with increasing amount of filamentous algae (Pihl et al. 1995). This can be explained by (1) extreme structural complexity of algal mats that prevent fish larval immigration as well as adult fish migration, (2) altered or reduced food resources, and (3) reduction in oxygen levels. Laboratory experiments have shown that juvenile cod actively avoid filamentous algae when offered alternative habitats (Borg et al. 1997). Furthermore, algal mats affect foraging success of juvenile cod negatively. A vegetation cover of as little as 30 to 40% significantly reduced the predation capacity of juvenile cod on three major prey species (Isaksson et al. 1994).

Shallow soft bottoms are for many fish species bottlenecks in their lifecycle, being the preferred habitat where settled juveniles experience high growth and survival rates (Gibson 1994). As mentioned previously, lowered oxygen levels under algal mats may reduce the abundance of benthic infauna, which serve as an important food source for fish (Pihl 1982, Wennhage and Pihl 2002). Further, exudates produced by algae in combination with low oxygen levels have been shown to increase mortality rates of larvae (crabs and flatfish) during settlement (Johnson & Welsh 1985, Larson 1997). Mats of filamentous algae on soft bottom sediments have negative impact on settlement, survival, growth and distribution of juvenile plaice (Wennhage and Pihl 1994). By using a numerical model Pihl et al. (in prep) studied the effects of algal mats (30-50 % cover) on the recruitment of plaice. The result showed that out-put of juveniles from the nursery ground could be reduced by 30 to 40 % during different scenarios of larval supply to the coast (Pihl et al. 2004, in prep). Assuming that this finding is valid also for Danish nursery grounds, this reduction is likely to affect the plaice population and thus catches in the whole plaice fishery in Kattegat and Skagerrak. In the last decade, the total catch in this fishery has been about 9,000 t yr⁻¹, which corresponds to a total gross income to fishermen of about SEK 180 million yr⁻¹ (Fiskeriverket 2001, ICES 2001). If the 30-40 per cent reduction in the output of juveniles ultimately would result in a corresponding decrease in total catch, total gross income to fishermen would be reduced by SEK 54-72 million yr⁻¹. While a complete economic valuation of the reduction in juvenile output has to take into account several other factors, such as changes in fishermen's behaviour and costs, these figures still illustrate the economic importance of shallow soft bottoms as a nursery.

The structural and functional properties of the alternative state with algal mats will offer opportunities for some species associated to dense vegetation to expand their distribution. In Swedish costal areas the shore crab (*Carcinus maenas*) and fishes like sticklebacks (*Gasterosteus aculeatus* and *Pungitius pungitius*) seem to be well adapted to the complex structure of filamentous algal mats. Early benthic stages of the shore crab are utilizing algal mats as a refuge from predation during settlement (Hedvall et al. 1998), and the adult crabs are dominant among epibenthic species in the system with algal mats (Wennhage and Pihl 2004). Sticklebacks do not occupy bare sediment habitat, but are the most dominant fish species when the system shifts into a state with algal mats (Wennhage and Pihl 2004). Thus, a shift into an alternative state with algal mats will result in profound changes of species and functional groups among epibenthic crustaceans, as well as fishes occupying shallow soft bottom systems (Fig. 3). The provision of ecosystem goods in terms of the production of fish species of commercial and recreational value will be significantly reduced, and replaced by non-commercial resident fishes and crustaceans.

Aesthetic and recreational values

Shallow soft bottom habitats also provide social and cultural services through aesthetic attraction and recreational uses. People probably enjoy the scenery of unvegetated shallows, which is reflected in the preference for constructing permanent or holiday residential houses, or the demarcation of scenic roads. The aesthetic values also provide the basis for recreational activities such as sunbathing, swimming, fishing, sailing, etc. The appearance of algal mats is a eutrophication effect, which means that the economic value of aesthetic attraction and recreational uses is likely to be included, at least partially, in the benefit estimates reported in section 6.1. To sort out the significance of aesthetic attraction and recreational uses requires more detailed

studies. For example, studies can be based on the relationship between aesthetic conditions and property values. Marine water quality and water clarity reduced by eutrophication have elsewhere been shown to influence property values (Leggett and Bockstael 2000, Poor et al. 2001). Whether such an influence has taken place in Sweden remains to be studied, but a number of studies indicate that an improved water clarity in Swedish coastal waters affected by eutrophication is economically valued by recreationists (Sandström 1999, Frykblom et al. 2004). Similarly, people have been found to be willing to pay for improvements of general bathing water quality at the Swedish West Coast (Eggert and Olsson 2003). These findings suggest that the Swedish coastal tourism industry is to a large extent coupled to the aesthetic attraction and recreational uses of coastal ecosystems. The visual cover of algal mats, the smell of decomposing algae and the physical disturbance on recreational activities, such as swimming and fishing, thus constitute a threat against the tourist industry and costly measures can be expected as a response. For example, camping ground owners in the island of Öland in the Baltic Sea every year take away tons of dead red filamentous algae in order to keep beaches attractive (Engkvist et al. 2001). As another example, the costs of mechanical harvesting of algal mats in bays with more than 60 per cent cover of algae in the northernmost municipality of the Swedish West Coast have been estimated to about SEK 660,000 y^{-1} , which correspond to about SEK 500,000 t^{-1} harvested N (Harlén and Zackrisson 2001).

SYSTEM STATE CONTROLLING VARIABLES AND RESILIENCE

Many studies have investigated possible ecological effects from increased occurrence of filamentous algal mats in coastal shallow areas (e.g. Hartog 1994, Sundbäck et al. 1990, Fong et al. 1993, Isaksson and Pihl 1992, Österling and Pihl 2001, Krause-Jensen et al. 1999, Trimmer et al. 2000, Astill and Lavery 2001), but few have attempted to explain the underlying driving forces for its establishment (Trimmer et al. 2000, Eilola and Stigebrandt 2001) or for its persistence (Hodking and Birch 1986, Stimson and Larned 2000, Tyler et al. 2003, Sundbäck et al. 2003). No study has to our knowledge discussed the observed changes from a possible regime shift between two possible alternative states, or discussed the phenomena from a resilience perspective. To gain a deeper understanding of system dynamics and insights into what factors that should be monitored for management purpose this perspective is utterly important. One system state may be undesired from a social perspective, i.e., by reducing the generation of beneficial goods and services (Table 2). Any efforts making the system reverse to its previous state (if possible) may be more costly compared to mitigation efforts before a shift has taken place. As described earlier the coastal ecosystems of Kattegat and Skagerrak have been exposed to gradually increasing discharges of nutrient over several decades, with total input of nitrogen from land and air deposition increasing by 300% since 1940 (Rosenberg et al. 1990). This enhanced nutrient loading has resulted in a doubling of phytoplankton production, with cascading effects through the food web. The surplus of primary production results in increased loading of particulate organic matter to the shallow soft bottom systems. Such increased import of particulate matter and nutrients (N) from external sources to the shallow coastal zone has been suggested to be the major factor facilitating growth of filamentous algae (Trimmer et al. 2000, Eilola and Stigebrandt 2001). The enrichment increases nutrient regeneration from local sediments (Hodking and Birch 1986, Thybo-Christensen 1993, Sundbäck et al. 2003), which together with external nutrient sources make up the available pool of nutrients for the establishment of algal mats. Recent *in situ* and laboratory experiments indicate

that nutrient fluxes from the shallow soft bottom sediment may constitute a significant share of the nutrient demand of macroalgae during the onset of blooms (during early summer) (Sundbäck et al. 2003). Once established on the sediment the filamentous green algae will exhibit fast growth, developing covering mats within 4 to 5 weeks (Pihl et al. 1996). Annual green algae not only have a high production but will also decompose rapidly (Owens and Stewart 1983, Thiel and Watling 1998), although the reduced oxygen conditions slow down this decomposition. The mineralization process releases inorganic carbon and nutrients to the water column (Sfriso et al. 1987) but the high rate of production and sediment accumulation during the summer results in a continuous input of organic matter to the sediment, forming a basic pool of carbon and nutrients for future algal production. The accumulation of over wintering spores and algal filaments in the sediment is an additional factor suggested to facilitate the onset and rapid growth of the algae in early summer (Sundbäck et al. 2003). Thus, the refilling of the sediment nutrient pool together with the readily available algae material restrain the shallow soft bottoms into self-regenerating systems (Lavery and McComp 1991, Norkko and Bonsdorff 1996). Such altered state of nutrient dynamics with higher recycling within shallow embayment, may therefore initially be resilient to any efforts in reducing external nutrient loading to the system. Eilola and Stigebrandt (2001) could by modelling show that even if nutrient concentration in coastal waters was drastically reduced by 50 %, the response time of changes in coverage of filamentous algae was in the order of 5 yrs to reach a 75% decrease in algae cover. Modelling with a more realistic nutrient reduction (10-20%) resulted in a 35-50 % decrease of algae cover after the same time period (Eilola and Stigebrandt 2001). Thus, none of these nutrient reduction levels resulted in complete disappearance of algae, and the self-generating characteristics of the system probably keeps it locked into a filamentous state. Eilola and Stigebrandt (2001) also identified water depth and water exchange as important factors for filamentous algae growth. Shallow bays characterised by high water turnover and wave exposure are probably more resilient against development of algae mats due to continuous transfer of organic material out from the system and re-occurring events of strong physical forces disturbing the establishment of algae mats.

Even if not unambiguous, existing information from studies investigating shifts to algae dominating systems enables us to suggest what the controlling factors are and how they can be managed. Also for management purposes it is crucial to know the configuration of both systems (with and without algae), and have knowledge about what disturbance that is causing a shift. Thus, we need to know what sustains the systems capacity to undergo disturbance and maintaining its functions and controls. This information gives us a measure of the systems resilience and what changes in environmental conditions that can undermine it. Shallow bays along the Swedish West coast are characterized by high benthic primary production (Sundbäck et al. 1990), high turnover rates of organic materials and high fluxes of nutrients between sediment and overlaying water. Recalling the question “*resilience of what to what*” raised by Carpenter et al. (2001) “*resilience of what?*” would for the soft bottom system be a vegetation free state with a diverse and productive macro-faunal community. Dominant controlling feedback acting under such “normal” condition is the activity of benthic and epibenthic fauna (together with more mobile non resident fauna). A rich sediment community increases decomposition and facilitate transfer of organic compounds up the food web and also an export of carbon and nutrients from the bay. The organisms making burrows in the sediment facilitate through

denitrification a transfer of nitrogen into the atmosphere. The role of MPB should also to be included as this production buffer against nutrient availability for the macroalgae and can, thus, prevent its development. It is, however, uncertain how MPB community structures and activities have changed due to long term build-up of nutrients in the sediment. Some MPB have shown potential to persist in sediments with macroalgae mats, even though their activity been significantly reduced (Sundbäck and Miles, in press). It has also been suggested that a diverse MPB community will increase the systems resilience, i.e. mitigate the onset and build up of macroalgae mats (Sundbäck and Miles in press).

A short answer to the question “*resilience to what?*” is eutrophication, and more specifically the build-up of organic material and nitrogen pool in the sediment. The “normal” state of shallow bays has, despite increased coastal eutrophication, been sustained for long time. Thus, the system has been resilient against changes in increased input of organic material, i.e. the many functions within the bay have been sustained. However, the emergence of algae covered bays now indicates that many shallow systems have lost, or lowered, their resilience (Fig. 3). The shift to an algae dominated state and its persistence are most likely due to 1) increased loading of organic material; 2) build-up of sediment nutrient pool available for algae growth, and 3) increased pool of algae regeneration material in the sediment. Thus, the algae being produced create positive feedbacks that keep the system locked into the new system state.

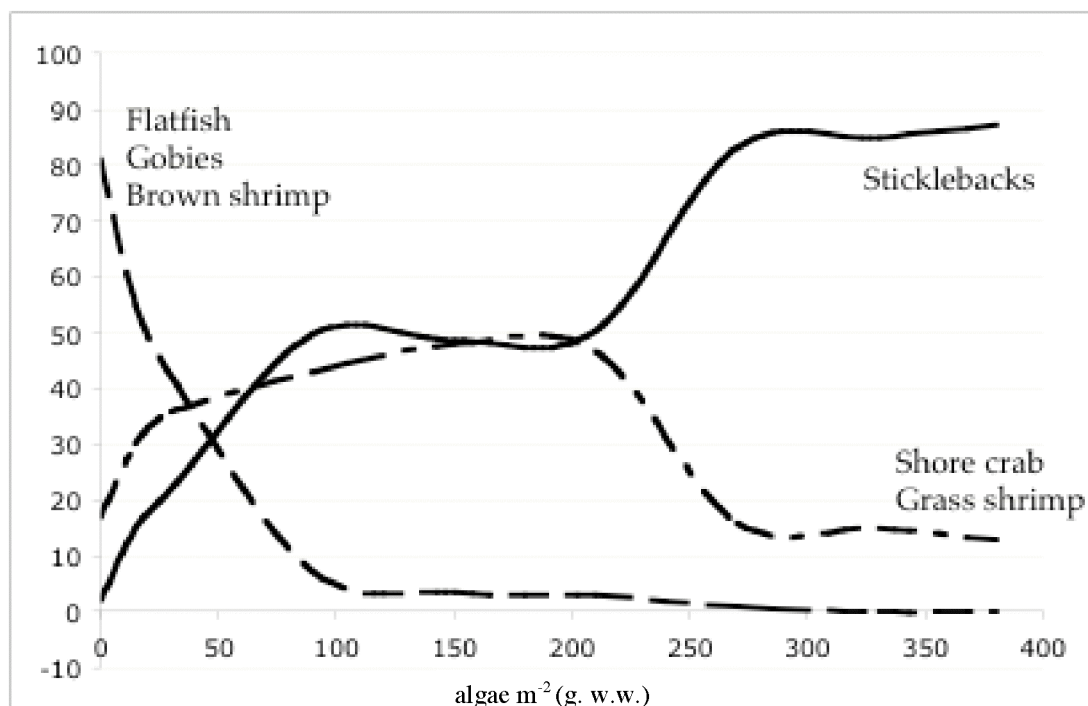


Figure 3. An overview of changes in community structure with increasing densities of filamentous algae. (Based on data from the Swedish West Coast. (Based on data from Wennhage and Pihl, in prep.).

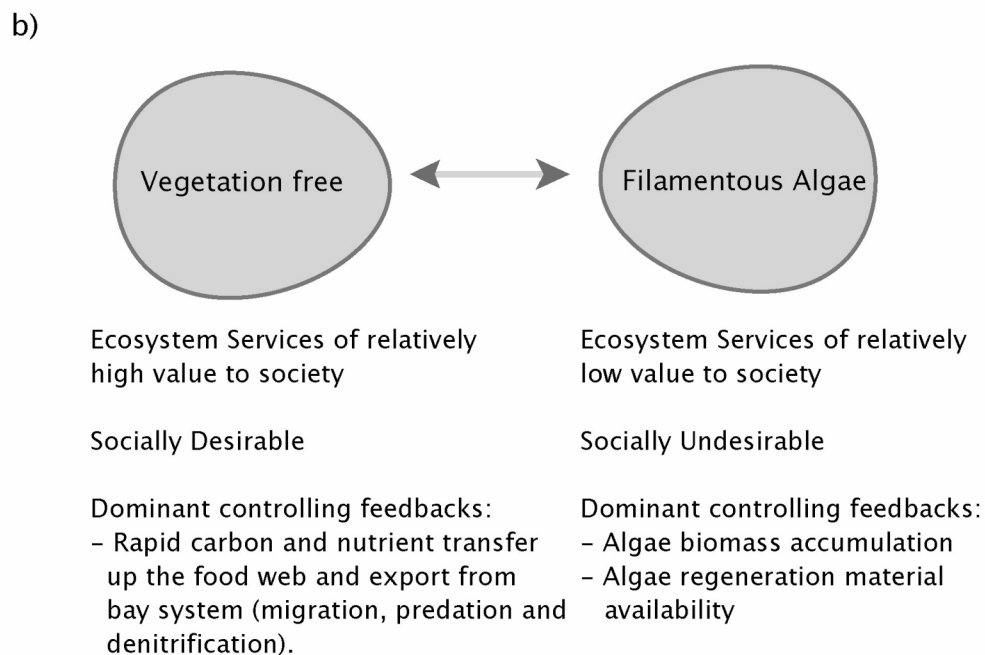
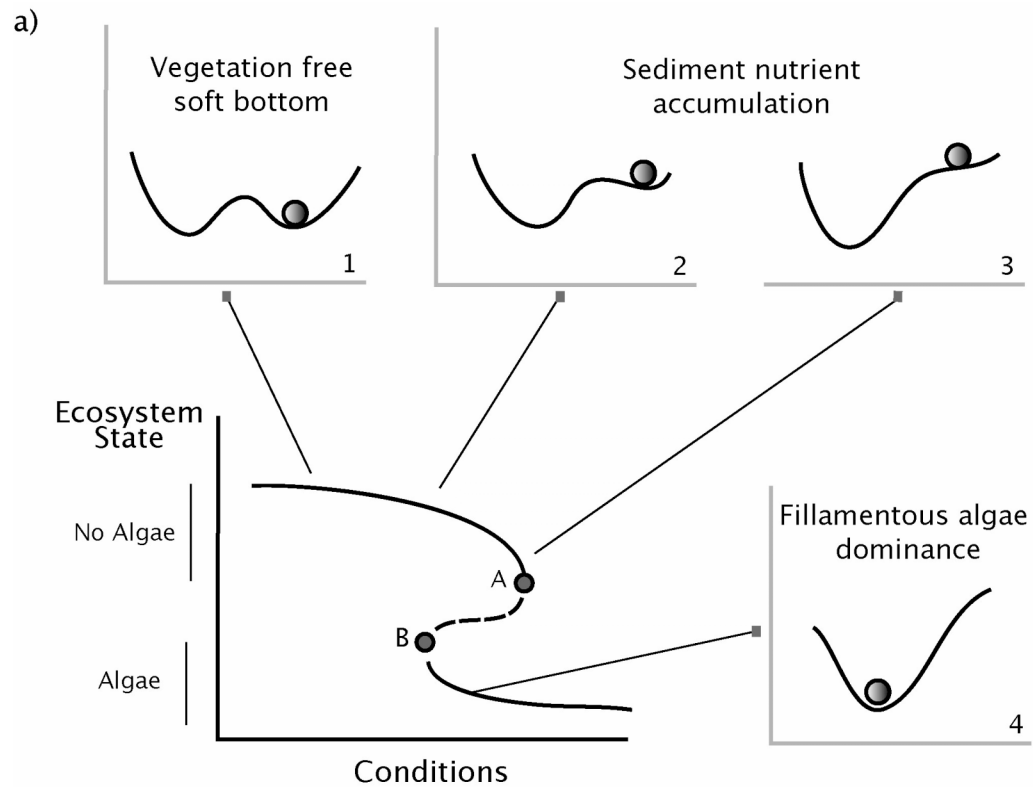


Figure 4. Graph showing how changes in external conditions can cause a shift from one system state to another. A slow build-up of the sediment nutrient pool (2-3) (i.e. change in Conditions) has been the driver for a shift from unvegetated shallow soft sediments (1) to filamentous algae dominated (4). b) The transition to a system having different structures and functions imply negative social effects.

If we can estimate how organic (or nitrogen) content in the sediment has changed during time, and link it with the occurrence of filamentous algae, this could be a valid parameter to monitor in the field. However, even if we find a strong correlation between organic content and algae, and manage to identify when we approach possible shifts, it may still be difficult to prevent such shifts taking place. Further, to determine if the shift really constitute a true alternative state there is a need for vigorous experimental testing with the aim to see if the conditions for alternative stable states outlined by Petraitis and Dudgeon (2004) are fulfilled. We do not elaborate in depth on this matter as no field experiments with the aim to test for occurrence of thresholds associated with changes in parameter values (e.g. environmental conditions) been carried out (see Petraitis and Dudgeon 2004 for discussion of experimental designs for detecting alternative states). Further, the existing field data on sediment property in shallow bays are limited to more recent time.

While reduction of large-scale coastal eutrophication is already prioritized by many EPA:s, we need to be aware of that even if action is taken today and we manage to decrease eutrophication there seem to be a momentum within the system that sustains already established algal mats (see Eilola and Stigebrandt 2001), and possibly also trigger development of new algae mats. The time it will take to return back will, thus, depend on the resilience of the algal dominated state. In this case resilience is an unwanted character of the system as it locks it into a state that is likely to have a relatively low value for society (Fig. 4).

The shift to a filamentous algae dominated ecosystem is thus likely to be a eutrophication effect caused by high anthropogenic nutrient loads to the sea during several decades. Preventing algal mats and other marine eutrophication effects requires nutrient reduction measures such as nitrogen removal in sewage treatment plants. However, once the transition to a filamentous algae dominated state has occurred, reactive measures such as mechanical removal of algal mats might have to be taken repetitively for reducing recreational and aesthetic nuisance at a considerably higher costs than those of preventive measures; 17 times higher costs t^{-1} removed N (SEK 500,000/ SEK 30,000) are indicated by the examples given earlier in section 6. While the comparison is halting because it cannot be predicted exactly what eutrophication effects preventive measures will reduce, it illustrates the extra costs that society incurs from a shift to an undesirable ecosystem state that cannot easily be reversed.

CONCLUSIONS

The rapid increase of filamentous algal cover in previously unvegetated shallow areas may render in severe negative consequences for society. This is partly because these coastal habitats constitute important feeding and breeding grounds for commercially valuable fish species. They also sustain valuable ecosystem services by facilitating for coastal nitrogen removal through denitrification and function as important recreational areas with aesthetic values. We suggest that the observed shift is driven by increased coastal eutrophication, i.e. more specifically reaching a threshold for development of filamentous algae. Organic materials accumulate and increase the sediment nitrogen pool. The algae themselves, both the accumulating biomass and the living structure, keep the system locked into a state with reoccurring algae development by facilitate further sediment accumulation and storing algae fragments for re-growth. The emergent system seems to be resilient against restoration efforts implying increased costs for the society.

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Table 1. Examples of system shifts in marine ecosystems

| Ecosystem Type | Alternative state 1 | Alternative state 2 | References |
|------------------------|--|---|---|
| Marine Systems | | | |
| Coral reefs | <i>hard coral dominance</i> <i>hard coral dominance</i> | <i>macroalgae dominance</i> <i>sea urchin barren</i> | Knowlton 1992, Done 1992, Hughes 1994, McCook 1999, Glynn 1988, Eakin 1996, Nyström et al. 2000 |
| Kelp forests | <i>kelp dominance</i> <i>sea urchin dominance</i> | <i>sea urchin dominance</i> <i>crab dominance</i> | Steneck et al. 2002, Konar & Estes 2003 Steneck et al. 2002 |
| Shallow lagoons | <i>seagrass beds</i> | <i>phytoplankton blooms</i> | Gunderson 2001, Newman et al. 1998 |
| Coastal seas | <i>submerged vegetation</i> <i>rockweeds</i> | <i>filamentous algae</i> <i>musselbeds</i> | Jansson & Jansson 2002, Worm et al. 1999 Petraitis and Latham 1999 |
| Benthic foodwebs | <i>rock lobster predation</i> | <i>whelk predation</i> | Barkai & McQuaid 1988 |
| Ocean foodwebs | <i>fish stock abundance</i> | <i>fish stock depleted</i> | Steele 1998, Walters & Kitchell 2001, de Roos & Persson 2002 |
| Shallow soft sediments | <i>Diatoms, silty sediment</i> <i>soft bottom sediments</i> | <i>sandy sediment</i> <i>filamentous algae</i> | Van De Koppel et al. (2001) This study |

Table 2. Net changes in the provision of ecosystem services after phase shift from unvegetated to algal mat covered shallow soft bottom habitats on the Swedish west coast.

| Key parameter** | Key ecosystem services | Net change | Spatial scales affected** | |
|--|---|------------|---------------------------|--------------------|
| | | | local | regional Internat. |
| MITIGATION OF EUTROPHICATION | | | | |
| • Water circulation(reduced) | • Denitification • Mineralisation • Efficient energy transfer to higher trophic levels | - | * | * |
| • Sedimentation and accumulation of organic matter(increased) | | - | * | * |
| • Oxygen levels in water and sediment (reduced) | | - | * | * |
| • Abundance of suspension and surface deposit feeder (reduced) | | | | |
| SEAFOOD PRODUCTION | | | | |
| • Oxygen level in water column | • Quality as nursery, feeding and breeding habitat for fishery species of commercial and recreational value | - | * | * |
| • Mechanical prevention of larval immigration | | | | |
| • Foraging efficiency for fish | | | | |
| • Abundance of food organisms | | | | |
| SOCIAL AND CULTURAL SERVICES | | | | |
| • Visual cover of algal mats | • Aesthetic attraction • Recreational uses • Cultural and artistic values | - | * | |
| • Physical disturbance on recreational activities | | - | * | |
| • Smell of decomposing algae | | - | * | |

* Changes from algal mat cover within brackets

** Describing on what scale the change in ecosystem service is relevant, i.e. accounting for distribution of user groups and service of more global concern.