

Synthesis

Regime shifts and ecosystem services in Swedish coastal soft bottom habitats: when resilience is undesirable

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ABSTRACT. Ecosystems can undergo regime shifts where they suddenly change from one state into another. This can have important implications for formulation of management strategies, if system characteristics develop that are undesirable from a human perspective, and that have a high resistance to restoration efforts. This paper identifies some of the ecological and economic consequences of increased abundance of filamentous algae on shallow soft bottoms along the Swedish west coast. It is suggested that a successive increase in the sediment nutrient pool has undermined the resilience of these shallow systems. After the regime shift has occurred, self-generation properties evolve 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 one, resulting in less valuable ecosystem goods and services generated for society. In Sweden, loss of value results from the reduced capacity for mitigating further coastal eutrophication, reduced habitat quality for commercial fishery species, and the loss of aesthetic and recreational values.

Key Words: *alternate stable states; shallow soft bottoms; eutrophication; filamentous algal mats; resilience; ecosystem function; ecosystem goods and services.*

INTRODUCTION

Many coastal marine ecosystems worldwide are subject to increased supply of nutrients from direct point discharges (sewage, industries, etc.), terrestrial run-off, and atmospheric deposition. Nitrogen loading in the Skagerrak and Kattegat regions on the Swedish west coast has increased about four-fold since 1930 (Rosenberg et al. 1990, Aure et al. 1996, Rosenberg et al. 1996). A small tidal amplitude, generally less than 20 cm, makes the coastal zone and, especially the inner archipelago, sensitive to increased nutrient loading. Phytoplankton production has doubled, from around 100 g-C-m⁻²-y⁻¹ in the 1950s and 1960s, to 200 g-C-m⁻²-y⁻¹ during the period of 1980 to 2000 (Richardsson and Heilman 1995, Lindahl 2003). Over the same time period, coastal sedimentation has increased about five-fold, from 30 to 140 g-C-m⁻²-y⁻¹ (Lindahl 2003). Observed indications of eutrophication include increased frequencies of phytoplankton blooms and reductions of oxygen in bottom waters (Baden et al. 1990), as well as an

increased occurrence of filamentous algae on shallow soft bottoms along the Swedish west coast (Afzelius 1978, Wennberg 1987, Österling and Pihl 2001). The average cover of green algal mats in 10 shallow (0-1 m) bays on the Swedish Skagerrak Coast, increased significantly from <3% during the period of 1976 to 1978, to 40% in 1992 to 1994 (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, and the average cover of green algal mats ranged from 30 to 50% of the total shallow soft bottom habitat in the archipelago (Pihl et al. 1999).

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) the capability of the system for self-

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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 (Scheffer et al. 2001, Dent et al. 2002, Scheffer and Carpenter 2003, Petraitis and Dudgeon 2004). Until then, the system may not give any indication of vulnerability, particularly if we monitor the flows of ecosystem goods and services (e.g., fish productivity). Since the theory of multiple states was first developed (May 1977), a number of examples of alternative states have appeared in the literature (see references in Folke et al. 2005).

This paper identifies two alternative system states of shallow soft sediment along the Swedish west coast. The main aim is to increase our understanding about how the generation of ecosystem goods and services differ between the two system states. In addition, we describe structural and functional changes, identify main system drivers, and discuss inherent self-generating properties from a resilience perspective.

STRUCTURE AND FUNCTIONS OF COASTAL SHALLOW SOFT BOTTOM ECOSYSTEM

Soft bottom sediments constitute >70% of the shallow zone (0-1 m) along the Swedish west coast (Pihl and Rosenberg 1982). This habitat is usually free from macrovegetation, but in some areas a patchy coverage of the macrophytes *Zostera marina* and *Ruppia* sp. or macroalgae, such as *Fucus* spp., exists. This is a key coastal ecosystem because of its wide distribution and its role in sustaining important ecological functions. The main energy source for the shallow soft bottom system is primary production imported from pelagic phytoplankton (Möller et al. 1985). Phytoplankton is utilized by filter-feeders and deposit-feeders, which capture and transfer energy to other benthic and epibenthic organisms, including fish (Cloern 1982, Officer et al. 1982, Loo and Rosenberg 1989). In addition, microphytobenthic algae attached to sediment particles make a significant contribution to the primary production of the shallow system (Sundbäck et al. 1990).

Soft sediment bottoms are characterized by a high

infauna and epibenthic fauna production (Pihl and Rosenberg 1982, Möller et al. 1985). The high food production and reduced predation pressure from deep water fish make the shallow soft bottom ideal nursery grounds for many commercial species of fishes (Zijlstra 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 (<3 m) 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 undertake seasonal or diurnal foraging migrations to utilize the rich production of the sandy beaches (Pihl and Wennhage 2002, Wennhage and Pihl 2002).

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

ALTERNATIVE SYSTEM STATE - NET CHANGES IN ECOSYSTEM GOODS AND SERVICES

The formation of algal mats in shallow areas results in considerable changes in ecosystem structure and functions, many of which are important for the generation of ecosystem goods and services. We will here concentrate on the net effect on three groups of ecosystem services: (1) mitigation of eutrophication, (2) seafood production, and (3) aesthetic and recreational values (Table 1). These ecosystem services were selected on the basis of their substantial socio-economic importance as well as the availability of background data.

Table 1. 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	international	
• Water circulation (reduced)	<i>MITIGATION OF EUTROPHICATION</i>	Denitification	-	*	*	*
• Sedimentation and accumulation of organic matter (increased)		Mineralisation	-	*	*	
• Oxygen levels in water and sediment (reduced)		Efficient energy transfer to higher trophic levels	-	*	*	
• Abundance of suspension and surface deposit feeder (reduced)						
• Oxygen level in water column	<i>SEAFOOD PRODUCTION</i>	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						
• Visual cover of algal mats	<i>SOCIAL AND CULTURAL SERVICES</i>	Aesthetic attraction	-	*		
• Physical disturbance on recreational activities		Recreational uses	-	*		
• Smell of decomposing algae		Cultural and artistic values	-	*		

* *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.*

Mitigation of eutrophication

Bays with recurrent algal mats on the Swedish west coast have an average organic carbon and nitrogen sediment content that is three times higher than algae-free bays (Pihl et al. 1999, Svensson and Pihl

2001). Besides localized nutrient inputs, elevated nutrients can be explained by increased sedimentation due to reduced water circulation caused by algal mats, and by the algae acting as mechanical filters for organic matter in the water column. Furthermore, parts of the algal mats

decompose during the summer season and as much as 50% of the annual production can be incorporated in the sediment when dead algae accumulate (Owens and Stewart 1983, Thiel and Watling 1998). The initial net result is enhanced accumulation of organic matter that, through a number of feedback mechanisms, changes the nutrient dynamics of the sediment. The organic enrichment may increase oxygen consumption that, together with the reduced water exchange, result in decreased oxygen levels in both the water column and the sediment. Mineralization efficiency in the sediment is reduced due to lowering of decomposition rates with decreasing oxygen levels. The ecosystem service of converting organic particles to inorganic matter is thus reduced.

The number of species, and the density and biomass of benthic macrofauna is 40-50% lower under mature algal mats (Svensson and Pihl 2001). The impoverished community structure under algal mats is partially attributable to deteriorating oxygen conditions, but may also be a consequence of algae forming a barrier to settling larvae, thus preventing new faunal recruitment to the sediment (Olofsson 1980). Species composition of the infauna may shift in response to algal mats, resulting in dominance of tolerant opportunistic species (Norkko and Bonsdorff 1996a, b). Suspension feeders and surface deposit feeders, which are dependent on good water circulation for feeding and respiration, are drastically reduced in sediments under algal mats. Burrowing deposit feeders and predators, however, remain more or less unaffected (Fig. 1) (Österling and Pihl 2001). The loss of suspension and surface deposit feeders will dramatically decrease the capacity of the benthic system to absorb and transfer organic matter to higher trophic levels, 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 by lower oxygen concentrations. The overall reduced efficiency of this ecosystem service will lead to an increased net accumulation of organic matter, which may reinforce the elevated nutrient load of shallow coastal systems.

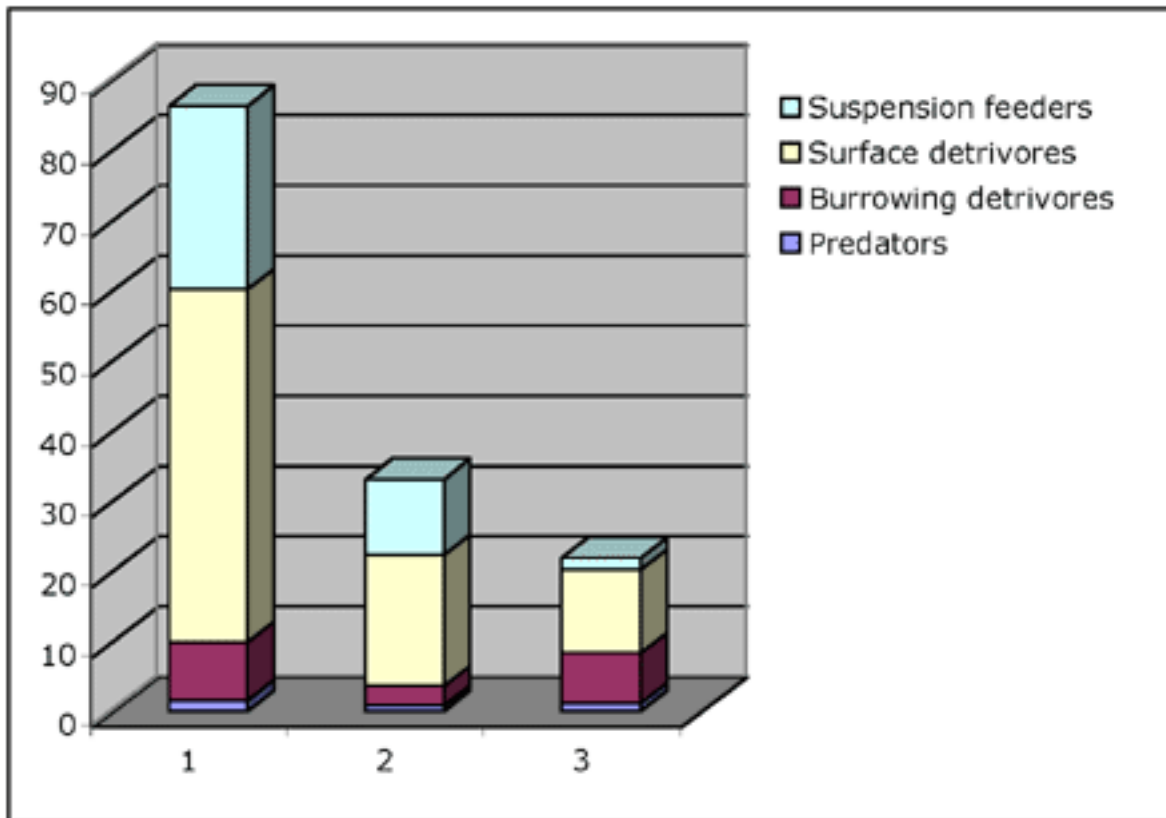
Organic enrichment may also create negative impacts when algal mats are transported to deeper bottoms. Such transfer can occur continuously by water currents during the summer, but is especially evident following autumn storm events. Deeper

coastal areas are sensitive to increased levels of sedimentation because the decomposition of organic matter commonly results in oxygen deficiency in the bottom water and sediments (reviewed in Diaz and Rosenberg 1995). Several fjord systems on the Swedish west coast show a significant negative trend in oxygen concentration in the bottom water over the last several decades (Rosenberg 1990), which is believed to be caused by sedimentation of excess micro- and macroalgal blooms. There is, however, a need for studies to examine such linkage in more detail.

Denitrification is another ecosystem service that is negatively affected by algal mats (Table 1). 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 (DIN) from the system. Studies from temperate regions have shown that the rate of denitrification is reduced by an order of magnitude in sediments enriched with algae (Hansen and Blackburn 1991, Tuominen et al. 1999). The contribution of infaunal activity to increasing denitrification processes and DIN fluxes is well documented (Hansen and Kristensen 1997, Berg et al. 2001, Gilbert et al. 2003). The reduced infauna beneath algal mats can lower the denitrification rate by two mechanisms. Firstly, by reducing the amount of sediment surfaces suitable for the denitrification process, and secondly by increasing micro-phytobenthos (MPB) activity due to reduced sediment mixing. Shallow soft sediments function as sinks for nutrients, but under anoxic conditions (resulting from development of macroalgae mats) these sediments can instead become sources leaching N and P to the water column (Tyler et al. 2003). Even if both macroalgae and MPB are sinks for nitrogen, the nutrients still remain in the ecosystem (albeit transformed). Denitrification rates are between 0.060 to 1 millimol-m⁻²-h⁻¹ (7 to 123 kg-m⁻²-yr⁻¹) in shallow sandy soft bottom habitats on the Swedish west coast (Sundbäck and Miles 2000, 2002), in the lower range reported from other shallow-water coastal sediments in temperate areas (Cabrita and Brotas 2000).

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. (2005) reported that the benefits of a one-metre improvement in summer Secchi depth in the Stockholm archipelago would amount to SEK

Fig. 1. Shift in species composition in response to cover by algal mats, illustrated by altered infaunal diversity (individuals per 0.01 m²) in different functional groups. 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. (ANOVA; $p < 0.01$) (based on Österling and Pihl 2001).



60-500 million-yr⁻¹ (on 31 January 2005, 7 SEK was equivalent to around one USD). One might also get indications of 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. (1997) reported that the costs of removing nitrogen in conventional Swedish sewage treatment plants are about SEK 30,000 t⁻¹ of 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 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 the 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 sediment to 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 (Table 1). Generally, macrovegetation such as kelp and seagrass has positive effects on

both abundance and diversity of fish assemblages in the coastal zone (Adams 1976, Carr 1989). However, in areas where filamentous green algae becomes dominant, the number of fish species and fish biomass decreases (Pihl et al. 1995). This can be explained by: (1) the extreme density of algal mats that prevent fish larval immigration as well as adult fish migration, (2) altered or reduced food resources, and (3) reduced oxygen levels. Laboratory experiments have shown that juvenile cod actively avoid filamentous algae when offered alternative habitats (Borg et al. 1997), and that algal mats negatively affect their foraging success (Isaksson et al. 1994).

Juvenile plaice mainly feed on benthic infauna (Wennhage and Pihl 2002), a food source that is greatly reduced under algal mats. Further, exudates produced by algae in combination with low oxygen levels increase mortality rates of plaice larvae during settlement (Larson 1997). Using a numerical model, Pihl et al. (2005) studied the effects of algal mats on the recruitment of plaice. Output of juveniles from nursery grounds was reduced by 30-40% during different scenarios of larval supply to the coast (Pihl et al. 2005). 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 the 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% reduction in the output of juveniles ultimately results in a corresponding decrease in total catch, total gross income to fishermen would be reduced by SEK 54 to 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 behavior and costs - nonetheless these figures illustrate the economic importance of shallow soft bottoms as a nursery.

The structural and functional properties of algal mats offer opportunities for some species associated with dense vegetation to expand their distribution. In Swedish coastal areas, the shore crab (*Carcinus maenas*) and fishes such as sticklebacks (*Gasterosteus aculeatus* and *Pungitus pungitus*) seem to be well adapted to the complex structure of filamentous algal mats. Early benthic stages of the shore crab utilize algal mats as a refuge from predation during settlement (Hedvall et al. 1998),

and adult crabs are dominant among epibenthic species associated with algal mats (Wennhage and Pihl *in press*). Sticklebacks do not occupy bare sediment habitat, but are the most dominant fish species in algal mats (Wennhage and Pihl *in press*). Thus, a shift to 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. 2). The provision of ecosystem goods, in terms of the production of fish species of commercial and recreational value, will be significantly reduced, as non-commercial resident fishes and crustaceans replace them.

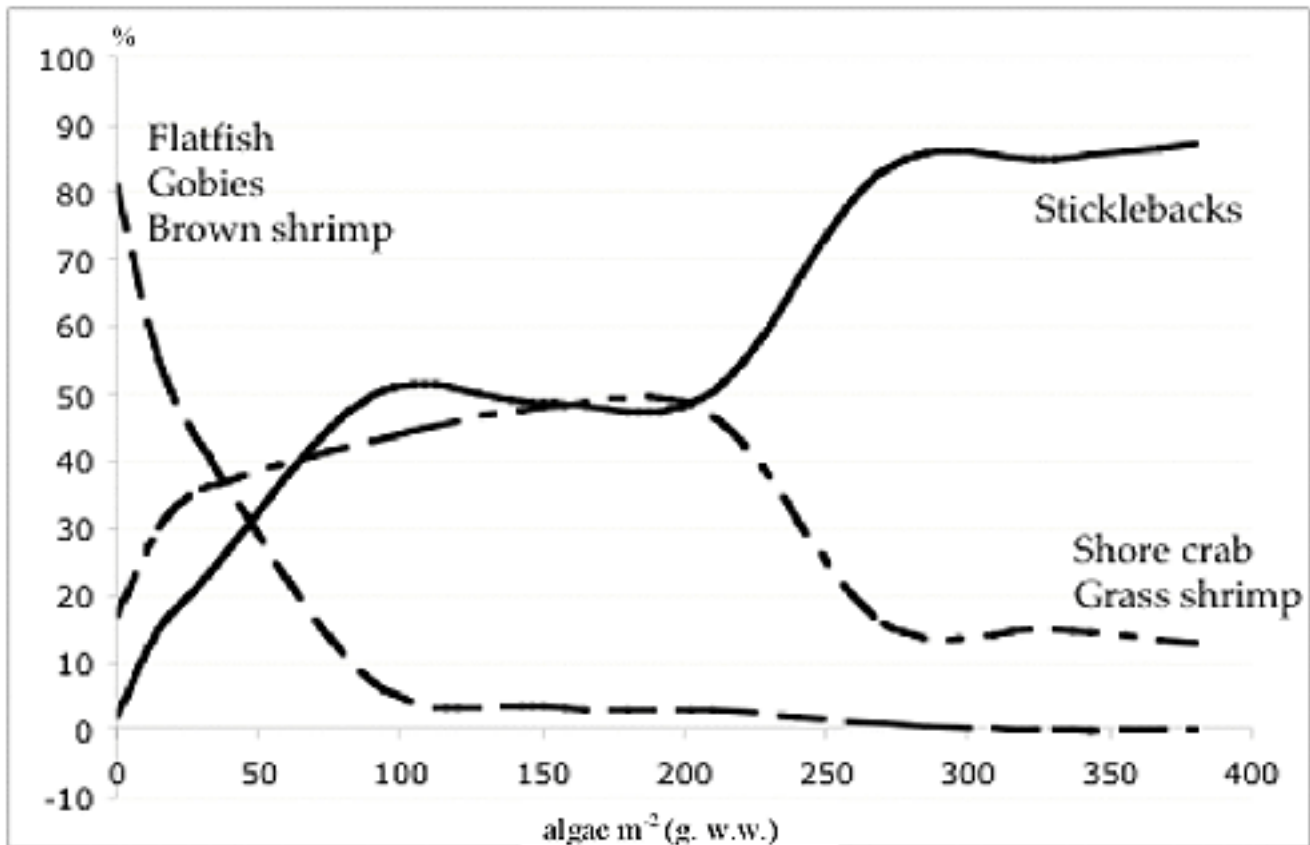
Aesthetic and recreational values

Social and cultural ecosystem services are affected by a high-density algae state through reduced aesthetic and recreational attraction (Table 1). The visual impact of algal mats, the smell of decomposing algae, and the physical disturbance on recreational activities such as swimming and fishing, constitute a threat to the Swedish coastal tourist industry. For example, camping ground owners in the island of land in the Baltic Sea remove tons of dead red filamentous algae every year in order to keep beaches attractive to tourists. On average, the annual cost is SEK 75 000 km⁻¹ of beach (Engkvist et al. 2001, Flodqvist and Hasselström 2004). The costs of mechanical harvesting of algal mats in the northernmost municipality of the Swedish west coast have been estimated to about SEK 660,000 y⁻¹ (Harln and Zackrisson 2001). Other studies confirm the importance of aesthetic conditions to recreationists, who put a high economic value on improved water quality and clarity in Swedish coastal waters (Sandström 1999, Frykblom et al. 2005). Similarly, people are willing to pay for improvements of general water quality on the Swedish west coast (Eggert and Olsson 2003). Effects on property values might also be significant (Leggett and Bockstael 2000, Poor et al. 2001).

SYSTEM STATE AND RESILIENCE

Many studies have investigated possible ecological effects from increased occurrence of filamentous algal mats in coastal shallow areas (e.g., Astill and Lavery 2001, Österling and Pihl 2001, and references therein), and some have attempted to

Fig. 2. A schematic/conceptual illustration of major changes in community structure with increasing density of filamentous algae. The smoothed lines (running average) were based on 400 quantitative samples (1 m²) of epibenthic fauna and filamentous algae to illustrate the significant change in community structure in relation to algae (ANOSIM-test: Global R = 0.751, p<0.001; Wennhage and Pihl *in press*).



explain the underlying driving forces for their establishment (Trimmer et al. 2000, Eilola and Stigebrandt 2001) or persistence (e.g., Sundbäck et al. 2003, Tyler et al. 2003). To our knowledge, no study has interpreted the observed changes as a regime shift between two alternative states, or discussed the phenomena from a resilience perspective. This perspective is essential in order to gain a deeper understanding of system dynamics and insights into factors that should be monitored. A particular system state may be undesirable from a social perspective, i.e. by reducing the generation of beneficial goods and services (Table 1). Efforts to reverse the system to its previous state (if this is possible) may be more costly compared to

intervention efforts before a shift has taken place.

As described earlier, the coastal ecosystems of the Kattegat and Skagerrak have been exposed to gradually increasing discharges of nutrients over several decades, with total input of nitrogen from land and air deposition increasing by 300% since 1940 (Rosenberg et al. 1990). The refilling of the sediment nutrient pool, together with the build-up of algal material, restrains the shallow soft bottoms into self-regenerating systems (Lavery and McComp 1991, Norkko and Bonsdorff 1996). Such an altered state of nutrient dynamics with higher recycling within shallow embayments may, therefore, initially be resilient to any efforts in

reducing external nutrient loading to the system. Even if nutrient concentrations in coastal waters were drastically reduced by 50%, the response time of changes in coverage of filamentous algae is in the order of 5 years for a 75% decrease in algae cover (Eilola and Stigebrandt 2002). Modeling 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 characterized by high water turnover and wave exposure are probably more resilient against development of algae mats due to continuous transfer of organic material out of the system and re-occurring physical disturbances that inhibit algae mats.

For management purposes, it is crucial to know about the functions of both systems (with and without algae), and the controlling variables that can cause a shift between them. 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 overlying water. The normal state of shallow bays has been sustained for a long time despite increased coastal eutrophication. 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 algal-covered bays indicates that the resilience of many shallow systems has been reduced (Fig. 3). The shift to an algae-dominated state and its persistence is most likely due to: (1) increased loading of organic material, (2) build-up of the sediment nutrient pool available for algae growth, and (3) an increased pool of algae propagules in the sediment. Thus, the algae state produces positive feedback that keep the system locked in.

conditions can cause a shift from one system state to another. A slow build-up of the sediment nutrient pool (conditions) (2-3) 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 leads to negative social effects.

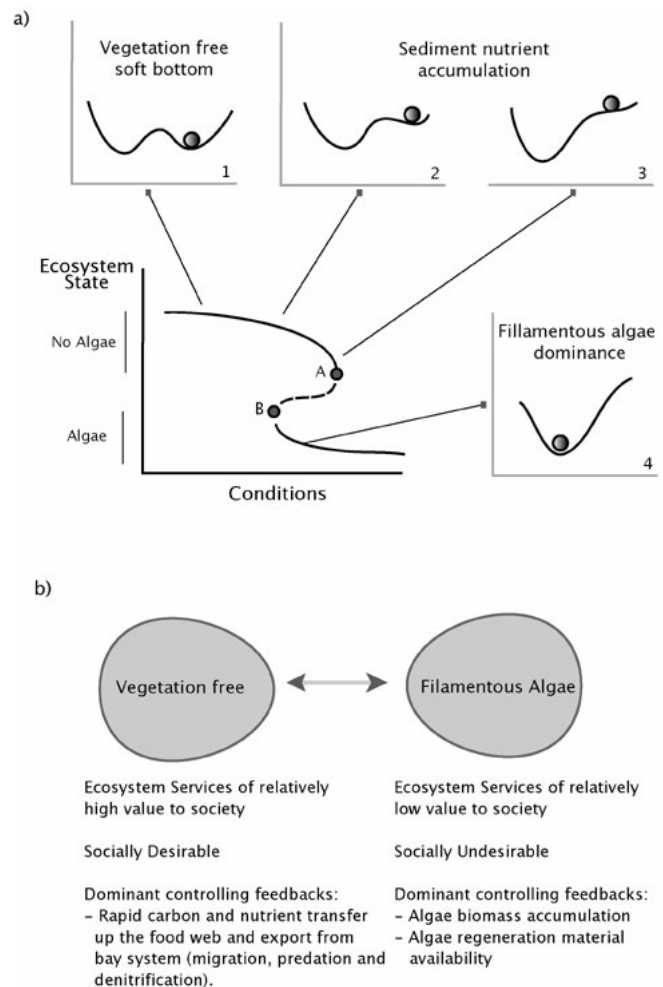


Fig. 3. a) "Ball and cup" metaphor to illustrate a shift from one alternative state to another (redrawn from Scheffer and Carpenter 2003). The ball illustrates the soft bottom sediment community and A and B alternative states. Changes in external

If we can estimate how organic (or nitrogen) content in the sediment has changed over time and link it to the occurrence of filamentous algae, this could be a useful parameter to monitor in the field. Even if a strong correlation between organic content and algae occurs, it may still be difficult to prevent such shifts taking place. Preventing algal mats 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 at considerably higher cost than those of preventive measures.

CONCLUSIONS

The rapid increase of filamentous algal cover in previously unvegetated shallow areas of Swedish coastal habitats may have severe negative consequences for society. This is partly because these habitats constitute important feeding and breeding grounds for commercially valuable fish species. They also sustain valuable ecosystem services by facilitating nitrogen removal through denitrification, and are important recreational areas with high aesthetic values. We suggest that the observed regime shift is driven by increased coastal eutrophication that exceeds a threshold for development of filamentous algae. Organic materials accumulate and increase the sediment nitrogen pool. The algae keep the system locked into a state with recurring algae development, by facilitating further sediment accumulation and storing algae fragments for regrowth. The alternate system seems to be resilient against restoration efforts, leading to increased costs for society.

Responses to this article can be read online at:
<http://www.ecologyandsociety.org/vol10/iss1/art30/responses/>

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