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Bottom-up and top-down forces in a tropical intertidal ecosystem

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GENERAL DISCUSSION

Interplay between bottom-up and
top-down forces in a tropical intertidal
seagrass system

Jimmy de Fouw

The main objective of the research in this thesis was to understand the relative importance of top-down and bottom-up forces on the functioning of tropical intertidal seagrass ecosystems. Key questions were: How can an intertidal seagrass ecosystem function under the ever-present risk of biochemical stress conditions (high sulfide levels) and what is the role of a migrant top-predator (top-down effects)? What is the function of the mutualistic interactions (bottom-up effects)? And finally, do bottom-up and top-down effects have interactive impacts on ecosystem functioning and does this help us predict how seagrass ecosystems may respond to the foreseen enhanced environmental stress conditions? In addition, I will reflect on the key questions and discuss some implications for conservation and the need for studies on ecosystem connectivity.

Coastal foundation species such as corals, kelp, mangroves, salt marsh plants and seagrasses play a pivotal ecosystem-structuring role through the creation of strong bottom-up effects by modifying resource availability, reducing physical stress and enhancing habitat complexity (Jones et al. 1994, Stachowicz 2001, van der Heide et al. 2007). Simultaneously, however, predators can also exert crucial community-structuring top-down effects through trophic cascades in the same ecosystems, suggesting that the interplay between top-down and bottom-up effects may be essential for the functioning of these ecosystems (Estes et al. 2011, van Gils et al. 2012, Hughes et al. 2013). If this is indeed the case, the combined anthropogenic disruption of bottom-up and top-down effects in these systems may to an important extent explain their global degradation. In this thesis, I investigated how the interplay between bottom-up effects created by seagrass *Zostera noltii* and its benthic invertebrate life, and top-down effects created by a migratory avian predator, the red knot *Calidris canutus*, may structure the intertidal tropical ecosystem of Banc d'Arguin in Mauritania (West Africa).

BOTTOM-UP FORCES

Seagrass beds are essential for coastal zones worldwide, because they provide coastal protection, act as carbon and nutrient sinks, and serve as keystone habitat for economically valuable species such as fish (Orth et al. 1984, Waycott et al. 2009, van der Heide et al. 2012). In addition, seagrass beds are known as 'ecosystem engineers' (Jones et al. 1994). Such ecosystem engineers are able to alter the physical conditions of their environment (Jones et al. 1994) which is not only beneficial for themselves, but for many associated species, thereby also called 'foundation species' (Figure 8.1A) (Bruno and Bertness 2001). For example, seagrass meadows create a positive feedback by reducing hydrodynamics, stabilizing sediments and accumulating organic matter from the water column (Figure 8.1D) (Folmer et al. 2012, Hansen and Reidenbach 2012). As a consequence, however, seagrass beds ultimately create a negative feedback, because accumulation of organic matter stimulates decomposition controlled by sulfate-reducing bacteria that produce sulfide, highly toxic to most forms of life including seagrasses (Bagarinao 1992, Lamers et al. 2013). How seagrass beds cope with sulfide stress remained a mystery for a long time.

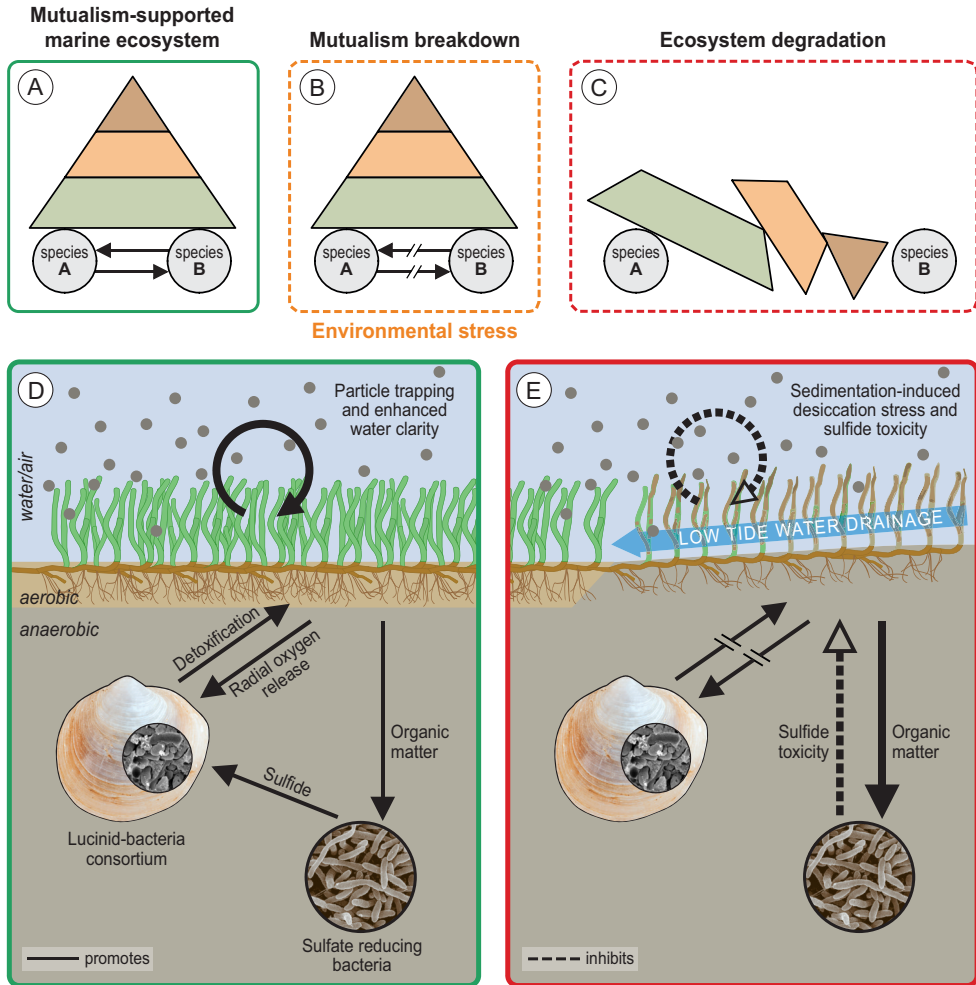


Figure 8.1 (A) Conceptual representation of a mutualism forming the foundation of a marine ecosystem. (B) Environmental change can disrupt such mutualisms, (C) which may initiate habitat degradation as observed in coral reefs (Knowlton 2001, Stachowicz 2001, Hay et al. 2004, Hoegh-Guldberg et al. 2007, Kiers et al. 2010). (D) We investigated the generality of this phenomenon by testing if breakdown of a facultative mutualism is an important driver of observed intertidal seagrass degradation (Chapter 3). (E) We hypothesize that the breakdown is triggered by enhanced desiccation, caused by high temperatures, strong winds and/or prolonged exposure at neap tide (van Lent et al. 1991, Seddon et al. 2000, Massa et al. 2009), and aggravated where local sedimentation differences result in water drainage from elevated patches.

It has been suggested that a facultative three-stage mutualistic interaction between seagrasses, Lucinid bivalves and their sulfide-oxidizing, gill-inhabiting bacteria play an important role (Larkum et al. 2006, Reynolds et al. 2007). Paleo records suggest that Lucinids and their symbiotic gill bacteria arose in the Silurian period (~340 m.y.) and the

family remained very low in diversity, however, a remarkable evolutionary radiation occurred at the end of the Cretaceous when the seagrasses and mangroves arose (Taylor and Glover 2000, Taylor et al. 2011, Stanley 2014). The Cretaceous was a period with a relative warm climate, coinciding with sea level-rise creating shallow inland seas (Pearson et al. 2001, Stanley 2014). In the warm shallow waters, the warm-adapted Lucinids benefited from the sulfide-rich muddy sediments provided by seagrasses. This indicates on a beneficial relationship between Lucinids and seagrasses during their rapid evolutionary radiation. Till date the Lucinids still have their highest diversity in shallow seas in seagrass beds (Stanley 2014). Many studies have investigated the effects of toxic sulfide on aquatic plants (see review Lamers et al. 2013) and the symbiosis between the lucinids and their gill-inhabiting bacteria (e.g. Distel 1998, Taylor and Glover 2006), but empirical proof of a *three-stage* mutualistic relationship remained unexplored.

In chapter 2 we experimentally tested the hypothesis that a three-stage mutualistic interaction plays an important role in these seagrass meadows. We experimentally showed that seagrasses engage in a mutualistic interaction with Lucinid bivalves *Loripes lucinalis* and their sulfide-oxidizing, gill-inhabiting bacteria to reduce sulfide stress, resulting in a positive feedback (chapter 2: Figure A2.1). In turn, the bivalves and their endosymbionts not only profit from sulfide that is indirectly provided by seagrasses due to organic matter trapping, but also from oxygen released by seagrass roots. Therefore we concluded that this mutualism was essential for the functioning of seagrass ecosystems in general and our study system in particular.

There are strong indications that temperature determines mutualistic dependency, as Lucinids are less common in the temperate zone (56%) and very common in the tropics where 97% of the seagrass beds contained Lucinids (chapter 2). The anaerobic decomposition by sulphate-reducing bacteria, producing toxic sulfide as a metabolic end-product, is strongly temperature-dependent (Garcia et al. 2013, Lamers et al. 2013). Therefore, it is likely that mutualism strength will depend on temperature. In addition, sediment conditions (e.g. organic matter, iron- and carbonate content) also affect sulfide production and thus likely mutualism dependency (Lamers et al. 2013). Apart from temperature and sediment conditions, the detoxification capacity of seagrass can play an important role in sulfide toxicity avoidance and tolerance (Holmer and Hasler-Sheetal 2014, Hasler-Sheetal and Holmer 2015). Regardless of the plant capacity, it seems that there is a gradient of mutualism-dependency related to the interaction between sediment conditions and temperatures this hypothesis needs to be further investigated.

DISRUPTION OF BOTTOM-UP FORCES

The alteration of the bottom-up forcing can lead to major disturbance of the ecosystem (Valiela et al. 1997, Vitousek et al. 1997, van Gils et al. 2006b). For instance, disturbances such as habitat loss and fragmentation, eutrophication, and global warming have led to biodiversity loss (van Gils et al. 2006b, Tylianakis et al. 2008). Simultaneously, they

may change the interaction between bottom-up and top-down forcing (Power 1992, Worm et al. 2002, Hughes et al. 2013). As in our seagrass system, many other marine foundation species, like salt marches and corals, depend on mutualistic interactions where they additionally reduce physical stress or gain recourses (Dayton 1972, Knowlton 2001, Stachowicz 2001, Hay et al. 2004, Hoegh-Guldberg et al. 2007, van der Heide et al. 2012, Angelini et al. in press). The strong community-wide dependence on these interactions also incurs a clear risk: they bind multiple species to one common fate, and disruption of the bottom-up forces may therefore lead to habitat degradation and biodiversity losses (Figure 8.1A-C) (Kiers et al. 2010). Up to now, most of the studies have used experiments, field surveys, descriptive data or models separately to investigate causes and consequences of mutualism breakdown (Hoegh-Guldberg et al. 2007, Tylianakis et al. 2008, Kiers et al. 2010, Lever et al. 2014). In this thesis, we are using a *combination* of these approaches, including GIS analyses to investigate the breakdown of a facultative three-stage mutualistic interaction.

Even though multiple stressors have been related to the global decline of seagrass (Waycott et al. 2009), only just recent research provided the evidence for seagrass declines as direct effects of increased temperatures or heat events (Marba and Duarte 2010, Jorda et al. 2013, Fraser et al. 2014, Thomson et al. 2015). Initial observations in our study system, the tropical marine intertidal flats of Banc d'Arguin in Mauritania (West-Africa), suggested that a seagrass die-off event occurred in 2011. In tropical regions, low-tide desiccation is a common stressor for seagrasses (van Lent et al. 1991). In 2010 and 2011, however, the region experienced intense drought and heat (with monthly anomalies of +2–3.5°C, with respect to long-term monthly temperatures) (Blunden et al. 2011, 2012, Masih et al. 2014). Although highly speculative, this may have been linked to the strong 2010–2011 La Niña event that affected the entire Northern Hemisphere (Masih et al. 2014), an intriguing hypothesis which needs further investigation. In chapter 3 we investigated whether the die-off could be related to low-tide desiccation stress caused by drought, wind and heat anomalies, and if disruption of a feedback was an important factor of the observed decline. In addition, in chapter 4 we quantified the stabilizing role of the mutualistic feedback in our seagrass study system.

Analysis of Normalized Difference Vegetation Index (NDVI – a proxy for seagrass cover) suggests a decrease of seagrass in the same period as the drought and heat events and was followed by a sharp decline. Although both 2010 and 2011 in Mauritania were reported warm and characterized by drought, our analyses of local climate data suggest that the summer of 2011 was particularly warm, windy and dry leading to a high evaporative demand (chapter 3: Figure 3.2). Before showing changes over time, we performed spatial analyses showing that NDVI was lower at higher elevation, suggesting that desiccation stress during low-tide exposure reduces seagrass cover at higher elevations. This landscape-scale wide NDVI decrease was supported by ground observations demonstrating a 50% decrease in seagrass cover between 2009 and 2013. Field surveys demonstrated that locally seagrass die-off seemed to typically occur on slightly elevated patches, where water drainage towards lower patches enhanced desiccation stress at low tide,

most likely due to subtle differences in local sedimentation rates (Figure 8.1E). Water drainage during low tide from higher towards lower patches in turn caused elevated patches to dry much quicker than lower areas. In fact, our measurements show that healthy patches were typified by a thin water layer on the mudflat, whereas the surface of degraded patches became dry within a few hours after exposure. In addition, field surveys also showed that degrading seagrass patches had significant lower Lucinid densities and higher sediment sulfide levels compared to healthy patches. Experimental manipulation of Lucinid densities confirmed that the loss of mutualism strength, triggered by desiccation stress, enhances seagrass degradation (chapter 3). Whether the Banc d'Arguin will fully recover after 2011 remains unanswered, as till date NDVI values kept rather low since (Figure 8.2).

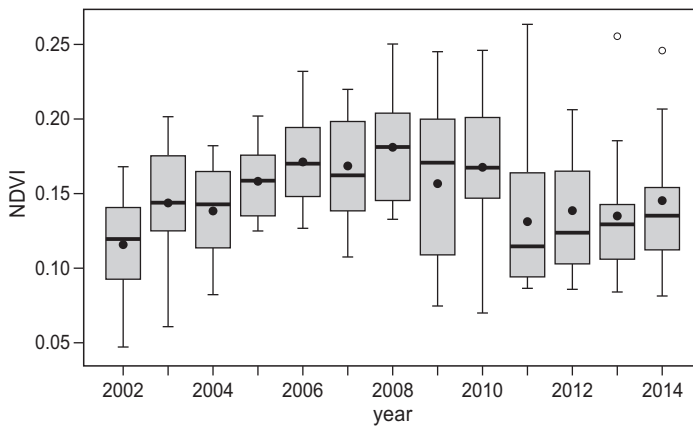


Figure 8.2 (Changes in NDVI in the study area over the period 2002 and 2014. Note that variation in NDVI is large due to seasonality and images were not corrected for low ground atmospheric condition (e.g. haze due to sandstorms).

Ecosystem shifts following gradual environmental change or perturbations of strong positive feedbacks have been described for a wide range of ecosystems (Scheffer et al. 2001, van der Heide et al. 2007). Several studies have shown that subtle temperature increase can lead to shifts in ecosystems states. For example, small climate change-related phenological shifts between plants and their pollinators have been observed to cause a mismatch between mutualistic partners (Burkle et al. 2013, Miller-Struttman et al. 2015); in coral reef mutualisms, subtle temperature increases have been suggested as an important cause of ‘coral bleaching events’ (Loya et al. 2001, Hoegh-Guldberg et al. 2007). Strong positive feedbacks can cause alternative states (i.e. bistability) (Scheffer et al. 2001), due to the changing environmental conditions a critical threshold is crossed causing a shift to an alternative state. If subsequently the conditions improve, they have to progress beyond the point of collapse, before recovery to the initial state takes place, a phenomenon called hysteresis. In seagrass meadows, such hysteresis may occur at high

water column ammonia loading, as ammonia toxicity can only be alleviated through joint uptake and detoxification of ammonia by ample seagrass meadows of high density (van der Heide et al. 2008, van der Heide et al. 2010b). The feedbacks described in our seagrass ecosystem may indicate that there might be alternative stable states (bistability) (chapter 3). In chapter 4 we used a parametrized differential equation model to investigate the importance of the mutualistic interaction for seagrass ecosystem stability, and test how low-tide desiccation stress affects ecosystem resilience. In addition, to examine whether our system shows bistability we used potential analysis, a method for detecting feedbacks and alternate states (Livina et al. 2010; Scheffer et al. 2012). If seagrass changes gradually in response to enhance desiccation stress over the elevation gradient, the frequency distribution of seagrass cover should be unimodal, whereas feedback-driven sudden shifts between two states would typically result in a bimodal distribution frequency. A potential analysis can identify peaks in the frequency distribution (‘attractors’) over an environmental stress gradient.

As argued in chapter 2 (Figure A2.1), our model simulation results show that accumulation of organic matter in an intertidal seagrass meadow results in a negative feedback created by seagrass itself. The organic matter accumulation results in enhanced sulfide production and toxicity over time, causing the system to collapse. However, incorporation of the mutualistic interaction into the model causes the negative effect of seagrass on itself to be buffered by *Loripes* by alleviating sulfide toxicity. Simulations of minor increase in seagrass mortality (as a proxy for desiccation stress), however, triggers disruption of the mutualistic interaction where *Loripes* is not able to consume all sulfide produced. This causes sulfide to accumulate slowly to the point where it becomes toxic, triggering sudden seagrass degradation enhanced by disruption of the mutualistic interaction, sending the system back into cyclic collapse and recovery dynamics. So, our simulation results were indeed consistent with our empirical findings reported in chapter 3.

Although the potential analysis of NDVI data and model simulation results suggests feedback-driven sudden shifts instead of a gradual response, we did not find evidence for alternative stable states. Instead, the strong mutualistic feedback causes the occurrence of so-called “slow-fast” cycles when environmental stress is enhanced, – a phenomenon very similar to what was proposed as a potential explanation for cyclic shifts in shallow lakes (van Nes et al. 2007). In our case, the system shows abrupt transitions between a seagrass- and barren state, the states are not stable but tend to stay relatively long in these conditions. In the background, however, environmental conditions change (sulfide concentrations in this case), this effectively causes cycles with alternating states (seagrass and bare) and fast changes (collapse and recovery) in between (see for details chapter 4). Potential analysis on the model results showed that slow-fast dynamics create the same kind of bimodality in frequency distributions as alternative stable states. So far, this kind of multimodality has been attributed to alternative stable states (Hirota et al. 2011, Scheffer et al. 2012, van Nes et al. 2014). However, we need to be cautious drawing conclusion on potential analysis as there are multiple examples of systems which may have slow-fast dynamics (Ludwig et al. 1978, Barkai and McQuaid 1988, Rinaldi and Muratori

1992b, a, van Nes et al. 2007, Dakos et al. 2015). Therefore, it is important to have sound mechanistic insights of the system when interpreting potential analysis. Obviously, there is a need for debate and further investigation on this topic to put these findings into perspective.

TOP-DOWN EFFECTS?

Predators have a strong top-down regulating effect on the community structure in ecosystem (Hairston et al. 1960, Paine 1980), and changes in the highest trophic level may lead to a trophic cascade altering ecosystem functioning (Estes et al. 2011). In this thesis we investigate the role of an abundant avian predator which feeds intensively on benthic prey, therefore, cascading top-down ecosystem effects can be expected (van Gils et al. 2012). Banc d'Arguin is the main wintering area of the red knot, the subspecies *C. c. canutus* feeds in the intertidal seagrass beds on molluscs which they ingest whole and crush in their gizzard (Piersma et al. 1993). The size of their gizzard is rapidly adjusted with hardness of their food, flesh-to-shell ratio (Dekinga et al. 2001, van Gils et al. 2006a). Maintaining a large gizzard is energetically costly and a prey with a high flesh-to-shell ratio is preferred (van Gils et al. 2005). In Banc d'Arguin red knots mainly have a mixed diet of the two most abundant bivalves *Dosina isocardia* and *Loripes*. The latter is by far the most abundant prey and has a higher flesh-to-shell ratio as *Dosina* (chapter 5, van Gils et al. 2013, Oudman et al. 2014). Therefore, one would expect *Loripes* to be the main prey for red knots, potentially creating a strong top-down effect by disrupting the bottom-up mutualistic seagrass-*Loripes* interaction. In other words, by eating *Loripes*, toxic sulfide concentrations will increase and may affect seagrass mortality!

In contrast to these expectations, however, faeces analysis revealed that on average only 50% of the red knot diet consisted out of *Loripes* (chapter 5), and the local depletion ('giving-up-densities'- GUD) was far less than expected based on earlier experiments on bare mudflats (see box 1.1) (Piersma et al. 1995, van Gils et al. 2003). Subsequent studies have shown that the lower dietary contribution of *Loripes* could be explained by mild toxicity of these bivalves due to the stored sulfide compounds (van Gils et al. 2013, Oudman et al. 2014). Therefore, red knots prefer the non-toxic bivalve *Dosina*, however, this bivalve is less abundant and red knots need to counterbalance their diet with *Loripes* (van Gils et al. 2013, Oudman et al. 2014). In addition to any toxicity effects, the higher GUDs still came as a surprise as red knots have a unique sensory organ in the tip of the bill to detect hard-shelled prey buried in soft wet sediments without direct contact ('remote touch') (Piersma et al. 1998). So, *a priori* one would expect that red knots would be capable of locally depleting *Loripes* in the soft sediments of the seagrass beds. On the contrary, a pilot experiment revealed that in high seagrass densities red knots could hardly detect their prey (see box 1.1). So, we asked ourselves how is it possible that a molluscivore specialist with a spectacular remote prey detection was not able to deplete its prey in habitat where they spend two-third of their life?

Over the last two decades, several studies have shown that insights into the morphology and functionality of sensory organs in animals have contributed basic understanding of habitat selection and foraging distribution of animals searching for prey (Miller and Surlykke 2001, Sleep and Brigham 2003, Nebel et al. 2005, Cunningham et al. 2010, Piersma 2012). Predators have evolved multiple ways to detect hidden prey with advanced sensory organs, however, in some environmental contexts sensory information may be obscured (Boonman et al. 1998, Wilson et al. 2013). Yet, the relation between sensory organs, obstruction, and searching efficiency remains little explored. In chapter 6 we experimentally examined whether seagrasses can obstruct prey detection by red knots. We showed that searching efficiencies decreased with prey depth in seagrass patches, it appears that the unique sensory organ in the tip of the bill of red knots is obstructed by the structural complexity of the root system in dense seagrass beds. Capitalizing on this empirical evidence, physical modelling of the pressure field build-up around a probing bill showed that in seagrass the pressure field no longer reveals the presence of the prey. In bare wet sediment the probing bill of the red knot imposes a spherical pressure gradient, which drops off from high to low pressure. A buried prey will disturb this gradient as the flow needs to go around the bivalve. The subtraction of the response of the imposed pulse with the shell in place and without the shell in place informs the red knot about the presence of a prey at some radial distance and direction (chapter 6: Figure 6.2) (Piersma et al. 1998). However, when the shell is situated within a layer of rhizomes, the permeability of this substrate is reduced, and the difference between the induced and the imposed pressure is dominated by the direct reflection due to the presence of the rhizomes layer. This overwhelms the much weaker pressure difference due to the reflection by the shell and obscures the directional prey information. Therefore, we concluded that in seagrass red knots 'lose their sixth sense' and can only detect their prey by direct touch rather than remotely. Relatively few studies have examined remote prey detection and habitat complexity (but see Cunningham et al. 2010) and to my knowledge especially not in this mechanistic detail as we have shown in chapter 6.

What are the consequences for red knots when foraging in seagrass rich habitat? In bare sediment red knots obey the assumptions of Holling's type II functional response, with a constant searching efficiency this implies that intake rate in relation to prey density levels off at high prey densities (Holling 1959, Piersma et al. 1995). In seagrass, however, searching efficiency is negatively related to seagrass biomass (chapter 6 and 7), in other words a foraging knot will encounter different searching efficiencies depending on seagrass density. Therefore, seagrass biomass indirectly influences the shape of the functional response and it may become dome-shaped across a gradient of seagrass densities (Figure 8.3). In addition, one could argue that it would be necessary to include prey depth, as in seagrass searching efficiency strongly decreased with depth (chapter 6: Figure 6.3A). Here I would argue that the seagrass-depth dependency of searching efficiency is an important factor to take into account. A large step has been made by van Gils et al (2013), in addition to search and handling time and digestive constraints he included the toxic constraint (toxic-digestive rate model, TDRM). An interesting next step would be to

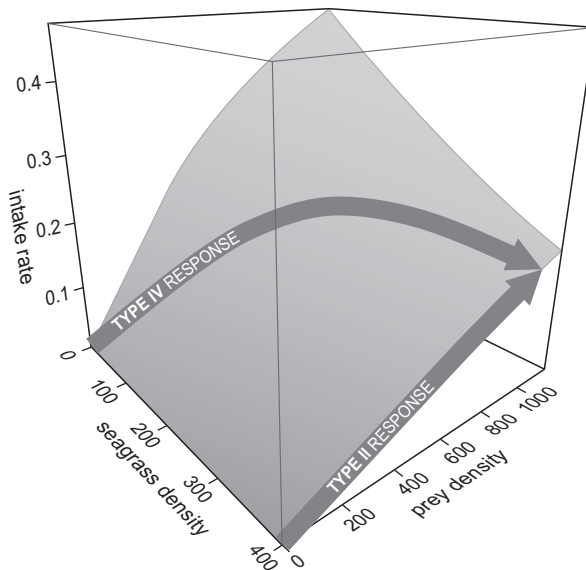


Figure 8.3 Functional response type II changing over a gradient of seagrass density with a positive association between seagrass density and prey density. As searching efficiency is negatively related to seagrass biomass, it will indirectly influence the shape of the functional response and it may become dome-shaped (type IV response) across an increasing gradient of seagrass density (grey arrow).

incorporate seagrass dependent searching efficiency when estimating intake rates of red knots in the Banc d'Arquin.

In many more ecosystems, plant structures are good candidates to affect predator-prey interactions and the acceptance of the existence of 'higher-order-interactions' or 'trophic interaction modifications' (TIM's) go back a few decades (Charnov et al. 1976, Abrams 1983) and have received more attention over the last decade (Brown and Kotler 2004, Brown 2010). Yet, despite the importance of TIM's, the net outcome for predator-prey dynamics where plant structure is related to attack rate of the predator has rarely been studied. Holt et al. (2010) discussed the interaction between plant level and attack rate and explored this phenomenon with a Lotka-Volterra model. This indicates on interesting opportunities for research on red knots and their bivalve prey!

It is interesting to speculate about the red knot – *Loripes* interaction in an evolutionary context. Predator and prey are often caught in an arms race (Vermeij 1987). This phenomenon is described as the so called 'red queen hypothesis' or the 'hypothesis of escalation': prey have evolved to stay in the same place to keep up with their predator and the other way around (Van Valen 1973, Vermeij 1987). In other words, two interacting species continue to change, and possibly in directional ways, in response to each other. Bivalves living in soft sediments show a typical food-safety trade-off which is reflected by their burrowing depth, which they use as a strategy to reduce predation risk (Zwarts and

Wanink 1989, Sih 1997, Bom et al. in prep), but increasing burrowing depth reduces food intake. Not surprisingly, their main avian predators have evolved long bills to find their buried prey by touch in the sediment by probing (Hulscher 1982). In the case of the red knot, in addition to their relatively long bills (note that *C. c. canutus* subspecies has on average the longest bill, Piersma et al. 1992, Tomkovich 1992), they evolved a spectacular and unique sensory organ in the tip of bill (Piersma et al. 1998), but, as discussed above, on the seagrass meadows of Banc d'Arguin this organ is obstructed by the dense belowground root network of seagrass. In fact, seagrass protect its sulfide detoxifier against its main predator. On top of this, due to its toxicity, *Loripes* is the less favourable prey of their two main prey types (Oudman et al. 2014), this may suggest an unknown chemical defence mechanism for bivalves, which was also described for *polychaetes* with similar symbiotic relation with endosymbionts (Kicklighter et al. 2004). From an evolutionary arms race perspective one could argue that *Loripes* has taken a leap in the arms race, by effectively escaping their predator (i.e. outpacing the red queen!).

In conclusion, seagrass indirectly conceals its detoxifier for its main predator, by obstructing the remote touch, and, in combination with the toxicity of the bivalves, preventing disruption of the mutualistic feedback. It appears that a strong trophic cascade interfering with the mutualistic seagrass-Lucinid interaction, which could be expected based on the large population size of the avian predator, is lower than expected. In degrading seagrass beds, however, the top-down effect may start to play a role because the decrease in seagrass has an additional consequence: it may increase the searching efficiency of the knots again (see above). In chapter 6 we argued that the searching efficiencies of red knots decreased with seagrass biomass, as a consequence red knot should choose feeding patches with no or low seagrass densities and high prey densities. However, in chapter 7 we could show that such sites hardly exist in Banc d'Arguin. The mudflats here are either sparsely covered by seagrass (low densities of prey that should be relatively easy to find) or densely covered (high densities of prey that should be harder to detect). Intake-rate maximizing red knots would have to find an optimum at intermediate seagrass densities. Indeed, as predicted, our experiments showed that red knots gained high searching efficiencies at low prey densities in little or no seagrass, and low searching efficiencies with high prey densities in dense seagrass beds. Using field observations on red knot densities, we showed that red knots in the field aim for the optimum at intermediate seagrass densities where intake rates potentially are maximized. Although we could not differentiate between active choice or random choice. Regardless the mechanism behind their distribution, intake rate were highest on degrading seagrass (chapter 7), therefore, the top-down effects of red knots may interact with the die-off event by eating the detoxifying Lucinid bivalves and possibly accelerating seagrass degradation.

INTERPLAY BETWEEN BOTTOM-UP AND TOP-DOWN EFFECTS AND ECOSYSTEM COLLAPSE

To investigate the top-down effect of red knots I extended the model presented in chapter 5. Here, I added predation pressure by red knots by assuming an intake rate according a functional response type II (Holling 1959), *Loripes* depletion rates based on the toxic-constraint (van Gils et al. 2012, Oudman et al. 2014), and assumed a negative relationship between searching efficiency and seagrass shoot density, based on our experimental findings in chapter 6. Finally, red knots are for about two-third of the year present in Banc d'Arguin, so I used 240 red knot simulation days per year (66% of the year).

Interestingly, the model predicted that red knots may not be able to disrupt the mutualistic feedback. One may expect that this is due to the obstruction of seagrass, but in contrast this was the consequence of the toxic constraint. Red knots are limited in their *Loripes* intake rate to a maximum of $0.12 \text{ mg flesh AFDM s}^{-1}$ (Oudman et al. 2014). From this we can calculate the daily *Loripes* consumption: assuming an average *loripes* energy content is 7.3 mg AFDM (van Gils et al. 2012), and 12 hours feeding per day an individual red knot can maximally consume $710 \text{ loripes day}^{-1}$ ($0.12/7.3 \times 3600 \times 12 \text{ h} = 710 \text{ day}^{-1}$). On an annual basis, taking the local average red knot population density into account (10 ha^{-1} (van Gils et al. 2009)), red knots thus should consume around $170 \text{ Loripes m}^{-2}$ ($710 \times 0.001 \text{ m}^2 \times 240 \text{ days} = 170 \text{ m}^{-2}$). Given that *Loripes* densities in healthy seagrass beds are generally very high (up to 3700 ind. m^{-2}) (van der Geest et al. 2011, Ahmedou Salem et al. 2014) a strong numeric effect of knots on the *Loripes* population is not likely there. Indeed, bifurcation analysis showed that predation pressure should be extremely high to have an effect on the system. Red knot feeding densities should exceed on average $170 \text{ birds ha}^{-1}$ (Figure 8.4) to consume enough *Loripes* to push the system over a critical threshold to disrupt the mutualistic feedback causing unstable cyclic behaviour

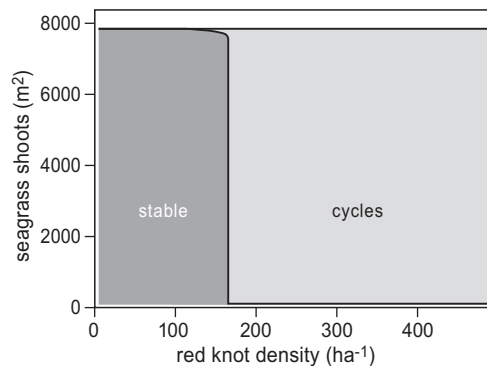


Figure 8.4 (A) Bifurcation analysis of the seagrass ecosystem with mutualistic interaction in relation with red knot density (top-down effects). The analysis of red knot density predicts that in a healthy system (default: seagrass mortality m_n : 0.007) the system is unstable showing cycles after red knot densities are unrealistically high, up to 170 ha^{-1} (field observations: max. 10 ha^{-1}).

(Figure 8.4) (note that average red knot densities in Banc d'Arguin may reach 6–10 ha⁻¹: Zwarts et al. 1990, van Gils et al. 2009). However, as argued above, a more thorough modelling examination showed that red knots could affect the dynamics of a seagrass bed in a degrading state. Here, red knots, in natural densities (10 ind. ha⁻¹), are indeed capable to speed up the degrading event by depleting *Loripes* causing further accumulation of sulfide (Figure 8.5A-C). In fact, resilience of the mutualistic partnership is diminished causing the system to collapse earlier (Figure 8.5C). Therefore, we may conclude that the

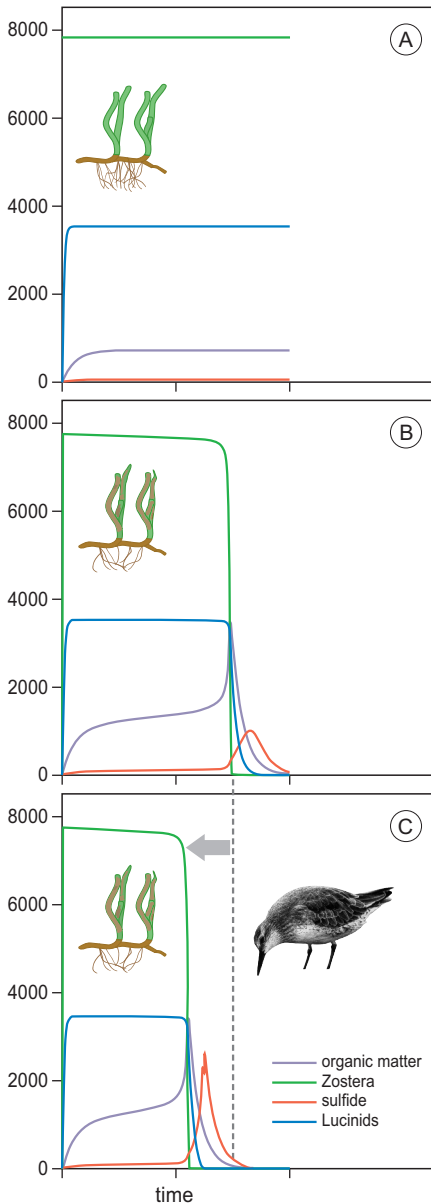


Figure 8.5 Model simulations of seagrass density Z (shoots m⁻²), sulfide concentrations S (μmol L⁻¹), organic matter OM (% × 100) and *Loripes* density L (ind. m⁻²) (A-C). (A) Model simulations at default setting (see chapter 7) with mutualistic interaction; any produced sulfide is removed by *loripes* and the system remains stable. (B) A minor increase (from $m_n = 0.007$ to $m_n = 0.011$) of seagrass background mortality, causes cyclic collapse-and recovery behaviour in which the mutualism temporarily buffers against sulfide toxicity, but is not able to remove all sulfide produced, eventually causing seagrass collapse. (C) When adding predation pressure on *Loripes*, resilience of the mutualistic partnership is diminished causing the system to collapse earlier (grey arrow).

top-down effect of red knots likely accelerates seagrass degradation. Although it appears that results from our empirically parameterized model may match the field situation, it is nevertheless a simplification of reality and interpretation of these results should be taken with cautious. However, I hope this theoretical exercise is a step in the direction to better understand the interplay between top-down and bottom-up forces in general, but especially for the Banc d'Arguin intertidal seagrass ecosystem.

ADDITIONAL EFFECTS

Prey giving-up densities are likely seagrass-dependent as searching efficiencies, and may therefore increase with seagrass densities, this relation is unknown and to really understand the direct top-down effect one should quantify this relationship, this should be addressed in future work. In addition, the model simulation does not include a number of effects that we did observe in the field. Apart from desiccation-induced seagrass die-off and increased sulfide levels, we observed a number of effects that occurred after initiation of the degradation event. First of all, we observed diatoms locally colonized the degraded parts and grew over the remaining healthy seagrasses. Secondly, the simultaneously eroded sediments increased sedimentation rates on the surrounding seagrasses. Finally, it seems that these effects improved the living conditions of other algae and organisms which also appeared on the degraded parts (e.g. *Vaucheria* sp. and *Uca* sp., Figure 8.6). Consequently, these effects appeared to aggravate the rate of the decline and may enhance the downward spiral of habitat degradation.

Apart from eating *Loripes*, there might be another surprising top-down effect, as recent observations suggest that red knots eat seagrass rhizomes (van Gils et al. in prep.). At first sight it is hard to believe that red knots could have an effect, as one m² of seagrass beds on average contains 645 gram wet mass of rhizomes and roots. However, unpublished field- and experimental observation show that red knots seem to choose for the most energy rich part of seagrass rhizomes, the apical meristem (own observation J. de Fouw and J. A. van Gils). The apical meristem is the growing part of seagrass (Larkum et al. 2006) and eating these parts may negatively affect seagrass growth and in turn seagrass mortality. In addition, the demolishment of the belowground physical structure may also enhance mortality. So, another open question is to get insight in what part of the seagrass red knots exactly eat and in which amount (future work M. Jewell). Finally, although *Loripes* is in most years the most abundant bivalve and has important community structuring effects, in this thesis we did not take other benthic species in to account. As mentioned before, *Dosinia*, for example, plays an important role and the amount of *Loripes* in red knot diet and is strongly correlated with *Dosinia* (van Gils et al 2013). In addition, increased predation pressure on *Dosinia* increased per capita growth rates of *Loripes* (van Gils et al. 2012), hinting at complex interacting population dynamics which also needs further investigation.

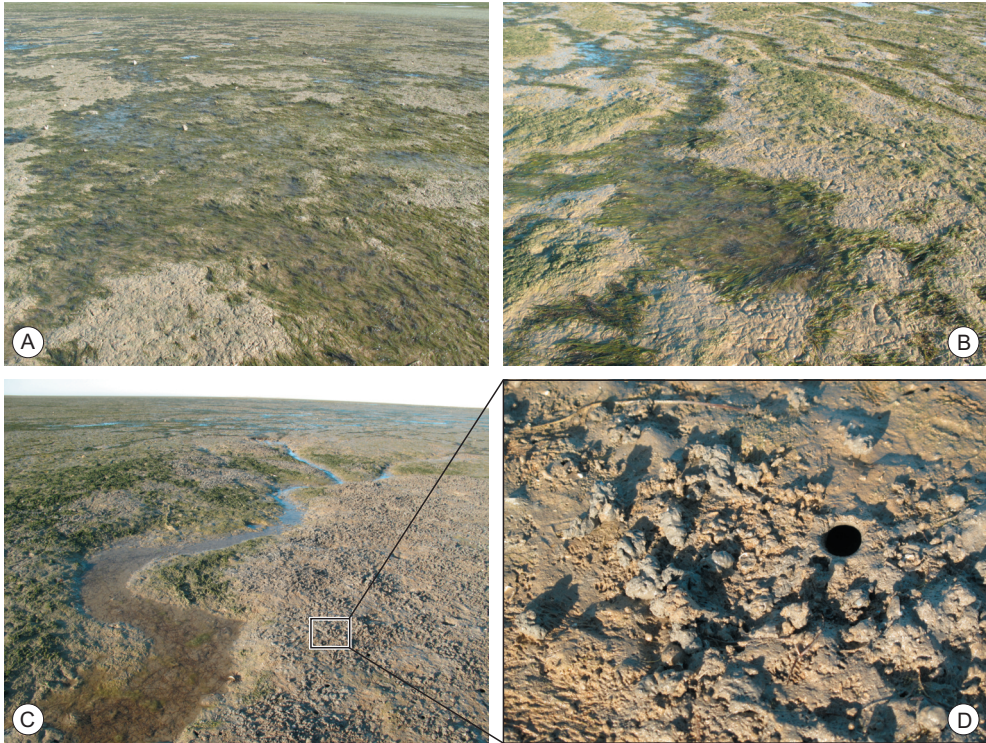


Figure 8.6 Additional effects in a degrading seagrass ecosystem. (A) The simultaneously eroded sediments increased sedimentation rates on the surrounding seagrasses. (B) Diatoms locally colonized the degraded parts and grew over the remaining healthy seagrasses and (C-D) seem to improve the living conditions of other algae and organisms which also appeared on the degraded parts (e.g. *Vaucheria* sp. and *Uca* sp.).

IMPLICATIONS FOR CONSERVATION

This thesis shows that bottom-up forces are important drivers of the Banc d'Arguin ecosystem, although, bottom-up and top-down effects have synergistic impacts on ecosystem functioning and their interaction could in theory explain rapid and large-scale ecosystem collapse. This thesis also points out a risk of facultative mutualism dependent marine ecosystems: environmental change can disrupt inherent facultative mutualism-driven positive feedback, causing severe ecosystem change. I therefore suggest that, apart from gaining in depth knowledge, conservation and restoration should not be based on the knowledge of a single species or stressor type, but should instead develop a more process-based integrated network approach taking in to account trophic and non-trophic interactions (e.g. mutualism, predation and habitat modification) to be able to predict ecosystem response to environmental change.

Seagrasses are degrading at an accelerating rate worldwide (Waycott et al. 2009) and losses are often linked to climatic extremes such as storms, high seawater temperatures, and low-tide desiccation events in intertidal beds (Seddon et al. 2000, Larkum et al. 2006, van der Heide et al. 2010a, Fraser et al. 2014, Thomson et al. 2015). This thesis shows that global change may also become a serious risk for the Banc d'Arguin seagrass ecosystem. The seagrass degradation was initially triggered by enhanced low-tide desiccation stress caused by high evaporation during a drought event. It seems likely that desiccation stress will become a more common phenomenon as long as the world heats up (IPCC 2014). There are other climate change related effects (e.g. sea-level rise, eutrophication, siltation events and dust-storms) which may have effect on seagrass meadows (Orth et al. 2006). Therefore, the ongoing monitoring of e.g. bird numbers, benthic community and seagrass meadow state should be given high priority to keep track of changes which possible could be linked to future global change.

Banc d'Arguin is a classic example where an intertidal seagrass ecosystem harbours a large diversity of large marine life (cetaceans and sea turtles), seabirds, shorebirds, fish and smaller marine life, which has a very important socio-economical value nationally and internationally. At this stage the Banc d'Arguin appears relatively pristine, but at the shelf-break area just outside the park large industrial fisheries are operating. In addition, recently there are developments of an offshore oil industry in Mauritanian waters (Burton and Camphuysen 2003, Camphuysen and van Spanje 2013)

The ongoing developments may in fact be a risk for the protected intertidal seagrass areas and may disruption bottom-up and top-down forces. It is increasingly recognised that marine ecosystems are open and interconnected and seagrass meadows are an integral and essential part of this larger marine network (Gillis et al. 2014, McKinnon et al. 2014, van de Koppel et al. 2015). The marine sequence of mangroves, seagrass beds, coral reefs, continental slope and deeper ocean waters are a typical example of inter-linked ecosystems that together form the basis of productivity and biodiversity in tropical coastal zones (Heck et al. 2008, van de Koppel et al. 2015). Between these ecosystems there is active and passive exchange of nutrients, detritus, small pelagic fish, predatory fish, seabirds and marine mammals. This strong reciprocal dependency between seagrass meadows and other ecosystems makes ecosystem connectivity a functional foundation of marine biodiversity. A sound understanding of ecological connectivity seems to be crucial, but it is currently often not taken into consideration in the absence of concrete information. Thus, rather than studying ecosystems in isolation, I argue that the Banc d'Arguin system should be studied on a broader ecosystem landscape scale. A key component and challenge for the future would be to increase mutualistic interactions between researchers studying top-down effects, bottom-up effects, cross-habitat ecological connectivity (e.g. intertidal versus pelagic) but last but not least between science and the social-economical needs within the Banc d'Arguin.

