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

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Document Version

Publisher's PDF, also known as Version of record

Publication date:
2016

[Link to publication in University of Groningen/UMCG research database](#)

Citation for published version (APA):

de Fouw, J. (2016). *Bottom-up and top-down forces in a tropical intertidal ecosystem: The interplay between seagrasses, bivalves and birds*. [Thesis fully internal (DIV), University of Groningen]. Rijksuniversiteit Groningen.

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Introduction

Jimmy de Fouw

SHORT INTRODUCTION

Worldwide there is growing concern that global environmental change (e.g. climate change, eutrophication, coastal development, overfishing) negatively affects coastal ecosystems and the rich suite of services they provide to humanity and global biodiversity (Costanza et al. 1997, Orth et al. 2006, Waycott et al. 2009). The importance of coastal ecosystems for humankind has traditionally been exceptionally large, and human settlements predominately occurred along the coast. Currently, almost half of the human population lives in coastal areas and both this proportion and their total numbers are still increasing (<http://www.oceansatlas.org/>, Halpern et al. 2008). Since 1700 all this human activity has led to the disappearance of 87% of the wetlands in the world (Davidson 2014). Given the ongoing and planned coastal developments around the world, a deeper understanding of the mechanisms driving biodiversity and other essential ecosystem functions in coastal systems is therefore urgently required to inform conservation management, should human society decide the remaining wetlands are worth preserving and managing!?

The main objective of the research in this thesis is to understand the relative importance of bottom up and top-down forces on the ecosystem functioning of tropical intertidal seagrass meadows. Seagrass beds play an important ecosystem-structuring role through the creation of strong bottom-up effects. At the same time, predators can also exert crucial community structuring top-down effects through trophic cascades in these ecosystems (Hairston et al. 1960, Paine 1980, Estes et al. 2011), and suggesting that the interplay between top-down and bottom-up effects may be essential for the functioning of these ecosystems (Hughes et al. 2013).

Key questions in this thesis were: How can an intertidal seagrass ecosystem function under the constant risk of biochemical stress conditions (bottom-up effects, high sulfide levels) and what is the role of a migrant top-predator (top-down effects)? What is the function of mutualistic interactions (bottom-up effects)? And finally, do bottom-up and top-down effects have synergistic impacts on ecosystem functioning and does this give us better insight into how seagrass ecosystems may respond to possible enhanced environmental stress condition?

STUDY AREA – BANC D'ARGUIN

The research in this thesis was carried out in the intertidal seagrass meadows of the Parc National du Banc d'Arguin (PNBA) in Mauritania. Here, the mudflats border the Sahara, with a very dry climate which is characterized with monthly average temperatures 18–23°C, often strong northerly winds and very low precipitation (Wolff and Smit 1990). In 1976 the coastal area encompassing almost all Mauritanian's intertidal flats and extensive areas of shallow seas were designated national park status and in 1989 the PNBA became a UNESCO Natural World Heritage site. The intertidal mudflats comprise about

500 km² of mudflat dominated by mixed meadows of *Zostera noltii*, *Halodule wrightii* and *Cymodocea nodosa* (Figure 1.1A-C) (Wolff et al. 1993, Folmer et al. 2012), that retain consistent aboveground biomass throughout the year (Duarte 1989, Vermaat et al. 1993). In this ecosystem seagrass meadows accumulate large amounts of silty, organic matter-rich sediment (up to 1-m thick) and are inhabited by extremely high densities (over 3700 ind. m⁻²) of the lucinid bivalve *Loripes lucinalis* (Honkoop et al. 2008, van der Geest et al. 2011, van Gils et al. 2013, Ahmedou Salem et al. 2014).

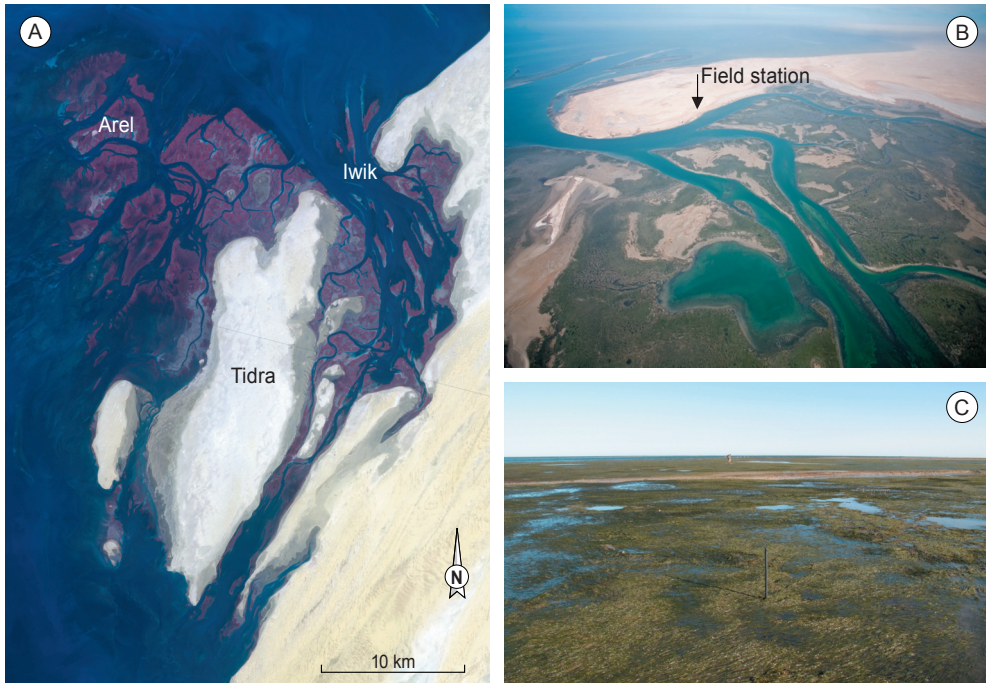


Figure 1.1 (A) False colour image based on Landsat satellite images, red areas depict intertidal seagrass. (B) Aerial picture of Baie d'Aouatif area (Photo: © Hellio - Van Ingen). (C) Intertidal seagrass mudflat during low tide.

BOTTOM-UP EFFECTS – TROPICAL SEAGRASS MEADOWS

Seagrasses are flowering plants which are closer related to terrestrial plants than marine plants like macroalgae. There are more than 50 different species worldwide which comprise five different families and represent least three lineages which independently entered the marine environment (Green and Short 2003, Larkum et al. 2006). Seagrasses evolved under different climate conditions (e.g. temperature, CO₂) which may lead to different tolerances to changing environmental conditions (Larkum et al. 2006). They can

live in mixed species or single-species meadows from intertidal to subtidal zone in temperate to tropical coastal areas. The upper limit in the intertidal zone is often determined by desiccation stress due to wind and solar exposure between tidal inundations and hydrodynamic conditions (van Lent et al. 1991, Philippart 1995, Leuschner et al. 1998, van der Heide et al. 2007). The deeper depth limit depends in general on light availability, varying from 1 to 50 meter in turbid- to clear water systems respectively (Duarte 1991).

Worldwide seagrasses form one of the ecological pillars of coastal zones due to the many habitat niches they offer to support a high biodiversity and their extremely high primary productivity. Seagrass meadows are of great socio-economic importance in these areas, because they serve as carbon and nutrient sinks, coastline stabilization and protection (e.g. storm buffers) and serve as a keystone habitat for economically valuable species such as fish (Waycott et al. 2009, van der Heide et al. 2012). However, the rapid worldwide decline of seagrass beds is a major concern, their decline is comparable with threatened ecosystems like coral reefs and tropical forest (Waycott et al. 2009). In the Dutch Wadden Sea, for example, a dramatic decline of seagrass meadows took place after the construction of a large dam and the occurrence of the wasting disease (van der Heide et al. 2009).

Seagrass beds alter the physical conditions of their environment (i.e. ecosystem engineers) (Jones et al. 1994), which is not only beneficial for the species involved but for many associated species, thereby also called ‘foundation species’ (Bruno and Bertness 2001). In more detail, seagrasses influence their own growing conditions by reducing hydrodynamics, stabilizing sediments and by accumulating organic matter and nutrients from the water column (Hansen and Reidenbach 2012). This will also increase water clarity which is beneficial for photosynthesis and growth (Koch 2001, Larkum et al. 2006, de Boer 2007) Apart from this positive feedback, the decomposition of organic matter in marine sediments is strongly controlled by sulphate-reducing bacteria that produce sulfide, which is highly toxic to seagrasses and all other aerobic life (Bagarinao 1992, Lamers et al. 2013). The high sulfide levels should lead to limitations of productivity and distribution, however, this is not the case and the mechanism how seagrass beds cope with sulfide stress remained a mystery for a long time. Nevertheless, it has been hypothesised that seagrasses engage in a mutualistic interaction with lucinid bivalves and their sulfide-oxidizing, gill-inhabiting bacteria to reduce sulfide stress (Larkum et al. 2006, Stanley 2014).

TOP-DOWN EFFECTS – RED KNOTS

Migratory shorebird species intensively use coastal wetlands to make migratory stopovers to replenish their exhausting energy reserves and as wintering grounds (van de Kam et al. 2004, Piersma et al. 2005). In the last decade, it has been clear that worldwide shorebirds are in decline due to habitat loss, climate change and overexploitation (Piersma and Lind-

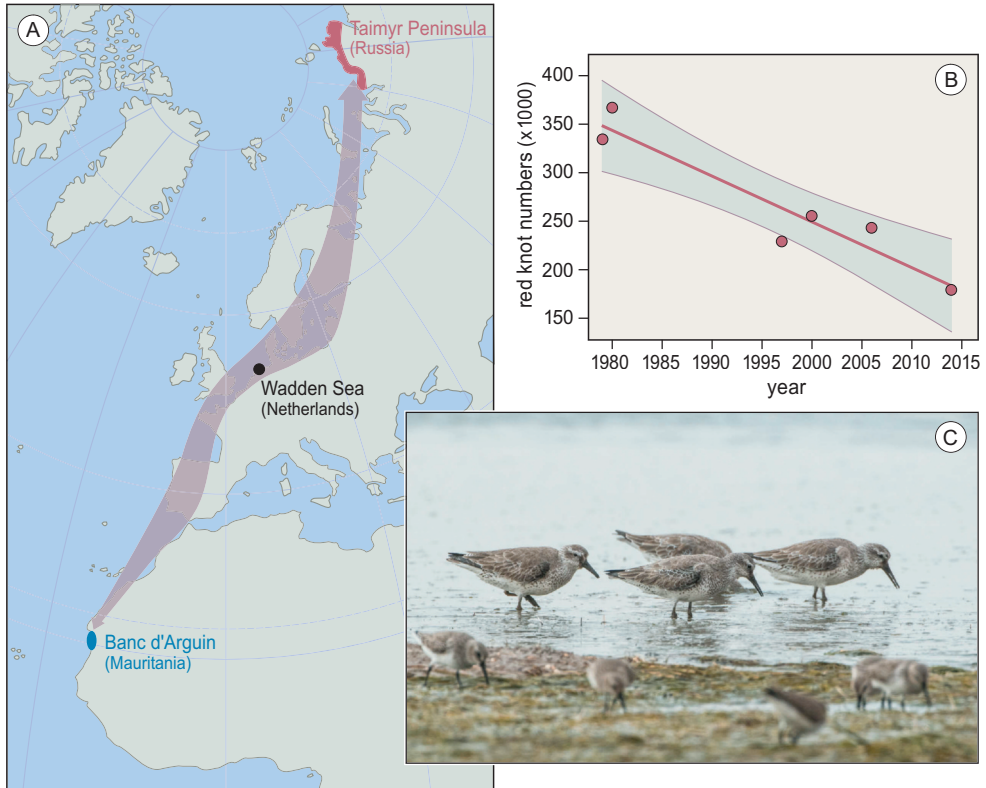


Figure 1.2 (A) Migration route of red knots *Calidris canutus canutus*. The subspecies can be found on the West-African coast during non-breeding season, with the main numbers in Mauritania, Banc d'Arguin. During summer they breed in the High Arctic at Taimyr Peninsula and during migration they can be found in high numbers on their main stop-over site the Dutch Wadden Sea. (B) Population trend of red knots at the Banc d'Arguin (produced from van Roomen et al. (2015)). (C) Red knot foraging in seagrass beds in Banc d'Arguin (picture: Jan van de Kam).

ström 2004, van Gils et al. 2006, Delany et al. 2009, Boere and Piersma 2012, van Roomen et al. 2015). These migratory top-predators travel around the planet, in doing so they connect ecosystems on a global scale, therefore, link biodiversity and ecosystem functioning on a large scale and play an important role in structuring global biodiversity (Bauer and Hoyer 2014). Being at the top of the food-web their role (top-down effect) seems to be crucial and losing the highest trophic level may lead to a trophic cascade accelerating biodiversity loss (Estes et al. 2011).

The red knot, the subspecies *Calidris canutus canutus*, is a migratory shorebird that breeds in the high Arctic tundra and has its main wintering site in Banc d'Arguin (Figure 1.2A). Within the East-Atlantic migratory flyway the red knot shows a sharp decline, including its main wintering site in Mauritania (Figure 1.2B) (van Gils et al. 2013, van Roomen et al. 2015). These changes may be due to anthropogenic impact (e.g. fisheries,

habitat destruction) on their stop-over sites in the temperate areas in Europe (van Gils et al. 2006); however, recent research showed that feeding conditions at their wintering grounds may play an important role (van Gils et al. 2013). Whatever the exact underlying reason, however, red knot population is declining and being still the most abundant shorebird cascading top-down ecosystem effects can be expected at the Banc d'Arguin.

Red knots are specialized molluscivorous birds which usually forage on bivalves buried in the soft sediments of intertidal mudflats (Piersma 2007). Because, *Loripes* and *Dosnina isocardia* are the most abundant prey, one would expect that *Loripes* is an important prey for red knots (van Gils et al. 2013, Oudman et al. 2014). In addition, 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') (Figure 1.3A-B) (Piersma et al. 1998). So, a priori, one would expect that red knots are capable of depleting *Loripes* in the soft sediments of the seagrass beds, potentially creating a strong top-down effect on the ecosystem (van Gils et al. 2012). In contrast to these expectations, however, a pilot experiment showed that local depletion ('giving-up-densities') was far less than expected based on earlier experiments on bare mudflats (Box 1.1).

A strong tool to understand the top-down effect of a forager is the functional response, which describes the relationship between food intake rate and prey density, and

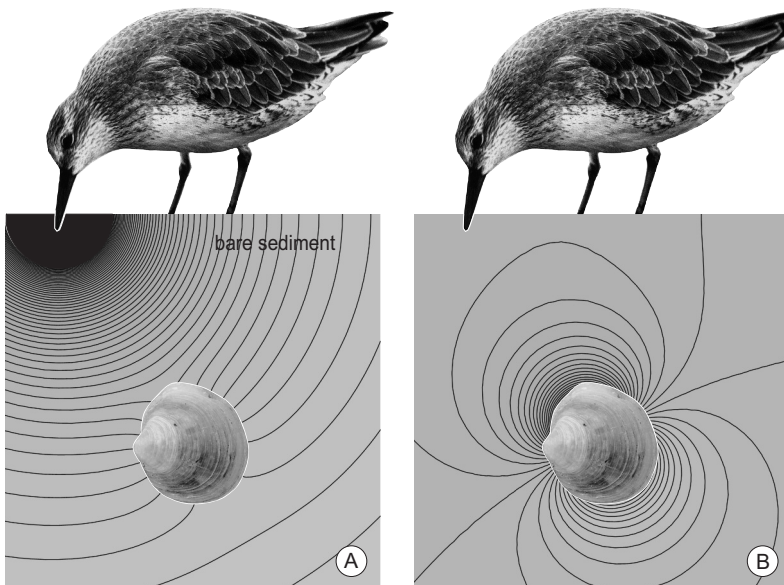


Figure 1.3 Cross section of a hypothetical mudflat with the pressure patterns produced by the probing knot's bill, located at the upper surface of the wet sediment. (A) The presence of a shell prevents the pressure field to move away. (B) The pressure pattern induced by the presence of the shell is defined by subtracting the response of the initial pulse with the spherical shell in place and without the shell in place. This difference is sensed and informs the knot about the presence of a prey, in the form of radial distance and direction (adapted from Piersma et al. 1998).

mechanistically includes searching, handling and digestion as factors constraining prey intake (Jeschke et al. 2002). On bare sediment red knots obey the assumptions of Holling's disc equation (functional response type II) (Holling 1959, Piersma et al. 1995). It is usually assumed that foragers will try to maximize their intake rates which should occur at the highest (harvestable) prey densities (Holling 1959, Stephens and Krebs 1986, Zwarts and Wanink 1993). However, as in seagrass beds habitat is more complex than in bare sediment, we asked ourselves the question whether this would influence the intake rate of red knots? Seagrass has a positive effect on species richness and abundance (Orth et al. 1984, Honkoop et al. 2008, van Gils et al. 2015). On the other hand, the increased habitat complexity may negatively affect the prey detectability of the red knots. Therefore, in seagrass habitat the intake rate and habitat choice by foraging red knots may not be simply a function of prey density but also of habitat complexity created by seagrass.

OUTLINE OF THE THESIS

In this thesis I investigate the relative importance of bottom-up effects created by seagrass and its benthic invertebrate life, and top-down effects created by the migratory avian predator, the red knots, on an intertidal tropical ecosystem.

In **chapter 2**, we investigated the functioning of a three-stage mutualism between seagrass, Lucinid bivalves and their sulfide-oxidizing, gill-inhabiting bacteria. By using a meta-analysis, a field study, and a laboratory experiment, we investigated the importance of this three-stage mutualism in seagrass meadows on a global and local scale for our study area. Next, in **chapter 3**, we empirically reveal that the breakdown of this three-stage mutualism due to climate extremes (heat and drought event) is a key driver of rapid landscape-scale degradation in intertidal seagrass beds. Furthermore, in **chapter 4**, in a combined investigation using a differential equation model, remote sensing analyses combined with potential analyses we showed that the mutualistic interaction stabilizes lethal feedback in seagrasses ecosystems.

To understand the top-down importance on the ecosystem we first determined the diet and intake rate of red knots on *Loripes*. In **chapter 5**, faeces analysis revealed that on average only 50% of the red knot diet consisted out of *Loripes*. In addition, earlier observations showed local intake rates where far less than expected based on earlier experiments in bare sand. In **chapter 6**, we determined the prey searching efficiency of red knots and showed that when foraging on bivalves hidden in seagrass beds, red knots 'lose their sixth sense' and can only detect their prey by direct touch rather than remotely. In **chapter 7**, we investigated how prey detectability and prey density combined determines the habitat choice of red knots in seagrass ecosystem. Finally, in **chapter 8**, I discuss the synergistic impacts of bottom-up and top-down effects on ecosystem functioning, in addition, I discuss how these insights give us better understanding in how marine ecosystems response to environmental stress condition.

BOX 1.1. RED KNOTS IN THE FIELD EXPERIMENTS

The red knots is an ideal model species in foraging experiments, with experiments carried out both under controlled laboratory conditions as well as in the ‘wild’. Since the 1980s, observational and experimental studies have been conducted, resulting in very important insights published in many peer-reviewed scientific journals and PhD thesis’s (e.g. Piersma 1994, Zwarts 1997, van Gils 2004, Vahl 2006, Reneerkens 2007, Buehler 2008, Kraan 2010, van den Hout 2010, Leyrer 2011, Folmer 2012, van der Geest 2013, Bijleveld 2015). This could only be done due to the support and experience of the NIOZ staff at the laboratory facilities. Inspired by the idea to bring captive knots in the field (an idea originally posed by the late Rudi Drent and later on followed up in the Dutch Wadden Sea by van Gils 2004), we copied this approach in Banc d’Arguin in order to understand top-down effect of red knots on the seagrass dominated ecosystem. Basically, we aimed to create patches with and without *Loripes lucinalis*, depleted in a natural way by our captive red knots. Based on the experience in the Wadden Sea (see chapter 1), initially we were convinced that red knots should be able to deplete *Loripes* in the soft sediments of the seagrass beds. In contrast to these expectations, however, after about 10 minutes of searching for prey our red knots stopped foraging, as they hardly found any prey and where resting for the next 50 minutes during the pilot experiment! It became clear that the knots were teaching us a lesson and showed us that we did not understand their foraging behaviour in seagrass rich environments, therefore, we first needed to get insight in what was going on here? So, we went step-by-step and adjusted our way forward dictated by the red knots, eventually resulting in new important insights of chapter 6.

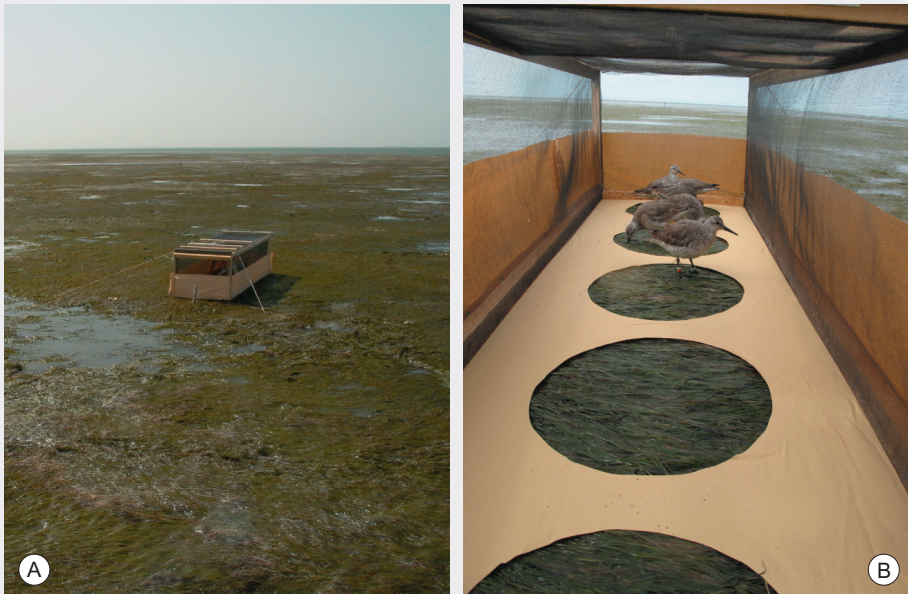


Figure B1.1 (A-B) A pilot experiment with red knots in dens seagrass at Banc d’Arguin, Mauritania (October 2010).

