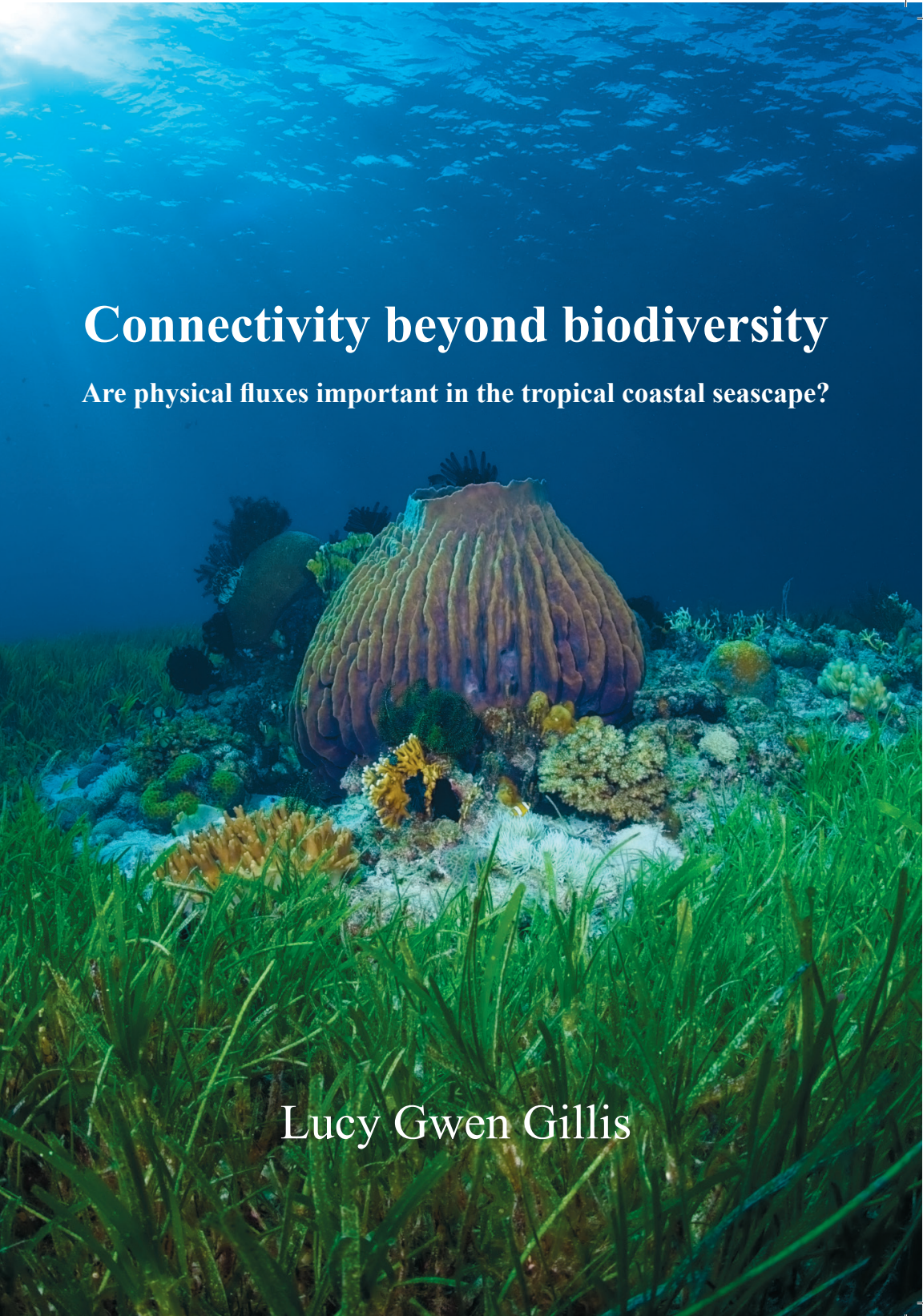


An underwater photograph showing a large, barrel-shaped sponge with vertical ridges in shades of purple, pink, and orange. The sponge sits on a sandy seabed covered with various corals and seagrass. In the foreground, there is a dense patch of green seagrass. The background shows the blue water of the ocean with light filtering down from the surface.

Connectivity beyond biodiversity

Are physical fluxes important in the tropical coastal seascape?

Lucy Gwen Gillis

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ISBN/EAN: 978-90-8891-922-0

Cover design: Proefschriftmaken.nl || Uitgeverij BOXPress

Cover photographs copyright: Steve De Neef

Correspondence: lucygwen.gillis@nioz.nl

Connectiviteit voorbij biodiversiteit:

Het belang van fysisch transport in de tropische kustzone

Proefschrift

ter verkrijging van de graad van doctor
aan de Radboud Universiteit Nijmegen
op gezag van de Rector Magnificus prof. mr. S.C.J.J. Kortmann,
volgens besluit van het college van decanen
in het openbaar te verdedigen op dinsdag 4 september 2014
om 14.30 uur precies

door

Lucy Gwen Gillis
geboren op 21 oktober 1980
te Dumfries (United Kingdom)

Promotoren:

Prof. dr. P.M.J. Herman
Prof. dr. A.D. Ziegler (NUS, SG)

Copromotor:

Dr. T.J. Bouma (NIOZ)

Manuscriptcommissie:

Prof. dr. L.P.M Lamers
Prof. dr. R. Aerts (VU Amsterdam)
Prof. dr. S. Bouillon (KU Leuven)

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General Introduction

The tropical coastal seascape

Within the tropical seascape, mangrove forests, seagrass beds and corals reef are important ecosystems, providing many services to society. Ecosystem services can in general be categorized as supporting services (e.g erosion control and coastal defence), provisioning services (e.g. maintenance of fisheries and raw materials), regulating services (e.g. nutrient cycling and water purification) and cultural services (e.g. spiritual and recreational benefits) (Barbier et al. 2011). Some of the most important ecosystem services provided by mangroves are erosion control and stabilization of sediment, as well as nutrient filtering (Barbier et al. 2011). Seagrasses provide fisheries nursery habitat and re-mineralization of inorganic and organic material (Barbier et al. 2011). Coral reefs are an important support for offshore fisheries and dissipate waves before they reach the coast (Barbier et al. 2011). The recognition of the ecosystem services provided by these coastal ecosystems means that they are increasingly valued.

Unfortunately, there has been a considerable global decline in occurrence and health of mangroves, seagrass beds and coral reefs over the last 100 years. Worldwide, seagrass beds are thought to be declining about 7 % year⁻¹ since 1990 (Waycott et al. 2009). Mangroves are decreasing in surface area by 1-2 % year⁻¹ (Valiela et al. 2001) and coral reefs by 1-7 % year⁻¹ (Bellwood et al. 2004). With human pressures on coastal areas expected to increase in the coming decades, this decline will continue unless counteracted by actively imposing protective laws or by restoring these ecosystems when they become degraded for ecosystem service purposes.

One possible explanation for restoration failures can be the lack of large-scale facilitative interactions between adjacent ecosystems, due to the absence of a sequence of connected ecosystems along the depth gradient, as may have been present in the undisturbed coastal seascape (illustrated in Fig. 1). Marine ecosystems such as mangrove forests, seagrass beds and coral reefs will always be interconnected via the seawater. This connection means that there can be an exchange of physical (hydrodynamic) energy, chemical (sediment and nutrient) and biological (organism) elements (Fig. 1). As a consequence of this interconnection, changes in one specific ecosystem may have consequences on neighboring ecosystems both in close proximity or further away. In case adjacent ecosystems improve each other's growing conditions, one could speak of large-scale facilitative or positive interactions. It should be noted that only a limited number of large-scale facilitative interactions require ecosystems to be directly neighbouring (e.g., hydrodynamic facilitation). For other facilitative interactions the ecosystems may be further apart and appears disconnected (e.g., for transport of riverine/marine sediment and POM export, Fig. 1).

It is poorly known to what extent such large-scale facilitative interactions exist, even though they may offer great opportunities for restoration. For example, to restore a

seagrass bed, it may be better to create coral-reef like structures that attenuate hydrodynamic energy and allow seagrass to establish in the sheltered conditions, rather than trying to directly plant seagrass. Moreover, the coral reef like structures may also enable corals to settle. My research aims at identifying the importance of large-scale facilitation by ecosystem connections as critical factors needed for ecosystem-based designs. Ultimately, I hope that this thesis will provide a scientific basis for broadening design and restoration practices in the tropical coastlines from a small-scale target-ecosystem approach up to an integrated large-scale approach. We need to understand if damaging or losing one ecosystem may, via different modes of connectivity, have cascading effects to adjacent ecosystems, even though based on such distance that the ecosystems may appear to be apparently unconnected. In the worst-case scenario, restoration efforts on a single ecosystem may be futile if an adjacent ecosystem is gradually degraded. On the other hand, restoration of a target ecosystem might be most successful by both *i)* creating suitable conditions via restoring or improving an adjacent ecosystem (i.e., large-scale facilitation) and *ii)* focussing restoration goals on re-establishing at the local-scale positive feedbacks that characterise these ecosystems.

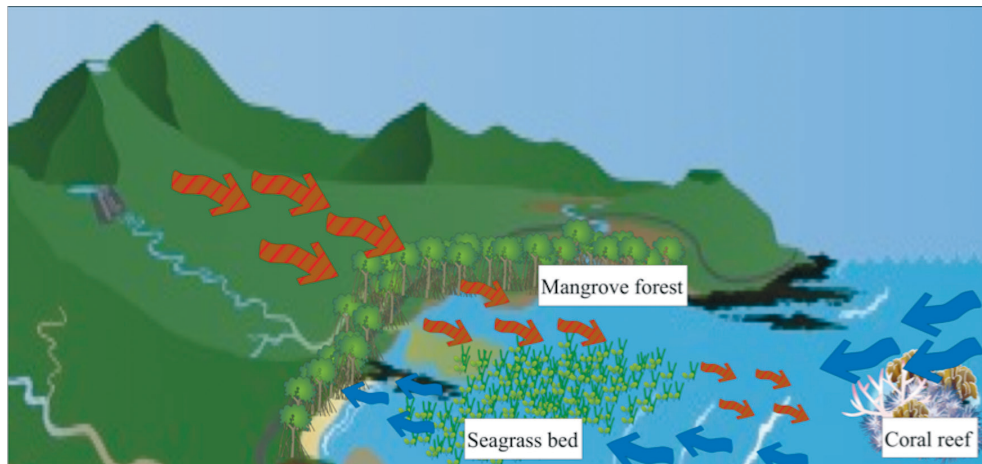


Figure 1 Conceptualization of connections between land, mangrove forests, seagrass beds, coral reefs and ocean systems. Arrows indicate the direction and approximate magnitude (arrow width) for three exchange fluxes considered in this thesis: sediment and nutrients (brown and red striped) and hydrodynamic energy (blue).

Objectives of this thesis

The research in this thesis aims at identifying the importance of large-scale facilitation by ecosystem (and especially organic nutrient) connections as critical factors needed for ecosystem-based designs, ecosystem conservation and ecosystem re-establishment. This objective will be met by the combination of the three principal research activities:

- i) Literature analyses to obtain quantitative insight in the potential importance of different types (hydrodynamics, sediment, nutrients and organismal) of large-scale facilitative interactions (chapter 1).
- ii) Elaborating experimentally large-scale facilitative interactions via material (especially organic nutrients) fluxes (chapters 2, 3 and 5).
- iii) Experiments to determine the role of local-scale facilitation in ecosystem resilience and (re-) establishment (chapters 4 and 6).

Below, we elaborate this in detail and indicate the importance of each chapter within the context of the overall objectives.

Research activity i) In **chapter 1** we completed an extensive literature review to establish if and how large-scale facilitative cascades of physical, chemical (nutrients and sediment) and biological fluxes may occur in the tropical coastal seascape between mangrove forests, seagrass beds and coral reefs. This activity forms the foundation of the thesis, as it is to our knowledge the first time that the concept of large-scale facilitative interactions is explicitly explored.

Research activity ii) One of the least studied connectivity routes between ecosystems is the exchange of (organic) nutrients, even though material fluxes between ecosystems have the potential to be highly important, regardless of whether these systems are directly neighbouring or further apart. Therefore we investigated by field sampling the material fluxes of organic matter between mangrove forests, seagrass beds and coral reefs on the landscape scale across several sites in the Phuket region of southern Thailand (**Chapter 2**). To facilitate future modelling of such exchange processes, we subsequently investigated nitrogen exchange in the form of particulate organic matter fluxes (seagrass and mangrove leaves) between mangrove forests, seagrass beds and coral reefs (**Chapter 3**). We also investigated at the landscape scale, how land-use affects the nutrient status (eutrophic vs. oligotrophic) of mangrove forests across sites in the Phuket region (**Chapter 5**).

Research activity iii) To determine how local-scale facilitation may affect particulate organic material (POM) exchange between ecosystems, we completed flume experiments with mimic mangrove roots and seagrass canopies. This allowed us to elucidate the trapping capacity of each ecosystems and therefore their potential to retain POM (**Chapter 4**). We experimentally studied the possibility that stony corals may utilise seagrass and mangrove derived particulate organic material (POM) as a direct food and nutrient source, combining field and laboratory incubations (**Chapter 6**). Whereas for seagrass and corals there is a growing body of work on how dissolved organic materials can be used as a nutrient source, very little is known about the role of POM for corals.

Research activity iv) Finally we developed guidelines on using the concept of facilitation interactions between foundation species for monitoring, restoration and management of the tropical coastal seascape (**Chapter 7**). We explored the premise that

monitoring of specific variables in ecosystems could provide information on the health of habitats in close proximity. In addition our aim was to establish if specific ecosystem engineering species could provide essential functionality that has been lost in the tropical seascape. A combination of effective monitoring and efficient restoration should provide robust management guidelines.

Chapter 1

Introduction

Potential for landscape-scale positive interactions among tropical marine ecosystems: A review

L.G. Gillis, T.J. Bouma, C.G. Jones, M.M. van. Katwijk, I. Nagelkerken, C.J.L. Jeuken,
P.M.J. Herman and A.D. Ziegler.

STATUS: Published at Marine Ecology Progress Series



Abstract

Fluxes of energy, materials and organisms among ecosystems are consequences of their openness to exchange and lead to the consideration of reciprocal connections among adjacent ecosystems. Reciprocal connectivity may have implications for ecosystem functioning and management but it is generally studied only for a single factor, rather than for multiple factors. We examined the extent to which these fluxes may apply at the landscape scale for 3 ecosystems: mangrove forests, seagrass beds and coral reefs. From a literature review and analysis, we semi- quantitatively assessed fluxes based on attenuation of wave height and exchanges of sediments, nutrients and algivores. We found that coral reefs and seagrass beds significantly attenuated wave height and that this effect depended on specific physical conditions. In the case of coral reefs, the attenuation capacity depended on the section of the reef the wave breached, whilst for seagrass beds, we hypothesized that the density of the plants was the controlling factor. Mangrove forests' ability to reduce sediment fluxes was related to the mangrove forest area. Seagrass plants have a capacity to decrease sediments in the water column. Both mangrove forests and seagrass beds retained nutrients within the ecosystems, which was a positive interaction. Isolated reefs showed a decrease (30 to 95 %) in algivore biomass compared to situations where the 3 habitats were in proximity to each other. The findings show that there is potential for reciprocal connections among coastal ecosystems. Our results indicate that these exchanges at the ecosystem scale can be placed into the context of facilitation in the field of community ecology. Future research should focus on which natural and anthropogenic factors determine reciprocal facilitation between these ecosystems and determine how ecosystem-based management can be improved with this knowledge. The considerable potential for reciprocal facilitation implies that ecosystem managers may need to place greater emphasis on the landscape scale.

Keywords: Mangrove forests; Seagrass beds; Coral reefs; Ecosystem Engineering; Nutrients; Hydrodynamics; Sediments; Algivores.

1.1 Introduction

Within the field of community ecology, positive interactions between species have an important impact on population establishment and thereby on overall community structure (Bertness & Callaway 1994, Silliman et al. 2011). Habitat-forming organisms (foundation species) that are able to change the physical conditions (i.e. ecosystem engineers cf. Jones et al. 1994, 2010) and buffer environmental stress can become the dominant community-structuring force. By becoming the core species and changing physical conditions within the habitat, ecosystem engineers can also change physical fluxes entering and exiting the system. Modifying these fluxes means they can also control connections between ecosystems, and thus, essentially form connective relationships between ecosystems.

All ecosystems are open to the exchange of energy, materials and organisms; ecosystems therefore are functionally connected in landscapes (Lovett et al. 2005). Understanding these connections is central to ecosystem-based management, particularly in the face of increasing human impacts. Connectedness relevant to management has been shown, for example, in riverine systems (Pringle 2001) (unidirectional), terrestrial ecosystems (Moilanen & Nieminen 2002) (unidirectional) and marine reserves (Kininmonth et al. 2011) (bi-directional). Two unconnected ecosystems can be managed as independent systems. If there is unidirectional influence, control over the donor ecosystem can be used in the management of the recipient ecosystem (e.g. hydrologic systems such as riparian/ rivers) (Pringle 2001). When there are reciprocal interactions, however, management will be more complicated, particularly if these interactions involve multiple, mutually reinforcing exchanges between ecosystems. In such cases, each ecosystem can facilitate the establishment or functional persistence of the other, but the opposite can also occur. Small declines in the functioning of one ecosystem can lead to functional diminution in the other, and eventually this can result in a decline in the functioning of the entire landscape.

Despite the need for a better understanding of reciprocal connections among adjacent ecosystems as an aid to integrated management, quantitative analyses of reciprocal connections have seldom been conducted. Moreover, analyses are typically restricted to a single rather than multiple exchanges. To exemplify the importance of this concept, we review evidence for large-scale reciprocal interactions by multiple exchanges for 3 kinds of tropical ecosystems that often occur in close proximity: mangrove forests, seagrass beds and coral reefs. The co-occurrence is not invariably observed, even taking into account that present-day observations are not always representative of historic connections. Large-scale positive interactions are defined as multiple connections, physical, biological or chemical, which help to improve adjacent ecosystems' growth or establishment conditions. We examine how ecosystem's spatial co-occurrence may influence mutual establishment and persistence

via positive, landscape-scale interactions mediated through multiple exchanges of energy, materials (i.e. sediment and nutrients) and/or organisms.

Mangroves, seagrasses and coral reefs occur along a depth gradient from tidal flats to deeper (60 m), near-shore oceans (Fig. 1; Ogden & Gladfelter 1983, Moberg & Folke 1999).

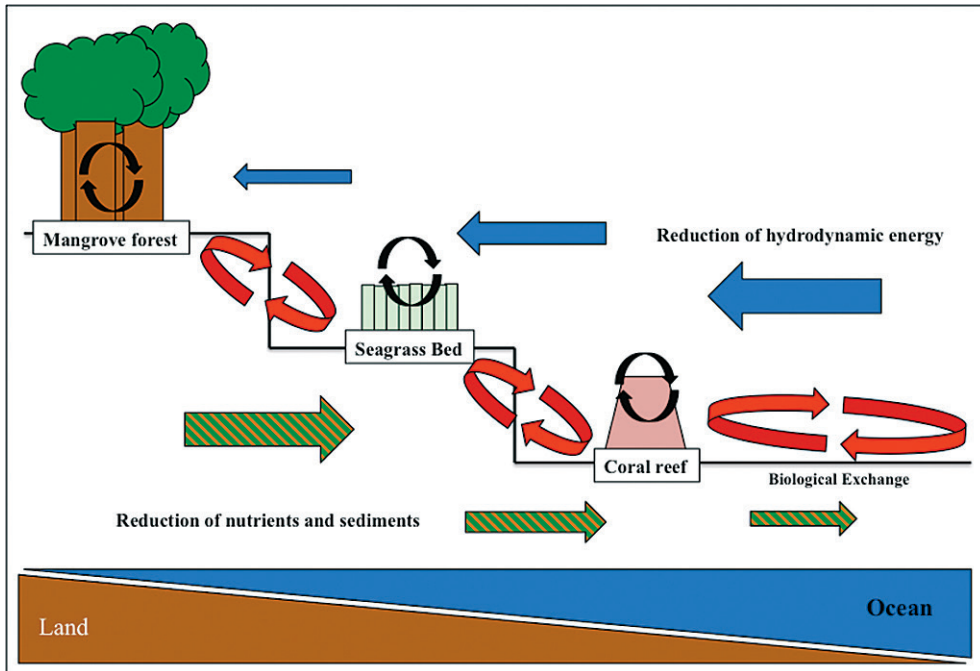


Figure 1 Conceptualization of connections between land, mangrove forests, seagrass beds, coral reefs and ocean systems. Arrows indicate the direction and approximate magnitude (arrow width) for 4 exchange fluxes considered in the present review: sediment and nutrients (orange and green striped), hydrodynamic energy (blue) and organism movement (red). Black arrows within mangroves, seagrass and coral reefs indicate internal exchanges of nutrients, sediment, hydrodynamic energy and organisms within each ecosystem.

Mangrove trees, seagrass plants and scleractinian corals are all foundation species that support entire ecosystems (Moberg & Folke 1999, Valiela et al. 2001, van der Heide et al. 2007). Via physical ecosystem engineering (Jones et al. 1994, 2010), nutrient uptake and organic matter production, these species can improve their own habitat and create the habitats and resources for many other species. Positive engineering feedbacks are important in the establishment and persistence of these foundation species, particularly under stressful conditions (Bruno et al. 2003, Halpern et al. 2007). Here, we review data on connections between these 3 kinds of ecosystems for 4 potentially important kinds of exchanges: wave height, sediment, nutrients and organisms (Fig. 1). The first 3 exchanges largely derive from

the extended spatial influence of physical ecosystem engineering by the foundation species within its ecosystem. This can then influence the establishment and persistence of recipient ecosystems. The fourth exchange derives from the creation of proximate habitat diversity in the landscape for other species occurring in > 1 ecosystem type. Modification of these exchange processes by mangroves, seagrasses and/or corals can feed back to influence the establishment and persistence of the foundation species.

The potential for connections between mangrove forests, seagrass beds and coral reefs has been demonstrated in many studies conducted worldwide (Roberts et al. 1977, Alongi & Christoffersen 1992, Hemminga et al. 1994, 1995, Kitheka 1997, Lugo-Fernández et al. 1998, Koch 2001, Dorenbosch et al. 2004, Mumby 2006, Bouillon & Connolly 2009, Davis et al. 2009, Nagelkerken 2009). However, these studies did not investigate the potential for multiple, mutually reinforcing exchanges where one ecosystem changes the physical parameters to allow for the establishment of another. We define connectivity as a sub-set of positive reciprocal exchanges. Studies of tropical coastal ecosystems have highlighted the importance of landscape mosaic configuration in the management of tropical fisheries (Pittman et al. 2004, Grober-Dunsmore et al. 2009) and mangrove restoration (Thinh et al. 2008), but the importance of reciprocal exchanges—in particular their influence on recruitment, establishment and persistence of the foundation species—have not been considered. Coral reef, seagrass bed and mangrove forest structures decrease hydrodynamic energy (Roberts et al. 1977, Koch 2001), but it is not clear if such effects are sufficient to result in landscape-scale interactions. Sediment trapping by the extensive root systems of mangroves is thought to significantly buffer coastal oceans from terrestrial sediment runoff (Valiela & Cole 2002, Adame et al. 2010), but the implications for adjacent ecosystems have not been elaborated. Only a handful of studies have quantified the net exchange of nutrients between mangroves and seagrass beds (Hemminga et al. 1994, Hyndes et al. 2013), but these studies have not considered the potential for reciprocal exchanges. Studies investigating biological connectivity have largely focused on the importance of nursery and spawning sites (Mumby 2006, Nagelkerken 2009), but few studies have determined the degree to which high production rates in coral reefs are due to ‘nursery’ or other effects of adjacent ecosystems or how such effects might influence reef persistence.

Here, our aims are to (1) identify the extents to which there are known physical, chemical and biological exchanges among adjacent mangroves, seagrass beds and coral reefs and (2) from this, deduce whether or not multiple, reciprocal interactions may exist among the ecosystem types when they co-occur in proximity. We use the literature to identify the optimum range of abiotic conditions for mangrove forests, seagrass beds and coral reefs for each kind of exchange variable. This capacity is reviewed from the literature, allowing a semi-quantitative assessment of (1) and (2) above. In the present paper, we hope to address

the question regarding to what extent the proximity of ecosystems allows for connecting, mutually positive mechanisms between them.

1.2 Co-occurrence of ecosystem types and consequences of loss of one type: Spatial co-occurrence.

The potential for reciprocal interactions will generally be restricted to situations where different ecosystem types occur in close proximity. For example, hydrodynamic energy effects via wave attenuation by coral reefs require the reefs to be close enough to seagrass beds and mangroves for waves not to build up again once they pass over the reef. Seagrass beds also have to be close to mangroves to have any influence on hydrodynamic energy exchange. Influence due to altered sediment and nutrient exchange will only occur if distances are short enough to 'carry over' changes in water quality before mixing from other areas 'dilutes' the impact. Biological effects require a sufficient proximity for juvenile and adult organisms to move between ≥ 2 of these ecosystem types, although this distance will vary substantially among species (Nagelkerken 2009).

Mangrove forests, seagrass beds and corals reefs have overlapping distributions across a latitudinal breadth encompassing East Asia, Australia, the Caribbean, the Red Sea and East Africa. The 3 types are often found together but do not always co-occur locally. For example, oceanic barrier islands often support only isolated mangrove ecosystems (Pilkey et al. 2009). Tropical seagrass beds exist in the absence of coral reefs (Orth et al. 2006). Atoll islands such as the Maldives have only a few co-occurrences of seagrass beds, and these habitats were introduced within the last 100 yr (Miller & Sluka 1999).

There has been a considerable global decline in occurrence and health of mangroves, seagrass beds and coral reefs over the last 100 yr. Worldwide, seagrass beds are thought to have been declining $\sim 7\% \text{ yr}^{-1}$ since 1990 (Waycott et al. 2009). Mangroves are decreasing in surface area by 1 to $2\% \text{ yr}^{-1}$ (Valiela et al. 2001) and coral reefs by 1 to $7\% \text{ yr}^{-1}$ (Bellwood et al. 2004). Even though the high rate of destruction of coastal ecosystems makes it difficult to map where these ecosystems were once neighbours, mangrove forests, seagrass beds and coral reefs were much more widespread and the frequency of spatial co-occurrence was very likely much greater in the past than it is today.

1.2.1 Consequences of loss: Mangrove forests.

Many mangrove forests have completely disappeared due to logging, coastal landfill and/or aquaculture (Valiela et al. 2001). Circumstantial evidence suggests that mangrove loss may have had functional consequences for neighbouring marine ecosystems, apart from their role in protecting terrestrial systems from major events such as tsunamis (Alongi 2008). For

example, in Sabah, Malaysia, mangrove loss likely contributed to increased turbidity during the rainy season via increased terrestrial sediment runoff that, in turn, caused large scale disturbance to seagrass meadows within the area (Freeman et al. 2008). Cleared mangrove forests can alter the algae composition in adjacent ecosystems, such as coral reefs (Granek & Ruttenberg 2008). The algal species *Dictyota* sp. and *Acanthophora* sp. were found growing on dead and living patch corals, adjacent to cleared mangrove areas (Granek & Ruttenberg 2008). They were absent in the vicinity of intact mangroves. Valiela & Cole (2002) showed that mangroves could intercept and store large amounts of terrestrial nitrogen. Mangrove forests that received an input of $< 20 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ intercepted all of it; this reduction in nitrogen load to the ocean positively correlated with increased seagrass biomass and reduced habitat loss (Valiela & Cole 2002).

1.2.2 *Consequences of loss: Seagrass beds*

Human activities in the coastal seascape can physically damage seagrass beds via coastal construction, boat movement, anchor damage and de-ballasting (Burkholder et al. 2007, Todd et al. 2010). Seagrass beds are susceptible to reduced light availability (Ralph et al. 2007, van der Heide et al. 2007) and to increases in nutrient concentrations and toxins (Orth et al. 2006, Freeman et al. 2008, Todd et al. 2010). Loss of seagrass beds has been associated with changes in neighbouring ecosystems. For example, in Motagu Bay, the Bahamas, the loss of patch reef over the last 50 yr is thought to be due to the loss of a seagrass bed (Sealey 2004). In Mauritius, many hotels are actively removing seagrass beds because they are deemed unsightly, and this has caused increased turbidity with potential damage to nearby corals (Daby 2003). Other negative impacts on seagrasses may also negatively affect linkages to coral reefs, such as the reduction in density or elimination of algivorous fish. Recently, it has been shown that seagrasses increase seawater pH, which in turn allows for an increase in calcification in corals of 18 % (Unsworth et al. 2012). The rise in calcification of coral reefs only occurred when seagrasses were neighbouring coral reefs (Unsworth et al. 2012). It can be inferred that the loss of seagrass beds adjacent to coral reefs will cause a decrease in calcification rates. This especially has implications for anthropogenic impacts such as climate change, which can result in acidification of the ocean.

1.2.3 *Consequences of loss: Coral reefs*

Coral reef persistence is threatened by large-scale influences such as global warming, ocean acidification and deteriorating water quality (increased turbidity and eutrophication) that can result in reduced productivity, mass mortality and consequent habitat loss for other species (Moberg & Folke 1999, Bellwood et al. 2004). Destroyed or heavily damaged coral reefs no longer provide an effective wave barrier; this change results in increased coastal erosion. A

study in the Seychelles (Sheppard et al. 2005) found that coral reef die-off caused in part by warming seas killed ~99 % of hard coral cover. This mortality increased the depth of the coral flat, decreased roughness, reduced ecosystem complexity and increased wave energy on the shoreline, resulting in increased beach erosion. Although that study did not discuss a possible de-stabilizing effect on seagrass beds or mangroves, it does illustrate the importance of coral reefs in coastal protection from wave action. Recent work has also highlighted the importance of ecosystem structural complexity to ecosystem services, especially in coral reefs (Graham & Nash 2013). Density and complexity of the coral reef was positively related to fish biomass (Graham & Nash 2013). Thus, a decrease in complexity will have concomitant effects on fish species, which connect coral reefs with seagrass beds and mangrove forests.

1.3 Materials and Methods

We completed a literature search (using sources from 1947 to the present) on Web of Science and Google Scholar using keywords including, but not limited to, the following: connectivity, facilitation, positive interactions + coral reefs + seagrass beds + mangrove forests, facilitation, positive interactions + tropical coastal seascape; wave energy, wave height + coral reefs + seagrass beds + mangrove forests; alteration of hydrodynamic energy + coral reefs + seagrass beds + mangrove forests; turbidity, sedimentation rates + coral reefs + seagrass beds + mangrove forests; outwelling + mangrove forests; nutrient concentrations, fluxes + coral reefs + seagrass beds + mangrove forests; biological connectivity + coral reefs + seagrass beds + mangrove forests; nursery areas + coral reefs + seagrass beds + mangrove forests; and ecosystem based management + coral reefs + seagrass beds + mangrove forests. Not all topics of study were completed in the same time period. The relation between coral reefs and hydrodynamics was studied well before reports on other aspects (e.g. hydrodynamics and seagrass beds or mangroves) were present in the literature. In our supplementary tables, we indicate the time periods during which the results for different ecosystems and exchanges were published, but for the analysis we did not constrain the data used to a particular time span.

We estimated the threshold value for sediment/nutrient fluxes and wave height at coral reefs, seagrass beds and mangrove forests. This threshold value was the mean value from the literature review of fluxes under which the ecosystem engineers (stony corals, seagrass plants and mangrove trees) can survive (Tab. S1, S3 & S5). We decided to use a mean value as being the most representative because the range (minimum and maximum values) could be skewed by very high and low values being recorded for a specific site or species, which were not characteristic of the entire data.

In each of the literature studies, we searched for reductions in wave heights, sediment fluxes and nutrient fluxes as these passed through an ecosystem. This was done by comparing

import and export per study. If an import value was not available but a retention rate was, we calculated import based on export and retention. Import and export of wave height, sediment or nutrients were plotted to establish if the ecosystem was reducing the flux and therefore providing a positive interaction. We also compared the export values from one system with the threshold values for the ecosystem engineers of the other systems.

Retention capacity of the different ecosystems was statistically analysed by regressing the export/import ratio versus area or length of the system with a Model II regression. To ensure normality and homogeneity of variances, the export/import ratios were log-transformed. This transformation also avoided any spurious correlation that could have been caused by a correlation between export or import and the dimensions of the system. Probability (p) was considered significant at $p < 0.05$. All statistical testing was completed in the R program.

1.4 Analysis of ecosystem exchanges and potential interactions

1.4.1 Attenuation of wave height

1.4.1.1 Habitat requirements of mangroves and seagrasses and ecosystem engineering feedbacks

Mangroves require low wave heights for seedling establishment and development of root systems (threshold wave height 0.5 m; Tab. 1, Tab. S1) (Balke et al. 2011). Seagrass beds grow in shallow water environments. Similar to mangroves, they require calm conditions for

Table 1 Literature-based threshold values of wave height (m) and sediment ($\text{g m}^{-2} \text{d}^{-1}$), nitrogen ($\text{g N m}^{-2} \text{d}^{-1}$) and phosphorus ($\text{g P m}^{-2} \text{d}^{-1}$) fluxes at which mangrove forests (MF), seagrass beds (SB) and coral reefs (CR) can establish or persist. Values were calculated based on a literature review; the mean value of the literature review values was chosen as the threshold value (Tab. S1, S3 and S5). Facilitation potential indicates whether one ecosystem type could positively affect the establishment and/or persistence of another by altering the corresponding abiotic variable (based on literature review); arrows indicate the direction of the facilitation potential. We have not considered differences in organic or inorganic nutrients and have combined all sources of N and P.

Threshold Variables	Mangrove forests	Seagrass beds	Coral reefs	Facilitation Potential
Wave height (m)	0.5	0.4	0.9	CR SB→MF
Total suspended sediment ($\text{g m}^{-2} \text{day}^{-1}$)	82	161	11.2	MF SB→CR
Water column nitrogen ($\text{g N m}^{-2} \text{day}^{-1}$)	0.07	0.04	0.009	MF SB→CR
Water column phosphorous ($\text{g P m}^{-2} \text{day}^{-1}$)	0.04	0.002	0.0002	MF SB→CR

initial establishment and expansion (threshold wave height 0.4 m; Tab. 1, Tab. S1) (van der Heide et al. 2007, Infantes et al. 2009).

Along coastlines subject to strong wave action, mangroves and seagrass beds could benefit from the physical barrier provided by coral reefs (Ogden & Gladfelter 1983, Moberg & Folke 1999). Coral reefs at the edge of the coastal zone are a physical barrier between the land and the ocean (Moberg & Folke 1999). Coral reefs can persist at high levels of hydrodynamic energy (threshold wave height 0.9 m; Tab. 1, Tab. S1). The reef's physical structure is spatially complex, resulting in high friction with the water currents. As a result, coral reefs create calm lagoons on the landward side and can prevent shoreline erosion (Ogden 1988, Moberg & Folke 1999, Sheppard et al. 2005). Established seagrass beds can also attenuate wave energy (Koch 2001, Bouma et al. 2005), but to a much lesser degree than coral reefs due to their flexible structure (Bouma et al. 2005, Infantes et al. 2009). In the present study the data show that reduction of wave heights is species- and location-specific. Seagrass beds and corals can contribute to sediment accretion and stabilization, thus decreasing water depth toward the shore. This reduction in depth can also alter wave height, but we did not take this factor explicitly into consideration.

1.4.1.2 Positive interactions from coral reefs and seagrass beds under average conditions

Coral reefs reduce wave heights to a fraction of the incoming wave height (Fig. 2A, Tab. S2). Assuming an initial wave height arriving at a coral reef of between 0.07 and 4 m, this would result in 0.02 to 0.8 m waves via attenuation of hydrodynamic energy (Fig. 2A, Tab. S2). There was no correlation between the distance the wave travelled and the retention capacity (linear regression $R^2 = 0.05$, $p > 0.05$). However, the data taken at the reef crest did show a negative relationship between export/import ratio and the distance the wave travelled (linear regression: $R^2 = 0.5$, $p < 0.05$). All studies showed a decrease in wave height between 20 and 97 %; this indicates the ability of coral reefs to reduce wave heights, thereby potentially facilitating the establishment of seagrass beds (Fig. 2A, Tab. S2).

After a wave passes a coral reef, seagrass beds will further reduce an initial wave height from 0.04–0.2 m to 0.01–0.08 m (Fig. 2B, Tab. S2). The reduction ratio (export/import) was not related to the physical dimensions of the bed or to the density of the seagrass, possibly because of the small data set (Tab. S2). However, all values were well below 1, demonstrating that wave height reduction is a consistent feature of all seagrass beds studied. Overall, these studies (Tab. S2) show the potential of seagrass beds to attenuate wave height for neighboring ecosystems.

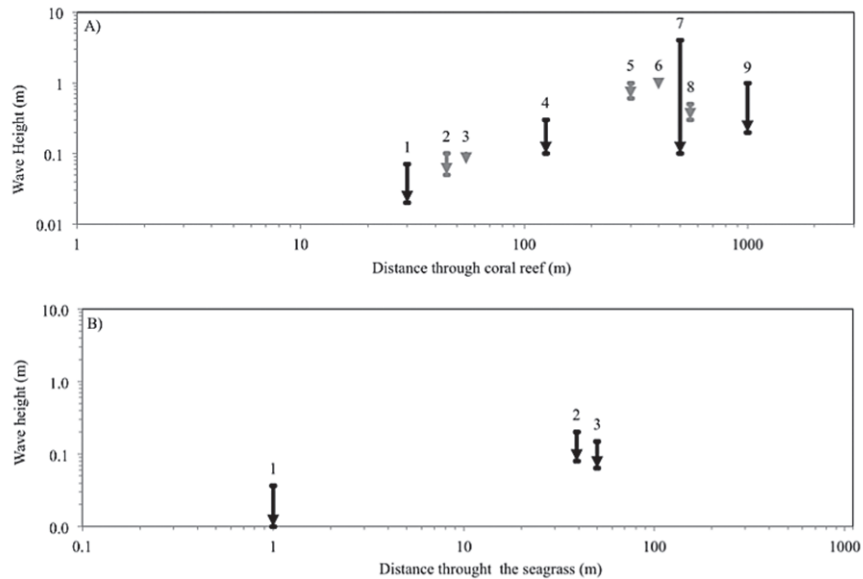


Figure 2 Change in wave height (m) over a distance (m, ocean to shore) of (A) coral reef and (B) seagrass bed. Each line/arrow represents a different study, where the highest point is the initial wave height, and, following the direction of the arrow, the lowest point represents the end wave height. In panel (A), grey lines represent studies taken at the reef crest; black lines represent studies taken at the fore or back reef. Each study calculated a different percentage change of the wave height over a given distance; the number directly above the line indicates the study number in Tab. S2.

1.4.1.3 Positive interactions from coral reefs to seagrass beds in storms and hurricanes

Coral reefs may be exposed to recurrent tropical storms and hurricanes with high hydrodynamic energy. The main factor influencing coral reef capacity for wave height attenuation is the physical dimension of the reef. Madin et al. (2006) reviewed various studies and found that 90 % of wave height and velocity was reduced in the first 300 m of a fringing reef. Various wave heights during storm swells have been recorded: for example, 1 to 2 m in the South Pacific and Indian Ocean, 10 m in the North Pacific and 3 to 5 m at Hawaii (Dollar 1982). Based on Madin et al. (2006), such waves would be substantially reduced by coral reefs, although remaining waves would most likely still exceed normal threshold conditions for seagrass beds (Tab. 1). Thus, seagrass beds will be damaged by hurricanes even in the presence of coral reefs (Lugo 2000). However, given the transient character of storms, in most cases, these ecosystems will be damaged but not eliminated, given sufficient time for prior establishment and for recovery between storms (Uhrin et al. 2011). The storm surge created by Category 5 Hurricane Katrina (New Orleans, USA) was ≥ 5.6 m with a wind speed of 60 m s^{-1} (Knabb et al. 2005). This force was sufficient to damage coral reefs, increase wave energy and height in the lagoon and move coral reef debris toward the lagoon

(Lugo-Fernández & Gravois 2010). Nevertheless, in the absence of coral reefs, damage to seagrass beds would most probably have been much greater. Healthy coral reefs are resilient to infrequent hurricanes, and if no additional major impacts occur immediately after the hurricane, they can continue to protect the shoreline (Lugo 2000).

1.4.2 Sediment exchange

1.4.2.1 Habitat requirements of coral reefs and seagrasses

With respect to total sedimentation and turbidity, the range of reported thresholds for establishment and/or persistence is lower in coral reefs than in seagrass beds and mangrove forests (Tab. 1, Tab. S3). Suspended sediments can limit coral reef productivity by reducing light penetration (Erftemeijer & Lewis 2006, van der Heide et al. 2007, Todd 2008). High sediment loads can also bury coral reefs (Muzuka et al. 2010, Erftemeijer et al. 2012b). More modest sediment loads can also reduce coral energy reserves by creating a continuous demand for sediment clearing by coral polyps and can reduce reproductive success (Brown 1997, Todd 2008, Erftemeijer et al. 2012a). Because reduced sediment loads can benefit coral reefs, the potential for positive interactions will depend on the extent to which mangroves and seagrass plants can trap sediments.

1.4.2.2 Habitat modification by mangroves and seagrass beds

Sediment trapping is largely a consequence of hydrodynamic energy attenuation, hence physical structure. The extensive root systems of mangroves, along with their pneumatophores and stems, can result in sediment accumulation rates of 0.5 to 10 cm yr⁻¹ (Wolanski et al. 1990, Adame et al. 2010). Therefore, the size of the forest may affect the capacity of mangroves to trap sediment. Because a greater amount of structure implies a greater reduction in hydrodynamic energy and more sediment accretion (Bouma et al. 2005), we expect mangrove forests with larger areas to trap more sediment; this results in greater potential for buffering of coral reefs.

Seagrass beds reduce hydrodynamic energy via leaf structure and stem density, which causes sediment deposition and reduced re-suspension (van der Heide et al. 2007). This could reduce sediment load and water turbidity of outgoing tides moving toward coral reefs (Koch 2001).

1.4.2.3 Positive interactions from mangroves and seagrass beds

From our review, all the mangroves reduced suspended sediment flux concentrations; the trapping capacity of the mangrove ranged from 1 to 90 %, indicating large variability (Tab. S4, Fig.3). We realize that this variability can come from sediment fluxes over different time

periods, but for simplicity, all data were transformed to $\text{g m}^{-2} \text{d}^{-1}$ values, even when based on incomplete year cycles, as indicated in Tab. S4.

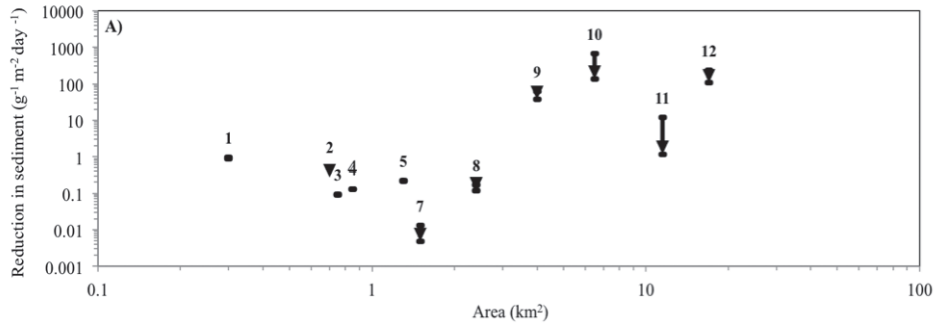


Figure 3 Oceanward flux of total suspended solids (TSS; $\text{g}^{-1} \text{m}^{-2} \text{d}^{-1}$) from mangrove forests to the coastal ocean, as a function of mangrove area (km^2). Each line represents a different study, where the highest point is the initial sediment input, and, following the lines in the direction of the arrow, the lowest point represents the exported sediment (see Tab. S4). Dash without arrow indicates no difference in imported and exported sediment. The number directly above the line indicates the study number in Tab. S4. Not all sediment fluxes have been measured over an entire year (Tab. S4).

We found a negative relationship between export/import ratio and area of mangrove forest ($p < 0.05$, $R^2 = 0.7$). This indicates that a larger mangrove forest has a greater relative retention capacity. In this analysis, we did not account for changes in fluxes of sediment from currents or increased water volume, which would certainly have an effect on the flux of suspended sediment in the water. Such analysis would require large-scale hydrodynamic modelling and is beyond the scope of this section. In conclusion, mangrove forests could provide a positive interaction with coral reefs via reduction in sediment load; however, further research is required on how the state (degraded or natural) of the mangrove forest could alter its ability to retain sediments.

Seagrass beds showed a reduction in turbidity (18 to 50 %) (Hendriks et al. 2008, 2010). It is difficult to draw firm conclusions because variability between studies is large and the data set is limited. For example, flume studies by Hendriks et al. (2008) show a very large initial concentration of sediment (1576 to 2575 g l^{-1}), which would not show any facilitative effect to coral reefs. Other ecological influences, e.g. local hydrodynamic conditions, nutrient status, disturbance, architecture of the seagrass canopy, resuspension potential and herbivory, are expected to affect the structures of the seagrass bed and therefore the perspective of positive sediment interactions from seagrass beds to coral reefs (Koch 2001, de Boer 2007, Infantes et al. 2009).

1.4.3 Nutrient exchange

1.4.3.1 Habitat requirements of coral reefs and seagrass beds

Corals reefs in pristine areas can be limited by nitrogen and/or phosphorus (Kuhlmann 1988, Hearn et al. 2001). Three major processes are involved in nutrient acquisition under these circumstances: nutrient depletion of the boundary layer; tight nutrient recycling within the ecosystem; and consumption of particulate matter (Kuhlmann 1988, Hearn et al. 2001, Todd 2008). Seagrass beds can also be limited by nitrogen and phosphorus in pristine areas (Lee et al. 2007) but are adapted to low nutrient availability. Seagrasses access the higher nutrient concentrations in sediment (Terrados et al. 1998) and can use organic sources as a nitrogen source both by trapping organic matter in porous sediment as well as by uptake of dissolved organic matter from the water column (Vonk et al. 2008a). Seagrass beds have efficient nutrient recycling in the sediment that is enhanced by invertebrates such as burrowing shrimp (Vonk et al. 2008b).

Changes in land use in the last 100 yr have resulted in high nutrient inputs to the coastal seascape (Uriarte et al. 2010). Consequently, many coral reefs and seagrass beds are no longer nutrient limited (Schaffelke et al. 2005, Burkholder et al. 2007). Nutrient loading to seagrass beds, particularly of terrestrially derived nitrogen, has been found to initially increase seagrass productivity and biomass (Lee et al. 2007). However, increased loading for longer periods generally causes a decrease in leaf density and cover, followed by shifts to macroalgae-dominated systems (Burkholder et al. 2007). Many studies of coral reefs have found that high nutrient concentrations have detrimental effects, including growth of macroalgae (Todd et al. 2010), increased occurrence of exotic species (Dubinsky & Stambler 1996) and physiological changes (e.g. in feeding strategies, reproductive abilities and zooxanthellae photosynthesis) (Tomascik & Sander 1985, 1987a,b).

In general, coral reefs have greater exposure to low nutrient ocean water than seagrass beds (Tab. 1, Tab. S5). Because reduced nutrient loads can benefit seagrasses and coral reefs, the potential for positive interactions will depend on the extent to which mangroves (for seagrasses and reefs) and seagrass beds (for reefs) affect nutrient loads.

1.4.3.2 Habitat modification by mangroves and seagrass beds

The mangrove outwelling hypothesis (Odum 1968, Lee 1995) postulates that detrital export supports adjacent ecosystems and food webs. For example, mangrove detritus has been found up to 3 km away in nearby seagrass beds (Hemminga et al. 1994, Lee 1995, Bouillon et al. 2007). Here, however, we focus on the reverse influence: can mangroves buffer seagrass beds, and possibly even coral reefs, from excess terrestrial nutrients? These forests receive nutrients from a variety of oceanic and/or terrestrial sources (Vilhena et al. 2010). Mangrove

ecosystems are biogeochemically complex, with high nutrient processing and outputs by associated fauna (Lee 1995, Kristensen et al. 2008). For example, invertebrates feeding on mangrove particulate organic matter can account for 10 to 80 % of exported carbon (Robertson 1986). Microbial activity has also been found to utilize up to 20 % of particulate organic matter, and microbial mineralization, nitrogen fixation and denitrification are significant processes within the nitrogen budget (Kristensen et al. 2008). High rates of biogeochemical cycling within mangrove ecosystems imply that nutrient export will be constrained to that exceeding internal requirements or that which cannot be retained at high discharge or under storm conditions (Boto & Wellington 1988).

Seagrass beds are known to trap and mineralize mangrove particulate organic matter and seston (Bouillon et al. 2007). Seagrass beds export nutrients via leaf shedding enhanced during strong hydrodynamic events and via marine herbivore consumption (Hemminga et al. 1994). In pristine seagrass beds, we expect most nutrients to be retained (Vonk et al. 2008b).

1.4.3.3 Positive interactions from mangroves and seagrass beds

Mangroves have been shown to be able to retain up to 100 % of terrestrial nitrogen import (Valiela & Cole 2002), making it important to understand which factors affect mangrove retention. We have collected data regarding nutrient retention in mangrove forests; many of these studies were using very different methods of measurement. To give broad understanding

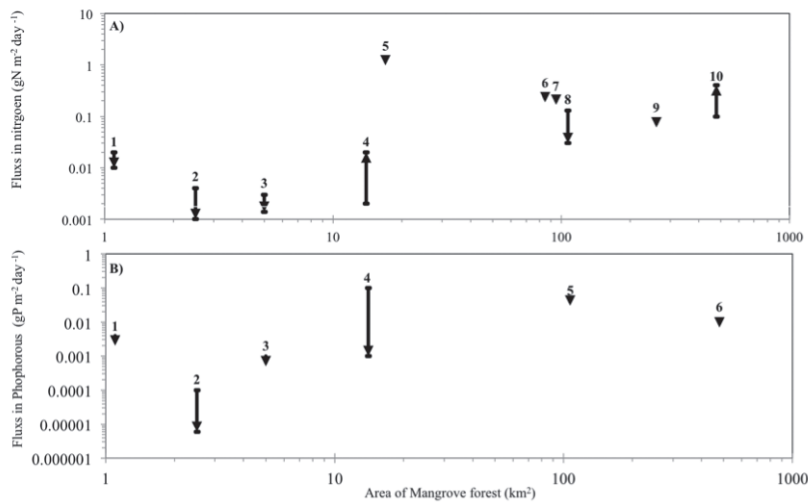


Figure 4 Fluxes of dissolved (A) nitrogen ($\text{g N m}^{-2} \text{d}^{-1}$) and (B) phosphorus ($\text{g P m}^{-2} \text{d}^{-1}$) from and within mangroves forests with different surface area (km^2). Each line/arrow represents a different study, where the initial flux is represented by the highest point, and the end concentration flux is indicated by the arrow (see Tab. S6). The arrow also shows if the nutrient flux is increasing (facing upwards) or decreasing (pointing downwards). Decreasing fluxes indicate that the mangrove forest is net absorbing nutrients; increasing fluxes indicate that it is net exporting. The number directly above the lines indicates the study number in Tab. S6

of nutrient retention in mangroves, we compared all these studies, despite the limitations in this analysis. Eight studies (Tab. S6, Fig. 4A) reported less export than import of dissolved nitrogen in the water column (N, DIN + DON, TN), indicating a potential facilitative effect to seagrass beds (Tab. S6, Fig. 4A). Two other studies showed a higher export than import of nitrogen in the water column (Tab. S6, Fig. 4A). No relationship was seen between mangrove area and retention capacity ($R^2 = 0.1$, $p > 0.05$).

This could not be explained by any environmental influence that the authors were aware of for these studies. The same pattern was not seen with respect to fluxes of dissolved phosphorus in the water column (P, TP, DIP + DOP, DOP + PO_4) (Tab. S6, Fig. 4B); all studies retained phosphorus. However, there was no correlation between mangrove areas and export/import ratio for phosphorus ($R^2 = 0.1$, $p > 0.05$).

Seagrasses absorb dissolved nitrogen and phosphorus from the water column and sediment porewater, and they export nutrients primarily as organic detritus. All the studies showed seagrass retaining dissolved nutrients in the water column, with retention rates of 5 to 79 % for nitrogen and 35 % for phosphorus, indicating a large range (Tab. S7, Fig. 5). No relationship was seen between the retention capacity for nitrogen and the area of the seagrass beds ($R^2 = 0.1$, $p > 0.05$).

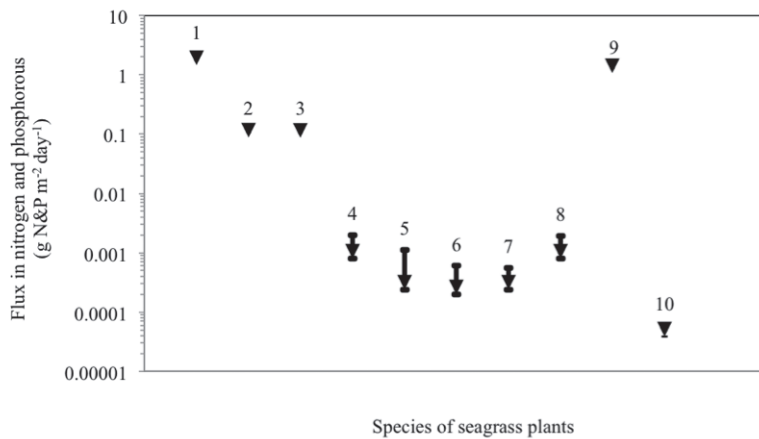


Figure 5 Reduction of dissolved nitrogen (black) and phosphorus (grey) fluxes ($g\ N\ or\ P\ m^{-2}\ d^{-1}$) via uptake from seagrass plants. Each line/ arrow represents a different study, where the highest point is the initial flux; following the arrows down, the lowest point represents the end concentration flux (see Tab. S7). Each study calculated a different percentage change of nutrient uptake for a given species of seagrass bed, which we re-calculated to a flux; the number directly above the lines correlates with the study number in Tab. S7. Studies 1 & 2 refer to *Cymodocea sp.*, Study 3 is a *Halodule sp.*, Studies 4 & 5 refer to *Posidonia sp.*, Studies 6–8 refer to *Thalassia sp.*, and Studies 9 and 10 are both *Zostera sp.*

In part, this is because the experiments were incubations or flumes, and therefore, the area is not a controlling variable. We did not complete statistics for phosphorus as there was only 1 data point.

Epiphytes also strongly contribute to nutrient retention in seagrass beds. Cornelisen & Thomas (2006) found that seagrass epiphytes absorb 43 to 47 % of nitrogen from the water column. If seagrass beds and their associated epiphytes were the only buffer between coral reefs and the land, they obviously would provide an important service in absorbing nutrients, especially in the event of pulse nutrient enrichment. Nutrient-rich conditions in seagrass beds are mainly the result of increased organic matter concentrations (McGlathery et al. 2007). Organic matter addition experiments have shown a decline in above- and below-ground biomass (20 to 50 %) due to plant mortality and greater leaf abscission (Perez et al. 2007). The resulting increase in particulate organic matter, along with sediment destabilization, would likely lead to greater export to mangroves or coral reefs under these conditions. Note that reduced aboveground biomass will reduce the potential of seagrass to attenuate hydrodynamic energy and to retain sediment.

1.4.4 Organism exchange

1.4.4.1 Increased densities of algal consumers can affect coral reefs and seagrass beds.

As noted earlier, corals and seagrasses require relatively high light levels and are adapted to low nutrient conditions. In nutrient-rich environments, they can be overgrown by algae and epiphytes, which may compete for light (Ralph et al. 2007, van der Heide et al. 2007). For example, Heck & Valentine (2006) showed that seagrass declined due to surface epiphyte overgrowth following nutrient enrichment. The latter was especially problematic when no epiphytic grazers were present, as grazers can reduce epiphyte biomass by up to 30 % (Neckles et al. 1993). Moreover, a small increase in grazing can result in a substantially greater resilience of coral reefs (Mumby & Hastings 2008, Berkström et al. 2012). Algivores (e.g. some species of juvenile butterflyfish, goatfish, surgeonfish and parrotfish) can thus play a major role in maintaining the vigour of coral reefs and seagrass beds (Neckles et al. 1993). Thus, the presence of adjacent ecosystems may have facilitative effects on another ecosystem by enhancing populations of mobile algivores and thereby algal consumption. Piscivores/invertebrate feeders can also utilise all 3 systems as juveniles; 17 to 59 % of these predator fishes use seagrass beds and mangrove reefs as nursery areas (Berkström et al. 2012). The predatory species can affect the stability of coral reefs via reduction of prey species such as sea urchins, starfish and gastropods, which can in large numbers cause bioerosion on stony corals (Berkström et al. 2012). However, based on available data, we will consider this

question mainly for parrotfish, which are regarded as predominantly algivores with positive effects on seagrass and corals.

1.4.4.2 Positive interactions from mangroves and seagrass beds by enlarging algal consumer populations

Several studies in Tanzania and the Caribbean have shown increases in density of parrotfish when coral reefs were adjacent to mangroves and seagrass beds (Nagelkerken & van der Velde 2002, Dorenbosch et al. 2006); for example, parrotfish density increased > 95 % in Curaçao compared to coral reefs isolated from the other 2 systems (Fig. 6). The increased density of parrotfish for co-occurring ecosystems indicates a potential facilitative relationship for coral reefs and seagrass beds, as the fish can reduce algal loading via herbivory.

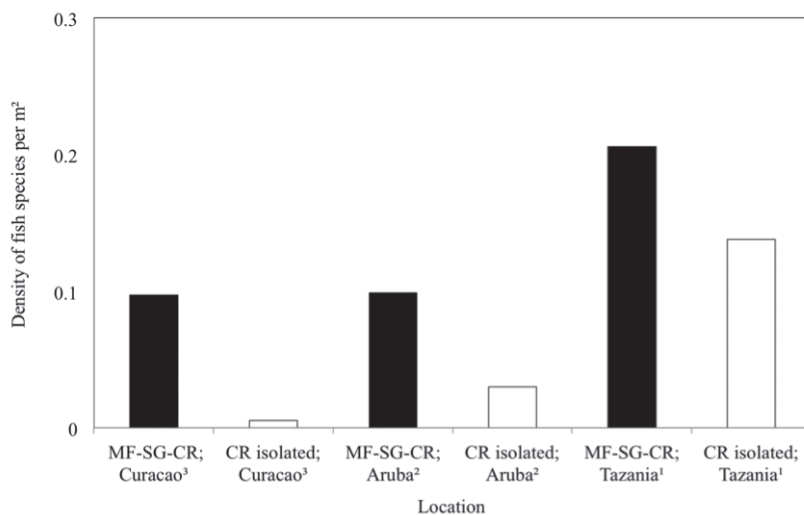


Figure 6 Three examples of the positive effect of the co-occurrence of coastal ecosystems (MF: mangrove; SG: seagrass; CR: coral reef) on the density of parrotfish measured at the coral reef. MF-SG-CR indicates mangrove forests, seagrass beds and coral reefs occurring in close proximity (black columns); CR alone denotes coral reefs that have no other ecosystems nearby (grey columns). Data from ¹Dorenbosch et al. (2005), ²Dorenbosch et al. (2007), ³Nagelkerken et al. (2002).

Mumby et al. (2004) also found an increased biomass of reef fish when coral reefs were near to abundant mangroves, compared to coral reefs with few or no mangroves. Mangrove forests, seagrass beds and coral reefs are distributed across incremental depths from the land to the open ocean, and significant ontogenetic transfers from one ecosystem to another (i.e. juveniles to the shallows, mature organisms to the deep) (Kimirei et al. 2013) may occur in addition to transfer with daily tides (Forward & Tankersley 2001) and diurnal movements (Krumme 2009). With respect to the nursery function of adjacent ecosystems, Mateo et al. (2010) demonstrated that distance is not necessarily the primary influence on the origin of

juveniles and that distance effects can be species-specific. Recent laboratory and *in situ* studies also find that juveniles of some fish species show strong preferences for specific habitats (Grol et al. 2011); this indicates that any potential for positive interactions would depend on a blend of species, distance and habitat types. Overall, it is clear that inland mangrove and seagrass bed areas form an important nursery habitat for parrotfish (Nagelkerken 2009) and that mangrove forests or mangrove-seagrass systems contribute high fractions of the populations of various reef fish species (Nagelkerken et al. 2002). Nursery or spawning areas in adjacent ecosystems may have lower predation risks for juveniles, which might explain why coral reefs close to nursery or spawning areas show enhanced species diversity or secondary production (Dorenbosch et al. 2004, Mumby et al. 2004, Nagelkerken 2009).

1.5 Interacting effects between multiple fluxes

The majority of previous studies have investigated single connections between systems (Hemminga et al. 1994, Bouillon et al. 2007, Nagelkerken 2009). We argue that multiple fluxes need to be taken into account in evaluating the importance of adjacent ecosystems. However, such multiple environmental factors may interact and thereby result in responses that differ from what would be expected based on a single factor. However, interactions between multiple fluxes are still too poorly studied to fully account for all interactions within this perspective. It is clear that certain exchanges are likely to co-occur (e.g. high hydrodynamic energy and turbidity) (de los Santos et al. 2010). Wolanski (2007) showed that physical and chemical parameters are often linked to biological aspects of ecosystems. In the case of mangrove forests, the physical structure of mangroves will influence outwelling and consequently offshore fisheries.

Combining 2 factors may cause different types of interactions: synergistic, antagonistic and independent (de los Santos et al. 2010, La Nafie et al. 2012). A clear example of one exchange fully overruling a second exchange was shown by de los Santos et al. (2010), who demonstrated that light availability (related to turbidity) was much more important for seagrass health than changes in hydrodynamic energy. In contrast, La Nafie et al. (2012) showed that waves and high nutrient loads jointly decrease the survival but separately affect morphological and biomechanical properties of the seagrass *Zostera noltii*. Recent work has also shown that herbivores will limit the establishment of algae, in turn limiting sediment accumulation (Rasher et al. 2012). All of the factors mentioned above (light availability, hydrodynamic energy, nutrient loads, herbivore numbers and sedimentation) are critical for the growth and establishment of these ecosystems.

We have concentrated on the positive interactions, but there could be negative interactions as well. Fluxes leading to negative direct effects may have a positive indirect effect. For example, increased nutrient fluxes to coral reefs or seagrass beds, with negative

effects due to eutrophication, may cause increased herbivore numbers, a positive effect. Some species of parrotfish *Leptoscarus vaigiensis* are known to only feed on seagrass leaves (Gullström et al. 2011). Thus, an increase in numbers for this specific herbivore because of proximity to a coral reef may cause a decrease in seagrass biomass and be therefore classified as a negative interaction. Furthermore, these potential negative interactions may be cancelled out, e.g. mega-herbivore grazing (green turtle) has been shown to increase seagrass tolerance to eutrophication (Christianen et al. 2012), and fish herbivore grazing has been shown to increase shoot density (Valentine et al. 1997, Heck & Valentine 2006). These simple examples illustrate the complexity of these ecosystems and how fluxes of both positive and negative interactions can have results not explicitly considered.

Obtaining a better understanding of multiple flux interactions is of vital importance for the future. Global climate change combined with anthropogenic influences is likely to cause simultaneous changes in multiple factors in the near future and, as highlighted in the present perspective, the disappearance of one ecosystem can cause simultaneous changes in multiple fluxes with adjacent ecosystems.

1.6 Perspective: Landscape facilitation?

The idea of facilitation is generally considered in ecological community theory (Bruno et al. 2003). The importance of the idea of facilitation or positive interaction in community ecology raises the question of whether this concept can be used as an analogy at the landscape level. Where ecosystems in close proximity are connected by flows of energy, materials and organisms, 3 minimal requirements must be met for landscape-scale positive interactions to occur. First, there should be a sufficiently large exchange between the systems of a relevant resource, such as nutrients, sediment, energy or organisms. This requires the systems to be close enough spatially, relative to the typical length scale governing dispersal and exchange mechanisms. Second, exchanges must have the potential to be beneficial to at least one of the systems, donor or recipient. Systems must either have a requirement for a specific resource or must be dependent on the stress-buffering capacity of another system. Third, the requirement for alteration in resources suggests that substantive ecosystem engineering by some species may well play an important role in landscape-scale facilitation. However, it is clear that only those ecosystems that cause a clear change in resources and/or stresses are relevant to consider and that such ecosystems may be expected to often contain strong ecosystem engineers.

This exploration of positive reciprocal interactions for mangrove forests, seagrass beds and coral reefs indicates a potential for landscape facilitation. We have shown that these systems show an exchange of relevant resources (nutrients, sediment, energy or organisms), that these exchanges can be beneficial to donor ecosystems (via sediment/nutrient buffers,

wave reduction and nursery areas) and that a potential requirement is that ecosystem engineers are a substantial component of the donor or receiving systems (e.g. mangrove trees, seagrass plants and stony corals). Progress has been shown with regard to species interactions (Altieri et al. 2010) and more recently within habitat interactions (Thomsen et al. 2010) at the small scale; follow-up work should upscale and investigate multiple connections at the ecosystem scale. To our knowledge, quantitative analyses are typically only measured for single rather than multiple exchanges and more often for directional than reciprocal exchanges. Fortunately, interest in this type of research is gaining ground from the ecosystem services perspective (Barbier et al. 2008).

1.7 Conclusions

In the present review, we found that the changes in fluxes (wave height, sediment/nutrient and organismal exchange) will be vital for (1) establishment of foundation species and (2) when ecosystems are already under stress from eutrophic or natural affects. We acknowledge that threshold conditions may have already been surpassed before the interaction of the donor ecosystem. In many countries, these 3 ecosystems are managed by different entities. To ensure effective management, a more coordinated approach is required (Berkström et al. 2012). A priority should be ecosystem-based management (EBM), which is considered the most holistic approach to managing ecosystems (Mora et al. 2006, McLeod & Leslie 2009, Wilkinson & Salvat 2012). At present, it is highly speculative to generalize about the universal importance of ecosystem-level facilitation at the tropical coastal seascape. However, we suggest that the potential for the process is large and moreover that it may have substantial management implications.

1.8 Supplementary Material

Wave heights

Table S1 Reports of field wave heights at (A) mangrove forests (from 1990 to 2011), (B) seagrass beds (from 2001 to 2012) and (C) coral reefs (from 1975 to 2012). The studies are in ascending order according to wave height (m). nd: no available data, NA: not applicable. The mean wave height across studies can be seen in Tab. 1 in the main article.

Ecosystem Location	Ecosystem attributes	Depth (m)	Wave Height (m)	Area (km ²)	State	Reference
A) Mangrove forests						
Hinchinbrook Channel, Australia	-	NA	0.2	164	Modified	Wolanski et al. (1990)
Flume	-	NA	0.4	-	-	Suzuki et al. (2011)
Can Gio mangrove forest, Vietnam	-	NA	0.4	757	-	Phuoc & Massel (2006)
Tong King delta, Vietnam	-	NA	1	4.5	Re-planted	Mazda et al. (1997)
B) Seagrass beds						
Whangapoua Estuary, New Zealand	<i>Zostera sp.</i>	1.2	0.02-0.1	> 0.1	Fragmented	Bryan et al. (2007)
Duck Point Cove, USA	<i>Ruppia sp.</i>	1	0.1	-	Recovered	Newell & Koch (2004)
Santa Rosa Island, USA	<i>Thalassia sp.</i>	1.5	0.1	-	Stable	Bradley & Houser (2009)
South Bay, USA	<i>Zostera sp.</i>	1.4-2.3	0.2	0.0007	-	Hansen & Reidenbach (2012)
Cala Millor, Majorca Island	<i>Posidonia sp.</i>	6-35	0.2-0.4	1.2	-	Infantes et al. (2009)
Naruto, Japan	<i>Zostera sp.</i>	-	2	-	-	Cited from Koch (2001)
C) Coral Reefs						
Hawaii, USA	Fringing reef	0.05	0.09	-	-	Filipot & Cheung (2012)
St. Croix, USA	Back reef	2	0.1	-	-	Roberts et al. (1988)
St. Croix, USA	Reef crest	3	0.1	-	-	Roberts et al. (1988)
St. Croix, USA	Reef crest	3	0.3	-	-	Roberts et al. (1988)
St. Croix, USA	Fore reef	5	0.5	-	-	Lugo-Fernandez et al. (1998)
Torres Strait, Australia	Fore reef	2.5	0.5	-	-	Brander et al. (2004)
Margarita reef, Puerto Rico	Reef crest	0.3-6	0.6-1.5	-	-	Lugo-Fernandez et al. (1994)
Grand Cayman Island, Barbados	Reef shelf	13	1	-	-	Roberts (1975)
Great Corn Island, Nicaragua	Reef crest	0.5	1	-	-	Suhayda & Roberts (1977)
Guam, USA	Reef edge	8	4	-	-	Pequignot et al. (2011)

* Area of basin.

Table S2 Studies showing a percentage reduction in wave height travelling across (A) coral reefs and (B) seagrass beds from ocean to shore. H(enter) denotes the wave height at the edge of the seaward side of the ecosystem. H(exit) represents the wave height after passing through the coral reef or seagrass bed. Reduction (R) (%) is the percentage reduction in the initial wave height after travelling over a given distance of the coral reef or seagrass bed. H(exit) was calculated by $H(\text{enter}) - [H(\text{enter}) \times (R/100)]$. Export/import ratio gives an inverse wave retention potential of the forest and bed. The studies are in ascending order according to distance (m).

Ecosystem	Ecosystem attributes	Distance (m)	Depth (m)	H _{enter} (m)	H _{exit} (m)	Reduction (R) (%)	Export/Import ratio	Reference	Study
A) Coral reefs									
St.Croix, USA	Back reef	30	2	0.07	0.02	74	0.3	Roberts et al. (1988)	1
St.Croix, USA	Reef crest	45	3	0.1	0.05	56	0.5	Roberts et al. (1988)	2
St.Croix, USA	Reef crest	55	3	0.1	0.07	46	0.7	Roberts et al. (1988)	3
St.Croix, USA	Fore reef	125	5	0.3	0.1	54	0.3	Lugo Fernandez et al. (1998)	4
Great Corn Island, Nicaragua	Reef crest	300	5	1	0.6	40	0.6	Suhayda & Roberts (1977)	5
Grand Cayman Island	Reef crest	400	13	1	0.8	20	0.8	Roberts (1975)	6
Ipan, Guam	Fore reef	500	8	4	0.1	97	0.03	Pequignet et al. (2011)	7
Torres Strait, Australia	Fore reef	556	3	0.5	0.3	58	0.6	Brander et al. (2004)	8
Margarita reef, Puerto Rico	Reef crest	1000	0.3	1	0.2	72	0.3	Lugo Fernandez et al. (1994)	9
B) Seagrass beds									
			Density (Shoots m ⁻²)						
Flume	<i>Zostera sp.</i>	1	875	0.04	0.01	81	0.3	Fonseca & Cahalan (1992)	1
Virginia Coast reserve, USA	<i>Zostera sp.</i>	1.4-2.3	560	0.2	0.08	58	0.4	Hansen & Reidenbach (2012)	2
Santa Rosa Island, USA	<i>Thalassia sp.</i>	50	110	0.1	0.07	30	0.7	Bradley & Houser (2009)	3

Sediment

Table S3 Reports of total suspended solid fluxes ($\text{g m}^{-2} \text{d}^{-1}$) for (A) mangrove forests (from 1990 to 2010), (B) seagrass beds (from 1995 to 2003) and (C) coral reefs (from 1974 to 2004). Mean total suspended solid fluxes ($\text{g m}^{-2} \text{d}^{-1}$) values across studies can be seen in Table 1 in the main article. The studies are in ascending order according to total suspended solid (TSS) flux values ($\text{g m}^{-2} \text{d}^{-1}$). *: mean values. nd: no available data.

Location	Ecosystem attributes	TSS* ($\text{g m}^{-2} \text{day}^{-1}$)	Area (km^2)	State	Reference
A) Mangrove forest					
Ngerdorch, Palau	River	0.001	1.5	developed catchment area	Victor et al. (2004)
Nudgee Creek, Australia	Tidal creek	0.09	~0.8	extensively modified	Adame et al. (2010)
Bald Hills Creek, Australia	Tidal creek	0.1	0.8	extensively modified	Adame et al. (2010)
Caboolture River, Australia	River	0.2	2.4	modified	Adame et al. (2010)
Eprapah Creek, Australia	Tidal creek	0.2	1.3	modified	Adame et al. (2010)
Tingalpa, Australia	River	0.3	1.3	extensively modified	Adame et al. (2010)
Ngerikiil, Palau	River	0.5	0.7	natural, but poor surrounding land use	Victor et al. (2004)
Mooloolah River, Australia	River	1	0.3	modified	Adame et al. (2010)
Klong Ngao estuary, Thailand	Tidal creek	12	11.5	natural	Wattayakorn (1990)
Pohnpei, Federated states of Micronesia	River dominated	62	~0.4	-	Victor et al. (2006)
North coast, Kenya	River	233	17	moderately & extensively degraded	Kitheka et al. (2003)
Middle Creek, Australia	Tidal creek	675	6.5	less developed catchment area	Furukawa et al. (1997)
B) Seagrass bed					
China Sea, Hong Kong	<i>Zostera sp.</i>	0.003-0.02	-	-	Lee (1997)
Bay of Calvi, Mediterranean	<i>Posidonia sp.</i>	3.6	-	-	Dauby et al. (1995)
Silaqui, Pislatan, St. Barbara, Buenavista, Umalagan, Philippines	<i>Enhalus sp. Cymodocea sp. Halodule sp. & Thalassia sp.</i>	19-175	-	-	Gacia et al. (2003)
Fanals point, Spain	<i>Posidonia sp.</i>	1.5-500	-	-	Gacia & Duarte (2001)

Bai Tien, Dam Gia, My Giang, Vietnam	<i>Enhalus sp. Cymodocea sp. Halodule sp. & Thalassia sp.</i>	76-681	-	-	Gacia et al. (2003)
C) Coral reefs					
Phuket, Thailand	<i>Acropora sp. Porities sp.</i>	0.02	-	-	Chansang et al. (1992)
Puerto Rico, USA	<i>Agaricia sp. Monstratea sp.</i>	0.03-0.2	-	-	Loya (1976)
Puerto Rico, USA	<i>Acropora sp.</i>	0.2	-	-	Rogers (1979)
Great Barrier reef, Australia	<i>Acropora sp.</i>	0.5	-	-	Fabricius & Wolanski (2000)
Puerto Rico, Caribbean	<i>Porities sp. Siderastrea sp.</i>	1	-	-	Torres & Morelock (2002)
Papua New Guinea	<i>Acropora sp.</i>	1.4	-	-	Kojis & Quinn (1984)
Puerto Rico, USA	<i>Monstratea sp.</i>	1.9	-	-	Torres (1998)
Discovery Bay, Jamaica	<i>Monstratea sp.</i>	1.9	-	-	Dodge et al. (1974)
Aquarium experiment	<i>Favia sp.</i>	2	-	-	Todd et al. (2004)
Great Barrier reef, Australia	<i>Leptoria sp. Porities sp.</i>	2.5	-	-	Stafford-Smith (1992)
Palawan, Philippines	<i>Montipora sp. Porities sp.</i>	3	-	-	Hodgson (1990)
Natal, South Africa	<i>Favia sp. Favites sp. Gyrosmillia sp. Platygyra sp.</i>	20	-	-	Riegl (1995), Riegl & Bloomer (1995)
Dampier Archipelago, Australia	<i>Acropora sp.</i>	20-30	-	-	Simpson (1988)
Curacao, Caribbean	<i>Acropora sp.</i>	43	-	-	Bak & Elgershuizen (1976)
Laboratory experiment	<i>Astrangla sp.</i>	< 60	-	-	Peters & Pilson (1985)

Table S4 S Studies showing flux of total suspended solids (TSS; $\text{g m}^{-2} \text{d}^{-1}$) exported from a mangrove forest (column 4) compared to the initial import into the forest (column 5) ($\text{g m}^{-2} \text{d}^{-1}$). Some fluxes were not based on a full year of observation, and this can cause large variability. Nevertheless, for simplicity, all fluxes have been expressed as $\text{g m}^{-2} \text{d}^{-1}$. Location indicates where the study was performed. Classification and area of the mangrove forest is information from the original data source except where indicated. Trapping capacity was calculated as $100 - (\text{Import}/\text{Export} \times 100)$, which gives the percentage of the influx retained by the ecosystem. Column 7 is the export/import ratio, which gives an inverse retention potential of the forest. We also include the original units, how the export and import were calculated and the type/location of measurements for transparency, which are all taken from the original studies. The studies are in ascending order according to mangrove area (km^2). *: data were taken from www.ozcoasts.au. Data from Adame et al. (2010) are estimations because these data were taken during a spring tide when inundation was higher, and this could affect the sedimentation rates.

Location	Classification	Mangrove area	Export	Import	Trapping capacity	Export/Import	Original units	Calculated from	Type of measurement	Location of measurement	Study
Reference		km^2	$\text{g m}^{-2} \text{day}^{-1}$	$\text{g m}^{-2} \text{day}^{-1}$	(%)	(ratio)					
Mooloolah River, Australia Adame et al. (2010)	River dominated	0.3*	0.9	1	8	0.9	$\text{mg cm}^{-2} \text{spring tide}^{-1}$	Sedimentation rate	Sediment traps	Depositional side of river/tidal creek	1
Ngerikil, Palau Victor et al. (2004)	River dominated	0.7	0.4	0.5	25	0.7	$\text{tons km}^{-2} \text{yr}^{-1}$	Export rate	Sediment traps	Edge of river bank/perpendicular to river	2
Nudgee Creek, Australia Adame et al. (2010)	Tide dominated	-0.8*	0.090	0.094	5	1.0	$\text{mg cm}^{-2} \text{spring tide}^{-1}$	Sedimentation rate	Sediment traps	Depositional side of river/tidal creek	3
Bald Hills Creek, Australia Adame et al. (2010)	Tide dominated	0.8*	0.130	0.131	1	1.0	$\text{mg cm}^{-2} \text{spring tide}^{-1}$	Sedimentation rate	Sediment traps	Depositional side of river/tidal creek	4
Epparah Creek, Australia Adame et al. (2010)	Tide dominated	1.3*	0.21	0.22	5	1.0	$\text{mg cm}^{-2} \text{spring tide}^{-1}$	Sedimentation rate	Sediment traps	Depositional side of river/tidal creek	5
Tingalpa Creek, Australia Adame et al. (2010)	River dominated	1.3*	0.2	0.3	37	0.6	$\text{mg cm}^{-2} \text{spring tide}^{-1}$	Sedimentation rate	Sediment traps	Depositional side of river/tidal creek	6
Ngerdorch, Palau Victor et al. (2004)	River dominated	1.5	0.005	0.01	64	0.4	$\text{tons km}^{-2} \text{yr}^{-1}$	Export rate	Sediment traps	Edge of river bank/perpendicular to river	7
Caboollure River, Australia Adame et al. (2010)	River dominated	2.4*	0.1	0.2	31	0.7	$\text{mg cm}^{-2} \text{spring tide}^{-1}$	Sedimentation rate	Sediment traps	Depositional side of river/tidal creek	8
Pohnpei, Federated states of Micronesia Victor et al. (2006)	River dominated	~4	37.3	62	40	0.6	$\text{mg cm}^{-2} \text{day}^{-1}$	Export rate	Oceanographic instruments	Bay	9
Middle creek, Australia Furukawa et al. (1997)	Tide dominated	6.5*	135	675	80	0.2	$\text{mg cm}^{-2} \text{day}^{-1}$	Sedimentation rate	Sediment traps	Along boardwalk	10
Klong Ngao estuary, Thailand Wattayakorn et al. (1990)	Tide dominated	11.5	1	12	90	0.1	kg day^{-1}	Export rate	Water samples	In estuary at three different depths	11
Mwachhe mangrove, Kenya Kihuka et al. (2003)	River dominated	17	107	233	54	0.5	$\text{g m}^{-2} \text{tide}^{-1}$	Sedimentation rate	Water samples	Along tidal creek	12

Nutrients

Table S5 Reports of fluxes in the water column (g N or $\text{P m}^{-2} \text{d}^{-1}$) for (A) coral reefs (1983 to 2011) and (B) seagrass beds (1985 to 2010) of total dissolved nitrogen (N) and phosphorous (P). Mean nutrient flux (g N or $\text{P m}^{-2} \text{d}^{-1}$) values across studies can be seen in Table 1 in the main article. The studies are in ascending order according to the year of the study. *: average values; nd: no available data.

Location	Type	Nutrient*	($\text{g m}^{-2} \text{day}^{-1}$)	Study
Ecosystem				
A) Fluxes in the water column at coral reefs				
Guam, Mariana Islands	Fringing reef	N	P	Matson (1993)
	Offshore reef	0.02	0.0004	
Florida, USA	Barrier reef	0.004	0.00002	Corbett et al. (1999)
Yucatan, Mexico	Barrier reef	0.002	0.00007	Hernández-Terrones et al. (2010)
B) Fluxes in the water column at seagrass beds				
Chesapeake Bay, USA	<i>Zostera sp.</i>	0.01	-	adapted from Lee & Olsen (1985)
Long Island, USA	<i>Zostera sp.</i>	0.02	-	adapted from Lee & Olsen (1985)
Long Island, USA	<i>Zostera sp.</i>	0.03	-	adapted from Lee & Olsen (1985)
Long Island, USA	<i>Zostera sp.</i>	0.02	-	adapted from Lee & Olsen (1985)
Buttermilk Bay, USA	<i>Zostera sp.</i>	0.02	-	Valiela & Costa (1988)
Chincoteague bay, USA	<i>Zostera sp.</i>	0.01	-	Boynton et al. (1996)
Sage Lot Pond, USA	<i>Ruppia sp.</i>	0.003	-	McClelland et al. (1997)
Sage Lot Pond, USA	<i>Zostera sp.</i>	0.02	-	Hauxwell et al. (1998)
Charlestown Pond, USA	<i>Zostera sp.</i>	0.02	-	adapted from Nixon et al. (2001)
Great South Bay, USA	<i>Zostera sp.</i>	0.004	-	adapted from Nixon et al. (2001)
Great Bay, USA	<i>Zostera sp.</i>	0.01	-	adapted from Nixon et al. (2001)
Great Bay, USA	<i>Zostera sp.</i>	0.09	-	adapted from Nixon et al. (2001)
Buttermilk Bay, USA	<i>Zostera sp.</i>	0.05	-	adapted from Nixon et al. (2001)
Kertinge Nor, USA	<i>Zostera sp.</i>	0.01	-	adapted from Nixon et al. (2001)
Florida, USA	<i>Thalassia sp.</i>	0.001	-	Comelissen & Thomas (2006)
Florida, USA	<i>Thalassia sp.</i>	0.002	-	Comelissen & Thomas (2006)
Spermonde Archipelago, Indonesia	<i>Cymodocea sp.</i>	0.1	-	Vonk & Stapel (2008)
Spermonde Archipelago, Indonesia	<i>Halodule sp.</i>	0.1	-	Vonk & Stapel (2008)
Spermonde Archipelago, Indonesia	<i>Thalassia sp.</i>	0.1	-	Vonk & Stapel (2008)
Sonion, Greece	<i>Posidonia sp.</i>	0.04	0.002	Apostolaki et al. (2010)

Table S6 Studies showing water column fluxes (g N or P m⁻² d⁻¹) of dissolved (A) nitrogen (N, TN, DON + DIN) and (B) phosphorus (TP, SRP + PO₄, DIP, DOP) to and from a mangrove forest. All data are expressed as fluxes per day, but not all studies covered a full year, which will give rise to variability. Different studies are also variable because of differences in methodology. Import flux (column 6) indicates the nutrient being fluxed into the mangrove forest, and export flux (column 5) is nutrients, which are being fluxed out from or within a mangrove. Location (and reference) indicate where and by whom the study was completed. Export/import ratio (column 7) gives an inverse retention potential of the forest. The studies are in ascending order according to mangrove area inundated (km²). We also included the original units, how the import & export was calculated and the type/location of measurements for transparency, which are all taken from the original studies. nd: no available data, *.wetland area, not inundation area.

Location Reference	Mangrove area inundated (km ²)	Type of Nutrient	State	Export g m ⁻² day ⁻¹	Import g m ⁻² day ⁻¹	Export/Import ratio	Original Units	Calculated from	Type of measurements	Location of measurements	Study
A) Nitrogen											
Shenzhen, South China Li (1997)	1.1	N	Relatively undisturbed	0.01	0.02	0.5	kg ha ⁻¹ year ⁻¹	Uptake & Export rate	Nutrients in woody components	In mangrove trees	1
Taylor River, America Davis et al. (2001)	2.5	TN	-	0.001	0.004	0.3	μmoles m ⁻² hour ⁻¹	Uptake & Export rate	Water samples	River	2
Coral Creek, Australia Boto & Wellington (1988)	5	DIN + DON	-	0.001	0.003	0.5	kg day ⁻¹	Export & Import	Water samples	Creek water column	3
Bahía de Lobos, Mexico Sánchez-Carrillo et al. (2009)	14	TN	Eutrophication problems	0.02	0.002	10	kg ha ⁻¹ day ⁻¹	Export & Import	Water samples	Mouth of channel	4
Sarasota Bay, USA Cited from Valiela & Cole (2002)	17*	N	-	0.1	0.2	0.5	kg ha ⁻¹ year ⁻¹	Export & Import	-	-	5
Tampa Bay, USA Cited from Valiela & Cole (2002)	85*	N	-	0.12	0.13	0.9	kg ha ⁻¹ year ⁻¹	Export & Import	Suspended and dissolved N	Bay	6
Moreton Bay, USA Cited from Valiela & Cole (2002)	95*	TN	-	0.1	0.12	0.8	kg ha ⁻¹ year ⁻¹	Export & Import	Water samples	River mouth, plumes and ocean	7
Red river, Vietnam Wösten et al. (2003)	107	DIN + DON	-	0.03	0.1	0.2	kmol day ⁻¹	Export & Import	Water samples	Estuary	8
Charlotte Harbour, USA Cited from Valiela & Cole (2002)	261*	N	-	0.06	0.07	0.9	kg ha ⁻¹ year ⁻¹	Export & Import	-	-	9
Tapi Estuary, Thailand Wattayakorn et al. (2001)	480	DIN + DON	-	0.4	0.1	4	mol m ⁻² day ⁻¹	Export & Import	Water samples	Estuary	10

B) Phosphorus										
Shenzhen, South China Li (1997)	1.1	P	Relatively undisturbed	0.002	0.004	0.5	kg ha ⁻¹ year ⁻¹	Nutrients in woody components	In mangrove trees	1
Taylor River, America Davis et al. (2001)	2.5	TP	-	0.0001	0.0002	0.5	μmoles m ⁻² hour ⁻¹	Water samples	River	2
Coral Creek, Australia Boto & Wellington (1988)	5	DOP + PO ₄	-	0.0005	0.001	0.5	kg day ⁻¹	Water samples	Creek water column	3
Bahia de Lobos, Mexico Sánchez-Carrillo et al. (2009)	14	TP	Eutro- phication problems	0.001	0.1	0.001	kg ha ⁻¹ day ⁻¹	Water samples	Mouth of channel	4
Red river, Vietnam Wösten et al. (2003)	107	P	-	0.06	0.09	0.7	kmol day ⁻¹	Water samples	Estuary	5
Tapi Estuary, Thailand Wattayakorn et al. (2001)	480	DOP + DIP	-	0.017	0.02	0.9	mol m ² day ⁻¹	Water samples	Estuary	6

Table S7 Studies showing seagrass bed import and export of dissolved nitrogen sources (nitrate/nitrate, ammonium and urea) and phosphorus ($\text{g m}^{-2} \text{d}^{-1}$) fluxes. Site and species indicates the location and type of seagrass of each individual study; each study looked at different dissolved nitrogen sources. To understand fluxes of import and export of nutrients, we totaled all of the types of nutrient (NH_4^+ , NO_3^- , urea) as an import; we understand this is a coarse estimation, but it allowed us to compare export of nutrients. Nutrient export denotes the concentration flux in the water column at the end of the experiment; nutrient import represents the concentration flux at the beginning of the experiment. The export/import ratio is an indication of the inverse retention potential of the seagrass bed (column 7). The reduction (%) is the percentage of nutrient and phosphorus retained by the seagrass plants and is calculated as $100 - (\text{export/import} \times 100)$. Type of measurement and the original units are taken from each study. The studies are in ascending order according to alphabetical order of the names of seagrass species. NA: not applicable.

Site	Species	Area m^2	Type of nutrient	Nutrient export $\text{g m}^{-2} \text{day}^{-2}$	Nutrient import $\text{g m}^{-2} \text{day}^{-2}$	Export/ import ratio	Reduction %	Type of measurements	Original units	Study
Cádiz, Spain Van Engeland et al. 2013	<i>C.nodosa</i>	-	NH_4^+ , NO_3^- , Urea	1.5	2	0.7	30	Incubations	$\mu\text{gN m}^{-2} \text{hour}^{-1}$	1
Spermonde Archipelago, Indonesia Vonk & Stapel 2008	<i>C.rotundata</i>	0.5	N	0.09	0.1	0.8	22	Model verified with litterbags	$\mu\text{mol l}^{-1} \text{hour}^{-1}$	2
Spermonde Archipelago, Indonesia Vonk & Stapel 2008	<i>H.uninervis</i>	0.5	N	0.106	0.112	1.0	5	Model verified with litterbags	$\mu\text{mol l}^{-1} \text{hour}^{-1}$	3
Sitía, Greece Apostolaki et al. 2012	<i>P.oceanica</i>	0.08	NH_4^+ , NO_3^-	0.0001	0.0003	0.3	60	Incubations	$\mu\text{gN m}^{-2} \text{hour}^{-1}$	4
Psaromoura, Greece Apostolaki et al. 2012	<i>P.oceanica</i>	0.08	NH_4^+ , NO_3^-	0.0002	0.001	0.2	79	Incubations	$\mu\text{gN m}^{-2} \text{hour}^{-1}$	5
Spermonde Archipelago, Indonesia Vonk & Stapel 2008	<i>T.hemprichii</i>	0.5	N	0.1	0.1	0.9	67	Model verified with litterbags	$\mu\text{mol l}^{-1} \text{hour}^{-1}$	6
Florida, USA Cornelisen & Thomas 2006	<i>T.testudinum</i>	3.7	NH_4^+ , NO_3^-	0.0002	0.0006	0.4	57	Flume	$\text{gN (gDW)}^{-1} \text{s}^{-1} * 10^{-9}$	7
Florida, USA Cornelisen & Thomas 2006	<i>T.testudinum</i>	3.7	NH_4^+ , NO_3^-	0.0008	0.002	0.4	58	Flume	$\text{gN (gDW)}^{-1} \text{s}^{-1} * 10^{-9}$	8
Cádiz, Spain Van Engeland et al. 2013	<i>Z.noltii</i>	-	NH_4^+ , NO_3^- , Urea	1.1	1.5	0.7	30	Incubations	$\mu\text{gN m}^{-2} \text{hour}^{-1}$	9
Algeciras Bay, Spain Perez-Llorens & Niell 1995	<i>Z.noltii</i>	NA	P	0.00004	0.0001	0.7	35	Incubations	$\mu\text{gN m}^{-2} \text{hour}^{-1}$	10

Chapter 2

Tiny is mighty: Seagrass beds have a disproportionally large role in the export of organic matter in the tropical coastal zone.

L.G. Gillis, A.D. Ziegler, D. van. Oevelen, C. Cathalot, P.M.J. Herman and T.J. Bouma.

STATUS: Submitted



Abstract

Ecosystems in the tropical coastal zone may exchange particulate organic matter (POM) with adjacent systems, but relative differences in this function among ecosystems remain poorly quantified. Seagrass beds are often a relatively small section of the coastal zone, but have a potentially much larger ecological influence than suggested by their surface area. Using isotope tracers of oceanic, terrestrial, mangrove and seagrass sources, we established the origin of particulate organic matter in coastal areas in Phuket, Thailand. Using an mixing model, based on C:N ratio, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, we found that oceanic sources dominated suspended particulate organic matter samples along the mangrove, seagrass open ocean gradient. Sediment trap samples showed contributions from all four sources. Based on ecosystem area however, the contribution of suspended particulate organic matter derived from seagrass beds was disproportionally high, relative to their size. The contribution from mangrove forests was roughly equal to their surface area, whereas terrestrial sources were under represented to suspended organic particulates. The relatively large role of seagrass beds in organic matter export should be considered in coastal zone management.

Keywords: Isotopes, seagrass beds, mangrove forests, catchment area, nutrients, landscape

2.1 Introduction

The tropical coastal zone is comprised of ecosystems along the coastline ranging from the open ocean, over coral reefs and seagrass beds towards the terrestrial zone including mangrove forests. These systems form a well-structured and gradual interface between the land and the sea that comprises some of the most productive and biogeochemically active ecosystems in the world (Gattuso et al. 1998). In part, the productivity is maintained by the inputs of nutrients in the form of particulate and dissolved organic material (POM & DOM), from both terrestrial and oceanic sources (Gattuso et al. 1998). Environments within this zone have high production and storage capacity in addition to readily exchanging POM between them and with the ocean (Gattuso et al. 1998).

The quantity of the influx of terrestrial organic material depends on the size and the land-use within the catchment area and importantly, on the linkage between organic matter sources and the river system draining toward the coast (Krusche et al. 2002). Estuaries, which are tidally dominated, have large exchanges of water with the ocean and therefore also receive ocean-derived dissolved and particulate organic material (Kuramoto & Minagawa 2001, Thimdee et al. 2003, Meksumpun et al. 2005). The mangrove outwelling hypothesis (Odum 1968, Lee 1995) postulates that export of mangrove-derived organic matter supports adjacent ecosystems and food webs. Mangroves are biogeochemically complex, with high nutrient processing by associated fauna (Lee 1995, Kristensen et al. 2008).

Another potentially important nutrient source and sink within the tropical coastal zone are seagrass beds. Seagrass plants trap suspended POM originating from both external sources and from leaf shedding inside the seagrass bed (Terrados & Duarte 2000, Vonk et al. 2008b). Trapping results directly from the physical structure of the meadow and from settling induced by changes in the hydrodynamic conditions; both are related to plant density and leaf characteristics (Fonseca & Cahalan 1992, Hendriks et al. 2008). Once POM is deposited within seagrass beds, plants in the meadow limit re-suspension and most of the POM degrades within the bed thereby releasing dissolved nutrients that are taken up by the seagrass (Hemminga et al. 1999, Koch & Verduin 2001, Infantes et al. 2009) or are released to the water column (Terrados & Duarte 2000, Wilkie et al. 2012).

Due to the different habitats in the seascape, the high production of ecosystems and the potential for import and export from a variety of sources it is challenging to separate different sources of organic material. A useful chemical tracer approach is to use a combination of carbon to nitrogen ratios (C:N), with carbon and nitrogen stable isotope ratios ($\delta^{13}\text{C}$ & $\delta^{15}\text{N}$, respectively) (McConnachie & Pettricrew 2006, Schindler Wildhaber et al. 2012). Each of these tracers has a specific signature for each source (oceanic, seagrass, mangrove and terrestrial), which can be used to identify the contribution of different sources in a mixture (McConnachie & Pettricrew 2006, Schindler Wildhaber et al. 2012).

Kuramoto & Minagawa (2001) investigated source contributions in Southern Thailand and found that seagrass plants contributed between 36-42 % of organic material to sediment trap samples. Hemminga et al. (1994) and Bouillon et al. (2007) found that mangrove and seagrass material dominated suspended POM in the water column at Gazi Bay, Kenya. These studies indicate it is likely that these results depend on the local conditions. In this paper, we build upon the foundations of previous work to investigate the origin of POM in the coastal zone in Phang-nga Bay in southern Thailand across several sites to gain a greater understanding of export of POM from different ecosystems at the tropical seascape scale. Specifically we compare the amount of organic material originating from seagrass beds versus mangrove, oceanic, and terrestrial sources across a number of different sub-habitats in the region and compare this to their respective surface areas.

2.2 Methods

2.2.1 Study Area and Physical attributes

Within the Andaman Sea, along the south west coast of Thailand is the province of Phuket, which borders Phang-nga bay (Fig. 1).



Figure 1 Map showing location of the nine sampling sites (black circles) in Phang Ngu bay, Southern Thailand. All sites were sampled and treated identically, but for easier presentation only the figures of the white filled points (A, B & C) are shown. The data for all sites can be found in the supplementary material.

Our sampling sites are located along Phang-nga Bay, which is 68 km long (head to mouth), 82 km long and a surface area of 3000 km² (Fig. 1). The southern part of the bay is open to the Andaman Sea and the northwest area is open to the sea via the Pak Pra Inlet, which separates Phuket island from the mainland (Fig. 1). Estuarine salinity conditions dominate in the north, whilst marine conditions dominate in the south (Limpsaichol et al. 1998). Circulation in the bay changes depending on the dry (May to October) or wet season (November to April), which alters the wind direction and surface water currents. Mean annual rainfall is about 2300 mm and mean temperature is 28 °C. Land-use around Phang-nga bay has changed from natural forest to initially tin mining (1600-1800); this area in Southern Thailand has substantial deposits of valuable earth minerals such as tin and quartz (Limpsaichol et al. 1998). However tin mining intensity has decreased in recent years. Other land-uses have gained greater importance such as rubber and palm oil plantations as well as shrimp and fish farms (Limpsaichol et al. 1998), and recently the rapid urbanisation related to tourism in Phuket.

For convenience, the data and results of the other sites are shown in the supplementary material (Fig. S1 and 2 and Tab. S1), but are included in the discussion. All sites were outside the reach of direct river discharge and experienced a strong tidal exchange with the ocean. Therefore, all sites classify as tidal mangroves (Woodroffe 1992).

2.2.2 Sample collection and data processing

At each site we established transects beginning at the edge of the mangrove and extending towards the ocean through an adjacent seagrass patch. Samples were taken, when logistically possible, at all distances of 0 (seaward edge of mangrove forest), 50, 100, 200, 300, 400, 500, 1000, 1500 and 2000 m along the transect perpendicular to the seaward edge of the mangrove forest towards the open sea. Three types of samples were collected: core samples of surface sediment, trap samples of suspended material above the bed and suspended particulate matter in the water column. At least half of the sampling points (for core, trap and water samples) were in the seagrass beds, the other half were taken at points landward or seaward of the bed depending on the physical constraints of the different sites. Sediment core samples were taken at each point with a 5-cm length hand-held PVC corer that extracted a volume of 90 cm³. Sediment traps (at each point) were secured to steel rods and anchored at each point to the substrate at a height of 0.05 m above the sediment: they were emptied once after approximately 24 hours. On the day of core sample collection and trap installation, 2 liter surface water samples were taken at each point above the traps at the water surface during high tide. All samples were collected in March 2011.

Table 1 Land-use in the catchment areas and the physical attributes of the marine ecosystems for each site and the associated bay. Physical attributes of each site. Land use in the catchment area was determined by analysing Quickbird, WorldView-1 and WorldView-2 satellite imagery. The land use in the catchment area was visually qualified as mangrove forest, natural forest (terrestrial), plantations (rubber & palm oil), rice paddies, shrimp farms, clearings (cleared land) or buildings (urban areas). The physical attributes associated with the marine ecosystems were determined during the experiment.

Site	Catchment area land-use	Area (km ²)	Marine ecosystem attributes	
A	Natural forest	0.3	Seagrass bed (SB)	
	Plantations	23.3	Area (km ²)	0.5
	Rice paddies	0.1	Species	<i>Enhalus sp.</i>
	Shrimp farms	1.2	Mangrove forest (MF)	
	Buildings	0.4	Area (km ²)	3.3
	Clearings	1.0	Species	<i>Rhizophora sp, Ceriops sp & Xylocarpus sp</i>
	Fish farm	0.0009		
	Total catchment area	26.3	% MF in catchment area	13
B	Natural forest	0.4	Seagrass bed (SB)	
	Plantations	1.0	Area (km ²)	2.1
	Shrimp farms	0.4	Species	<i>Enhalus sp.</i>
	Buildings	3.9	Mangrove forest (MF)	
	Clearings	1.8	Area (km ²)	0.9
			Species	<i>Rhizophora sp</i>
	Total catchment area	7.5	% MF in catchment area	12
C	Natural forest	0.4	Seagrass bed (SB)	
	Plantations	1	Area (km ²)	0.8
	Rice paddies	0	Species	<i>Enhalus sp, Halodule sp, Halophila sp & Thalassia sp</i>
	Buildings	4	Mangrove forest (MF)	
	Clearings	1.8	Area (km ²)	0.4
			Species	<i>Rhizophora sp, Ceriops sp & Xylocarpus sp</i>
	Total catchment area	7.2	% MF in catchment area	6

Four POM sources were considered in this study: terrestrial vegetation, mangrove leaves, seagrass material and oceanic plankton. For the terrestrial vegetation, three replicates of 3-4 leaves from rubber trees (*Hevea sp.*) and native vegetation (*Delonix sp.*) were collected on the island of Koh Yai. This material represents the source value for the terrestrial organic material used in the mixing model. Mangrove and seagrass leaves were collected during the trap deployment. Oceanic samples were taken for plankton samples were sampled with weighted plankton nets with mesh sizes 400 µm and for SPM samples 5 x 1 litre water

samples were collected. These were collected at a point, which was thought to have the majority of oceanic influence (7°52.573'N and 98°35.635'E) at a depth of 10 m. The mean of the C and N content and $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ value of each POM source was taken as respective end-member to determine the contribution of each source to the organic matter along the transect.

All solid samples (sediment and leaves) were placed in separate sample bags, stored in a cooling box and then transported immediately to the field laboratory where they were dried at 60°C for 48 hours. Water samples for SPM and plankton were filtered through pre-combusted glass fiber filters (GF/F) (0.7 μm pore diameter). The GF/F filters were then dried at 60°C for 48 hours. Both solid material (sediment & leaves) and GF/F filters were packed in airtight containers and transported to the laboratory of Royal Netherlands Institute for Sea Research (NIOZ) for elemental and isotope analysis.

2.2.3 Elemental and isotope analysis

Sediment and leaf material samples were ground for homogenisation. The trap, plankton and SPM were acidified to remove all carbonates from the samples (Nieuwenhuize et al. 1994), while the leaves were not acidified. All samples were analysed for total organic carbon (TOC), total nitrogen (TN), and the isotopes $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ by means of elemental analysis isotope ratio mass spectrometry (EA-IRMS) using a Thermo Finnigan Flash 1112.

Stable isotope ratios are expressed as δ values (‰) relative to conventional standards (VPDB limestone for C and atmospheric N_2 for N), as shown in equation (1):

$$\delta x = ((x_{\text{sample}} - x_{\text{standard}}) / x_{\text{standard}}) * 1000 (\text{‰}) \quad (1)$$

where δx is either $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$; x_{sample} is the $^{13}\text{C} / ^{12}\text{C}$ or $^{15}\text{N} / ^{14}\text{N}$ ratio of the sample; x_{standard} is the $^{13}\text{C} / ^{12}\text{C}$ or $^{15}\text{N} / ^{14}\text{N}$ ratio of the standards (0.01118 for ^{13}C and 0.00368 for ^{15}N).

2.2.4 Elemental and isotope analysis examination

We considered the following potential sources (Fig. 2): terrestrial vegetation (*Delonix sp.* & *Terminalia sp.*), mangrove material (*Rhizophora sp.*), seagrass leaves (*Enhalus sp.*, *Halodule sp.* & *Halophila sp.*) and oceanic production (plankton and SPM). Values for the four end members in the carbon and isotope analysis were taken as the means of the collected data for each source (Tab. 2). Only SPM and trap samples were analysed with the mixing model.

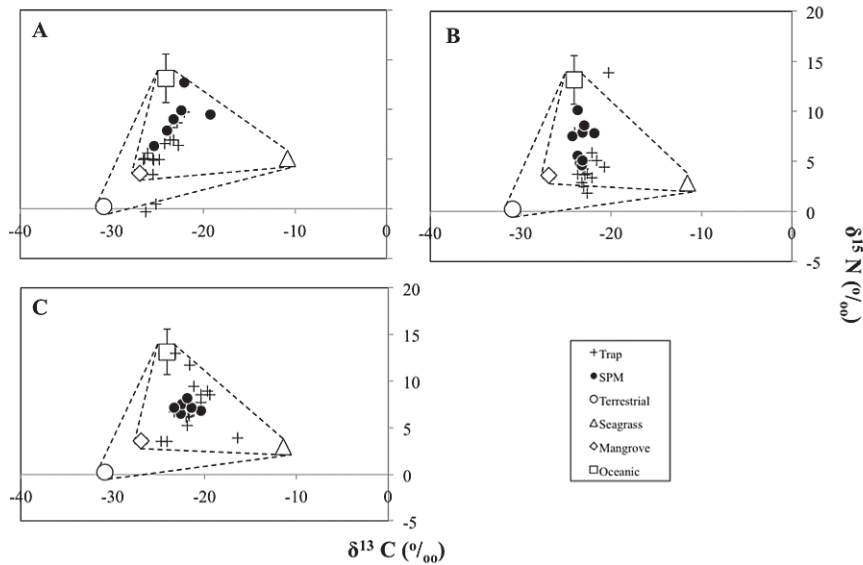


Figure 2 Carbon ($\delta^{13}\text{C}$ ‰) and nitrogen ($\delta^{15}\text{N}$ ‰) isotopic composition for organic matter from trap and SPM samples from the three sites A, B & C. The end members shown are as follows white circles is the terrestrial value, white square represents oceanic sources, white triangle symbolises the seagrass plant end-number and white diamond is the mangrove plant values. The trap and SPM samples are represented by crosses and black circles respectively. Values for the end members are means ($\pm$ SE). For the end members of the oceanic, terrestrial, seagrass plants and mangrove plants sources, $n = 6, 9, 44$ & 45 respectively. This is 2 dimensional representation of the data with only isotope sources, table 3 represents the analysis of the results with all three components (carbon, nitrogen isotopes and C:N ratios).

A linear mixing model was used to determine the contributions of the different sources to the SPM and trap sediment samples (Phillips & Gregg 2001, Phillips & Koch 2002). The mixing model uses the means of $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and the C:N ratios (corrected for differences in %C and %N between sources) of individual trap or SPM samples to determine the contribution (f) of each of the four sources (oce = oceanic, ter = terrestrial, man = mangrove trees & sea = seagrass plants) to this mixture. The variation between the replicates is small, justifying the use of the means. The mixing model has four equations (eqs. 2-5) that are solved simultaneously to recover a unique solution of the four source contributions (f_{oce} , f_{ter} , f_{man} , f_{sea}). The model was implemented and solved in R (R Core Team 2012), using the *lsei* function from the LIM package (Van Oevelen et al. 2010).

$$f_{\text{oce}} + f_{\text{ter}} + f_{\text{man}} + f_{\text{sea}} = 1 \quad (2)$$

$$\delta^{13}\text{C}_{\text{mix}} = \delta^{13}\text{C}_{\text{oce}} \cdot f_{\text{oce}} + \delta^{13}\text{C}_{\text{ter}} \cdot f_{\text{ter}} + \delta^{13}\text{C}_{\text{man}} \cdot f_{\text{man}} + \delta^{13}\text{C}_{\text{sea}} \cdot f_{\text{sea}} \quad (3)$$

$$\delta^{15}\text{N}_{\text{mix}} = \delta^{15}\text{N}_{\text{oce}} \cdot f_{\text{oce}} + \delta^{15}\text{N}_{\text{ter}} \cdot f_{\text{ter}} + \delta^{15}\text{N}_{\text{man}} \cdot f_{\text{man}} + \delta^{15}\text{N}_{\text{sea}} \cdot f_{\text{sea}} \quad (4)$$

$$0 = (\%C_{\text{oce}} - \text{CN}_{\text{mix}} \cdot \%N_{\text{oce}}) \cdot f_{\text{oce}} + (\%C_{\text{ter}} - \text{CN}_{\text{mix}} \cdot \%N_{\text{ter}}) \cdot f_{\text{ter}} + (\%C_{\text{man}} - \text{CN}_{\text{mix}} \cdot \%N_{\text{man}}) \cdot f_{\text{man}} + (\%C_{\text{sea}} - \text{CN}_{\text{mix}} \cdot \%N_{\text{sea}}) \cdot f_{\text{sea}} \quad (5)$$

Table 2 Mean values of $\delta^{13}\text{C}$ & $\delta^{15}\text{N}$, carbon, nitrogen ratios (C:N) and standard error for terrestrial trees, mangroves trees, seagrass plants and oceanic. The overall values for each source (highlighted) are the means of the different contributions (species for terrestrial, mangrove and seagrasses & SPM/plankton for oceanic). These values are defined as the end members (organic matter sources), which are used in the mixing to determine the different mixture of fractions for organic matter. The organic matter was collected in the sediment trap and suspended sediment matter samples. The carbon isotope value is represented by $\delta^{13}\text{C}$ and the nitrogen by $\delta^{15}\text{N}$ and C:N equates to the atomic carbon (C)/nitrogen (N) ratio. n , is the number of samples and SE is standard error.

Sources	Species	$\delta^{13}\text{C}$		$\delta^{15}\text{N}$		C		N		n
Group		Mean	SE	Mean	SE	Mean	SE	mean	SE	
		(‰)		(‰)						
Terrestrial	<i>Havea sp</i>	-31.8	0.5	0.4	0.001	46.8	0.2	4.2	0.04	3
	<i>Delomix sp</i>	-30.1	0.5	0.6	0.001	46.9	0.3	2.6	0.2	3
	<i>Terminalia sp</i>	-31.2	0.5	1.9	0.001	44.8	0.2	3.6	0.006	3
Overall terrestrial	-	-31.0	0.4	1.0	0.0004	46.1	0.2	4.01	0.08	3
Overall Mangrove trees	<i>Rhizophora sp</i>	-26.9	0.6	3.6	0.2	37.5	0.6	1.2	0.07	45
Seagrass plants	<i>Halodule sp</i>	-11.4	0.7	2.9	0.15	21.4	2.6	1.4	0.2	7
	<i>Halophile sp</i>	-11.6	0.5	2.8	0.9	21.4	2.1	1.3	0.2	19
	<i>Enhalus sp</i>	-10.1	0.3	5.2	0.3	25.6	1.6	1.9	0.1	17
Overall seagrass plants	-	-11.0	0.6	3.6	0.2	21.7	1.4	1.5	0.1	3
Oceanic	SPM	-24.1	0.13	18.3	3	1.2	0.07	0.2	0.01	3
	Plankton	-24	0.04	7.9	0.03	4.6	0.5	0.8	0.1	3
Overall oceanic	-	-24.1	0.06	13.1	3.5	2.9	0.8	0.5	0.1	6

Using the contribution results from the mixing model, we then calculated if each source was under contributing or over contributing compared to its relative surface area (equation 6).

$$F_x/A_{fx} \quad (6)$$

This index was not calculated for POM derived from oceanic sources, because no representative surface area for the 'ocean' could be defined. The contribution (F_x ; %) per source in each sample was then divided by the percent of total surface area (A_{fx}) occupied by the particular system (catchment area-terrestrial, mangrove forest, seagrass bed). This gives a dimensionless number in which 1 implies that the ecosystem contributes proportionally to its relative surface area and below or above 1 would indicate that the proportional contribution is lower or higher, respectively.

2.2.5 Statistical analysis

From the results of equation 6 we used step-wise regression analysis to determine if the contribution was related to relevant physical aspects of the nine sites. For this analysis we only used the mixing model results at 0 m on the transect as this was comparable across all three sites. Contributions from terrestrial, mangrove and seagrass to SPM and trap samples were correlated with physical attributes of each site. The mangrove contribution was tested against area of mangrove forest (m^2), area of bay (m^2), urbanisation in the catchment area (%), ratio of width and length of bay and width of mangrove forest (m). Terrestrial contribution was analysed against catchment area (m^2), area of bay (m^2), urbanisation in the catchment area (%), ratio of width and length of bay. Finally seagrass was tested with area of the seagrass bed (m^2), area of bay (m^2), urbanisation in the catchment area (%), ratio of width and length of bay.

The surface area of the mangrove forests and seagrass beds was determined during the sampling campaign. Land use in the catchment area, width and length of the bay was determined by analysing Quickbird, WorldView-1 and WorldView-2 satellite imagery. All statistical analysis was completed in R (R Core Team, 2012), where probabilities (p) were expressed at $p > 0.05$ and are referred in the text as a significant result.

2.3 Results

In the isotope plot of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (Fig. 2), almost all samples (trap and SPM) were between oceanic, terrestrial, mangrove and seagrass plant end-members. We consider that the three trap samples that fell out of the triangle indicate that these contained POM that had undergone substantial processing and degradation that had altered the CN and stable isotope ratios (see Discussion below). Interestingly, all trap samples along the gradient showed different sources of organic material (Fig. 2). At site A, the majority of trap samples were between terrestrial, mangrove and oceanic sources, with some influence from seagrass (Fig. 2). The trap samples from Site B centred in the middle of the triangle. Apart from a substantial contribution from mangrove trees at 0-100 m a greater influence from oceanic and seagrass plant sources could be seen (Fig. 2 & Tab. 3).

Suspended sediment samples showed similar patterns to trap samples, but with a stronger contribution from the oceanic end member (Fig. 2). Trap samples from site C were located equidistantly between the terrestrial and seagrass plant end members but with a slight increase in $\delta^{15}\text{N}$ values indicating an inclination towards the oceanic source (Fig. 2).

The mixing model determined the fraction of each source end-member (mangrove & seagrass plants, terrestrial & oceanic) in the mean of 2-3 individual sediment traps and SPM samples for the three sites (Tab. 3). Site A showed little variation in suspended

Table 3 End member contributions of each source (terrestrial, mangrove, seagrass and oceanic) to each sediment sample (SPM & trap) calculated from the mixing model. Distance (m) represents the distance along the transect from land (0 m) to the ocean for each site (A, B & C). SPM and trap are sample type, SPM is suspended particulate matter taken from the water column. Whilst trap represents sediment samples captured on the sediment floor over a 48 hour period. (ns) means that the model did not find a solution. (^) represents sediment traps located in seagrass beds.

Site	Sample	Distance (m)	0	50	100	200	300	400	500	1000	1500
		Source	Contribution (%)								
A	SPM	Mangrove		2	0.3		1	0.2			
		Oceanic	66	86	90		83	85			
		Terrestrial	12	7	5		12	4			
		Seagrass	5	4	4		4	10			
	Trap	Mangrove	15	13	6^		46^	24^			
		Oceanic	67	71	79^		35^	52^			
		Terrestrial	7	7	9^		13^	17^			
		Seagrass	11	10	6^		6^	7^			
B	SPM	Mangrove	1	6	9	11	7	15	22	15	ns
		Oceanic	69	58	53	55	75	71	67	74	ns
		Terrestrial	23	25	24	20	7	4	3	1	ns
		Seagrass	8	11	13	13	11	10	8	10	ns
	Trap	Mangrove	20	ns	20	ns	ns^	ns^	16^	8^	7
		Oceanic	48	ns	22	ns	ns^	ns^	31^	58^	40
		Terrestrial	17	ns	34	ns	ns^	ns^	29^	19^	34
		Seagrass	15	ns	23	ns	ns^	ns^	24^	15^	19
C	SPM	Mangrove	6	4	5	1	6	ns	4	0	NA
		Oceanic	69	77	71	72	72	ns	76	82	NA
		Terrestrial	14	11	11	14	10	ns	13	10	NA
		Seagrass	11	8	13	13	13	ns	7	7	NA
	Trap	Mangrove	22	ns	9	10	3	4^	2^	3^	NA
		Oceanic	59	ns	68	62	71	72^	84^	78^	NA
		Terrestrial	6	ns	10	12	15	8^	5^	8^	NA
		Seagrass	13	ns	13	16	11	17^	9^	12^	NA

particulate matter source contributions. The samples were predominantly oceanic (66-90 %) for all distances (0-400 m) (Tab. 3). Mangrove and terrestrial plants showed the highest contribution to SPM at the coast (0 m); 17 and 12 % respectively (Tab. 3). A low but consistent contribution from seagrass sources, in the order of 5 %, was inferred. For suspended sediment samples in site B, oceanic sources still showed the strongest influence (53-75 %). There was no clear pattern of contribution from mangroves (1-22 %), whilst for seagrass, values remained comparatively low (8-13 %) for SPM (Tab. 3). The contribution of terrestrial sources decreased in SPM from the coast (23 % at 0 m) to the ocean (1 % at 1500 m). The influence of the terrestrial sources for SPM along the transect at site C did not show the same decreasing trend with distance from the coast as at site B. Terrestrial contributions varied between 10-14 % along the gradient (Tab. 3). A similar fluctuation without a clear

trend with distance is shown by the mangrove contribution (0-6 %) and seagrass plants (8-13 %). Oceanic input dominated along the entire gradient (69-82 %) (Tab. 3). The trap samples in site A showed spatial patterns that were unrelated to distance from the source (Tab. 4).

Table 4 Dimensionless index indicating the relative contribution of terrestrial, mangrove and seagrass sources for SPM and trap sediment samples (SPM & trap). This was calculated from dividing the mixing model contribution result (Tab. 3) with the per cent of total surface area occupied by the particular ecosystem at the sites A, B & C. Distance (m) represents the distance along the length of the transect from the land (0 m) to the ocean for each site (A, B & C). SPM and trap are sample type, SPM is suspended particulate matter taken from the water column. Whilst trap represents sediment samples captured on the sediment floor over a 48 hour period. (ns) equates to the model not solving for these points. (^) represents sediment traps located in seagrass beds. MF= mangrove forest, SB= seagrass bed and CA = catchment area.

Site	Area of ecosystem (km ²)	Sample	Distance (m)	0	50	100	200	300	400	500	1000	1500
			Source	Contribution (%)								
A	MF: 3.3 CA: 26.3 SB: 0.5	SPM	Mangrove	2	0.2	0.03 [^]		0.06 [^]	0.02 [^]			
			Terrestrial	0.1	0.1	0.1 [^]		0.1 [^]	0.05 [^]			
			Seagrass	3	3	3 [^]		3 [^]	7 [^]			
		Trap	Mangrove	1	1	1 [^]		5 [^]	2 [^]			
			Terrestrial	0.1	0.1	0.1 [^]		0.1 [^]	0.2 [^]			
			Seagrass	7	6	4 [^]		4 [^]	4 [^]			
B	MF: 2.1 CA: 7.5 SB: 0.9	SPM	Mangrove	0.03	0.3	0.5 [^]	0.6 [^]	0.4 [^]	0.8 [^]	1 [^]	0.8 [^]	ns
			Terrestrial	0.3	0.3	0.3 [^]	0.3 [^]	0.1 [^]	0.1 [^]	0.04 [^]	0.02 [^]	ns
			Seagrass	1	2	2 [^]	2 [^]	1 [^]	1 [^]	1 [^]	1 [^]	ns
		Trap	Mangrove	1	ns	1 [^]	ns [^]	ns [^]	ns [^]	0.8 [^]	0.4 [^]	0.4
			Terrestrial	0.2	ns	0.5 [^]	ns [^]	ns [^]	ns [^]	0.4 [^]	0.3 [^]	0.4
			Seagrass	2	ns	3 [^]	ns [^]	ns [^]	ns [^]	3 [^]	2 [^]	3
C	MF: 0.4 CA: 7.2 SB: 0.8	SPM	Mangrove	1	0.5	1	0.1	1		1 [^]	0.1 [^]	
			Terrestrial	0.2	0.1	0.1	0.2	0.1		0.2 [^]	0.1 [^]	
			Seagrass	1	1	1	1	1		1 [^]	1 [^]	
		Trap	Mangrove	3	ns	1	1	0.4	0.5	0.2 [^]	0.3 [^]	
			Terrestrial	0.1	ns	0.1	0.1	0.2	0.1	0.1 [^]	0.1 [^]	
			Seagrass	1	ns	1	1	1	1	1 [^]	1 [^]	

The oceanic contribution dominated in most samples (mean 54%). In the range 300-400 m there was a relatively large mangrove contribution. Overall mangroves had the second strongest influence (mean 23%) followed by terrestrial contributions (mean 14%) and lastly seagrass plants (mean 8%) (Tab. 3). The oceanic (22-58 %) signal in trap samples of site B was weaker than in trap samples of the other sites. It did not vary clearly with distance. Seagrass plants (15-24 %) and terrestrial (17 -34 %) had similar contributions to the trap samples in site B (Tab. 3), whilst mangrove forest influence decreased away from the forest (20 % at 0 m to 7 % at 1500 m). The trap samples of site B had the most equal distribution over sources of the three sites. Mangrove forest at site C showed a strong contribution at 0

m (22 %) decreasing towards the ocean at 1000 m (3%) (Tab. 3). Terrestrial sources showed no clear pattern in contribution in relation to distance from shore 0 m (6 %) to ocean 1500 m (8 %) (Tab. 3). Seagrass plants at site C showed a steady influence through the length of the transect (9-16 %) (Tab. 3). Oceanic sources were responsible for about three quarters of the material.

The majority of SPM and trap samples (~70 %) contribution from seagrass plants in sites A and B showed an over contribution compared to the seagrass bed sizes (Tab. 4). In site C, seagrass plants contributions, were comparable to the surface area of the ecosystem both for SPM and trap samples (Tab. 4). A high quantity of mangrove forests (60 %) showed a lower contribution to the SPM and trap samples (sites A, B and C) comparative to the forest surface area, whilst 30 % showed a contribution relative to the size of the forest, the remaining indicated a over contribution (Tab. 4). The terrestrial source across sites A, B and C for SPM and trap samples were all under contributing compared to the area of the source (Tab. 4).

Step-wise regression found no relationship between terrestrial contributions and associated physical attributes of the sites (catchment area, urbanisation within the catchment area, ratio of width and length of the bay and bay area) for SPM and trap samples ($p > 0.05$; Tab. 5). Seagrass contribution showed a negative correlation with larger areas of the seagrass bed for trap samples ($y = 16 - 17x$: $R^2 = 0.5$), no relationship was seen for seagrass contribution (SPM and trap samples) and other physical variables ($p > 0.05$; Tab. 5). Mangrove trap sample contributions showed no correlation with area of mangrove forest, area of bay, percentage of urbanisation in the catchment area, ratio of width and length of bay and width of mangrove forest ($p > 0.05$; Tab. 5). Suspended sediment samples for mangrove contribution did show a positive relationship with width of mangrove forest ($y = -0.9 + 0.9x$: $R^2 = 0.8$), but no other relationship was seen for SPM samples and physical variables from mangroves.

2.4 Discussion

This study was designed to clarify the origin and exchange of organic material within tropical bays using chemical tracers. Despite the high local primary production in mangrove and seagrass stands, we found that oceanic sources dominated trap and SPM samples along the entire transects. The mixing model showed that mangrove forests and terrestrial sources had major contributions especially to trap samples. Seagrass meadows, although occupying the smallest area of all the potential sources, also had a substantial contribution to organic material in the majority of trap and SPM samples.

Table 5 Showing physical variables of all sites, which were used, in step-wise regression statistical analysis. The site letters in *italics* and **bold** data are shown in this paper (Fig. 2 & Tab. 4), whilst the others (non-*italics* and non-**bold**) are indicated in the supplementary material (Fig. S2 & Tab. S1). CA equates to catchment area. Site B and C were located along a exposed coast and therefore did not have any bay areas which could be used in the analysis.

Sample Type	Site	Physical attributes						
		Area of mangrove forest	Area of catchment	Area of seagrass bed	Width of bay	Length of bay	Ratio width:length	Urbanisation in catchment
		km ²	km ²	km ²	km	km		%
SPM	A	3	30	1	1	1.5	0.7	5
	<i>A</i>	3.3	29.6	0.5	1	1.5	0.7	5
	B	10	3	0.1	na	na	na	40
	C	0.6	0.2	0.3	na	na	na	21
	D	7.5	0.6	0.8	1.8	1.1	1.6	4
	E	3.2	0.7	0.04	1.4	0.7	2	4
	F	1.5	12.3	0.8	3.8	3.3	1.1	5
	<i>B</i>	9	2.1	0.9	1.2	2.9	0.4	7
	<i>C</i>	4.7	0.4	0.8	2	1.1	1.9	70
Trap	A	3	30	1	1	1.5	0.7	5
	<i>A</i>	3.3	29.6	0.5	1	1.5	0.7	5
	B	10	3	0.1	na	na	na	40
	C	0.6	0.2	0.3	na	na	na	21
	D	7.5	0.6	0.8	1.8	1.1	1.6	4
	E	3.2	0.7	0.04	1.4	0.7	2	4
	F	1.5	12.3	0.8	3.8	3.3	1.1	5
	<i>B</i>	9	2.1	0.9	1.2	2.9	0.4	7
	<i>C</i>	4.7	0.4	0.8	2	1.1	1.9	70

2.4.1 Mixing model

Mixing models are often used to estimate contributions to a mixture (Phillips & Gregg 2001, Phillips & Koch 2002). Some of the samples could not be solved with this model which indicates that they violate some of the implicit assumption of the linear mixing model formulation, such as imprecise measurement of the end-members' values, the existence of unidentified sources, or degradation processes that have altered the isotope or CN ratios of the mixture. For our study site, we are confident that we included the dominant POM sources

in our design and these end-members were very consistent and were estimated with a very low uncertainty (Tab. 2). We therefore believe that the few samples that fell outside the mixing polygons (Fig. 2) had already undergone substantial biogeochemical modification, which can lead to a decrease of $\delta^{15}\text{N}$ values and/or N contents through mineralization and denitrification (Cline & Kaplan 1975, Kuramoto & Minagawa 2001). We think that the trap samples that fell out of the polygon contained predominantly re-suspended bottom sediment (not unlikely given the close proximity to the sediment) due to hydrodynamic processes. Re-suspended bottom sediment is a potential source of material caught in the trap that had been subjected to biogeochemical modification.

There was a strong oceanic signal in the trap samples for the three sites suggesting that oceanic derived organic material must also be settling out (Fig. 2). The influence of oceanic source in the SPM and trap samples, indicating a substantial POM oceanic input in agreement with previously studies (Dittmar & Lara 2001, Hunsinger et al. 2010). The fact that the ocean shows any contribution to the organic material within the bays indicates that industries such as offshore fish farms or similar may have an impact (both positive and negative) on nutrient availability with the water column. The organic matter of the trap samples at Site A and B showed a strong contribution from terrestrial and mangrove sources. These sites have large channels coming from the inner terrestrial and mangrove area, which may explain the increased contribution of terrestrial and mangrove organic matter. Sites B & C trap samples within the seagrass bed show an inclination towards the seagrass plant end-member and this indicates that the seagrass canopy trap seagrass organic material (Evrard et al. 2005, Vonk et al. 2008b, Van Engeland et al. 2011).

2.4.2 *Landscape patterns of organic material fluxes*

Suspended particulate material (SPM) was dominated by the oceanic source (Tab. 3). Our data indicate that nitrogen and carbon from oceanic sources may be an important POM source in the water column. Although terrestrial and mangrove plant sources contributed to SPM samples, we found that in terms of particulate organic matter in the water column, the ocean was a dominant source. The oceanic, terrestrial and mangrove plant sources influenced trap samples, but the oceanic did not dominate the contributions as much as in the SPM samples. Mangrove and terrestrial plants showed the next strongest influence to trap samples supporting the outwelling theory that mangrove-derived nutrients support adjacent ecosystems and food webs (Odum 1968, Lee 1995).

Interestingly mangrove contribution did not correlate with the size of the mangrove forest but correlated positively with the frontal width of the mangrove forest. This indicates that the export of mangrove detritus may partly be controlled by the exposure of the trees to hydrodynamics (waves and tidal exchanges), thus more trees with direct contact to the ocean

will show a forest with a higher contribution. In fact no other physical parameters showed a correlation with any terrestrial or mangrove contribution. As no relationships were found, we assume that there is another controlling factor that has not been measured at the present time. Past research have found that the presence of waves can increase the movement of POM through mimic mangrove roots and seagrass beds (Gillis et al. 2014b), other hydrodynamics in-situ could be also be an important factor and a future research perspective.

If one compares the potential amount of influx of organic material sources in relation to their relative size, seagrass is a much more important relative source than mangrove forest (Tab. 4). In addition seagrass beds with smaller areas contributed significantly more than larger seagrass beds, which indicates that small beds can also have an important influence. There was a remarkably similar pattern where terrestrial and mangrove samples were within a small range between sites. Considering the 9 other sites, we calculated the source contribution for trap and SPM samples per area (catchment, mangrove forest, seagrass bed) for each site (Fig. 3).

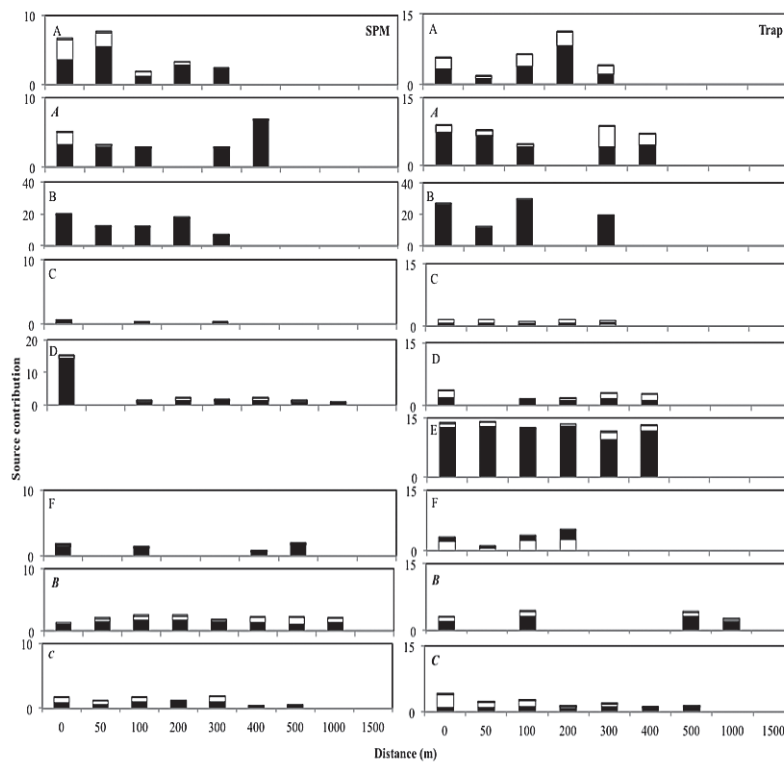


Figure 3 Map showing distance along transect (m) and mean contributions of source material from mangrove forest and seagrasses beds for suspended sediment samples and sediment traps. Each chart represents a site location, see letter at top left hand side of chart (Fig. 1 & Fig. S1). The site letters in italics and bold data are shown in this paper (Fig. 2 & Tab. 4), whilst the others (non-italics and non-bold) are indicated in the supplementary material (Fig. S2 & Tab. S1). Black areas represent seagrass beds, white and grey areas symbolise mangrove forests and terrestrial sources respectively.

This allows us to obtain an estimation of the variability of the contributions among sites (Fig. 3). For suspended sediment and trap material the sites A, B & C followed a very similar pattern to the other 6 sites, where seagrass derived POM source over contributed (mean trap: 5 & SPM: 3) compared to mangrove (mean trap: 1 & SPM: 1) and terrestrial (mean trap: 0.2 & SPM: 0.1) sources (Fig. 3).

2.5 Future perspective and management implications.

We have shown that seagrass beds are a comparatively large source of POM for adjacent ecosystems. A decrease in the size or productivity of the ecosystem could have implications for the seagrass beds' role as a nutrient source for other ecosystems and organisms. Natural impacts such as strong wave action, storms or hurricanes could cause major uprooting of the plants thus reducing the size and productivity of the beds (van der Heide et al. 2007, Infantes et al. 2009). In addition nutrient enrichment or increased turbidity from changes in catchment area surrounding coastal areas where seagrasses are located can also cause physiological problems which can reduce the area and biomass of the ecosystem (Todd et al. 2010). These alterations in the integrity of the system could also have consequence on their ecosystem function as a nutrient sink or buffer for excess nutrients for sensitive adjacent ecosystems such as coral reefs. Therefore a key role in management of these areas is to ensure the health and physical/physiological structure of seagrass beds; these two factors can be related to quantities of POM being trapped and outwelled (Burkholder et al. 2007, Perez et al. 2007). We monitored nine sites and in all sites seagrass beds showed an over contribution to POM in trap samples (> 1), even sites with minor seagrass beds (smallest site 0.08 km²).

Mangrove forests were not found to be as an important input for organic material compared to oceanic influence or seagrass material. Furthermore, recent research has found that mangrove forest may be an effective POM trap and therefore a strong nutrient sink (Gillis et al. 2014b). For this reason the integrity of the forest should always be ensured, as further work is required to understand how their role of trapping fits within the tropical coastal seascape. Importantly this study provides further evidence that connective particulate fluxes, which occur between environments in the tropical coastal seascape, do exist. The existence of these connections is important and could have implications for strengthening management especially from an ecosystem-based perspective.

2.6 Supplementary Material

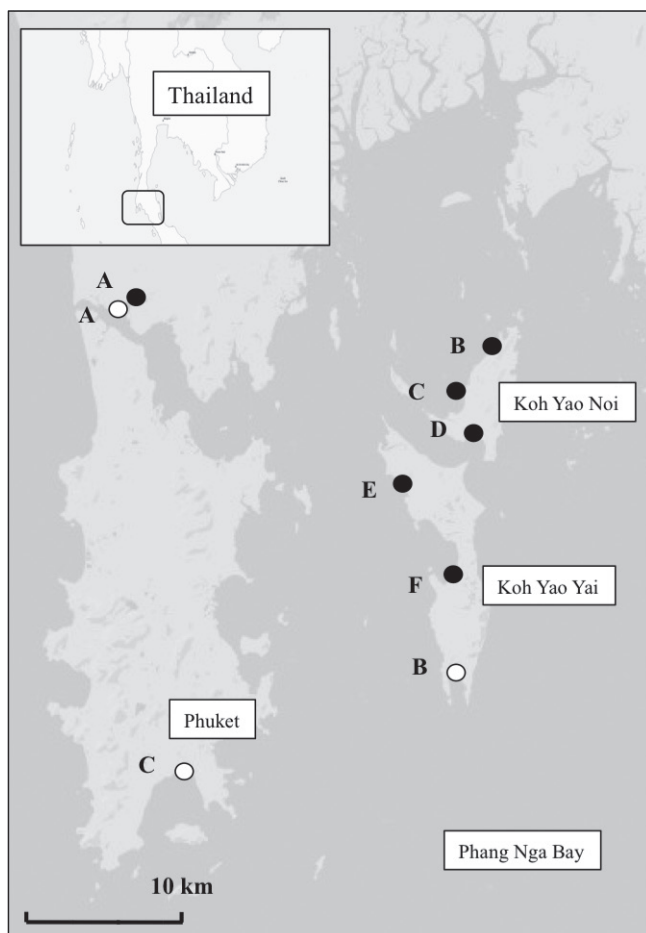


Figure S1 Map showing location of the nine sampling sites (black circles) in Phang Ngu bay, Southern Thailand. Red filled points (A, B & C) data is shown in the paper (Figs. 3 & Tab. 3). Black filled circles are the sites which are generalised in the paper and the data are presented below (Figure S2 & Table S1).

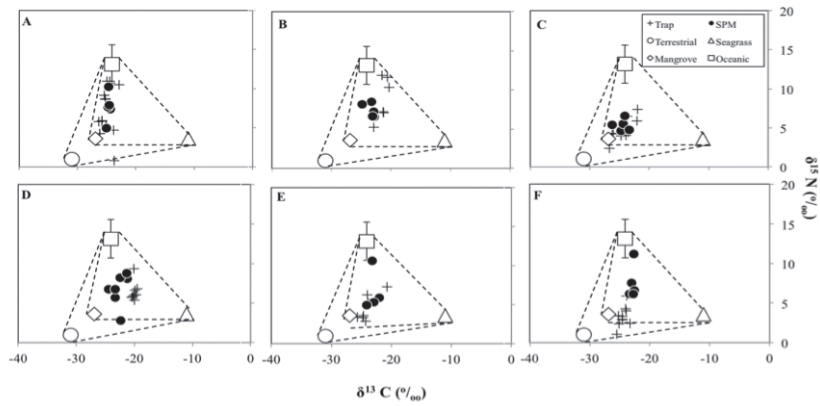


Figure S2 Carbon ($\delta^{13}\text{C}$ ‰) and nitrogen ($\delta^{15}\text{N}$ ‰) isotopic composition for organic matter from trap and SPM samples from the five sites A, B, C, D, E & F. The end members shown are as follows white circles is the terrestrial value, white square represents oceanic sources, white triangle symbolises the seagrass plant end-number and white diamond is the mangrove plant values. The trap and SPM samples are represented by crosses and black circles respectively. Values for the end members are means ($\pm$ SE). For the end members of the oceanic, terrestrial, seagrass plants and mangrove plants sources, $n = 6, 9, 44$ & 45 respectively.

Table S1 End member contributions of each source (terrestrial, mangrove, seagrass and oceanic) to each sediment sample (SPM & trap) calculated from the mixing model. Distance (m) represents the distance along the length of the transect from the land (0 m) to the ocean for each site. SPM and trap are sample type, SPM is suspended particulate matter taken from the water column. Whilst trap represents sediment samples captured on the sediment floor over a 48 hour period. (ns) equates to the model not finding a solution for these points.

Site	Sample Type	Distance (m)	0	50	100	200	300	400	500	1000
Source Contributions										
A	SPM	Mangrove	3	2	0.6	0.3	0.2			
		Terrestrial	0.2	0.2	0.04	0.2	0.1			
		Seagrass	4	5	1	3	2			
	Trap	Mangrove	2	0.7	3	3	2			
		Terrestrial	0.1	0.03	0.1	0.2	0.1			
		Seagrass	3	1	4	8	2			
B	SPM	Mangrove	1	0	0.1	0.5	1			
		Terrestrial	0.1	0.1	0.2	0.1	0.1			
		Seagrass	19	12	12	17	6			
	Trap	Mangrove	1	0.04	1		0.2			
		Terrestrial	0.2	0.03	0.3		0.1			
		Seagrass	26	12	29		19			
C	SPM	Mangrove	0.03		0.01		0.02			
		Terrestrial	0.3		0.2		0.2			
		Seagrass	0.3		0.2		0.1			
	Trap	Mangrove	1.0	0.9	0.4	0.9	0.4			
		Terrestrial	0.4	0.4	0.4	0.4	0.6			
		Seagrass	0.2	0.3	0.4	0.3	0.5			
D	SPM	Mangrove	1		1	1	0.1	0.8	0.5	0
		Terrestrial	0.2		0.1	0.1	0.2	0.1	0.2	0.1
		Seagrass	14		1	1	1	1	0.8	0.8
	Trap	Mangrove	2		0	0	1	1		
		Terrestrial	0.1		0.2	0.2	0.1	0.2		
		Seagrass	2		1	1	2	1		
E	SPM	Mangrove	0.01							
		Terrestrial	0.05							
		Seagrass	2							
	Trap	Mangrove	1	1	0.1	0.2	2	1		
		Terrestrial	0.4	0.2	0.1	0.5	0.3	0.2		
		Seagrass	13	13	12	13	9	12		
F	SPM	Mangrove	0.1	ns	0.2	ns	ns	0.1	0.1	
		Terrestrial	0.2	ns	0.1	ns	ns	0.02	0.2	
		Seagrass	1	ns	1	ns	ns	1	2	
	Trap	Mangrove	2	0.7	2	3	ns	ns	ns	
		Terrestrial	0.1	0.03	0.1	0.2	ns	ns	ns	
		Seagrass	0.9	0.3	1	2	ns	ns	ns	

Chapter 3

Toward understanding the roles of mangrove and seagrass particulate matter as a nitrogen source in tropical coastal ecosystems.

L.G. Gillis, A.D. Ziegler, C. Cathalot, W. Kiswara, P.M.J. Herman and T.J. Bouma.

STATUS: Submitted.



Abstract

The location of tropical mangrove forests and seagrass beds along coastlines and shallow water areas enables them both to receive and outwell particulate organic matter (POM), as well as inorganic and organic nitrogen in dissolved forms. Little is known about the potential importance of POM transfer between mangrove forests and seagrass beds as a nutrient source. Transportation experiments using both mangrove and seagrass leaves showed that the mangrove leaves were the dominant POM source exported to seagrass beds, but there was little difference between the export of seagrass or mangrove leaves to the ocean. Incubations showed that dissolved organic nitrogen came primarily from seagrass leaves. Mangrove and seagrass leaves had different degradation patterns independent of the location of the degradation. The slower degradation of mangrove leaves could potentially mean that they may transport nutrients over longer distances than seagrass leaves, which degrade rapidly. Because of the fast seagrass leaf degradation and resultant dissolved organic nitrogen release, seagrass leaves are likely to recycle within the bed and may not be an important nitrogen source for other ecosystems. Results overall, indicate that under normal conditions, seagrass beds compared with mangrove forests retain most of their nutrients, rather than exporting them to adjacent nutrient-sensitive ecosystems such as coral reefs.

Key words: mangrove forests, seagrass beds, particulate organic material, nitrogen, nutrients, connectivity

3.1 Introduction

In nutrient-limited conditions (Hearn et al. 2001, Lee et al. 2007), particulate organic matter originating from adjacent ecosystems may form an important source of nutrients for keystone organisms, such as stony corals and seagrass plants, and their associated species (Alongi 1990, Lee & Dunton 1999, Granek et al. 2009). Given the large standing biomass and high productivity of mangrove forests and seagrass beds, POM originating from leaves could be an important nutrient source to adjacent ecosystems (Lee 1995, Hemminga et al. 1999). In this respect mangrove and seagrass leaves may provide positive interactions with adjacent ecosystems at the tropical seascape scale, but experimental evidence is very limited to date.

Mangrove nutrient recycling is thought to occur predominantly *in situ* within the forest, with unused nutrients exported to coastal waters, in part via leaves and other types of POM (Boto & Wellington 1988, Ewel et al. 1998, Adame & Lovelock 2011). Decaying leaves release both organic and inorganic forms of dissolved nitrogen. Leaves are also utilized by organisms, such as crabs that process nitrogen to more palatable forms that can be used by other organisms (Lee 1995, Kristensen et al. 2008). Mangroves growing in nutrient-rich conditions may therefore export considerable amounts of nutrients in their leaves.

Seagrass beds typically have high productivity, even within nutrient-poor environments (Hemminga et al. 1999, Touchette & Burkholder 2000). One explanation for the ability to flourish in such conditions is internal recycling of nutrients released by senescent leaves or those shed by hydrodynamic forces—provided that degradation starts before leaves are exported from the beds (Hemminga et al. 1999, Koch & Verduin 2001, Infantes et al. 2009). Alternatively, some of the nutrients may come from the import of POM from adjacent sources, including mangroves.

Previous studies have focused on the importance of leaves as a nitrogen and carbon source mainly through incubation degradation experiments (Kristensen et al. 1998, Holmer et al. 1999, Kristensen et al. 2000, Holmer et al. 2001) but they did not account for transport processes. Bouillon et al. (2007) investigated the transfer of organic material between mangrove forests and seagrass beds, but did not look at re-mineralization of processes. As far as we are aware, no study has tried to combine both components: transportation and re-mineralization of POM. To understand the potential role of POM originating from mangrove forests and seagrass beds as nitrogen sources for adjacent ecosystems, one must both understand the rates of tidal export of POM from mangroves and seagrasses. As well as nutrient release rates from degrading leaves and how this depends on the location where the degradation occurs i.e. in the sediment or while in suspension in the water column.

Our aim is to determine the process rates that are needed for understanding nutrient exchange via POM transport between mangrove and seagrass. We address the following questions: 1) To what extent are mangrove & seagrass leaves exchanged between both

ecosystems under normal tidal conditions; 2) What is the rate of degradation of mangrove and seagrass leaves depending on the location degradation takes place; (3) How do C:N ratios change with degradation; (4) Do mangrove/seagrass leaves efflux dissolved organic and inorganic nitrogen in different ways; (5) How much nitrogen exchange may potentially occur between mangrove forests and seagrass beds as a result of the interchange of particulate organic matter; and (6) Is the nutrient donation of mangrove POM sufficient to meet nitrogen demand for seagrass beds to persist. These questions are addressed through a series of field- and lab-based experiments.

3.2 Study Area

The study site for all field-based experiments was located in Koh Chong Lat Noi bay, on the island of Yao Yai, in Pang Nga Province in Southern Thailand ($7^{\circ}54'28.26''\text{N}$, $98^{\circ}35'12.47''\text{E}$) (Fig. 1). The mangrove forest area was 2,093,775 m^2 and seagrass bed was 960,000 m^2 . The forest received no river discharge; and we assume the only fresh water it received was from rainfall or land run-off (Fig. 1).



Figure 1 Study site for shallow water environments on the island of Yao Yai, Phang Nga bay, southwest coast of Thailand (inset). The white area shows the extent of the mangrove forest (grey lines are channels); and the black area indicates the seagrass bed. Black rectangles indicate the location of the POM flux nets, the dashed line indicates the side of the nets POM were collected from. The dark grey lines refer to the widths of the mangrove forest (900 m) and the seagrass beds (landward 560 m and seaward 680 m) used in Equation 1. The black arrow indicates the direction of the water at flood tide.

The mangrove forest has two longitudinal tidal creeks, one of 2.6 km and another smaller creek of 0.8 km. Tidal range in the area varies from 1 m at neap tide to 3 m at spring tide. The direction of the current is from south to north, during spring low tide the whole seagrass bed is exposed. Incubation experiments were completed in the marine research station, also

located on the island. Seagrass and mangrove leaves, sediment and water for the degradation and incubation experiments were taken from Chong Lat Noi bay during July 2011. Mean water temperature during sampling was 27-30°C and salinity was 28-33 ppt.

We compared degradation rates in three habitat types: (1) the edge of the mangrove forest (MF); (2) the tidal flat (TF) at approximately 300 m from the mangrove forest; and (3) the seagrass bed (SB) located approximately 600 m from the mangrove forest (Fig. 1). The mangrove forest was composed of fringing *Rhizophora sp.*, *Ceriops sp.* and *Xylocarpus sp.* The seagrass beds comprised *Enhalus sp.*, *Halodule sp.*, *Halophila sp.* and *Thalassia sp.* with *Enhalus sp.* being the climax species with highest biomass. For the experiments we used leaves from *Rhizophora sp.* and *Enhalus sp.* The seagrass, tidal flat and fringing mangrove were exposed at low tide for 1-4 hours.

3.3 Methods

3.3.1 Incubations to measure release rates of dissolved nitrogen from seagrass and mangrove leaves

Sediment and mangrove/seagrass leaf samples were collected at low tide. Care was taken to pick leaf samples with similar length (mangrove leaves: 0.1 m, seagrass leaves: 0.45 m) and physical state (whole green leaves with no imperfections in the leaf structure). Water samples were collected in the bay at high tide and transported to the marine laboratory in an icebox. Salinity and temperature were recorded during sampling. Water samples were filtered to remove large particles (> 2 mm). Three dark-incubations with mangrove leaves were completed in parallel over a 24-hour period. The first incubation contained only seawater collected at the mangrove site (control treatment); the second, mangrove sediment plus seawater (sediment treatment); and the third, fresh mangrove leaves with sediment and seawater from mangroves (leaves treatment). Three replicate experiments on all treatments were performed.

Samples were incubated in the dark in 19.2-L chambers (radius: 0.1 m, height: 0.3 m). For the sediment and leaf treatments, a 0.1 m thick sediment layer was placed on the bottom and 12.9 L of seawater was added. The temperature was kept constant by placing the chambers in a water bath in which the temperature was maintained manually. Temperature (27-30 °C) and salinity (28-33 ppt) were held within narrow ranges that corresponded with the sampling conditions. A magnetic stirrer was used to maintain water flow during the 24-hour incubations. Water samples (25 ml) were taken every 6 hours (at 0, 6, 12, 18, 24 hours) and temperature and salinity were recorded at the times of sampling. The water in the incubation chamber was replaced by seawater from the site that had been kept at the sample temperature and salinity. Samples were immediately frozen for analysis at a later date. After transporting to Royal Netherlands Institute for Sea Research (NIOZ), the samples were analyzed for dissolved

organic and inorganic nitrogen (DON & DIN). For determining seagrass release of DON and DIN, we followed the same protocol described above for mangroves. Nitrogen release from mangroves or seagrass leaves was calculated as the difference of DON and DIN contents of the sediment treatment (seawater + sediment incubation) from those of the leaf treatment (leaves + sediment + seawater incubation).

3.3.2 *Transportation rate of seagrass and mangrove leaves - field experiment*

We estimated the residence time of mangrove and seagrass leaves deposited on the sediment within the mangrove forest (MF), tidal flat (TF) and seagrass bed (SB). In each of these habitat types, five marked (florescent paint) mangrove and seagrass leaf replicates were placed at low tide at edge (< 10 m from the ocean) and interior (100 m from the ocean) locations within a 1 m² quadrat area. The sites were monitored every tidal cycle to determine the time it takes until the leaves were transported from their initial locations.

We measured the import/export rates of leaf particles from each ecosystem with 50 (length) x 1 (height) m nets, mesh size 0.05 m, stretched across the seaward edge of the mangrove forest (net 1 in Fig. 1), the landward edge of the seagrass bed (net 2 in Fig. 1), and the seaward edge of the seagrass bed (net 3 in Fig. 1). We collected particulate matter over five consecutive low tidal cycles, separating the mangrove and seagrass leaves. Leaf material was only collected from the sides of the net facing the ecosystem (dashed red lines: Fig. 1) to ensure we only collected material exported from the mangrove forest or seagrass bed. Dry mass (g) was determined after drying for at least 48 hours at 60 °C.

Particulate organic material transportation rate per unit area of each ecosystem ($POM_{transport}$; mg m⁻² day⁻¹) was estimated following equation 1:

$$POM_{transport} = 2 \times POM_{net} \times (L_{eco}/L_{net}) / A_{eco} \quad (1)$$

where POM_{net} (mg tide⁻¹) is the total POM captured in the 50 m long net during one tidal cycle; L_{net} is the length of the net (50 m) and L_{eco} the total length of the fringe edge of the ecosystem which is donating the POM (~900 m for mangrove, 560 m for shoreward seagrass bed, 680 m for seaward seagrass bed); A_{eco} (m²) is the surface area of the entire donating ecosystem (mangrove forest 2,093,775 m² and seagrass bed 960,000 m²); and the constant 2 converts the transportation rate from per tide to per day.

We subsequently calculated the total nitrogen exported per unit area ($TN_{transport}$; μ mole m⁻² day⁻¹) as:

$$TN_{transport} = POM_{transport} * TN_{leaf} \quad (2)$$

where TN_{leaf} (%) is the total leaf N determined from the fresh mangrove/seagrass leaves used in the degradation experiments (see section 3.3). Collectively, these calculations provide a rough estimate of POM exchanged between ecosystems and the ocean, as we assume all trapped leaves contribute to the total POM exported/imported.

3.3.3 *In situ seagrass and mangrove leaf degradation experiment*

Fresh seagrass (*Enhalus sp.*) and mangrove (*Rhizophora sp.*) leaves of similar length (mangrove leaves: 0.1 m, seagrass leaves: 0.45 m) and physical state (whole green leaves with no imperfections in the leaf structure) were used in the degradation experiments. Leaves were collected at low tide and epiphytes were removed. Subsequently, leaves were separated into 180 groups; 90 for seagrass and mangrove (approximately 10 g wet weight each). Each group was then placed into a net bag of mesh size < 0.5 mm that allowed for small organisms to migrate in and out, but dispelled larger marine animals such as crabs. Additional seagrass and mangrove leaf samples (3 replicates each) were used to determine initial wet mass (M_{wet}), dry mass (M_{dry}), and C:N ratios. At each habitat type (MF, TF, SB), three replicates 50 m apart were established, creating three parallel transects. At each replicate, sets of 5 poles were driven into the substrate. The poles supported two sets of bags, one with mangrove leaves, the other seagrass leaves. The bags were attached 0.05 m above the surface, and one buried 0.05 m in the sediment. We collected one set of randomly chosen bags after periods of 2, 4, 6, 20 and 30 days to determine the leaf degradation rates. Changes in C:N ratios were determined from bags collected on days 6, 20 and 30 days. Following collection, the samples were dried in an oven for 48 hours at 60°C. They were then weighed and placed in labeled sealed plastic bags for transportation to NIOZ, where they were further analyzed for C: N ratios.

3.3.4 *Nitrogen requirements of seagrass beds*

To quantify to what extent nitrogen in mangrove POM exported to seagrass ecosystems could provide the seagrass plants with their nitrogen needs, we made an approximate calculation of the nitrogen requirements of *Enhalus sp.* and *Halophila sp.* meadows (N_R ; μ mole m^{-2} day^{-1}) using equation 3:

$$N_R = TN_{leaf} * B/LT \quad (3)$$

where TN_{leaf} is the total leaf N content (μ mole g_{leaf}^{-1}), B is the standing biomass (g m^{-2}) and LT is the leaf turnover (days). Where TN_{leaf} (μ mole g_{leaf}^{-1}) for *Enhalus sp.* is the total leaf N determined from the seagrass leaves used in the degradation experiment (1143μ mole g_{leaf}^{-1}). For *Halophila sp.* we used total N leaf content data from Zakaria et al. (2001): $34-54 \mu$ mole g_{leaf}^{-1} . Standing biomass of the seagrass per m^2 was calculated by determining the above

ground weight of *Enhalus sp.* and *Halophila sp.* per m². The leaf turnover (LT; days) for *Enhalus sp.* is 100 days and for *Halophila sp.* 30 days (Hemminga & Duarte 2000).

3.3.5 Chemical analyses

Following drying, leaf samples were ground to ensure homogenization using a mixer mill (Retsch, type MM301). The C, N & C:N ratios in dried leaves were determined using a Flash EA 1112 Elemental Analyzer (Thermo Finnigan). Dissolved inorganic (NH_4^+ , NO_3^- & NO_2^-) nitrogen (DIN) accumulated in the incubation water was determined calorimetrically using a SK12 nutrient analyser, Skalar & Seal (Middelburg & Nieuwenhuize 2000). Total nitrogen (TN) was determined from a GFF filter (Whatman) after alkaline persulphate destruction using the same instrument for dissolved nutrient concentrations (Grasshoff et al. 1999). Dissolved organic nitrogen was calculated from the difference between dissolved organic nitrogen (DIN) and total nitrogen (TN).

3.3.6 Statistical analysis

Prior to testing, normality in the data was tested using a D'Agostino-Pearson test. Three-way analysis of variance (ANOVA) with replication was used to test for differences in the following: *i*) decomposition of detritus related to habitat type (MF, TF, SB) versus time period (2, 4, 6, 20 and 30 days) for each environment (sediment and water column); and *ii*) C:N ratios of mangrove and seagrass leaves between habitat type (MF, TF, SB) versus time period (2, 4, 6, 20 and 30 days) for each environment (sediment and water column). A repeated measures test was also used to compare nitrogen release from mangrove leaves (DIN & DON) and time in the incubations. The same test was used for seagrass leaves. Because the data were not normally distributed, the Kruskal-Wallis (K-W) test was used to compare changes in DIN & DON release from mangrove and seagrass leaves at 24 hours in the incubation, to prevent serial correlation we used the final concentrations of DIN & DON. We also used Kruskal-Wallis to test differences between mangrove and seagrass leaf export to other ecosystems and to the ocean. Least squares difference (LSD) post-hoc testing was performed following ANOVA. Probabilities (p) were expressed at $p < 0.01$ & 0.1 , and are referred to in the text as significant. All statistical testing was completed in an R programming platform (R Core Team 2012).

3.4 Results

3.4.1 Incubation experiment

There was low release of DIN from *Rhizophora sp.* leaves in the incubation experiments, as the concentration did not significantly differ from zero whilst *Enhalus sp.* showed slight

negative values (Fig. 2). In contrast, DON concentrations increased during 24-h of seagrass leaf decomposition, with the maximum reaching a mean $93 \mu \text{ mole DON g}^{-1}$. DON-release from decomposing mangrove leaves was negligible (Fig. 2). A significant (K-W test: $p = 0.04$) increase in DON release from seagrass leaves compared with mangrove leaves occurred after 24 hours (Fig. 2).

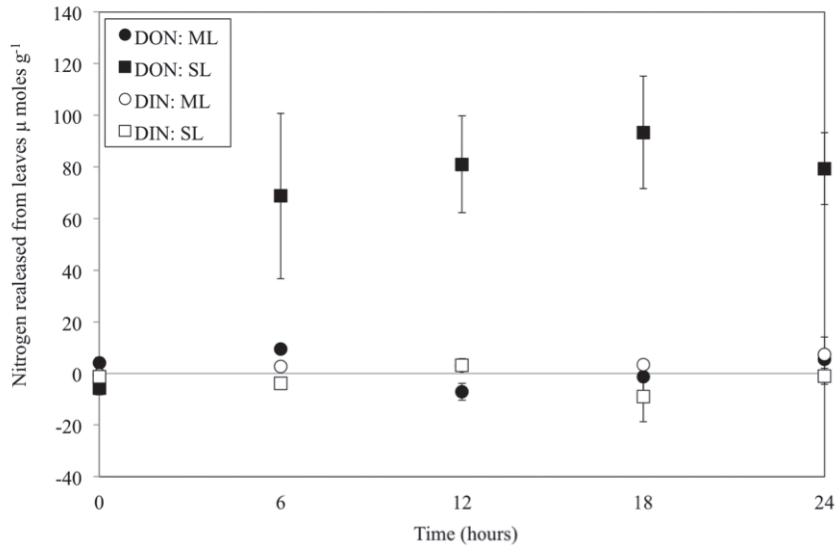


Figure 2 Incubations of fresh *Rhizophora sp.* leaves (circles) and *Enhalus sp.* leaves (squares). Shown are dissolved inorganic nitrogen (DIN) release (clear markers) and dissolved organic nitrogen (DON) release (filled markers) over 24 hours. Three-way ANOVA indicated seagrass DON concentrations varied over time ($p = 0.05$). The seagrass leaf DON response was significantly different from that for mangrove leaves (Kruskal-Wallis test: $p = 0.04$). Values are means $\pm$ on standard error of 3 replicates.

In addition, DON concentrations for seagrass increased significantly (repeated measures ANOVA: $p = 0.002$), then stabilized after 6 hours until the end of the experiment. Negative values indicate zero release and originate from the calculation of the nitrogen release from mangroves or seagrass leaves i.e. subtraction of the N values of the “seawater + sediment” incubation from the “leaves + sediment + seawater” incubation (Tab. SI).

3.4.2 POM and TN exchange calculations

All tagged leaves that were deposited at positions within the mangrove forest, tidal flat and seagrass bed were transported away from their original location within one tidal cycle (data not shown). However, it is not known if they were transported out of the system. Our flux measurements using nets across the bay indicated that the export of mangrove leaves moving into seagrass beds was significantly higher than the biomass of seagrass leaves moving inland toward the mangrove (K-W test, $p = 0.01$; nets 1 & 2; Fig. 3). The daily area-weighted mass of

mangrove leaves transported toward the seagrass beds ($3.7 \text{ mg m}^{-2} \text{ day}^{-1}$) was approximately six-fold greater than for seagrass material transported toward the mangroves ($0.6 \text{ mg m}^{-2} \text{ day}^{-1}$; Fig. 3; nets 1 & 2).

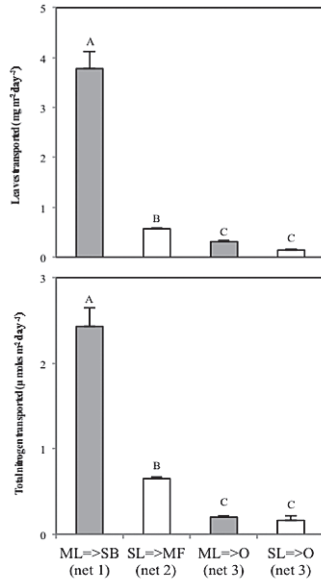


Figure 3 Transportation of total organic matter and nitrogen contained in *Rhizophora* sp. and *Enhalus* sp. leaves, between mangrove forests, seagrass beds, and the coastal ocean. X-axis labels represent the movement of leaf material between ecosystems. ML=>SB shows mangrove leaf (ML: grey) transportation from the mangrove forest (MF) to the seagrass bed (SB) (net 1); SL=>MF, seagrass leaf (SL: white) from the seagrass bed (SB) to the mangrove forest (MF) (net 2). The last two columns indicate leaf movement to the ocean (O) (net 3). The top panel indicates the total dry mass transported from each ecosystem per day ($\text{POM}_{\text{transport}}$; $\text{mg m}^{-2} \text{ day}^{-1}$), which was calculated using equation (1). Letters denote significant differences between total leaf mass transported ($\text{mg m}^{-2} \text{ day}^{-1}$), with different letters indicating a difference (K-W test; LSD test). The lower panel shows total nitrogen transportation in leaf content of *Rhizophora* sp. and *Enhalus* sp. Letters denote significant differences between total nitrogen transported ($\mu\text{mole m}^{-2} \text{ day}^{-1}$), where different letters indicate a difference (K-W test; LSD test). Values are means $\pm$ one standard error ($n = 5$).

The transport to the ocean of both mangrove ($0.3 \text{ mg m}^{-2} \text{ day}^{-1}$) and seagrass leaves ($0.1 \text{ mg m}^{-2} \text{ day}^{-1}$) was much lower than the exchange between mangroves and seagrass (Fig. 3; net 3). The total nitrogen in seagrass leaves conveyed to mangrove forests was approximately half of that transferred to seagrass beds from mangroves (K-W test, $p = 0.001$; Fig. 3). There was no detectable difference in TN exported to the ocean by mangrove and seagrass leaves (net 3).

3.4.3 Degradation experiments

Degradation of *Enhalus* sp. leaves followed an exponential decay pattern, where loss of mass showed a 50-75 % decrease within 6 days in the both the water column and in the sediment (Fig. 4B & D). At 20-30 days, leaves in the water column plateaued at about 25 % of original mass for all habitat types, in contrast leaves in the sediment had a huge variability; 10-50 % of the initial mass of seagrass leaves remained in the sediment (Fig. 4B & D). The degradation pattern of *Enhalus* sp. leaves was in direct contrast with that of the *Rhizophora* sp. leaves, *Rhizophora* sp. leaves showed only a 25 % loss in mass after 6 days, both in the water column and sediment (Fig. 4A & C). *Rhizophora* sp. leaf mass was still approximately 50 % of the initial mass at 30 days (Fig. 4A & C). A significant relationship for mangrove leaf

mass loss was seen between the water column and the sediment in the different environments (water column & sediment) at 20 days.

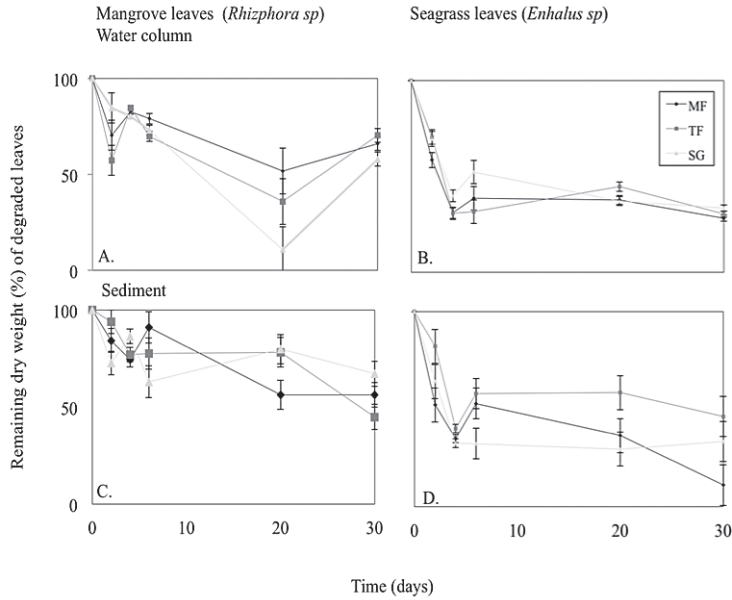


Figure 4 Remaining dry mass (%) of *Rhizophora sp.* (A & C) and *Enhalus sp.* (B & D) leaves during 2, 4, 6, 20 and 30-day degradation experiments conducted in different ecosystems: mangrove forest (MF: black diamonds), tidal-flat (TF: dark grey squares) and seagrass bed (SG: light grey triangles). Top graphs represent incubations in the water column (A and B); bottom graphs, within the sediment (C and D). The change in mangrove ($p = 0.01$) and seagrass leaf ($p = 0.1$) mass over time was highly significant ($p = 0.01$; Tab. 1), an interaction was also seen between the environment and time for mangrove ($p = 0.01$) and seagrass ($p = 0.1$) leaves (Tab. 1). Values are means $\pm$ one standard error ($n = 3$).

In the sediment the leaves showed a gradual decrease in contrast with the water column where leaves sharply decreased in mass remaining ($p = 0.01$; Tab. 1). Changes in seagrass leaf mass over time were significant at the level $p = 0.1$, seagrass leaf mass stabilized in the sediment, but their mass decreased more in the water column (Tab. 1). Both mangrove and seagrass leaves also indicated an interaction between time and the environment (water column vs. sediment) at $p = 0.01$ and $p = 0.1$ respectively (Tab. 1). No other mass changes were significant (Tab. 1).

C:N ratios of seagrass leaves increased in the water column and plateaued in the sediment (Fig. 5B & D) ; and these differences in the water column changed over time ($p = 0.01$; Tab. 1). A change in C:N ratios of seagrass leaves was found to be highly significant ($p = 0.01$) between the environments (Tab. 1). Different C:N ratios in the water column also changed over time, as shown by the time interaction (Tab. 1). Mangrove leaves showed a highly significant relationship ($p = 0.01$) between C:N ratios for time; and these were

affected by the site (Tabl.1; LSD test). Mangrove leaves showed a significant change ($p = 0.01$) between C:N ratios at 6 and 20-30 days (Fig. 5A & C); and these were affected by the site (Tab. 1; LSD test).

Table 1 Statistical summary of the 3-way ANOVA analysis of mangrove leaf (ML) and seagrass leaf (SL) degradation experiments, for leaf mass and C:N ratios variables. The data reflect statistically significant interactions between environment (water column versus buried in the sediment), site (seagrass bed versus mangrove forest), and time (mass : 0, 2, 4, 6, 20 & 30 days and C:N ratios : 0, 6, 20 & 30 days) variables.

Leaf type	Experiment	D'Agostino-Pearson	Environment	Site	Time	Environment *Site	Environment *Time	Site *Time	Environment *Site*Time
SL	mass	$p > 0.05$	-	-	*	-	*	-	-
	C:N ratios	$p > 0.05$	**	-	-	-	**	-	-
ML	mass	$p > 0.05$	-	-	**	-	**	-	-
	C:N ratios	$p > 0.05$	-	-	**	-	-	**	-

* P-value < 0.1

**P-value < 0.01

- Not significant

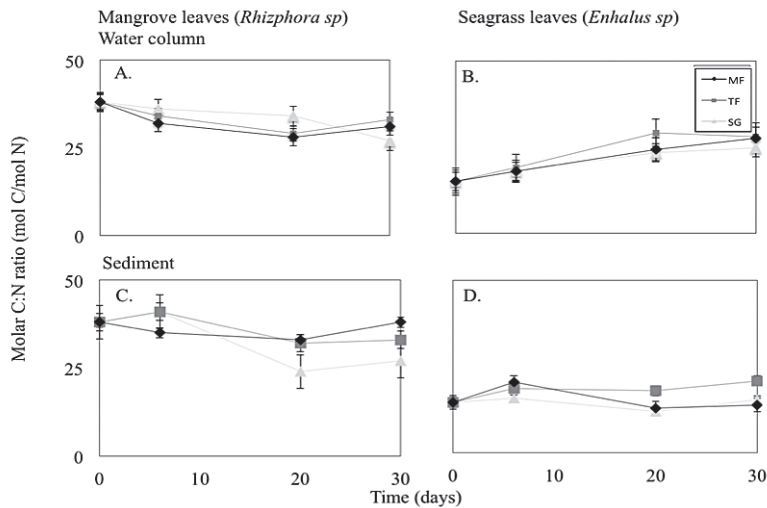


Figure 5 C:N ratios of *Rhizophora* sp. (A & C) and *Enhalus* sp. (B & D) leaves during 6, 20 and 30 days of degradation in different ecosystems: mangrove forest (MF: black diamonds), tidal-flat (TF: dark grey squares) and seagrass bed (SB: light grey triangles). Top graphs represent incubations in the water column (A and B); bottom graphs in the sediment (C and D). The change in mangrove ($p = 0.01$) and seagrass leaf ($p = 0.1$) mass over time was significant (Tab. 1). An interaction was also seen between the environment and time for mangrove ($p = 0.01$) and seagrass ($p = 0.1$) leaves (Tab. 1). Values are means $\pm$ one standard error ($n = 3$).

3.5 Discussion

Mangrove leaves were the dominant POM source transported between adjacent seagrass beds and mangrove forests, but had similar POM transport rates to the open ocean as seagrass beds (Fig. 3). However, our results show faster degradation rates of seagrass leaves than mangrove leaves (Fig. 4), suggesting that seagrass leaves are mainly internally recycled with high N-release in the bed. In contrast, mangrove leaves are a dominant particulate organic matter in the coastal area that can be transported before degrading and hence may be regarded as a potential source for dissolved nitrogen in other ecosystems. Importantly, combining transportation and degradation/incubation experiments provide novel insights in the processes and pathways in the tropical coastal seascape.

3.5.1 *Leaf litter nitrogen release from seagrass & mangrove leaves*

It has been thought that seagrass and mangrove detritus enhance nitrification and denitrification processes in the water column (Kristensen et al. 1998, Holmer et al. 2001). Detritus is a DIN/DON source through leaching and bacterial degradation. Fresh seagrass leaves had a much higher concentration of TN (total nitrogen) in the leaf than mangroves leaves (SL: 2 μ mole N g⁻¹, ML: 1 μ mole N g⁻¹). Importantly our data also showed that seagrass sediment has a much higher contribution to water column DIN than seagrass leaves (Tab. SI). The negative values found for efflux of DIN from seagrass leaves indicates that there was an influx of DIN into the seagrass sediment that is probably caused by enhanced denitrification from organic material derived ammonium (Holmer et al. 2001). Seagrass leaves showed a higher contribution to water column DON than seagrass sediment, indicating that DON production comes from the plants rather than from the sediment. Our incubation experiments indicate that initially (first 24 hours) seagrass leaves may be a more important source of DON in the coastal zone. The C:N ratios in the degradation experiments indicated that overall seagrass leaves released nitrogen, whereas mangrove leaves retained it, in agreement with previous studies (Kristensen et al. 1998, Holmer et al. 2001). Our incubations also verify this result over a 24 hour initial time period.

3.5.2 *Leaf litter transportation*

Although rough estimates, the results of our POM transportation experiment across ecosystems showed that significant amounts of mangrove leaves are exported to seagrass beds (3.7 ± 0.8 mg m⁻² day⁻¹; Fig. 3). Via leaf export, mangroves transport a substantial amount of POM to seagrass beds compared with fluxes from and to other ecosystems and the ocean. Only 8 % (0.3 mg m⁻² day⁻¹) of the mobilized mangrove leaves were transported from the seagrass bed to the ocean (Fig 3). We therefore estimate that 92 % of the mangrove leaves

remained in the seagrass bed, approximately $3.5 \text{ mg m}^{-2} \text{ day}^{-1}$ (Fig. 2). Other studies have shown that seagrass plants can trap mangrove leaves from mangrove forests located up to 3 km away (Hemminga et al. 1994). Exchanges of mangrove leaves (*Rhizophora sp.* & *Ceriops sp.*) to seagrass beds (*Thalassodendron sp.*) and then back to mangroves has been reported previously in Gazi Bay, Kenya (Slim et al. 1996).

In our transportation experiment, leaves trapped in the nets were fresh; degraded leaves were not present. This may suggest that degradation starts after leaves get trapped in either the mangrove roots or seagrass plants, ending their transport under normal hydrodynamic conditions. Retention of mangrove and seagrass leaves within tropical coastal systems can be quite substantial, and constitute a potentially important nutrient source, depending on the time scale of degradation and nitrogen release. In the case of seagrass beds, Vonk et al. (2008b) found that seagrass canopies could retain half of the nitrogen released from leaf litter within a 27-175 m^2 radius. Adame & Lovelock (2011) indicated that mangrove forests export carbon and nutrients as particulate organic matter to the coastal ocean and therefore seagrass beds. Furthermore mangrove forests will also import dissolved nitrogen usually at high tides and high concentrations, although further studies are required to form firm conclusions regarding nitrogen fluxes (Adame & Lovelock 2011).

3.5.4 Leaf litter Decomposition

Our observations agree with past degradation experiments with seagrass and mangrove litter (Newell et al. 1984, Holmer & Olsen 2002) but extend this knowledge by including different habitats and environment types. Differences in degradation rates between species are due to the higher structural content of mangrove leaves compared with seagrass leaves, thus much more important than location of degradation. Benner & Hodson (1985) found that lignocelluloses in mangrove particulate matter caused greater resilience to microbial degradation than other marine macrophytes such as seagrass leaves. Over 30 days, our degrading mangrove leaves lost about 50 % of their mass, which is comparable to other studies (Fig. 4) (d'Croz et al. 1989, Ashton et al. 1999, Bosire et al. 2005, Silva et al. 2007). The breakdown of the physical structure of mangrove leaves indicates a gradual bacterial colonization, which is also verified by the decrease in C:N ratio (Fig. 5).

Mangrove leaf C:N ratio showed little difference across both environments and habitat types, but they did show a decrease over the course of one month (Fig. 5). A decrease in C:N ratios could be attributed to carbon being the preferentially respired element as nitrogen is retained (Chale 1993, Holmer & Olsen 2002). However the rate of bacterial use of carbon is likely slow over 30 days, possibly due to tannin content in the mangrove leaves as well as the physical structure of the leaves, as found by Holmer & Olsen (2002). The C:N ratio of seagrass leaves buried in the sediment plateaued in the mangrove forest, seagrass bed and tidal

flat sediment, at a median value of about 15. The C:N ratio of the seagrass leaves incubated in the water column increased, indicating a decrease in nitrogen content. Differences in the evolution of the C:N ratios of seagrass and mangrove leaves during decomposition have been previously interpreted by the C:N differences of the starting material: the low C:N material of seagrass leaves have sufficient food quality to decompose rapidly, but microbes must accumulate N in order to degrade the high C:N material of mangrove leaves (Fourqurean & Schrlau 2003). Likely the increase in C:N ratio observed in seagrass leaves indicates a nitrogen release to the water column that will be available for other organisms.

3.5.5 *Exchange between Ecosystems: Facilitation potential*

For this study we investigated nitrogen fluxes via POM during the rainy season. We estimated maximum nitrogen requirements ($\mu\text{ mole m}^{-2}\text{ day}^{-1}$) for *Enhalus sp.* and *Halophile sp.* (via equation 3) to be approximately 21300 and 580-920 $\mu\text{ moles m}^{-2}\text{ day}^{-1}$, respectively. Comparing these values with the mangrove derived total nitrogen exported in POM to seagrass beds ($2.4\ \mu\text{ mole}^{-1}\text{ m}^{-2}\text{ day}^{-1}$; Fig. 3), indicates that mangrove forests only provide a negligible amount (0.01 %) of the N requirements for *Enhalus sp.* patches via the export of leaves per square meter of mangrove forest. For *Halophile sp.* mangrove leaves could provide approximately 0.3-0.4 % of nitrogen requirements of this species. Our study was completed in the wet season. In the dry season we would expect to see much less leaf shedding from mangrove trees, consequently mangrove forests may donate much less POM to seagrass beds or deeper water ecosystems. It should be noted that in this particular site, these two ecosystems area have a ratio of 2 (mangrove forest 2,093,775 m^2 and seagrass bed 960,000 m^2). But in a site with a larger area ratio, the potential for mangrove forests to provide seagrass beds with nitrogen will be greater. Furthermore, within the mangrove forest, degraded mangrove leaves will release dissolved organic material that will also be transported to seagrass leaves. This process represents an important direction for future research knowing that seagrasses can rapidly use DOM (Evrard et al. 2005, Vonk et al. 2008b, Van Engeland et al. 2011). Given that seagrass beds are found in oligotrophic water and consequently have developed effective nutrient retention and recycling, mangrove leaves may provide a small addition of nitrogen to seagrass beds.

3.6 Conclusion

In-situ transportation experiments showed that POM in tidal waters was composed more of mangrove leaves than seagrass leaves. Seagrass leaves degraded quicker across all habitat types, both in sediment and water column, than mangrove leaves. Furthermore, incubations indicated that DON release from seagrass leaves was higher than from mangrove leaves.

To improve insight into nitrogen interactions via particulate organic matter exchange between mangrove forests and seagrasses beds, further information should be obtained regarding the changes of DIN and DON release from degrading mangrove leaves over longer timescales (> 1 month). Data are also required on the productivity of the mangrove forest and seagrass ecosystems, potentially providing information on nitrogen dynamics, especially nutrient requirements within the ecosystem. Furthermore, the trapping capacity of mangrove roots and seagrass plants would support approximations of how much POM is outwelled from each system. Importantly the major findings of this study indicate that mangrove forests and seagrass beds are primarily found to withhold particulate derived nutrients within their own ecosystems.

Acknowledgments

Our thanks go to Kalaya Kantawong, Nam Wani, Boonchai Phrathaan, Bedeen Phrathaan and Mairi Fenton for their logistic help with the fieldwork in Thailand and to the NIOZ analysts for the laboratory measurements. This study was funded by the Building with Nature project (NUS SDWA Grant #R303-001-020-414).

3.7 Supplementary table

Table SI Concentrations ($\mu\text{mole l}^{-1}$) of dissolved inorganic (DIN) and organic (DON) nitrogen from seagrass (SL) and mangrove (ML) leaf incubation over 24 hours. The first column indicates the material (ML & SL) and the second column represents the number of hours (maximum 24 hours). Columns 3 & 5 show the nitrogen concentration change ($\mu\text{mole l}^{-1}$) from mangrove or seagrass leaves (ML & SL) with sediment (S) and water (W). Whilst columns 4 & 6 indicate nitrogen release ($\mu\text{mole l}^{-1}$) from only sediment (S) and water (W). To calculate the N release from mangrove or seagrass leaves ($\mu\text{mole g}^{-1}$) we subtracted columns 4&6 from 3&5 respectively, multiplied by the number of litres in the tank (19.2 L) and then divided by the weight of the material (g).

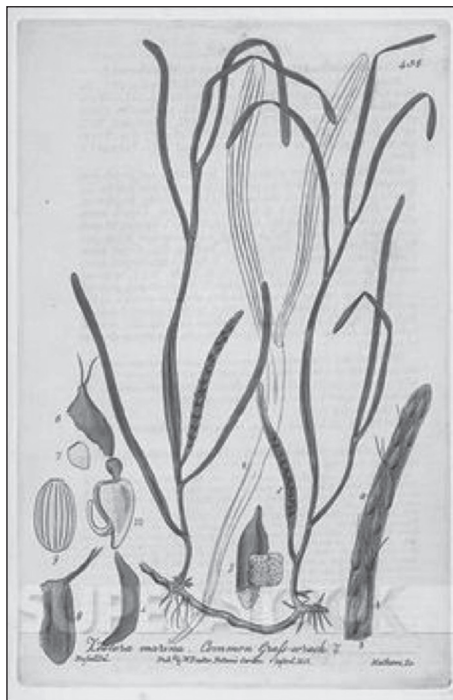
Material	Time (hours)	DIN	($\mu\text{mole l}^{-1}$)	DON	($\mu\text{mole l}^{-1}$)
		W + S + ML or SL	W + S	W + S + ML or SL	W + S
ML	0	0.6	0.6	15.4	13.9
ML	0	1.1	1.5	14.5	14.4
ML	0	0.6	0.8	14.1	10.0
ML	6	1.1	1.1	12.7	13.5
ML	6	3.1	1.7	32.9	18.0
ML	6	2.2	1.4	15.3	15.4
ML	12	1.3	1.8	10.2	16.1
ML	12	4.9	2.1	14.6	12.7
ML	12	2.4	1.8	11.7	15.8
ML	18	1.5	3.3	11.6	23.0
ML	18	8.5	2.6	20.4	12.7
ML	18	3.5	3.0	16.7	13.8
ML	24	1.6	2.1	12.1	11.9
ML	24	16.4	3.9	27.2	15.6
ML	24	0.7	3.0	11.3	13.5
SL	0	0.4	0.4	7.0	9.1
SL	0	0.3	1.0	8.4	14.3
SL	0	0.5	0.5	8.6	10.2
SL	6	0.5	2.0	12.0	7.2
SL	6	1.3	0.8	43.9	9.9
SL	6	1.8	1.3	64.1	9.8
SL	12	4.2	0.6	40.7	8.2
SL	12	1.0	0.9	38.0	6.9
SL	12	1.9	2.0	64.4	8.4
SL	18	1.2	0.9	44.1	8.6
SL	18	1.0	2.6	40.4	17.0
SL	18	1.8	2.1	72.9	7.4
SL	24	1.5	0.5	49.4	6.8
SL	24	0.7	2.0	33.9	9.5
SL	24	4.3	2.6	59.6	12.7

Chapter 4

Leaf transport in mimic mangrove forests and seagrass beds.

L.G. Gillis, T.J. Bouma, W. Kiswara, A.D. Ziegler and P.M.J. Herman.

STATUS: Published at Marine Ecology Progress Series.



Abstract

Mangrove forests and seagrass beds are thought to exchange particulate organic material, especially in the form of leaves. However, relatively little is known about the trapping capacity of mangrove aboveground roots and seagrass plants for leaf segments. We aimed to identify the major factors controlling the leaf-trapping capacity of mangroves and seagrasses in a flume study. For mangroves, we found that higher density mangrove roots enhanced trapping capacity whereas the presence of waves strongly reduced the trapping capacity. The latter might be explained by a reduced average collision time (i.e. the time a leaf was attached to a root structure) in the presence of waves. The ability for seagrass beds to trap leaves was dominated by the length/type of vegetation and the absence/presence of waves. Overall, our results suggest that mangroves-via their roots-have a more efficient trapping mechanism than seagrass beds. Mangrove roots extend through the entire water column the majority of the time, which enhances trapping capacity. In contrast, seagrass beds require particulate organic material to become entangled within the predominantly submerged shoots, making trapping dependent on the degraded state of the leaf and the water depth. Our results give an indication of parameters that could be used in a model of trapping capacity of these ecosystems. As leaves are associated with nutrients, we have identified factors, which will help to determine what parameters affect the nutrient retention or export of ecosystems. These include density of roots, hydrodynamic conditions (absence/presence of waves), location of initial deposition, degradation stage and type of leaf.

Key words: Particulate organic material, nutrients, trapping capacity, hydrodynamics, and flume experiment.

4.1 Introduction

Ecosystems are open to exchange materials with adjacent environments (Polis et al. 1997, Lovett et al. 2005). This is particularly true for mangrove forests and seagrass beds, which are often found in proximity to each other in the tropical coastal seascape (Ogden & Gladfelter 1983, Moberg & Rönnback 2003). Both systems are subjected to large tidal exchanges that facilitate the movement of particulate organic matter (POM) and dissolved nutrients from one ecosystem to another, or to deeper water (Lee 1995, Bouillon & Connolly 2009, Davis et al. 2009). POM can be classified as leaves, seeds, roots and other detachable parts of a plant. Of major importance is the nutrient potential of POM, i.e. how much of its associated nutrients can be made available to other ecosystems and organisms (Odum & Heald 1975, Bird et al. 1998, Polis et al. 1997). POM originating from ecosystems such as mangrove forests and/or seagrass beds is potentially an important source of nutrients for adjacent keystone organisms and their associated species (Alongi 1990, Lee & Dunton 2000, Granek et al. 2009).

Mangrove forests are intertidal ecosystems with large variability in the tree and root formation. Mangrove tree species can range from pioneering species such as *Avicennia* sp. (1 to 2 m tall) that has pneumatophores vertically extending from the ground, to *Rhizophora* sp. (5 to 40 m tall) with characteristic prop or stilt roots that can extend horizontally directly from the trunk (Giesen et al. 2006). Mangrove ecosystems can typically tolerate flow velocities of 0.02 to 0.2 m s⁻¹ and wave heights of 0.15 to 0.25 m (Quartel et al. 2007). In contrast, tropical seagrass species can range from the smallest *Halophila* sp. (leaf length 2 cm) to the largest *Enhalus* sp. (leaf length 30 cm) (Duarte 1991). The ecosystem can experience higher hydrodynamic energy than mangrove forests, flow velocities of 0.0004 to 1.5 m s⁻¹ and wave heights of 0.1 to 0.32 m (de Boer et al. 2000, Masini et al. 2001). Further, the extensive roots systems of many seagrass plants can reduce sediment erosion and facilitate sedimentation (Agawin & Duarte 2002, Gacia et al. 2002).

Because of their shape and density in the water column, mangrove roots and pneumatophores can trap POM (Alongi 1990, Lee 1995). Mangrove trees can decrease the water velocity and attenuate waves, causing calmer hydrodynamic conditions that facilitate trapping (Wolanski et al. 1998, Massel et al. 1999, Quartel et al. 2007). Factors such as density, species, root shape, and biomass as well as intertidal position of the mangrove forest can vary greatly (Friess et al. 2012). These factors affect the hydrodynamics and consequently the trapping capacity. Consequently, the interior of mangroves has greater trapping capacity compared with the seaward edges (Friess et al. 2012). Seagrass beds can also trap particles of POM inside the seagrass canopy (Terrados & Duarte 2000, Agawin & Duarte 2002). Trapping results directly from the physical structure of the meadow or from settling induced by changes in the hydrodynamic conditions, which are related to plant/root density, root type and leaf characteristics (Fonseca & Cahalan 1992, Agawin & Duarte 2002, Newell & Koch

2004, Uku & Bjork 2005, Hendriks et al. 2008). Once particulate material is deposited within seagrass beds, a high percentage will remain in place as the plants in the meadow limit re-suspension (e.g. see Terrados & Duarte 2000, Wilkie et al. 2012).

The majority of the studies on POM trapping in mangrove forests and seagrass beds focus on small detrital material (Terrados & Duarte 2000, Agawin & Duarte 2002, Wilkie et al. 2012). Large forms of particulate matter, for example mangrove and seagrass leaves, are a mobile source of POM in the coastal ocean (Hemminga et al. 1994, Davis et al. 2009). Mangrove forests and tropical seagrass can trap POM in the form of floating leaves (Alongi & Christoffersen 1992, Hemminga et al. 1994, Lee 1995, Kithaka 1997, Rivera-Monroy et al. 1998, Koch & Madden 2001, Bouillon & Connolly 2009). Changes in the water content of leaves through trapping or degradation can also affect their movement although this has only been verified for seeds (Chang et al. 2008). However, relatively little data are available on trapping capacity and transport velocities of various types of leaves in mangrove forests and seagrass meadows. Furthermore we are unaware of how changes in hydrodynamics, such as the presence of waves or increased velocity, can change the trapping capacity of these ecosystems.

To facilitate physical modeling of large POM exchange in the tropical coastal seascape, we used flume experiments to quantify the effects of plant/root density, current velocity, and the absence/presence of waves on the movement of leaves in mimic mangrove forests and seagrass meadows. Moreover, we measured settling velocities to determine the collision time needed for leaves to settle down and how increased moisture content of the leaf may affect its trapping potential. We investigated the following hypotheses regarding the physical trapping of POM within these ecosystems: (1) Higher density seagrass canopies and mangrove roots will increase trapping potential; (2) Longer leaf length will enhance the trapping capacity of mimic mangroves and seagrass ecosystems; (3) Addition of waves to the flow will generate an unbalanced leaf movement, creating a lower likelihood that a leaf will become trapped; (4) Mangroves will have greater trapping potential than seagrass because of their extension through the whole water column. Verifying these hypotheses will provide us with parameters that allow us to model what factors in different ecosystems will affect the transportation of leaves through the ecosystems.

4.2 Methods

4.2.1 Flume experiments

By means of a flume study, we quantified the retention of fresh mangrove and seagrass leaf segments by mimicking seagrass canopies and mangrove forests for a variety of hydrodynamic conditions. The experiments were conducted in the racetrack flume (17.5 m long, 0.6 m width and water depth of 0.3 m) at the Royal Netherlands Institute of Sea Research (NIOZ), Yerseke,

Netherlands, in May 2012. The design of the flume allows uniform flow conditions, and generates normal velocity profiles. The fresh leaves were transported in a cool box from Pari Island, Indonesia to NIOZ. The leaves were randomly selected from healthy plants and trees; care was taken to ensure leaves selected were the oldest fully-grown with uniform physical appearance. Leaves were either used immediately in the experiment or kept refrigerated until use. The hydrodynamic conditions tested included 2 current velocities (0.1 and 0.2 m s⁻¹) and 2 wave conditions (none and 0.1 m high, 1 s period waves). These conditions are similar to those typically reported in the literature for mangrove creeks and seagrass meadows (de Boer et al. 2000, Masini et al. 2001, Quartel et al. 2007). For our experiments, we did not investigate extreme tides or a storm, which would have increased the velocities and wave heights; our proposition was to look at the transportation under normal conditions.

Transport was measured for the following leaf segments: 0.1 and 0.3 m length, 0.02 m width and 0.0009 m thickness of fresh *Enhalus acoroides* leaves (seagrass); and 0.2 m length, 0.05 m width and 0.0008 m thickness of *Rhizophora apiculata* leaves (mangrove). In a 2.4 m² (4 m length × 0.6 m width) area of the flume, two densities of mangrove roots were mimicked: 4.5 roots m⁻² (low density) and 9 roots m⁻² (high density) using uncut bamboo canes (~0.1 m diameter, ~0.8 m length) (Van der Stocken et al. 2013). A 1.2 m² (2 m length × 0.6 m width) seagrass meadow was mimicked using highly flexible plastic strips (0.2 m tall and 0.02 m wide). Two leaf densities were tested: 200 leaves m⁻² (low density) and 400 leaves m⁻² (high density) (Folkard 2005). Both densities of mangrove roots and seagrass canopies were similar to physical properties of the ecosystems found in the field sites where we did the settling velocity experiments: 6 to 11 mangrove roots m⁻² and 170 to 510 seagrass leaves m⁻². Within the flume section, mangrove roots were randomly distributed over the available space. The mimic canopy was fully submerged in the flume, leaving 0.14 m depth of water overlying the seagrass canopy to mimic an incoming/outgoing tide, i.e. when POM transport may be expected to be highest.

Ten replicates were completed for each combination of parameters for a total of 48 treatments: 2 flow velocities (0.1 and 0.2 m s⁻¹), 2 wave conditions (waves and no waves), 3 leaf lengths/types (0.1 and 0.3 m seagrass leaves and 0.2 m mangrove leaves), 2 mimicked ecosystems (mangrove forest and seagrass meadow) and 2 densities (high and low) for each mimic ecosystems. For the mangrove forest treatments, individual leaves were released onto the water surface; throughout this experiment all leaves remained on the surface of the water. In the seagrass meadow treatments, individual leaves were released either onto the water surface or at the bottom within the mimicked seagrass canopy. In the mimic mangrove forest treatments, leaves were initially also released on the bottom. However, all leaves floated to the surface of water. Hence this aspect was not investigated in the mangrove experiments.

In total, 240 leaves were observed. We measured the time for leaves to move out of the system and we counted the number of collisions between released leaves and mimicked

mangrove roots or seagrass stalks. We also recorded the total time the leaves were stalled due to collisions with mimicked mangrove roots or seagrass material. Preliminary long-term flume runs showed no leaf release once the stall time exceeded 2 min. Hence, if the stall time exceeded 2 min, we considered them to be trapped indefinitely, meaning that to be released, a change in current direction would need to occur. Consequently, the trapping capacity for each system was determined as the percentage of leaves that stayed on a root or within a seagrass bed for > 2 min.

4.2.2 Leaf settling velocity experiments

Five fresh seagrass leaves 0.1 m and 0.3 m long were taken from the seagrass bed in Koh Chong Lat Noi bay, on the island of Koh Yao Yai, South Thailand (7°54'28"N, 98°35'12"E). We also collected five 0.2 m long mangrove leaves from the mangrove forest at the same location. Collected leaves were all green without imperfections in the leaf structure. The leaves were directly transported to the marine laboratory in a cool box. Epiphytes were removed from the collected mangrove and seagrass leaves where they occurred. The leaves (5 each of 0.1 and 0.3 m seagrass leaves and 0.2 m mangrove leaves) were placed into a net bag of mesh size < 0.5 mm that allowed for small organisms to migrate in and out, but dispelled larger marine animals such as crabs. At the mangrove forest a metal stake was placed into the substrate. The 3 net bags (i.e. 1 with mangrove and 2 with seagrass leaves) were then secured to the pole at a height of 0.05 m. These net bags were collected from the sampling sites after 5 d and leaves were used for measuring settling velocities.

Settling velocity (m s^{-1}) was measured using a settling chamber, which is a 0.3 m tall cylinder container, filled with water to a depth of 0.3 m. To determine settling velocities, the stopwatch was started when the leaf was placed into the surface of the water and stopped once the entire leaf was deposited on the bottom of the chamber. The time taken was recorded in seconds. Each 5 d degraded leaf was measured in this way, giving 5 replicates for 3 classes (0.1 and 0.3 m seagrass leaves and 0.2 m mangrove leaves). A 5 d degradation period was chosen because we found that at this time period leaves displayed rapid physical degradation.

4.2.3 Statistical analysis

We used ANOVA for analyzing cumulative collision time versus 2 seagrass densities, presence/absence of waves and leaf type in a mangrove forest (1-way ANOVA). A 2-way ANOVA was tested for trapping capacity versus presence/absence of waves in a mangrove forest. Lastly a 3-way ANOVA was used to test travelling times versus 2 velocities, absence/presence of waves and leaf length in the seagrass bed. One-way ANOVA was also used for the settling velocity versus leaf type. Prior to testing, normality in the data was assessed using a D'Agostino-Pearson test. Least squares difference (LSD) post-hoc testing was performed

following ANOVA. All statistical testing was completed using the R programming platform (R Core Team 2012).

4.3 Results

4.3.1 Flume Experiment – Mangrove forest

The trapping capacity of the high-density mangrove forests, estimated as the percent of leaves that remained trapped on a root for more than 2 min, was higher in the absence of waves ($68 \pm 4.4\%$) than in the presence of waves ($33 \pm 7.3\%$) (2-way ANOVA, $p = 0.0004$, $F = 17.3$, $n = 120$; Fig.1). The trapping capacity in high density mangroves was also significantly higher than in low density mangroves (2-way ANOVA, $p = 0.02$, $F = 6.2$, $n = 240$; Fig. 1), but the effect of vegetation density (trapping capacity $\sim 20\%$) was smaller than that of waves ($\sim 30\%$). No interactions were found between high and low densities of roots and the absence/presence of waves.

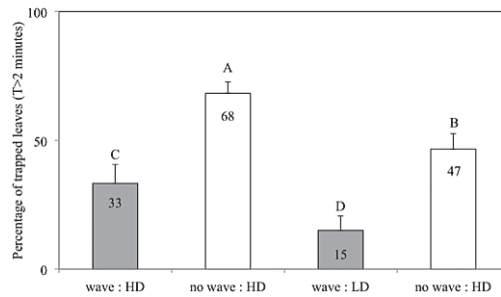


Figure 1 Percentage of trapped leaves (time > 2 minutes) in high density (HD) and low density (LD) mangroves for situations with waves (grey columns) and without waves (white columns). Percentages (numeric values in boxes) are calculated from 240 experiments ($n = 60$ for each treatment). Percentage of trapped leaves are means $\pm$ one standard error ($n = 6$). Letters denote significant differences (LSD test, $p = 0.05$).

Cumulative collision time was reduced in the presence of waves compared with absence of waves (1-way ANOVA, $p < 0.00001$, $F = 20.4$, $n = 240$; Fig. 2).

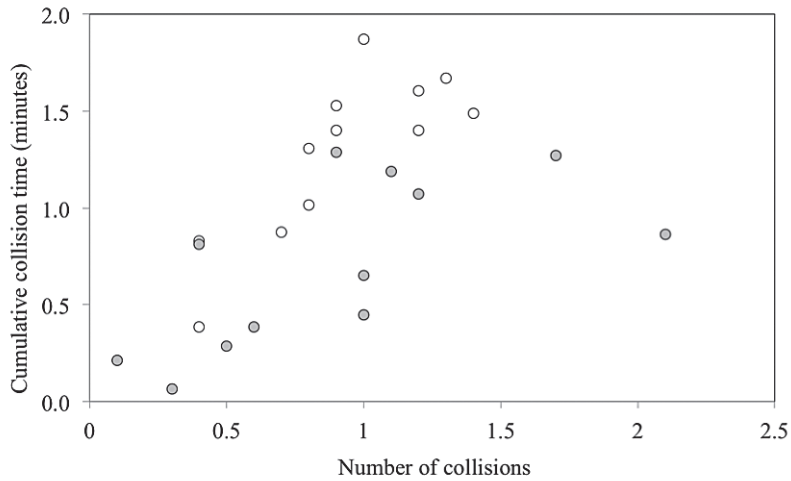


Figure 2 The relationship between number of collisions and cumulative collision time (minutes) for a single leaf for experiments with waves (grey circles) and without waves (white circles). In total 240 leaves were observed, 120 for each treatment. Circles are means of 10 flume runs. Cumulative collision times for wave and no wave conditions are significantly different (1-way ANOVA, $p < 0.00001$, $F = 20.4$, $n = 240$), but number of collision is not significant.

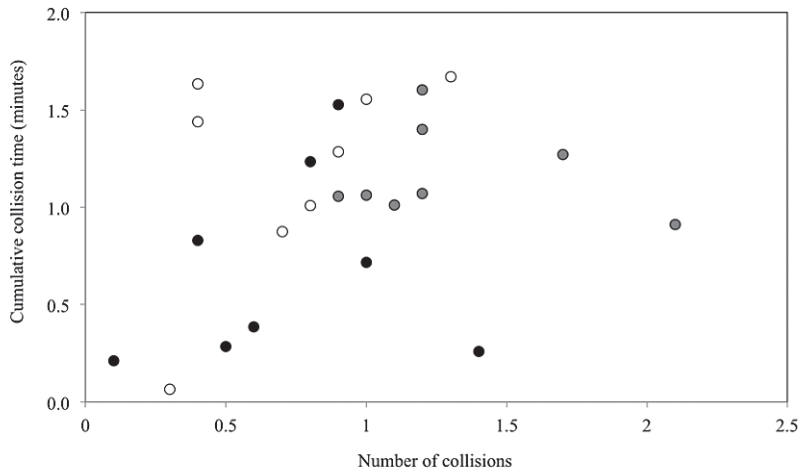


Figure 3 The relationship between the number of collisions and cumulative collision time (min) for 0.2 m long mangrove leaves (white circles) and 0.1 and 0.3 m seagrass leaves (black and grey circles respectively). Symbols represent the mean of $n = 10$ runs ($n = 80$ for each treatment). Mangrove leaves (0.2 m) and seagrass leaves (0.1 m) showed a reduced cumulative collision time compared to seagrass leaves (0.3 m) (1-way ANOVA, $p = 0.0003$, $F = 8.3$, $n = 240$). Values are averages ($n = 10$).

Among leaf types, the 0.3 m long seagrass leaves had the highest number of collisions as well as the longest collision time in the mimicked mangrove roots (Fig. 3). Seagrass leaves of 0.3 m length collided with the mangrove roots one or more instances the majority of the time ($93 \pm 3.9\%$) (Fig. 3). The 0.1 m long seagrass leaves and 0.2 m long mangrove leaves had fewer collisions. There was a positive relationship between the mean number of collisions and the cumulative collision time (minutes). A little more than half ($58 \pm 8.3\%$) of these leaves (0.1 and 0.2 m) had more than one collision with the mangrove roots. The cumulative collision time values for 0.2 m long mangrove leaves and 0.1 m long seagrass leaves were significantly lower than that of 0.3 m long seagrass leaves (1-way ANOVA, $p = 0.0003$, $F = 8.3$, $n = 240$; Fig. 3).

4.3.2 Flume Experiment – Seagrass bed

In the mimicked seagrass canopy experiments, all leaves released on the water surface moved over the meadow with no collisions. Higher velocity currents decreased travelling time significantly: 0.04 s versus 0.07 s (3-way ANOVA, $p < 0.00001$, $F = 486.6$, $n = 240$), however traveling time was not affected by the presence/absence of waves (3-way ANOVA, $p = 0.3$, $F = 1.1$, $n = 240$). On the bottom of the seagrass canopy, leaf type generated the greatest difference in travelling time (3-way ANOVA, $p = 0.0004$, $F = 9.2$, $n = 240$; Fig. 4). This difference was due to 0.3 m leaves becoming trapped for > 2 min in 3 out of 4 conditions (Fig. 4). In the presence of waves, travelling time for leaves was shorter: 0.9 min versus 1.5

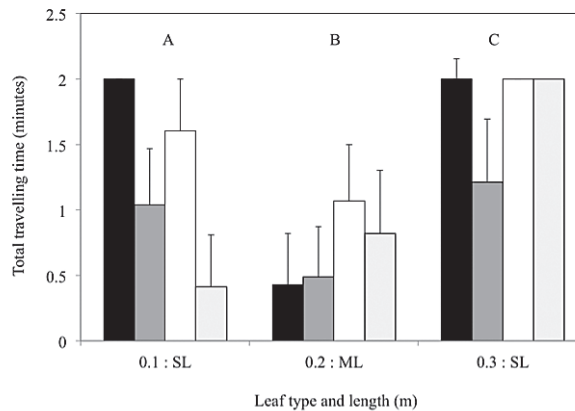


Figure 4 Total travelling time for leaves of different lengths through the bottom of the seagrass beds for four conditions and three combinations of leaf lengths and types. The x-axis refers to the following leaf lengths and types: 0.1 m seagrass leaves (SL); 0.2 m mangrove leaves (ML) and 0.3 m seagrass leaves. Boxes refer to the following conditions: no waves and 0.1 m s⁻¹ velocity (black); waves at 0.1 m s⁻¹ velocity (dark grey); no waves at 0.2 m s⁻¹ velocity (white); and waves at 0.2 m s⁻¹ velocity (light grey). Density was pooled for the figures. In total 240 leaves were observed, 80 of 0.1 m (seagrass), 80 of 0.2 m (mangrove) and 80 of 0.3 m (seagrass) leaves. Travel times are means for $n = 10$ runs $\pm$ one standard error ($n = 10$). Letters denote significant differences (LSD test, $p = 0.05$).

min (3-way ANOVA, $p = 0.02$, $F = 6$, $n = 240$; Fig. 4). Velocity did not change travelling time for leaves in the seagrass canopy (3-way ANOVA, $p = 0.5$, $F = 0.5$, $n = 240$; Fig. 4). Testing with a 3-way ANOVA revealed that there were no interactions between vegetation length/type, absence/presence of waves and current velocity. No significant difference was shown between the different densities of seagrass canopies (1-way ANOVA, $p > 0.5$, $F = 0.06$, $n = 480$), therefore the data was pooled for the high and low densities.

4.3.3 Settling velocity

Mean settling velocities of 5 d degraded mangrove leaves (0.2 m: 0.02 m s^{-1}) and seagrass leaves (0.1 m: 0.011 m s^{-1} ; 0.3 m: 0.01 m s^{-1}) in the settling chamber with standing sea water showed no significant differences between leaf origin ($p = 0.002$, $F = 10.4$, $n = 5$; Fig.5).

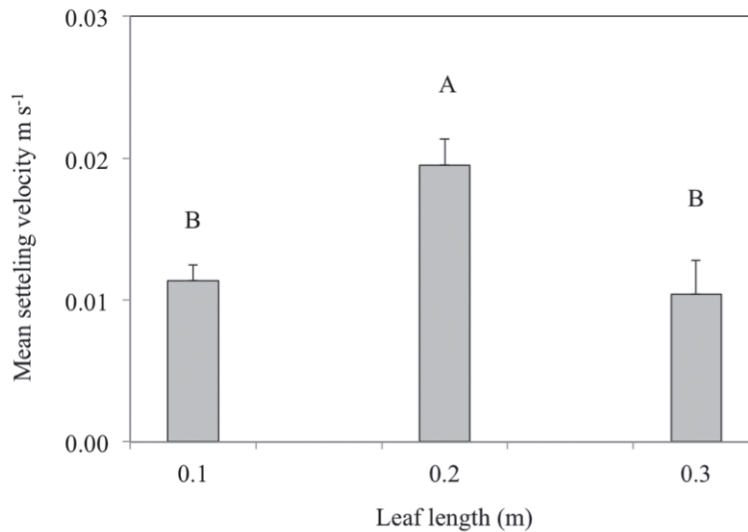


Figure 5 Mean settling velocities for different lengths of degraded leaves. Lengths of 0.1 and 0.3 m correspond to the seagrass leaves; 0.2 m, mangrove leaves. Settling velocities are means $\pm$ one standard error ($n = 5$). Letters denote significant differences ($p = 0.002$, $F = 10.4$, $n = 5$; 1-way ANOVA, LSD test).

4.4 Discussion

These experiments provide data for some important model parameters affecting the export of POM from mangrove forest and seagrass beds. Models for mangrove structure and dynamics such as FORMAN, KiWi and MANGRO and hydrodynamic models (for example Delft 3D) would be able to utilize this data for greater understanding of spatio-temporal changes in mangrove forests. Trapping capacity of mimicked mangrove roots was strongly dependent on the density of the roots and presence of waves (Fig. 1). Smaller leaves (0.1 m seagrass

leaves and 0.2 m mangrove leaves) did not have prolonged collisions with mangrove roots, and therefore had shorter collision times than the longer 0.3 m seagrass leaves (Figs. 2 & 3). Results from the seagrass canopy experiments indicated that leaves are trapped only if they come in contact with the bed, and the rate of trapping within seagrass canopies was determined largely by the length and/or type of vegetation (Fig. 4).

Prior studies have found that the hydrodynamics within a mangrove have a strong influence on dissolved and particulate matter transportation. For example, Wolanski et al. (1998) released a tracer into the upper areas of a mangrove swamp. After 15 d the tracer was still trapped within the edge of the forest. Wave action within mangrove forests decreases from the seaward edge of the mangrove forest towards the landward edge (Koch et al. 2009). Wolanski et al. (1998) showed that particles became trapped in the inner mangrove. Our results are in agreement: we found that trapping capacity increased (from 15-33 % to 47-68 %; Fig. 1) in the absence of waves (i.e. within the mangroves).

The dispersal of leaves could also be related to the tide cycle, where leaves released at high tide may become stranded beyond the high tide line—as Allen & Krauss (2006) and Clarke (1993) found for mangrove propagules. We found that smaller leaves were less likely to be trapped by mangrove roots, suggesting that small leaf fragments—e.g. broken by degradation or animals (e.g. crabs)—will have a greater chance of transporting nutrients to other systems. For this experiment we used a simplistic structure of mangrove roots; however, root density and shape has huge variability within mangroves forests depending on location and species. We did not establish transportation for leaves at the bottom of the mangrove roots, which can be moved by either hydrodynamics or biological aspects such as crabs. Movement of leaves into the sediment has ecological importance and should be the focus for future work. The present work is limited to physical transport with tidal flow, as can be applied in a flume setup.

The capacity of the seagrass canopy to trap POM depended on the initial location where the leaf was released: i.e. on the surface of the water column or within the seagrass canopy. The flexible seagrass canopy did not hinder leaves that floated on the surface. However, if leaves became entangled within the seagrass canopy, they were more likely to be trapped. Settling velocities of 0.01 to 0.02 m s⁻¹ indicate that in shallow water, short collisions are sufficient to cause degraded leaves to settle. Previous work has shown that seagrass canopies can reduce the re-suspension of small particles from within a meadow by approximately 98 % (Terrados & Duarte 2000). Thus, once seagrass leaves are deposited within beds, they likely will not be remobilized. Gacia et al. (2002) showed that particulate organic carbon in seagrass bed sediment can be made up of 43 % of *Posidonia oceanica* material. In Kenya, up to 30 % was made up from *Thalassia hemprichii* derived particulate matter (Hemminga et al. 1994). In our experiment, the seagrass canopy occupied two-thirds of the water column. This canopy will undoubtedly increase the trapping efficiency compared

to seagrass species with very small canopies. Furthermore, tide height at the time of leaf release would affect trapping potential. For example, a spring tide would reduce trapping even with species of seagrass with long leaves if plants are completely submerged. In our experiment we mimicked the incoming/outgoing tide, as POM exchange may be expected to be highest during these periods.

To gain greater insight into the trapping capacity of mangrove forests and seagrasses canopies, further information should be obtained regarding the different types of leaves (both terrestrial and marine). It would be insightful to establish how different types of leaves are trapped and then transported through the bottom of a seagrass bed or mangrove forests. Chang et al. (2008) found that the longer a seed was in water, the higher the water content, and this decreased the seed's buoyancy. A similar mechanism may occur in leaves. Biofilms that form on leaves can change the physical surface of the leaf by making it more tacky (Lindow & Brandl 2003, Bogino et al. 2013). However, in our mimic ecosystems we did not have any biofilms on the roots or canopies (to our knowledge), which may have reduced trapping capacity by reducing this stickiness. Leaves or roots with a higher potential for biofilm colonisations may have a greater trapping potential. Storm events could result in the simultaneous shedding of many leaves. The transport of a cohort of leaves may change the retention capacity of the ecosystems. This was however outside the scope of the current study.

Both seagrass beds and mangrove forests have different distributions and species assemblage in clear zonation patterns. In addition, differences in density among various species related to zonation potentially affect leaf trapping capacity. For example, in mangrove forests many species at the seaward edge such as *Avicennia* sp. and *Rhizophora* sp. can have extensive horizontal and vertical roots plus pneumatophores (Giesen et al. 2006). These roots and pneumatophores will increase leaf trapping, but their location at the seaward edge means they may experience a relatively high wave action (Giesen et al. 2006, Koch et al. 2009). In contrast, landward mangroves may have a lower root and pneumatophore density but also less exposure to wave action (Giesen et al. 2006, Koch et al. 2009). The present study suggests wave action has a stronger effect on leaf trapping than root density, but it requires further research to fully understand the spatial aspects of root density and wave exposure for leaf trapping. Further, many pioneer seagrass species such as *Halodule* sp. and *Halophila* sp. at the edge of the seagrass bed have smaller leaves and therefore lower trapping potential. We recommend that future work should concentrate on degradation and nutrient-release rates of trapped leaves, and what this means for nutrient retention in the mangrove forest or seagrass bed. Data on trapped degraded leaves would allow us to understand the time scale of nutrient release from leaves. New research should focus on how anthropogenic and natural impacts reduce the density or change the zonation of mangrove forests and seagrass beds. Modeling efforts should focus at the landscape scale and especially take into account how ecosystem

fragmentation affects trapping capacity, nutrient retention and nutrient outwelling to adjacent ecosystems or the adjacent estuary.

4.5 Conclusion

Our research indicates that mangrove roots have a more efficient mechanism for trapping leaves than seagrass beds because their roots and pneumatophores extend through much of the water column the majority of the time. In contrast, seagrass beds require POM to become entangled within the bed. Thus, trapping is dependent on the state of the leaf (degraded and non-degraded) and the water depth. These results give an initial idea of what processes need to be parameterized when modeling the transportation of POM from and between ecosystems: density of roots, hydrodynamic conditions (absence/presence of waves), location of initial deposition, degradation stage and type of leaf. In the present study we primarily concentrate on the physical transport of POM with tidal flow rather than biological transport. Further work is required to understand how biological aspects such as movement by organisms or bacterial degradation may affect leaf litter transportation. Finally, this work strengthens the viewpoint that the trapping capacity of POM in mangrove forests and seagrass beds could have a significant effect on the potential of retaining nutrients in leaves within the ecosystem. Importantly, understanding the trapping capacity of mangrove forests and seagrass beds also supports modeling of outwelling from ecosystems to estuaries in the tropical coastal seascape.

Acknowledgments

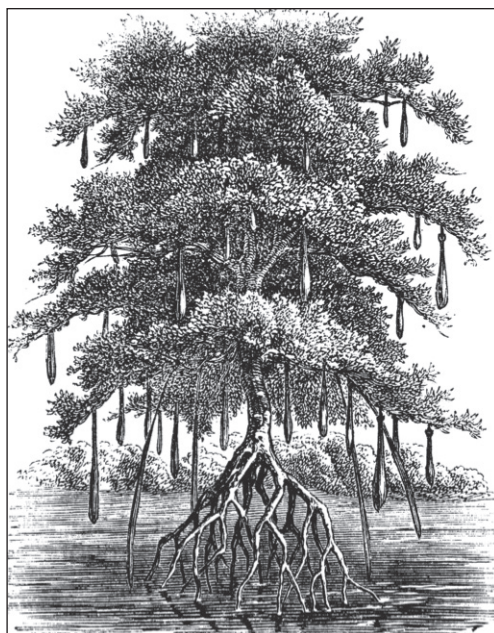
We would like to thank Achmad Arifin and Muhayar of the Research Centre for Oceanography-Indonesian Institute of Sciences for collection of the leaves used in the experiment. In addition the 4 anonymous reviewers for their constructive criticism. This work was funded by the Ecoshape/Building with Nature project.

Chapter 5

Land use effects on mangrove nutrient status in Phang Nga Bay, Thailand.

Jan-Willem Wolters, Lucy G. Gillis, Tjeerd J. Bouma, Marieke M. van Katwijk,
Alan D. Ziegler

STATUS: Submitted.



Abstract

Understanding the relationship between land use and the nutrient status of mangrove forests is important because the latter determines, in part, the amount of nutrients and sediment that is exported to adjacent marine ecosystems (e.g., seagrass beds and coral reefs). This study related land-cover distribution to mangrove nutrient status in several catchments in southwest Thailand. The investigation focused on indicators that integrate over relatively short time spans (i.e., porewater nutrient concentrations and sediment carbon & nitrogen content), as well as other indicators that integrate over longer time spans, including *Rhizophora apiculata* leaf carbon & nitrogen content & $\delta^{15}\text{N}$ signatures and the sesarmid crab *Parasesarma erythrodactyla* tissue $\delta^{15}\text{N}$ signature. Mangrove nutrient status was correlated with the degree of anthropogenic land use in the catchment. Nutrient availability was lowest in less-disturbed catchments with a high degree of natural vegetation cover; and it increased with higher levels of anthropogenic influence. Cleared and urban areas had a larger influence on mangrove nutrient status than other forms of land use, including plantations, rice paddies and shrimp and fish farms. All nutrient status indicators supported these correlations, but relationships were most profound for indicators that integrate over a longer period of time (i.e., *R. apiculata* leaves). Indicators that integrated over short time-spans (i.e., abiotic parameters) varied greatly between sites. Overall, the study showed that anthropogenic changes in land use clearly affect mangrove nutrient status.

Keywords: eutrophication, urbanization, South-East Asia, porewater, *Rhizophora apiculata*, sesarmid crab.

5.1 Introduction

Mangrove ecosystems play an important role in the tropical seascape by providing biotic and abiotic benefits to adjacent marine ecosystems, including seagrass beds and coral reefs. Biotic benefits may come in the form of providing a feeding habitat for animals that are not restricted to the mangroves themselves, such as fruit bats or fishes (Chong et al. 1990, Robertson & Duke 1990, Hogarth 1999). Mangroves also fulfil an important role as a nursery habitat for juvenile reef and seagrass fishes.

Abiotic benefits come in the form of coastal protection through the reduction of the hydrodynamic energy of incoming waves and currents (Othman 1994, Quartel et al. 2007). The intricate network of mangrove tree stilt roots, buttress roots, pneumatophores and stems provides resistance to flowing water, leading to a reduction in current velocity and the formation of flocs of suspended sediment that precipitate at slack tide. These processes result in the retention of sediment and associated nutrients within the mangrove forest (Eyre 1993, Furukawa & Wolanski 1996). They thereby aid in reducing turbidity in coastal waters, and thus, in maintaining sufficient light conditions required by sensitive seagrasses and coral ecosystems (Dennison & Alberte 1985, Telesnicki & Goldberg 1995). Another benefit of mangroves is that they absorb a part of the nutrients they receive from both oceanic and terrestrial sources, and in some cases, thereby protect adjacent seagrass beds and coral reefs from receiving excesses of nutrients (Boto & Wellington 1988, Dittmar & Lara 2001, Valiela & Cole 2002).

The capacity of mangrove forests to provide the aforementioned benefits partially depends on their nutrient status. Mangrove forests are generally nutrient-poor. It might therefore be expected that nutrients from external sources are at first taken up by the forest. In this way, the mangroves act as a buffer to protect adjacent marine ecosystems from an excess in nutrients. However, in cases of extreme nutrient enrichment, the buffering capacity may diminish. An increasing proportion of the received nutrients are then outwelled to the ocean (Boto & Wellington 1988, Dittmar & Lara 2001, Valiela & Cole 2002). Furthermore, nutrient enrichment in mangroves may lead to a relatively smaller biomass allocation to root structures (McKee 1995, Lovelock et al. 2009, Naidoo 2009). A decrease in root biomass results in fewer aerial root structures that can provide resistance to flowing water and facilitate sedimentation (Nepf 1999, Lopez & Garcia 2001, Bouma et al. 2009). It may be expected that nutrient-rich mangroves will therefore trap less sediment and absorb fewer nutrients than nutrient-poor mangroves. In such cases, the benefits they provide to adjacent systems will diminish.

Changes in catchment land use, particularly forest conversion to agriculture and urban areas, potentially affect nutrient status in downstream mangroves. For example, increased nutrient concentrations in the water column of streams and estuaries have been linked to

land use conversion. To our knowledge, however, no direct correlation between changes in land use and mangrove nutrient status has been determined to date. This study primarily focuses on the relationship between land use and nutrient status of mangrove forests on three islands in southern Thailand. We anticipated that the amount of available nutrients would be higher for catchments with greater anthropogenic activity. This hypothesis was based on the idea that compared with natural systems, disturbed catchments would export more nutrients, experience accelerated erosion and have a reduced capacity for nutrient retention (Vitousek & Melillo 1979, Reef et al. 2010). However, the study allows for an integrated, landscape-scale comparison of mangroves with differentially impacted catchments for tests of nutrient indicators operating at different time scales.

5.2 Assessing mangrove nutrient status

The nutrient status of the mangrove forests in this study was measured using a number of abiotic and biotic indicators of nutrient status that have different temporal periods of reference. These indicators include: (i) direct nutrient measurements, which display a large temporal variability (Lee & Joye 2006, Jennerjahn et al. 2009); (ii) composition of mangrove leaves, which reflects a longer period of nutrient uptake, ranging from around six months to a year (Boto & Wellington 1983, Feller et al. 2003); and (iii) sesamid crab muscle tissue stable isotope signature ($\delta^{15}\text{N}$), which is an indicator of nutrient status as it reflects on the stable isotope signatures of their various diet sources. Given the slow turnover rate of the muscle tissue, in the order of a few months (Gearing 1991, Raikow & Hamilton 2001, Lorrain et al. 2002), the muscle tissue provides a long term image of the isotopic signatures of the different food sources in crab diets and thus on the nutrient availability within the system.

Porewater from nutrient-rich mangrove forests was expected to contain more nutrients than porewater from nutrient-poor mangroves. It was furthermore hypothesised that sediment total organic carbon (TOC) and total nitrogen (TN) content would be higher in nutrient-rich mangroves due to the higher primary production and turnover rates in those areas (Machiwa 1998). In addition to these abiotic parameters, mangrove (*Rhizophora apiculata*) leaves were measured for TOC and TN content and stable isotope signature ($\delta^{15}\text{N}$), variables that reflect a longer period of nutrient uptake (Boto & Wellington 1983, Feller et al. 2003). The $\delta^{15}\text{N}$ signature of mangrove leaves is thereby related to nitrogen content (Fry et al. 2000, Teichberg et al. 2010; see below); and it also provides information on natural vs. anthropogenic origins of the nitrogen (Barile 2004, Lapointe et al. 2005). It might thus be expected that mangrove leaf TN content and $\delta^{15}\text{N}$ signature would be higher in mangroves leaves from nutrient-rich study sites because of the higher input of anthropogenic nitrogen at these locations. As a consequence, the C:N ratio was expected to be lower in those nutrient-rich study sites.

Finally, tissue stable isotope signatures of leaf eating sesarmid crabs (*Perisesarma erythrodactyla*), which were abundant in mangroves, were measured as an indicator of the stable isotope signatures of crab diets. The diet of leaf eating mangrove crabs consists mostly of mangrove leaf litter and other resources such as organic components of the sediment (degraded mangrove litter, microalgae and other microorganisms), encrusting algae on mangrove roots and small invertebrates (Linton & Greenaway 2007, Kristensen 2008). Because consumer stable isotope signatures reflects food source stable isotope signatures (Peterson & Fry 1987) it might be expected that a higher crab $\delta^{15}\text{N}$ indicate a higher $\delta^{15}\text{N}$ signature of the mangrove vegetation and detritus. This in turn provides information on the nutrient status of the mangrove forests and the origin of the nitrogen, because a high $\delta^{15}\text{N}$ signature is associated with high nitrogen contents and high inputs of anthropogenic nitrogen into the system.

The potential advantage of using a broad range of indicators that encompass multiple time-spans is that it may provide a more reliable view of the ecosystem, compared with an approach that only considers indicators of a similar time frame. However, we recognize that short-term indicators may be less reliable than their long-term counterparts for indicating nutrient status. Thus, a secondary focus of this study is determining which indicators are most effective for depicting nutrient status.

5.3 Study area

The study sites chosen in Phuket and Phang Nga provinces of southern Thailand provided good examples of mangrove forests with differing anthropogenic influences in their respective catchments areas. Field measurements were conducted in November 2011 in eight mangrove forests on the islands of Phuket, Yao Yai and Yao Noi (Figs. 1 & 2, Tab. 1). The mangroves were all classified as tidal, according to Woodroffe (1992). Seagrass beds were found adjacent to all study sites, although they were less developed for site 3. Coral reefs were only present next to the Koh Yao Yai sites 6 and 8.

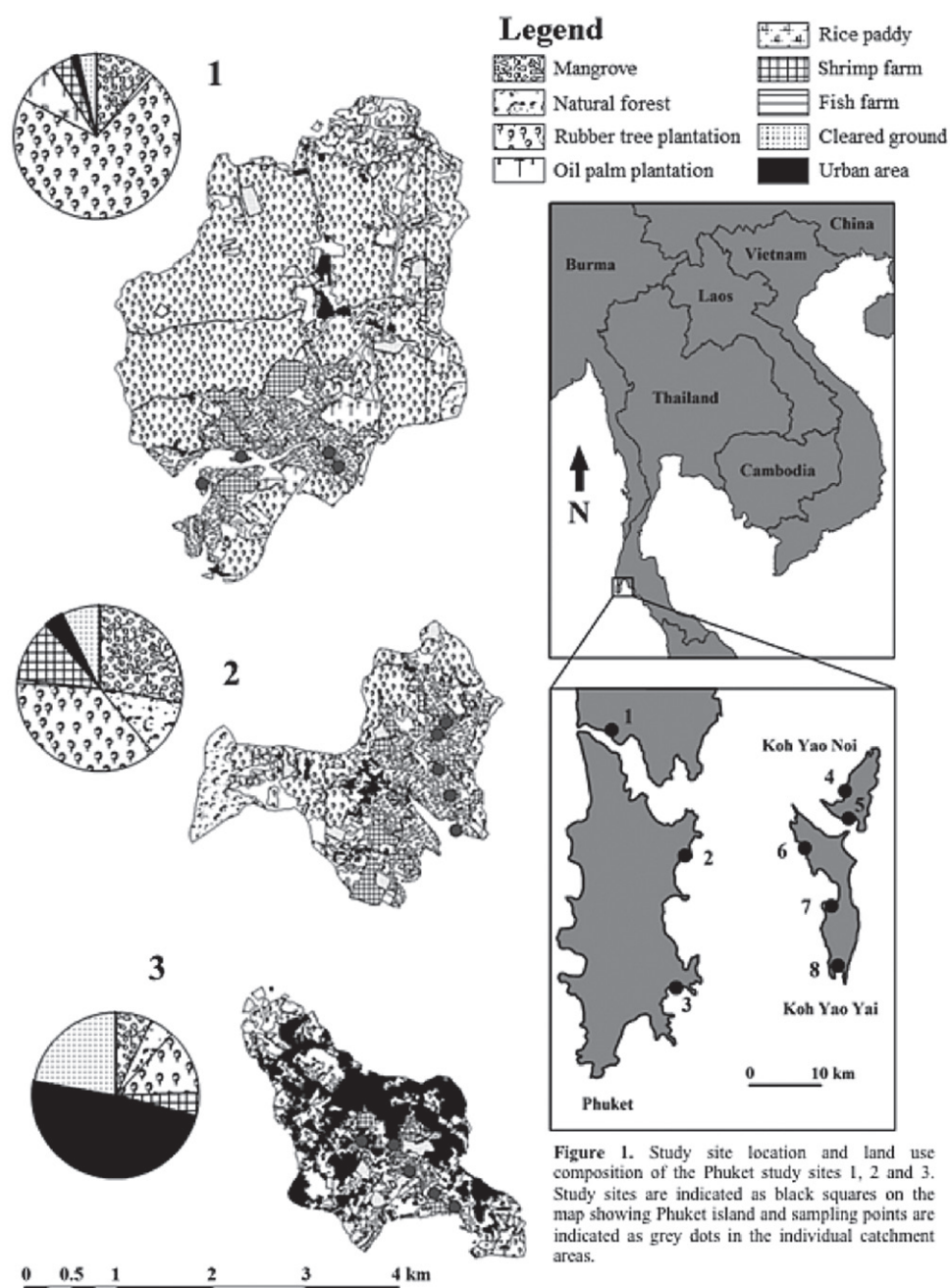


Figure 1. Study site location and land use composition of the Phuket study sites 1, 2 and 3. Study sites are indicated as black squares on the map showing Phuket island and sampling points are indicated as grey dots in the individual catchment areas.

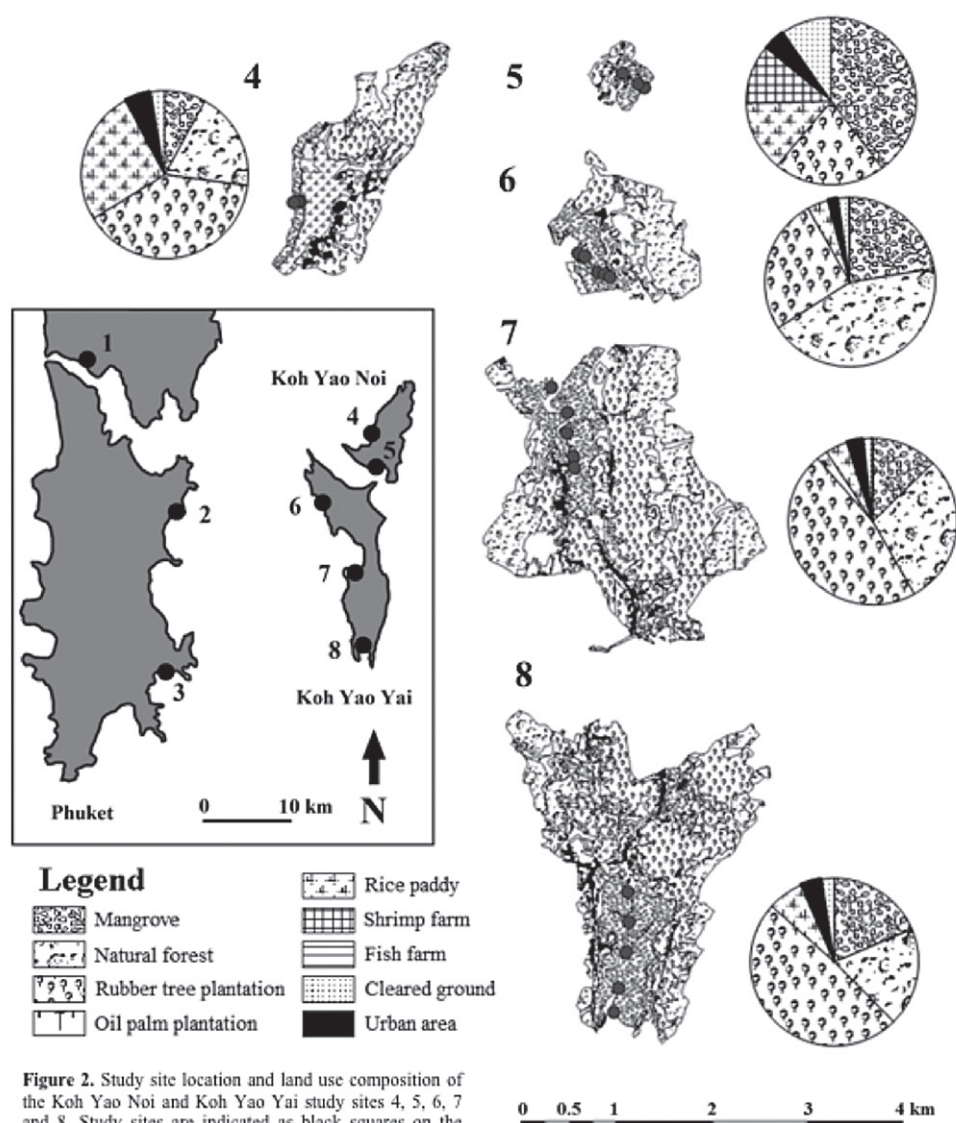


Figure 2. Study site location and land use composition of the Koh Yao Noi and Koh Yao Yai study sites 4, 5, 6, 7 and 8. Study sites are indicated as black squares on the map showing Phuket island and sampling points are indicated as grey dots in the individual catchment areas.

Table 1 Study site catchment area (km²) and catchment land use composition (%).

Site	Area	Mangrove	Natural forest	Rubber tree plantation	Oil palm plantation	Rice paddy	Shrimp farm	Fish farm	Cleared ground	Urban area
	(km ²)	(%)	(%)	(%)	(%)	(%)	(%)	(%)	(%)	(%)
1	29.6	11.0	0.9	70.7	8.2	0.2	4.1	$2.9 \cdot 10^{-3}$	3.5	1.3
2	9.9	27.8	11.2	37.1	0.7		12.0	$3.5 \cdot 10^{-2}$	7.3	3.8
3	8.1	7.0	4.7	12.7			4.5	$3.4 \cdot 10^{-2}$	22.2	48.8
4	4.7	8.0	19.1	39.2		26.0			2.7	5.1
5	0.6	39.7		21.3		13.5	11.4		9.7	4.4
6	3.2	22.4	43.6	25.8		4.0	$5.8 \cdot 10^{-2}$	$5.2 \cdot 10^{-2}$	2.2	1.9
7	12.3	12.6	29.3	46.8	2.1	4.2	$4.1 \cdot 10^{-2}$	$8.0 \cdot 10^{-3}$	1.8	3.1
8	11.3	18.6	19.0	49.0		6.9			2.4	4.1

The climate is monsoonal with a dry season from November to April and a wet season lasting from May to October. Mean annual rainfall and temperature are 2300 mm and 28 °C, respectively. At the time of study, the land use on all three islands was largely natural forest and rubber plantations, particularly in the more mountainous areas and on steep slopes. Other land use included rice paddies, shrimp and fish farms, cleared ground and urbanized areas. Rubber tree plantations and tourism (the latter particularly in Phuket) have largely replaced tin mining as a major source of income in the area. Phuket island was more developed and urbanized than the other two islands, of which Koh Yao Noi was more developed than Koh Yao Yai. During the last few years the entire study area has become more developed, with increasing urbanization, agriculture encroaching into terrestrial forest and shrimp farms encroaching on mangrove forests.

5.4 Materials and methods

5.4.1 Catchment area land use composition and measuring points

The borders of the catchment area of each study site were delineated in ArcMap Geographic Information Services (GIS) v.9.2, using the digital elevation data from the area. Using Quickbird, WorldView-1 and WorldView-2 satellite imagery, the land use in the catchment area was determined. The land use in the catchment area was classified as mangrove forest, natural terrestrial forest, rubber or palm oil plantations (henceforth mentioned as plantations), rice paddies, shrimp and fish farms, cleared land or urban areas.

At each of the five study sites, measuring points were located along the tidal creek running through the mangrove forest, ranging from the most seaward point where the creek reaches the ocean (0 % up the tidal creek) through the most landward point where the creek

begins (100 % up the tidal creek) and three points in between (25, 50 and 75 %). Sites were sampled, starting at the interior of the forest at high tide then following the retreating tide seaward. All measuring points were located within 10 m of the tidal creek in the forest. Indicators were only measured at three points (0, 50 and 100 %) at sites 4 and 5 due to the small size of the mangroves in those areas. The most seaward point at site 1 was also not measured due to high tide levels.

5.4.2 *Mangrove forest nutrient status*

5.4.2.1 Abiotic parameters: porewater and sediment sampling

Three replicate porewater samples were collected at each measuring point from the upper 10 cm of the sediment, in the active root zone at each measuring point using tension lysimeters. Samples (between 50 and 100 ml) were stored in polyethylene containers and transported to the field laboratory. Samples were analysed for nitrate (NO_3^-), nitrite (NO_2^-), silica (SiO_2) and ortho-phosphate (PO_4^{3-}), using a DR2800 portable spectrophotometer (Hach Lange GmbH, Germany) and Hach Lange powder pillows. Porewater NO_3^- , NO_2^- , SiO_2 and PO_4^{3-} were measured with the Cadmium reduction, Diazotization, Silicomolybdate and the PhosVer 3 (Ascorbic Acid) methods respectively (Hach Lange GmbH, Germany).

Three sediment cores were also collected at each measuring point by inserting handheld PVC core 5 cm into the sediment. These samples were then oven-dried in the field laboratory at 60-70 °C for at least 48 hours before they were stored temporarily. Within a month, the samples were taken to NIOZ Yerseke, the Netherlands for analysis. The samples were first ground, using a mixer mill (Retsch, type MM301), after which the carbonates were removed by acidification. Samples were then measured for total organic carbon (TOC) and total nitrogen (TN) content using a Flash EA 1112 Elemental Analyzer (Thermo Finnigan).

5.4.2.2 Mangrove leaf samples

Three green leaf and three brown leaf samples were collected at each measuring point. Each sample consisted of five *R. apiculata* leaves that were either handpicked from five separate living mangrove trees (i.e. green leaves), of heights ranging from 3 to 7 m or collected from the water and sediment (i.e. brown leaves). Before further analyses, brown leaves were rinsed with water to remove any attached sediment. The samples were oven-dried in the field laboratory, at 60-70 °C for at least 48 hours before they were stored and transported within a month to the NIOZ. The leaves were ground, using a mixer mill (Retsch, type MM301), and TOC and TN were measured using a Flash EA 1112 Elemental Analyzer (Thermo Finnigan). ^{15}N stable isotopes of the green leaf samples were measured using a Delta V Advantage

isotope ratio mass spectrometer (Thermo Finnigan) that was coupled, via a ConFlo III interface (Thermo Finnigan), to the Flash EA 1112 Elemental Analyzer (Thermo Finnigan).

5.4.2.3 Mangrove crab isotopes

Three to five individuals of the sesamid crab *P. erythrodactyla*, with a carapace width ranging from 10 to 25 mm, were hand caught at the majority of measuring points. Fewer crabs were caught at the most seaward measurement points, which were often inundated and seldom showed signs of crab presence. No crabs were caught at sites 1 and 4 due to high tide levels. Crabs were taken to the field laboratory where they were dissected. Only muscle tissue was extracted for isotope analysis. Structures such as the hepatopancreas and gonad tissue were avoided because they have high turnover rates and are therefore less reliable for reflecting the long-term $\delta^{15}\text{N}$ signature of the crab's diet. Muscle tissue was rinsed with deionized water and oven-dried at 60-70 °C for at least 48 hours. Samples were then stored dry and transported to NIOZ. The ^{15}N stable isotope signature was determined using the same methods as described for the green *R. apiculata* leaves.

5.4.3 Statistical analysis

The Shapiro-Wilk test was used to verify that measured parameters were normally distributed, although the power of the test was low due to the small sample size. Data were then checked for equality of error variances using Levene's test. Significant differences between groups were assessed using one-way ANOVA with a Tukey post-hoc test for equal variances or using a Welch test and a Games-Howell post-hoc test for non-equal variances. Relationships between different parameters were defined using the Pearson correlation coefficient and tested for significance using a two-tailed t-test.

Multivariate analyses of the different measured parameters ('response variables') and the land use in the catchment area ('explanatory variables') were performed in Canoco for Windows version 4.5. Because the response curve of the response variables could be best described by a linear response model rather than a unimodal model, principal component analysis (PCA) was performed. Occasional missing values were substituted by median values, after ter Braak & Smilauer (2002).

5.5 Results

5.5.1 Abiotic parameters, vegetation and fauna measurements

Porewater, sediment, *R. apiculata* leaves and *P. erythrodactyla* tissue parameters displayed great variability among sites (Tab. 2). Abiotic parameters varied more among sites (sometimes even a factor 10), than biotic parameters. A few significant relationships were observed

regarding nutrient availability within sites 3, 6, 7 and 8. Porewater nitrate, ortho-phosphate and silicate increased significantly further landward in site 3, 7 and 8 respectively ($r = 0.93$, $p = 0.022$, $r = 0.89$, $p = 0.043$, $r = 0.908$, $p = 0.033$ respectively, data not shown). Brown *R. apiculata* leaf TOC content and sediment C:N ratio decreased significantly further landward in sites 6 and 8 respectively ($r = -0.903$, $p = 0.036$, $r = -0.931$, $p = 0.022$ respectively, data not shown). Furthermore, the positive relationship between mangrove leaf $\delta^{15}\text{N}$ signature and nitrogen content, which is often cited in literature, was also found during this study ($r = 0.389$, $p = 0.021$, data not shown).

Table 2 Site average for all measured parameters, values are presented as mean $\pm$ S.E. Different letters indicate significant differences between sites at $p \leq 0.05$.

Variables	Study site							
	1 Phuket	2 Phuket	3 Phuket	4 Koy Yao Noi	5 Koy Yao Noi	6 Koy Yao Yai	7 Koy Yao Yai	8 Koy Yao Yai
Porewater nutrients								
Nitrate (μM)	0.40 $\pm$ 0.17	0.15 $\pm$ 0.05	0.16 $\pm$ 0.05		0.41 $\pm$ 0.19	0.24 $\pm$ 0.07	0.22 $\pm$ 0.08	0.25 $\pm$ 0.11
Nitrite (μM)	0.29 $\pm$ 0.10	0.30 $\pm$ 0.09	0.27 $\pm$ 0.10		0.11 $\pm$ 0.03	0.19 $\pm$ 0.04	0.12 $\pm$ 0.04	0.15 $\pm$ 0.03
Silicate (μM)	136.25 $\pm$ 27.39	96.21 $\pm$ 17.57	70.95 $\pm$ 12.59		212.92 $\pm$ 35.85	87.1 $\pm$ 14.42	149.62 $\pm$ 42.70	143.83 $\pm$ 32.60
Ortho-phosphate (μM)	23.31 $\pm$ 5.93 ^a	15.76 $\pm$ 4.32 ^{abc}	17.46 $\pm$ 4.18 ^{ac}		5.55 $\pm$ 2.30 ^{bc}	2.61 $\pm$ 0.33 ^b	6.03 $\pm$ 1.98 ^{bc}	7.42 $\pm$ 4.84 ^{bc}
Sediment								
Organic C (%)	2.57 $\pm$ 0.44	4.98 $\pm$ 0.39	2.20 $\pm$ 0.37	1.61 $\pm$ 0.47	3.09 $\pm$ 1.50	3.86 $\pm$ 0.42	2.83 $\pm$ 0.32	2.19 $\pm$ 0.21
Total N (%)	0.13 $\pm$ 0.03 ^{ab}	0.22 $\pm$ 0.01 ^a	0.11 $\pm$ 0.01 ^b	0.06 $\pm$ 0.01 ^b	0.13 $\pm$ 0.06 ^{ab}	0.17 $\pm$ 0.02 ^{ab}	0.13 $\pm$ 0.02 ^{ab}	0.11 $\pm$ 0.01 ^{ab}
C:N ratio	20.36 $\pm$ 1.08	22.16 $\pm$ 0.87	19.36 $\pm$ 1.18	23.60 $\pm$ 5.32	17.64 $\pm$ 2.47	23.35 $\pm$ 1.11	21.02 $\pm$ 0.54	20.45 $\pm$ 1.57
Brown <i>R. apiculata</i> leaves								
Organic C (%)	42.25 $\pm$ 0.79	41.06 $\pm$ 0.33	41.14 $\pm$ 0.33	42.29 $\pm$ 0.53	40.87 $\pm$ 0.35	41.89 $\pm$ 0.31	41.36 $\pm$ 0.26	41.61 $\pm$ 0.36
Total N (%)	0.30 $\pm$ 0.01 ^a	0.33 $\pm$ 0.01 ^{ab}	0.42 $\pm$ 0.02 ^b	0.39 $\pm$ 0.01 ^{ab}	0.29 $\pm$ 0.02 ^{ab}	0.32 $\pm$ 0.01 ^a	0.35 $\pm$ 0.02 ^{ab}	0.34 $\pm$ 0.01 ^{ab}
C:N ratio	142.79 $\pm$ 5.45 ^a	129.11 $\pm$ 5.33 ^a	99.96 $\pm$ 4.03 ^b	123.48 $\pm$ 13.12 ^{ab}	147.70 $\pm$ 13.37 ^a	130.94 $\pm$ 2.94 ^a	122.44 $\pm$ 5.15 ^{ab}	124.03 $\pm$ 2.22 ^{ab}
Green <i>R. apiculata</i> leaves								
Organic C (%)	41.49 $\pm$ 0.60	41.79 $\pm$ 0.76	41.18 $\pm$ 0.34	42.35 $\pm$ 0.32	42.17 $\pm$ 0.50	42.25 $\pm$ 0.41	42.15 $\pm$ 0.37	42.02 $\pm$ 0.27
Total N (%)	1.05 $\pm$ 0.06	0.95 $\pm$ 0.05	1.11 $\pm$ 0.05	1.01 $\pm$ 0.04	0.94 $\pm$ 0.06	0.91 $\pm$ 0.05	0.90 $\pm$ 0.05	1.08 $\pm$ 0.04
C:N ratio	41.27 $\pm$ 2.50	44.37 $\pm$ 1.59	37.96 $\pm$ 1.78	42.33 $\pm$ 1.50	46.19 $\pm$ 3.34	48.19 $\pm$ 2.50	49.36 $\pm$ 3.73	39.76 $\pm$ 1.56
$\delta^{13}\text{C}$ (‰)	-31.86 $\pm$ 0.49	-31.56 $\pm$ 0.27	-31.31 $\pm$ 0.44	-29.26 $\pm$ 0.45	-29.54 $\pm$ 0.64	-31.89 $\pm$ 0.32	-31.46 $\pm$ 0.34	-31.49 $\pm$ 0.37
$\delta^{15}\text{N}$ (‰)	3.80 $\pm$ 0.39 ^{ab}	3.18 $\pm$ 0.30 ^a	5.75 $\pm$ 0.83 ^b	3.76 $\pm$ 0.31 ^{ab}	2.76 $\pm$ 0.45 ^a	2.78 $\pm$ 0.19 ^a	3.19 $\pm$ 0.15 ^a	2.77 $\pm$ 0.22 ^a
<i>P. erythrodactylus</i> tissue								
$\delta^{13}\text{C}$ (‰)		-26.17 $\pm$ 1.49	-24.91 $\pm$ 2.03		-25.75 $\pm$ 3.53	-24.51 $\pm$ 0.26	-22.23 $\pm$ 1.68	-22.80 $\pm$ 2.09
$\delta^{15}\text{N}$ (‰)		8.81 $\pm$ 0.76 ^a	8.83 $\pm$ 0.24 ^a		4.48 $\pm$ 0.29 ^b	6.00 $\pm$ 0.12 ^b	6.65 $\pm$ 0.38 ^{ab}	4.79 $\pm$ 0.51 ^b

5.5.2 Relationship between land use and mangrove nutrient status

Significant linear correlations were found between total area occupied by certain forms of land use and parameters indicative of nutrient status (Tab. 3). Following the literature (see Introduction), brown *R. apiculata* leaf C:N ratios and green *R. apiculata* leaf TOC & C:N ratios were classified as parameters that decrease under nutrient-rich conditions in Tab. 3. Porewater ortho-phosphate concentrations, sediment TOC & TN, brown *R. apiculata* leaf TN and green *R. apiculata* leaf TN & $\delta^{15}\text{N}$ were on the other hand classified as parameters that increase under conditions of nutrient enrichment.

Table 3 Pearson's r values for all significant linear relationships between the percentage of a particular type of land use in the catchment area and parameters indicative of nutrient status. All presented relationships were found to be significant at the $p \leq 0.05$ level, while relationships with asterisks were significant at the $p \leq 0.01$ level. Only parameters and (combinations of) forms of land use for which significant relationships were found are shown.

	Parameters indicative of nutrient-poor conditions			Parameters indicative of nutrient-rich conditions				
	Green leaf org C	Green leaf C:N ratio	Brown leaf C:N ratio	Porewater PO_4^{3-}	Sediment N	Green leaf N	Green leaf $\delta^{15}\text{N}$	Brown leaf N
Natural Forest (NF)	0.790	0.766		-0.942**				
Mangrove (M)+NF	0.725	0.762		-0.860		-0.767	-0.746	
M+NF+Plantation (P)							-0.785	
Rice Paddy (RP)					-0.813			
Cleared ground (C)	-0.717						0.788	
Urban area (U)			-0.782				0.902**	0.728
C+U	-0.722		-0.718				0.883**	

The *R. apiculata* leaf were the only indicators that also showed significant relationships with anthropogenically impacted forms of land use like cleared and urban areas. The abiotic indicators had less significant relationships with land use, while *P. erythrodactyla* tissue $\delta^{15}\text{N}$ showed none at all (Tab. 3).

Area increases of anthropogenically impacted landscapes, in particular cleared and urban areas, were generally positively correlated with indicators of nutrient-rich conditions such as high *R. apiculata* leaf $\delta^{15}\text{N}$ values. Furthermore, the area occupied by urban and cleared lands was negatively correlated with indicators of nutrient-poor conditions, such as a high *R. apiculata* leaf TOC content and C:N ratio (Tab. 3). In contrast, mangrove and natural forest areas were positively correlated with indicators of nutrient-poor conditions such as a high *R. apiculata* leaf TOC content and C:N ratio. The area occupied by mangrove and natural forest was negatively correlated with porewater ortho-phosphate concentrations, *R. apiculata* leaf TN content and $\delta^{15}\text{N}$ signature, indicators of nutrient-rich conditions. No significant relationships were found for palm oil plantations, rubber plantations and aquaculture (shrimp and fish farms).

The principal component analysis provided further distinction between natural and anthropogenically-impacted land uses (Fig. 3). Mangroves and natural forests are situated in the upper left quadrant of the plot together with indicators of nutrient-poor conditions, including a high green and brown *R. apiculata* leaf C:N ratio. Anthropogenically impacted

land uses, such as cleared and urban areas, were located on the opposite side, in the lower right part of the plot. Indicators of nutrient-rich conditions, such as high porewater orthophosphate concentrations, were also positioned in this section of the plot. These findings illustrate the correlations between land use and nutrient status elaborated in the previous paragraph (Tab. 3). Agricultural land uses, including plantations and rice paddies, plot in the lower left section. Thus, they show more similarity with natural forms of land use than with cleared and urban areas. Silicate and nitrate also plot in this section. The first two PCA-axes in this plot explained 63 % of the variation in response data.

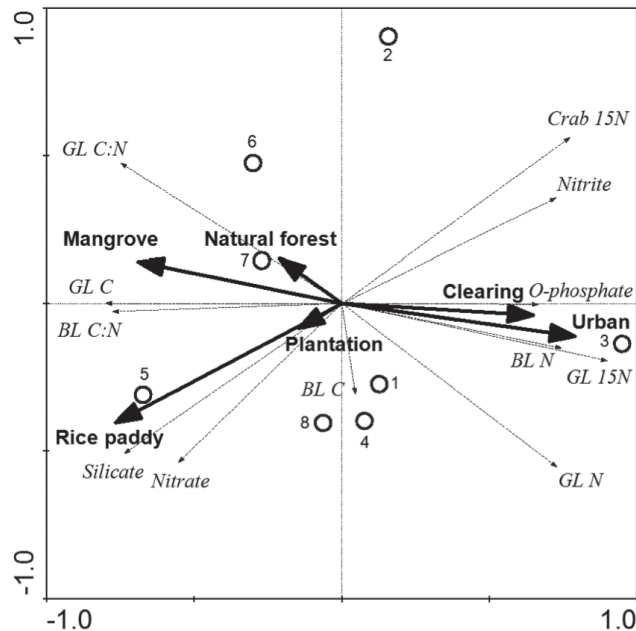


Figure 3 PCA triplot of the parameters indicative of nutrient status (dotted arrows) and the types of land use (solid arrows), the study sites are indicated as circles. GL and BL represent green and brown *R. apiculata* leaves and C and N carbon and nitrogen. Crab 15N represents *P. erythrodictyla* tissue stable isotope signature. Only the forms of land use which have significant relationships with parameters indicative of nutrient status are shown.

5.7 Discussion

To our knowledge this is the first study relating mangrove nutrient status to catchment land use. Understanding this relation is important because many of the services that mangroves provide to adjacent coastal ecosystems (e.g. seagrass beds and coral reefs) are potentially less effective under nutrient-rich conditions (e.g. Valiela & Cole 2002). Our results show that nutrient availability was lowest in catchments with higher coverage of natural vegetation (mangroves and natural forests). A higher availability of nutrients was associated with increasing levels of anthropogenic influence in the catchment area, such as land clearing and

urbanization. Nutrient availability of areas influenced by plantations, rice paddies and shrimp and fish farms was positioned between these two extremes.

Because the Phuket sites are generally richer in nutrients than the Koh Yao Noi and Koh Yao Yai sites, region specific effects might also be cited as the origin of the differences in nutrient status among the different sites (i.e. the Phuket sites are richer in nutrients because the surrounding ocean in that region is richer in nutrients because of runoff). Porewater ortho-phosphate concentrations indeed support this alternative hypothesis but other parameters that integrate over longer time-spans show fewer region-specific patterns. The PCA plot (Fig. 3) also shows that study sites 1, 4 and 8 (located on Phuket, Koh Yao Noi and Koh Yao Yai respectively) are more similar to each other than to the other study sites in the respective region. This finding further indicates that site-specific effects are more important than regional effects in determining the nutrient status of the mangroves. Furthermore, study sites from a specific region were not found to have a significantly different land use composition than sites from another region (Figs. 1 & 2, Tab. 1). Finally, the spatial spread of the different indicator values indicate that landward points are generally richer in nutrients than seaward points, thereby suggesting that nutrients mostly originate from the catchment area, not from the surrounding ocean. It can thus be concluded, because of the relatively even spread of the different forms of land use and data from various long-term nutrient status indicators that the differences in nutrient status among sites were caused by site specificity and not regional phenomena.

The results of this study stress the importance of the selection of appropriate nutrient status indicators. The TOC and TN content and $\delta^{15}\text{N}$ signature of *R. apiculata* leaves correlated the most with land use. *P. erythrodactyla* $\delta^{15}\text{N}$ signature displayed the same correlations with land use as found for *R. apiculata* leaves. These correlations however were only significant for the mangrove leaves. The abiotic indicators that integrated over shorter time-spans (i.e. porewater nutrients and sediment TOC and TN content) displayed the least correlations with the surrounding land use. These parameters tend to fluctuate over time, and they are therefore less reliable as long-term indicators of nutrient status (e.g. Lee & Joye 2006, Jennerjahn et al. 2009).

5.7.1 Relationship between land use and mangrove nutrient status.

The general trends, supported by all analyses, were that mangroves in catchments with substantial natural land cover conversion show increased nutrient availability and mangroves situated in less disturbed catchments displayed lower nutrient availability (Tab. 3, Fig. 3).

The area of mangroves and natural forest in the catchment was found to be positively correlated with mangrove leaf TOC and C:N ratio and negatively correlated with porewater phosphate concentrations, leaf TN and $\delta^{15}\text{N}$ signature. These relations indicate lower nitrogen

and phosphorus availability as well as a lower input of anthropogenic nitrogen. This suggests that these natural land use forms export fewer nutrients and are more efficient in retaining them (Vitousek & Melillo 1979, Reef et al. 2010).

Rubber and palm oil plantations in the catchment were also found to be correlated with nutrient-poor conditions in mangroves, although PCA analysis indicated this effect was not as profound as that caused by the presence of forest area (Fig. 3). Plantations at the study sites are therefore expected to export very few nutrients to the adjacent mangrove forests. Based on previous studies, rice paddies were expected to create nutrient-rich conditions in downstream mangroves by nitrogen leaching into the surrounding ecosystems (Choudhury & Kennedy 2005). However, our study showed no correlation between rice paddy area and indicators of mangrove nutrient status. This lack of correlation is possibly due to low fertilizer inputs during rice cultivation. The statistically insignificant positive correlation between plantation area and porewater nitrate and silicate concentrations observed in the PCA plot was not expected and the source of the correlation is unknown. Nitrate and nitrite are relative minor forms of nitrogen in mangroves and they are not expected to reflect great changes in the system. Ammonium was not measured during this study.

The amount of cleared or urbanized area was negatively correlated with *R. apiculata* leaf TOC and C:N ratio. It was also positively correlated with mangrove leaf nitrogen content and $\delta^{15}\text{N}$ signature. These correlations reflect a higher nitrogen availability, which was probably created by inputs of anthropogenic nitrogen. In general, urban areas are often a major source of nutrient enrichment of coastal areas and mangroves. Correlations between the area of cleared land and nutrient availability are probably related to increased surface runoff following clearance and reduced soil infiltrability. It should be noted that these correlations are mainly caused by the very high amounts of urban and cleared area from study site 3, a phenomenon that we did not observe for other forms of land use and other study sites. The lack of relationships between mangrove nutrient status and the area devoted to shrimp and fish farming was surprising. These types of aquaculture are recorded to export nutrients originating from applied shrimp feed or trash fish to surrounding ecosystems (Briggs & Funge-Smith 1994, Wu 1995, Hogarth 1999). It may be that the area devoted to these practices, or the intensity in which they are operated, is not sufficient to effect mangrove nutrient status at our sites. Prior research in the study area (site 2) also observed that shrimp farms had a very limited impact on mangrove nutrient status (e.g. Holmer et al. 2001, Kristensen & Suraswadi 2002). Other complicating factors, such as the position of aquaculture in the tidal creek and the temporal variability in nutrient loading, may also influence the magnitude of the aquaculture impact on the mangroves.

5.8 Management implications and recommendations

This study shows that nutrient status in mangrove forests is correlated with the degree of anthropogenic land use in the catchment. Nutrient availability was lowest in catchments with a high coverage of natural vegetation, and increased in catchments with a high degree of anthropogenic disturbance. These results show the potential for population increases and urbanization in Southeast Asia to cause nutrient enrichment in mangrove forests.

Increases in nutrient availability within mangroves not only have great effects on the forests themselves, but also potentially on adjacent ecosystems. In nutrient-enriched mangroves, a smaller portion of the received nutrients can be absorbed by the trees, thus more is exported to the ocean. The amount of exported sediment may also increase because the relative biomass allocation to root structures, which provide resistance to flowing water and thus facilitate sedimentation, decreases as a result of nutrient enrichment. These changes mainly affect the adjacent seagrass meadows and coral reefs, ecosystems that are already stressed by habitat destruction and ocean changes related to global warming. Our study shows that (1) for an optimal protection of mangrove forests, seagrass beds and coral reefs anthropogenic impacts on catchment land use should be minimized, and (2) the nutrient content and stable isotope signature of mangrove leaves are a suitable indicator to identify nutrient enrichment in mangrove forests.

Acknowledgements

Our thanks go to Kalaya Kantawong, Nam Wani, Boonchai Phrathaan and Bedeen Phrathaan for their logistic help with the fieldwork in Thailand and to the NIOZ analysts for the laboratory measurements. This study was funded by the Building with Nature project (NUS SDWA Grant #R303-001-020-414). The first author would also like to thank the Nijmegen University Fund for providing an individual travel grant.

Chapter 6

First experimental evidence of corals feeding on seagrass matter.

Lai S, Gillis LG, Mueller C, Bouma TJ, Guest JR, Last KS, Ziegler AD and Todd PA.

STATUS: Published at Coral Reefs.



Abstract

We present the first experimental evidence of a coral (*Oulastrea crispata*) ingesting and assimilating seagrass material. Tropical seagrass meadows export a substantial portion of their productivity and can provide an important source of nutrients to neighboring systems such as coral reefs; however, little is known about the mechanisms of this link. To investigate whether seagrass nutrient uptake via coral heterotrophy is possible, we conducted a feeding experiment with seagrass particulate and dissolved organic matter. Using gut extractions and stable isotope analyses, we determined that *O. crispata* ingested ^{15}N -enriched seagrass particles and assimilated the nitrogen into its tissue at a rate of $0.75 \mu\text{g N cm}^{-2} \text{h}^{-1}$. Corals took up nitrogen from dissolved matter at a comparable rate of $0.98 \mu\text{g N cm}^{-2} \text{h}^{-1}$. While other ecological connections between seagrass meadows and reef ecosystems are well known, our results suggest a previously unstudied direct nutritional link between seagrasses and corals.

Keywords: Seagrass, Coral heterotrophy, habitat connectivity, nutrient transfer.

6.1 Introduction

The interconnectivity between seagrass meadows, coral reefs and mangrove forests is known to be important for maintaining the health of these key habitats (Mumby et al. 2004, Dorenbosch et al. 2007). Research into nutrient connectivity from tropical seagrass meadows to coral reefs and mangroves has focused mainly on faunal migration or fauna-associated nutrient transport (Dorenbosch et al. 2007, Unsworth et al. 2008). Nutrient export from seagrass meadows via faunal intermediates, however, is generally thought to be less important than the quantities transported directly in seagrass material (Hemminga et al. 1991). Seagrass litter is exported in large quantities from seagrass meadows to other habitats, where it can be a significant nutrient source (de Boer 2000). Estimates place the percentage of net primary productivity exported from seagrass meadows at up to 77.34 %, with an additional contribution from dissolved organic matter (DOM) leaching from living and dead plant material (see Heck et al. 2008 for review). However, little is known about the mechanisms of coral uptake of nutrients from seagrass-derived organic matter, which is puzzling given the possible significance of such a relationship. Organic matter and nutrients from seagrasses can subsidise the metabolic needs of corals and may even promote growth and reproduction. While much of these requirements are derived from autotrophic symbiotic algae, corals also feed on a variety of planktonic organisms, with heterotrophy contributing substantially to their energy budget (see Houlbrèque & Ferrier-Pagès 2009). Osinga (2012) recently demonstrated that growth in the coral *Pocillopora damicornis* increased after being fed the marine diatom *Tetraselmis suecica*, highlighting that corals can derive nutrients from ingested phytoplankton. This result portends that seagrass matter could be eaten by corals and contribute to their growth. The discovery of a brush border enzyme pathway in the stony coral *Stylophora pistillata*, a pathway which invertebrates breaks down carbohydrates and peptides (Osinga 2012), further supports this notion. Given the large quantity of organic matter exported by seagrass meadows, their common occurrence near coral reefs in tropical regions (Short et al. 2007), and the propensity for corals to ingest particulate matter, it is entirely plausible that corals can and do acquire nutrients by feeding on seagrass material. We investigated a previously untested source of nutrient uptake in corals, direct ingestion of seagrass particulate matter, and compared it to the uptake rates of seagrass dissolved matter. We conducted a feeding experiment on the coral, *Oulastrea crispata*, and seagrass, *Halophila ovalis*, using a particle-suspension chamber. Through gut extractions and stable isotope analyses, we determined the extent to which corals assimilate nitrogen from seagrass material.

6.2 Materials and methods

6.2.1 Study species

In November 2012, 27 fragments (3–5 cm in diameter) from separate colonies of zebra coral, *O. crispata* (Fig. 1a), were collected from the south-west shoreline of mainland Singapore (1°18'44 N, 103°59'35 E). These fragments were acclimatised in a semi-indoor aerated aquarium at the National University of Singapore for 1 week. Approximately 800 g of seagrass *H. ovalis* were collected from a nearby island, Pulau Tekukor (1°13' 54 N, 103°50'12 E), and maintained in the same facility. The NH_4Cl (99 % ^{15}N , Cambridge Isotope Laboratories) to a concentration of $20\ \mu\text{mol L}^{-1}$; and a doubled concentration of $40\ \mu\text{mol L}^{-1}$ was applied 1 day before the experiment.

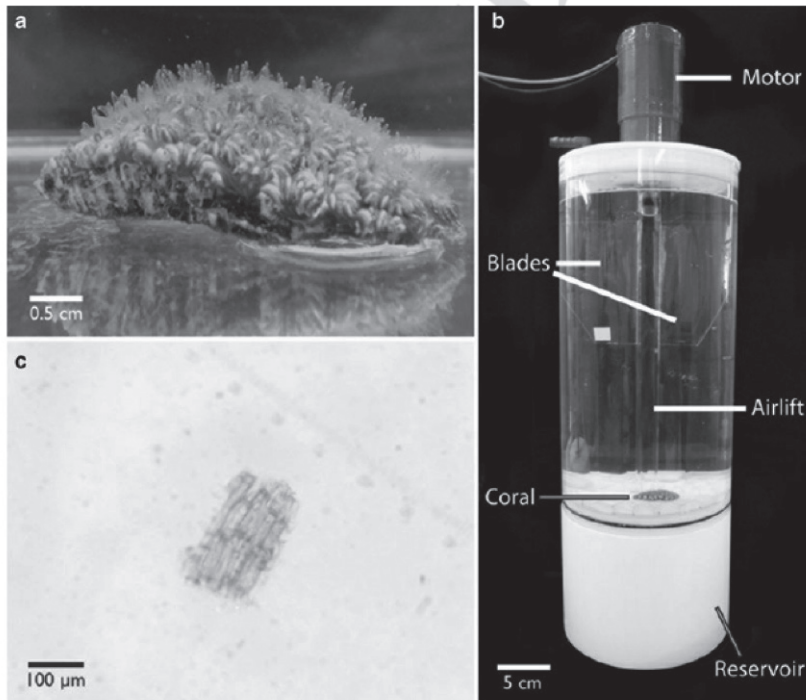


Figure 1 A *Oulastrea crispata* fragment with tentacles extended, b feeding chamber with coral, c seagrass particle extracted from the gut of a specimen in the POM treatment.

6.2.2 Preparation of seagrass POM and DOM

To create the feeding suspension of particulate organic matter (POM) and DOM, 200 g of rinsed seagrass (wet weight) was blended with 400 mL of sand-filtered seawater for 1 min. The suspension was sieved to obtain particulate sizes ranging from 75 to 500 μm for the POM, leaving the filtrate for the DOM solution. The POM was re-suspended in 400 mL

of seawater, centrifuged for 5 min at 6,000 rpm and decanted to remove the dissolved matter in the supernatant. This was repeated three times to remove as much dissolved matter as possible, so as to ensure that the great majority of the isotopic label was from the seagrass particles only (see Anthony 1999). The residue was then re-suspended in 800 mL of filtered seawater for the experiment. The DOM filtrate was further passed through a 20- μ m filter to remove more particles, and centrifuged three times for 5 min at 6,000 rpm, retaining only the supernatant each time. The POM and DOM solutions were refrigerated between each feeding experiment.

6.2.3 Coral feeding

Nine coral fragments were randomly assigned to individual feeding chambers filled with 5 L of sand-filtered seawater. The chambers, based on Davies et al. (2009), employed air-lifts to re-suspend particulate matter and rotating paddles to provide constant water flow (Fig. 1b). After 1 h of acclimatisation, 100 mL of the seagrass POM suspension was added to three randomly selected chambers, 100 mL of DOM was added to another three, and 100 mL sand-filtered seawater was added to the remaining three as the control. The average concentration of POM in the feeding chambers were 0.72 g L^{-1} ($\text{SD} \pm 0.01$) (dry weight) and had an average atom % N of 0.02 % ($\text{SD} \pm 0.01$). DOM concentration was 0.73 g L^{-1} ($\text{SD} \pm 0.01$), and average atom % N was 0.08 % ($\text{SD} \pm 0.02$). Corals were allowed to feed for 2 h before being rinsed to remove any residual label. They were then placed in seawater-filled individual 500-mL beakers until their polyps re-extended. Altogether, three rounds with three replicates of each treatment (POM, DOM and control) were conducted over a 2-d period ($n = 9$) in the semi-indoor aquarium with ambient photosynthetically active radiation and temperature conditions of $223\text{--}280 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$ and $27\text{--}29^\circ\text{C}$, respectively. Following Hill et al. (2008), 1-mL syringes with particles (recognised by the presence of rectangular cells), that particular fragment was considered to have a positive result for ingesting POM. The remaining polyps of each fragment were left to complete ingestion for an hour. To test whether the ^{15}N label was ingested and assimilated, the tissue was stripped into 20 mL of seawater using an air-pick and frozen. Samples were sent to the Royal Netherlands Institute for Sea Research for analyses of ^{15}N and total nitrogen (after zooxanthellae were removed by centrifugation) using a thermo Electron Flash EA 1112 analyser coupled to a Delta V isotope ratio mass spectrometer. In addition, samples of POM and DOM were analysed for ^{15}N content. Enrichment of the coral tissue in POM and DOM treatments was calculated following Veuger & Middelburg (2007). Values were divided by feeding time and coral surface area to obtain the uptake rate, expressed as N cm^{-2} of coral h^{-1} . Rates between POM and DOM treatments were compared using a Student's *t* test.

One sample of the POM treatment was spoiled during transport, so an unbalanced test was conducted using the uptake rates of the eight remaining samples.

6.3 Results and discussion

Gut extractions indicated that five out of the nine samples of the POM-fed *O. crispata* had seagrass particles in them (Fig. 1c); no particles were found in the DOM and control samples. The uptake rates for the corals through DOM and POM did not differ significantly (Student's *t* test, $p < 0.05$), with the corals in the POM treatment having a mean uptake rate of 0.75 ($SE \pm 0.30$) $\mu\text{g N cm}^{-1} \text{h}^{-1}$ and in the DOM treatment, 0.98 ($SE \pm 0.20$) $\mu\text{g N cm}^{-1} \text{h}^{-1}$. These results demonstrate for the first time that corals can assimilate ingested seagrass particles and absorbed dissolved seagrass matter and that the uptake rates through both mechanisms are comparable. The importance of corals being able to assimilate nitrogen and other nutrients from seagrass material is clearly dependent on the extent to which this occurs in situ. Seagrass meadows export large quantities of fresh and detrital litter, and it is therefore probable that high concentrations of seagrass particles are transferred to adjacent reefs. Seagrass matter transported to neighboring ecosystems can quickly fragment into smaller particles and leach their organic matter (Heck et al. 2008), which can lead to a lower nitrogen content in dead seagrass compared to the fresh matter used in this experiment. However, the sheer amount of dead material exported suggests that the derived nutrients, both particulate and dissolved, could still subsidise the metabolic needs of corals on typically oligotrophic reefs. Granek et al. (2009) found that the natural isotope signature of coral revealed a substantial organic matter contribution from *Thalassia testudinum* seagrass found in nearby meadows. The mode of the uptake in corals was not discussed, although heterotrophy was cited as one of the possible factors affecting nutrient incorporation. Direct ingestion could be the 'missing link' that explains how organic matter from seagrass meadows becomes assimilated into coral tissue. This has further implications on the type of organic matter corals can break down. If corals are capable of digesting plant matter, it opens up the possible route for nutrient transfer from other vegetal sources, e.g., mangroves, marshes, algal beds and coastal forests. The implications of a direct nutrient link from seagrass to coral reefs are profound, as the availability of nutrients can strongly influence the structure and function of reef systems (Hallock and Schlager 1986). An increase in inorganic nutrient levels, as seen in eutrophic reefs, can have a direct negative effect on corals, depressing growth rates, larval settlement and reproduction (Koop et al. 2001). Inorganic nitrogen is preferentially taken up by symbiotic zooxanthellae and used to promote their own growth, reducing the amount of photosynthetic product translocated the coral host resulting in slower coral growth (Stambler & Stimson 1991). Others, however, have documented an increase in growth and reproduction with organic nutrient enrichment (Bongiorni et al. 2003), suggesting the effect

of nutrients may be dependent on the overall concentration and chemical form (Ferrier-Pagès & Gattuso 2000). Corals have to supplement their phototrophic carbon diet with nitrogen-rich materials, such as zooplankton or DOM, as their capacity to assimilate inorganic nitrogen is low (Falkowski et al. 1984). As such, both particulate and dissolved organic nitrogen contributions from seagrass might promote coral growth without upsetting the balance between the zooxanthellae and their coral hosts. Our experiments demonstrate that corals can assimilate nitrogen-based nutrients by feeding directly on seagrass particulate matter and/or absorbing leached DOM. Additional investigations are essential to understanding the mechanisms involved, especially the enzymatic pathway used in plant matter digestion and the extent to which ingestion of seagrass particles occurs in situ. The importance of the reciprocal relationships between coral reefs and their neighboring habitats for conservation management has been emphasised many times. The potential nutrient transfer from seagrass meadows to coral reefs demonstrated here further underlines the interconnectivity between these critical ecosystems.

Acknowledgments

This research was carried out as part of the SDWAs Marine & Coastal Research Programme (Theme 2): ‘Dredging and infrastructure development near critical marine ecosystems’ (R-264-001-001-272).

Chapter 7

Discussion

Mind the gap: managing cross-ecosystem fluxes as key for preserving and restoring tropical coastal seascape.

LG Gillis, CG Jones, D van der Wal, AD Ziegler and TB Bouma

STATUS: In preparation



Abstract

Ecosystem engineers within key coastal ecosystems can have spatially extended positive influence on adjacent ecosystems, generating reciprocally reinforcing loops between adjacent engineering ecosystems. These positive interactions originate from so-called engineering-donor ecosystems that modify the physical environment. This modification can be done by a reduction of wave height or sediment and nutrient concentrations, and can be important for the persistence and establishment of recipient ecosystems. Hence, such positive interactions at the landscape scale should be included in successful management schemes, as well as in the creation of ecosystems for coastal defence purposes. Thus they should be a key focus of environmental monitoring. In practice, this means that management programs should include assessment of (1) the strength of the flux from the engineering-donor to the recipient ecosystems, and (2) the habitat modification by the engineering-donor in order to detect in what situation they can control fluxes. If monitoring shows that ecosystem engineers are so degraded that they cannot alter physical fluxes, restoration efforts may be most beneficial at larger scales, when specifically aimed on those ecosystem engineers that rapidly change specific physical/chemical fluxes. We hence specifically indicate fast growing engineering species as target for restoration, as they could quickly fulfil physical functions for other habitats. This paper presents a conceptualised outline of parameters that should be monitored for landscape-scale based management and suggest novel methods suitable for such monitoring in addition to providing recommendations for restoration of specific species. Thereby presenting a promising opportunity to use the physical aspect of ecosystem engineers to efficiently preserve and restore a highly connected seascape.

Key words: ecosystem engineers, connectivity, ecosystem based management, restoration, monitoring, mangrove forest, seagrass bed, coral reef.

7.1 Introduction

Because the openness of many ecosystems allows them to have reciprocally positive connections of energy, materials and organisms, they therefore can be functionally connected across landscapes (Lovett et al. 2005). Sheaves (2009) highlighted the importance of management of biological connectivity, but the importance of physical exchanges – in particular their influence on establishment and persistence of ecosystem engineers – has not been considered until recently (**Chapter 1**). Ecosystem engineers are an essential component of some ecosystems; they can physically modify the environmental conditions to allow for greater resource availability for their habitats (Jones et al. 1994, 2010). Furthermore, because they alter physical conditions (Jones et al. 1994, 2010) they can modify physical and chemical exchanges between ecosystems and thus have an extended spatial influence over long distances for example nutrient exchange (**Chapter 2**). Here we investigate how conserving/restoration and the monitoring of reciprocal positive connections between ecosystems in the tropical coastal seascape could be utilised to further improve ecosystem-based management (EBM).

Mangrove trees, seagrass plants and scleractinian corals are all keystone ecosystem engineers in that they support entire ecosystems (Moberg & Folke 1999, Valiela et al. 2001, van der Heide 2007). These habitat-forming organisms are able to change physical conditions (i.e., ecosystem engineers cf Jones et al. 1994, 2010) and therefore buffer environmental stress and become the local dominant community-structuring force (Bruno & Bertness 2001). In this paper we focus on the spatially extended effects of mangrove trees, seagrass plants and scleractinian corals. Specifically, three potential connections that have been proposed for these ecosystems (Ogden & Gladfelter 1983) are waves, sediments and nutrients (for nutrients see **Chapter 3 & 6**; Fig. 1 & Tab. 1). Modification of these exchange processes by mangroves, seagrasses and/or corals can provide a valuable function to another ecosystem (Tab. 1; Harborne et al. 2006). Hence, these interactions can potentially influence the establishment and persistence of recipient ecosystem engineers (Gillis et al. 2014a).

There has been a considerable global decline in occurrence and health of mangroves, seagrass beds and coral reefs over the last decades. That is, worldwide seagrass beds are thought to be declining about 7 % year⁻¹ since 1990 (Waycott et al. 2009), whereas mangrove areas are decreasing by 1-2 % year⁻¹ (Valiela et al. 2001) and coral reefs by 1-7 % year⁻¹ (Bellwood et al. 2004). These systems can be under a variety of threats by localised impacts such as changes in catchment area land use, which drains into the coastal seascape, causing greater nutrients and consequently potential eutrophication (**Chapter 5**). Because these tropical coastal ecosystems are very distinctive in that they function very differently, they have often been managed in a specific way, without focussing on connectivity and reciprocal interactions.

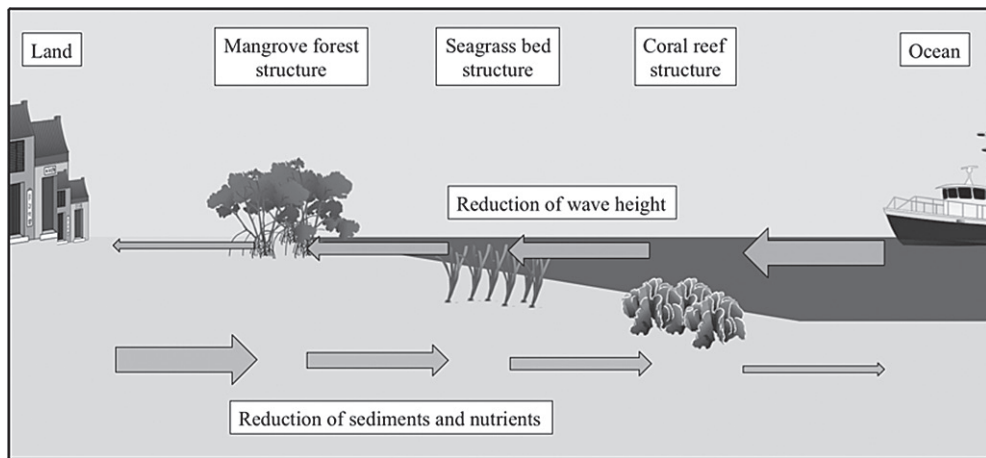


Figure 1 Conceptualization of functional physical connections between land, mangrove forests, seagrass beds, coral reefs and ocean systems. Arrows indicate the direction and approximated magnitude (arrow width) for three exchange fluxes considered: sediment & nutrients and hydrodynamic energy.

Table 1 Relationships between donor and recipient structures in the tropical coastal seascape. Donor structures are those who are altering the original flux via their physical presence. Recipient structures receive the altered physical flux from the donor structure. Showing literature based potential decrease in wave height, trapping of total suspended sediment and retention of nitrogen and phosphorous (%) for the donor structures.

Functional exchanges	Mechanisms	Donor structure	Recipient structure
Wave height (m)	Structural complexity of stony coral and seagrass leaves can reduce wave height	Coral reef Seagrass bed	Seagrass bed Mangrove forest
Potential decrease (%)	Coral reef Seagrass bed	20-97 ^(5, 15, 16, 17, 19, 20, 22) 30-81 ^(4, 6, 8, 10)	
Total suspended solids	Mangrove roots and seagrass leaves reduce current and allow for sediment accumulation	Mangrove forest Seagrass bed	Seagrass bed Coral reef
Potential trapping (%)	Mangrove forest Seagrass bed	1-90 ^(1, 9, 13, 24, 28) 18-62 ^(11, 12)	
Nitrogen (N) & Phosphorous (P)	Mangrove tree, seagrass plants and associated organisms can uptake particulate and dissolved nutrients.	Mangrove forest Seagrass bed	Seagrass bed Coral reef
Potential retention (%)	Mangrove forest Seagrass bed	N: 8-75 ^(3, 7, 14, 21, 23, 25, 26) P: 50-99 ^(3, 7, 14, 21, 23, 25) N: 5-79 ^(2, 27, 29) P: 35 ⁽¹⁸⁾	

1. Adame et al. (2010), 2. Apostolaki et al. (2012), 3. Boto & Wellington 1988, 4. Bradley & Houser (2009), 5. Brander et al. (2004), 6. Cornelisen & Thomas (2006), 7. Davis et al. (2001), 8. Fonseca & Cahalan (1992), 9. Furukawa et al. (1997), 10. Hansen & Reidenbach (2012), 11. Hendriks et al. (2008), 12. Hendriks et al. (2010), 13. Kithika et al. (2003), 14. Li (1997), 15. Lugo Fernandez et al. (1998), 16. Lugo Fernandez et al. (1994), 17. Pequignet et al. (2011), 18. Perez-Llorens & Niell (1995), 19. Roberts (1975), 20. Roberts et al. (1988), 21. Sanchez-Carillo et al. (2009), 22. Suhayda & Roberts (1977), 23. Wattaykorn et al. (1990), 24. Wattaykorn et al. (2001), 25. Wosten et al. (2003), 26. cited from Valiela & Cole (2002), 27. Van Engeland et al. (2013), 28. Victor et al. (2004), 29. Vonk & Stapel (2008).

Given that restoration of coral reefs, seagrass beds and mangrove forests can be very difficult and expensive (Yap 2000, Moberg & Folke 1999), a stronger focus on more effective and efficient management, which utilises the functions that ecosystem engineers provide at the landscape scale, is a promising avenue. This is becoming especially pressing now that there is a growing recognition of the ecosystem services they provide in coastal protection, and the growing desire and need to generate ecosystem-based coastal defences (Koch et al. 2009, Temmerman et al. 2013).

Ecosystem engineers and their associated change in fluxes at the local community scale have already been noted as having great potential for restoration (Crain & Bertness 2009, Montoya et al. 2012). Connective fluxes between ecosystems at the landscape scale will influence the establishment and expansion of the ecosystem (Gillis et al. 2014a). Thus a vital aspect to consider is the strength of the flux and how the ecosystem engineers affect the magnitude of the flux, for example mangrove roots and seagrass canopies can reduce hydrodynamic energy and retain particulate organic material (**Chapter 4**). We expand on these two concepts (i.e., the flux and how the flux is altered) by examining how decision-making in ecosystem-based management can benefit from putting focus onto reciprocal positive connections between ecosystems in the tropical coastal seascape. More specifically, we aim to identify what specific species within mangrove trees, seagrass plants and stony corals could be most useful for restoration and re-establishment of the functionality in terms of connectivity, and which monitoring tools have become available specifically for reciprocal positive connections.

7.2 Management of connected ecosystems

To ensure effective management that aims to conserve ecosystems requires a coordinated approach. Because of the functional connections, one cannot conserve one system without considering connections or interactions with other habitats (Berkström et al. 2012). Conserving ecosystems thus requires preserving favourable fluxes as generated by the key ecosystem engineering species. With respect to restoration, there is need to re-establish foundation species that provide the critical connectivity with adjacent ecosystems. Once these species are present again and surpass the critical biomass needed for ecosystem engineering (Jones et al. 1994 & 2010), the functional connections between ecosystems should in theory follow automatically.

If the ecosystems were being degraded because of a lack of functionally connective relationships, a viable program would be to restore specific species that could quickly provide essential habitat connective functions between ecosystems. We suggest utilising fast growing species of ecosystem engineers as an initial short-term management strategy. Fast growing species could provide the critical biomass (Yap 2000), which could then effectively

change fluxes from a donor to a recipient ecosystem. Once these species have become established, succession of other species within the ecosystem will follow. In addition, scale should be taken into account in situations where a restored ecosystem lacks essential physical characteristics (amongst others, distance between systems and a relevant minimal ecosystem size). If essential physical characteristics are not considered then connective fluxes between systems are unlikely to establish.

To conserve positively connected ecosystems, monitoring of fluxes must be an essential part of any management strategy. The monitoring should ideally include data on well-defined thresholds or early warning indicators. Moreover, within such monitoring programs, there needs to be an integrative approach to account for the effect of connections between adjacent ecosystems. That is, one should know how a specific engineering-donor ecosystem alter the incoming flux of specific physical variables that primarily affect the functional connections (i.e., waves coming from sea or nutrient/sediment loads coming from the land) before it passes on to the recipient (i.e., wave-shaded or downstream) ecosystem. We are aware that managers already monitor many physical fluxes, but the majority of this data are not yet used with respect to consequences in other connected ecosystems, especially if the connection is not directly visual. Moreover, new technologies, particular from remote sensing, may now offer the tools to monitor fluxes efficiently at a temporal and spatial time-scale that was previously impossible (see 2.2 for details).

7.2.1 Management of connective fluxes

Initiating an ecosystem-based management program based on reciprocal positive connections requires following the steps visualised in the flow chart (Fig. 2). As a 1st step, the relevant physical flux, the engineering-donor ecosystem and the reciprocal ecosystem all need to be identified (Fig. 2; step 1). Managers then need to monitor how the flux changes from the initial intensity through the engineering-donor ecosystem to the reciprocal environment (Fig. 2; step 2). Physical attributes of the ecosystem engineers need to be monitored (Fig. 2; step 2), these attributes will either directly control the flux (i.e. physical attenuation of waves from stony corals) or physical aspects could be correlated with a flux (i.e. a higher tree biomass would indicate greater nutrient uptake). The last step involves asking the question whether the reciprocal system is degraded or not (step 3). An affirmative answer would indicate the need for intervention, such as restoration of ecosystem engineers. If no degradation is present, monitoring should continue (Fig. 2; step 3).

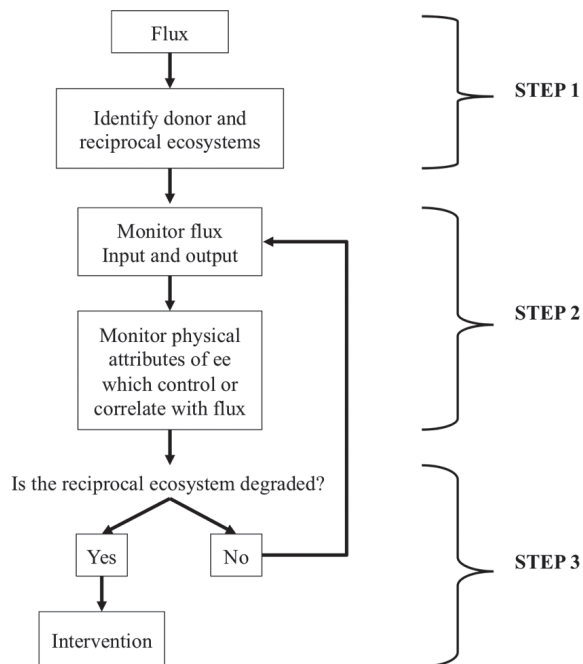


Figure 2 Flow diagram of management for ecosystems with connective fluxes. A flux, donor and reciprocal ecosystem is initially identified. Monitoring of the flux through the connective ecosystem is then completed. Whether the flux is detected or correlated with the physical structure of the ecosystem engineer is determined. Finally if the habitat is degraded then intervention is necessary but if not monitoring should continue.

7.2.2 Management of the tropical coastal seascape

The first step in implementing the flow diagram described above (Fig. 2) for the tropical coastal seascape is identifying the connective flux (wave height, nutrients and sediments) occurring between ecosystem engineers in the donor and recipient ecosystem (mangrove forests, seagrass beds and coral reefs) (Fig. 3; step 1). The second step is to monitor the flux and physical aspects in the donor system, which could provide us with an early warning system for the receiving ecosystem (Fig. 3; step 2b). Both the flux and the physical variables of the donor and receiving systems can be monitored with a combination of remote sensing and in-situ measurements (Fig. 3; step 2a).

The important aspect to monitor in coral reefs is the shape of the coral reef (rugosity) as this has the greatest influence for wave attenuation (Monismith 2007). Line and point intercept transect (LIT & PIT) methods are well-established techniques that can be used in conjunction with recent new technology such as high-resolution light detection and ranging (LIDAR) bathymetry. This can also provide 3-D perspective of the benthos over large areas (Walker 2008). It has also been used to detect surface wave energy fluxes and dissipation over coral reefs (Huang et al. 2012), whilst optical imaging remote sensing can yield estimates of the extent and health of the reefs (Mumby et al. 2004, Scopéllitis et al. 2010, Goodman et al. 2013).

Meadow density and health are the most important aspects to monitor in seagrass beds, as they control sediment and particulate accumulation (Hendriks et al. 2008, Hendriks et al. 2010). Airborne and satellite optical remote sensing have proven suitable in detecting sea grass beds and their dynamics, in the field at a smaller scale quadrats and transects can be used (Dierssen et al. 2003, Lyons et al. 2013). Advances in sensor technology and radiometric transfer modelling have resulted in the ability to account for the in-water light attenuation, bottom reflectance, and simultaneously retrieve water depth (Dierssen et al. 2003, Paul et al. 2011). Remote sensing also has the potential for monitoring dispersal of suspended sediments and nutrients in these ecosystems (Brodie et al. 2010).

Mangrove ability to absorb nutrients and accumulate sediment is dependent on the physical structure of the trees and surface area of the mangrove forest (Talbot & Wilkinson 2001, Lovelock et al. 2009). Initially ground truthing is needed to investigate if the forest is under stress via a transect or a quadrat approach (Talbot & Wilkinson 2001). Secondly the surface area of the mangrove forest should be mapped. Remote sensing techniques can be used to detect and monitor the distribution, biomass and health of mangrove forests. These methods range from aerial photography to high- and medium-resolution optical imagery and from hyperspectral data to active microwave data (notably polarimetric Synthetic Aperture Radar) and LIDAR (Kuenzer et al. 2011, Heumann 2011).

The third step is to establish a solution to the problem. If restoration is not required then detection of changes in the strength of the functional fluxes should continue (Fig. 3; step 3). However if restoration is required, then we should identify species that provide a ecosystem service to other habitats (Fig. 3; step 3). For example, restored stony corals need to provide high structural complexity, which can rapidly increase coral cover to attenuate waves. Seagrass beds need to be present to provide sediment and nutrient accumulation therefore we need to consider how quickly the plants will colonise the area (Yap 2000). When regarding the sediment trapping potential of mangrove forests an important aspect in ecosystem connectivity, rapid prop root growth that helps to trap sediment and stabilise the mass of the mangrove forests are thought to be of utmost importance. It is also important to note that ecosystems need to be restored within proximity of other ecosystems to have an effect on the strength of the flux. For example, in the case that a coral reef that is too far from seagrass beds and mangrove forests, attenuated waves may build up again after passing through the reef structure. They would therefore not be expected provide a positive interaction.

For integrative monitoring to truly work at the large-scale across individual ecosystems, monitored data from each ecosystem needs to be shared across sites with other managers or stakeholders. As building and maintaining cross-ecosystem collaborations and data sharing can be challenging, tools such as an internet-based directory for people with projects in the same area, grant sharing, workshops, consultations, online forums should

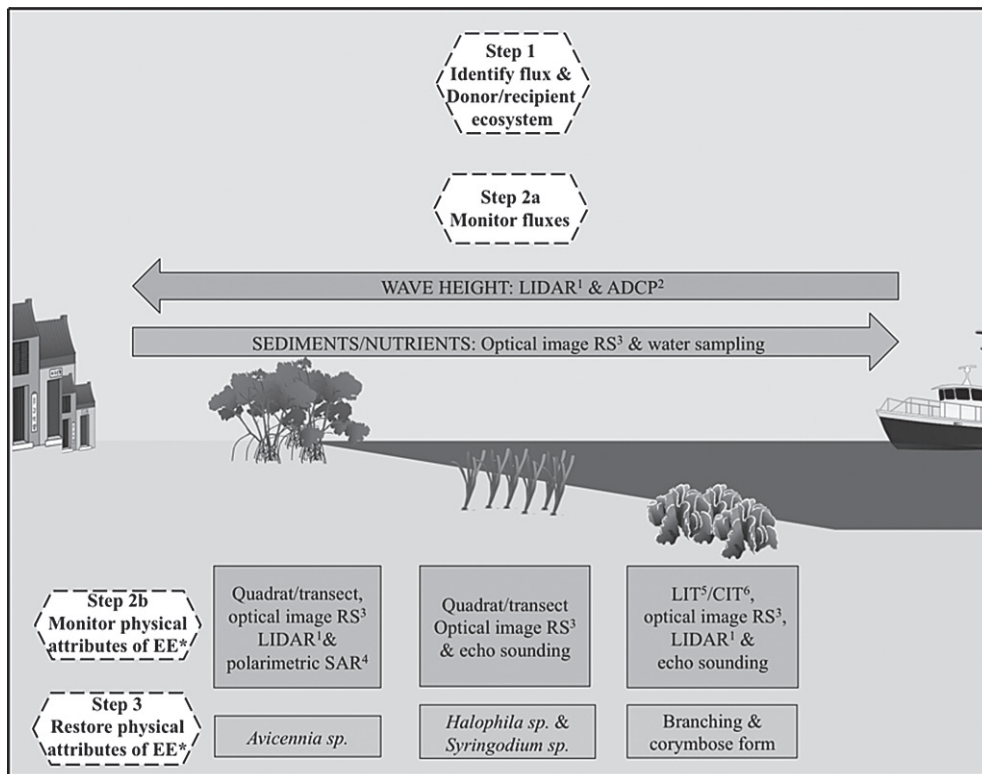


Figure 4 Diagram showing incorporation of connective ecosystems and their fluxes into management practises. The first step is to identify the flux and donor/recipient ecosystem. The first part of the second step it to monitor the flux that requires management. The second part of step 2 is to monitor the physical attributes of the ecosystem engineers (EE) in the donor system, which has the potential to alter the flux. The final stage is to establish if the ecosystem needs restoration of specific ecosystem engineering (EE) species.

¹ high-resolution light detection and ranging ² acoustic current depth profiler ³ remote sensing ⁴ synthetic aperture radar ⁵ line intercept transect ⁶ chain intercept transfer

be exploited fully (Vance-Borland & Holley 2011). Success stories that have maintained cross ecosystem monitoring include the Great Barrier Reef Marine Park (GBRMP) and the management of the greater everglades ecosystem (Lovett et al. 2005, Talbot & Wilkinson 2001).

7.3 Conclusion and future perspective

We suggest that positive physical interactions between ecosystem engineering ecosystems provide essential functions for other ecosystems at the landscape scale (Lovett et al. 2005, Gillis et al. 2014a). Because these interactions can be reciprocal, they can be particularly important for the persistence of the total of ecosystems as well as each ecosystem individually, and thus they need to be taken into account for successful management, conservation and

restoration. As restoration of coral reefs, seagrass beds and mangrove forests have all proven to be extremely complex, expensive, and difficult to predict the outcome (Yap 2000, Moberg & Ronnback 2003), a stronger focus on integrative monitoring of parameters that affect the connectivity between habitats and the sharing of such monitoring data is strongly advised. The re-establishment of specific ecosystem engineers whose primary effect is changing specific physical/chemical fluxes is a viable option to realise restoration goals in another ecosystem.

Currently we have only created a conceptual outline for identifying the monitoring techniques and parameters needed and provided general recommendations for selecting which species on which to focus restoration efforts. We have not taken into account the cost effectiveness nor accuracy assessments or local specific targets at the species level, these aspects are essential if management decisions are to be based upon monitoring results (Mumby et al. 1999, Jupiter et al. 2013). Managers are aware that these fluxes exist—and that they are important—they also need to establish where this information can be used within their own coastal zones. Hence, from a research perspective we require more information regarding how the physical functional connections between ecosystems manifest (**Chapter 1, 2, 3, 4 & 6**). Using ecosystem engineers that by their own physical structure affect landscape scale connectivity, in order to restore and conserve tropical coastal zones, is a great and challenging opportunity. In addition this concept allows us to integrate management across ecosystems, at a scale that expands beyond individual ecosystems. Moreover, it may coincide with the growing need to use nature for coastal protection.

Chapter 8

Summary

Nederlendse Samenvatting

Acknowledgments

Curriculum vitae

References

Summary

In the introductory literature review (Chapter 1), we established the potential for reciprocal connections (waves, sediment, nutrients and organisms) between mangrove forests, seagrass beds and coral reefs in tropical coastal seascapes. Our results indicate that, in the field of community ecology, these exchanges can be placed in the context of facilitation at the ecosystem scale. In this thesis, the experimental work concentrated on establishing nutrient connectivity between mangrove forests, seagrass beds and coral reefs at the landscape scale. The mangrove outwelling theory has been a central point of nutrient exchange in the tropical coastal seascape (Odum & Heald 1975, Lee 1995). Little work has tried to establish whether other highly productive ecosystems, such as seagrass beds, may provide particulate and dissolved nutrients to the coastal seascape. Furthermore, limited research has addressed whether mangrove forests act as nutrient sinks or buffers to other coastal ecosystems.

We found that in terms of area, seagrass beds contribute the most organic material compared to mangrove forests relative to their area (Chapter 2). The long degradation time of mangrove leaves and the negligible contribution of dissolved organic nitrogen ($93 \mu \text{ mole DON g}^{-1}$) to the water column, compared to seagrass leaves, meant the mangrove forests may not be a source of nitrogen for adjacent ecosystems and organisms as previously thought (Chapter 3). However, in terms of biomass (g), mangrove leaves transported outwards from the mangroves, were still the dominant form of particulate organic matter (POM) in the tropical coastal seascape (Chapter 3).

The ability of mangrove forests to retain nutrients/POM and to buffer adjacent systems from excess nutrients could also be affected by nutrient status. For mangroves, higher external nutrient availability may mean the forest cannot retain all nutrients and therefore some are outwelled in either dissolved or particulate form. Nutrient availability within a mangrove forest can be strongly affected by adjacent land-use. Most notably, urbanisations may pose higher external nutrient fluxes into a forest, while natural forests or plantations may cause upstream nutrient depletions and thus a decrease in external nutrient influx (Chapter 5).

Delivery of POM will in turn depend on the trapping capacity of both mangrove roots and the seagrass canopy. Using mimic mangrove roots and mimic seagrass canopies in a flume experiment with different hydrodynamic conditions, we found that mangroves have a much higher trapping capacity than seagrass canopies. This is in part because the mangrove roots extend through the entire water column, while the canopy of seagrass meadows typically extends until a certain distance from the bottom (Chapter 4). In this respect, mangrove forests may retain nutrient-rich particulate organic material, and in fact function as a buffer of dissolved and particulate organic material. These mangrove forests are therefore strongly connected to other coastal ecosystems.

Finally, we posed the question whether scleractinian or stony tropical corals could use fresh seagrass material, both in a dissolved and a particulate form, as a food source. Although dissolved material was assimilated in all tests and replicates, we moreover found that 55 % of corals also processed particulate seagrass material (Chapter 6). Our results indicate a new connective relationship, which has not been considered before, namely that seagrass-derived material is an available and usable source of both dissolved and particulate organic material.

Nederlandse Samenvatting

In onze literatuurstudie (Hoofdstuk 1) hebben we onderzocht op welke manier mangrovebossen, zeegrasvelden en koraalriffen elkaar kunnen beïnvloeden door uitwisseling van golven, sediment, nutriënten en organismen. Onze resultaten geven aan dat, op de schaal van gemeenschappen en ecosystemen, sprake kan zijn van faciliterende relaties als gevolg van deze uitwisselingen. De sterkte van de facilitatie is moeilijk te kwantificeren op basis van de literatuur. Het experimentele werk in dit proefschrift heeft bijgedragen aan het aantonen van nutriënten-connectiviteit op landschapsschaal tussen mangrovebossen, zeegrasvelden en koraalriffen. De mangrove *outwelling* theorie (Odum & Heald 1975, Lee 1995) is tot op heden het centrale concept wat betreft nutriënten-uitwisseling in de tropische kustzone. De rol van andere productieve mariene ecosystemen, zoals zeegrasvelden, als een bron van nutriënten en (particulair en opgelost) organisch materiaal voor de omringende kustzone, is slecht bekend. Daarnaast is er nog nooit onderzoek verricht aan de vraag of mangrovebossen fungeren als een *sink* van nutriënten of juist als buffers voor andere ecosystemen langs de tropische kustzone.

We hebben aangetoond dat zeegrasvelden meer organisch materiaal aan hun omgeving leveren dan mangrovebossen, gerekend op basis van oppervlakte-areaal (Hoofdstuk 2). In tegenstelling tot wat eerder werd aangenomen, vormen mangrovebossen geen significante bron van stikstof voor aangrenzende ecosystemen. Dit wordt verklaard door de lange degradatieperiode van mangrovebladeren en hun geringe bijdrage aan opgeloste organische stikstof (DON) in de waterkolom ($93 \mu \text{ mol DON g}^{-1}$), vergeleken met zeegrasbladeren (Hoofdstuk 3). Mangrovebladeren die vanuit de mangroven naar de daarbuiten gelegen ecosystemen worden getransporteerd, vormen wel, in termen van biomassa, de dominante flux van particulier organisch materiaal (POM) in de tropische kustzone (Hoofdstuk 3).

Het vermogen van mangrovebossen om nutriënten en POM te kunnen vasthouden en te fungeren als een (nutriënten)buffer voor aangrenzende ecosystemen, hangt af van het heersende nutriënten-regime. Als de beschikbaarheid van nutriënten in een mangrove hoog is, door invloeden van buitenaf, dan zal het bos niet al de voedingsstoffen kunnen behouden en zal een deel ervan uitspoelen naar aangrenzende systemen in de vorm van vaste deeltjes of als opgeloste stoffen. De beschikbaarheid van nutriënten in een mangrove kan worden beïnvloed door het landgebruik in aangrenzende gebieden. De meest opvallende voorbeelden hiervan zijn bebouwde gebieden, welke een hogere beschikbaarheid van nutriënten veroorzaken, terwijl natuurlijke bossen of plantages leiden tot een daling in de beschikbaarheid van nutriënten (Hoofdstuk 5).

De aanlevering van POM is op zijn beurt afhankelijk van de invangcapaciteit van de bovengrondse wortelstelsels van mangroves en van de bladeren van zeegrasvelden. We plaatsten nagmaakte modellen van mangrovetwortels en zeegrasbladeren in een stroomgoot

onder verschillende hydrodynamische omstandigheden. We vonden dat mangroven een veel hogere invangcapaciteit hebben dan zeegras. Dit komt voor een deel omdat, anders dan de zeegrasbladeren, de wortels van mangroven zich door de gehele waterkolom bevinden (Hoofdstuk 4). Hierdoor kunnen mangrovebossen gemakkelijk organische deeltjes vasthouden en vormen zij een buffer voor opgeloste nutriënten en POM in de kustzone. Deze bufferfunctie is verantwoordelijk voor een sterke connectie tussen mangroves en andere aangrenzende ecosystemen.

Vervolgens is de vraag gesteld of tropische harde koralen in staat zijn gedegradeerd zeegrasmateriaal, in zowel opgeloste als particuliere vorm, te gebruiken als voedselbron. De koralen namen het opgelost materiaal op tijdens alle gerepliceerde experimenten. Bovendien vonden we dat 55 % van de koralen ook fijn particulier zeegrasmateriaal verwerkten (Hoofdstuk 6). Onze resultaten wijzen op een nog niet eerder bekende verbindende relatie, namelijk dat gedegradeerd zeegrasmateriaal een beschikbare én bruikbare bron van particulier en opgelost organisch materiaal vormt voor harde koralen.

Acknowledgements

The premise of my PhD was too investigate how one ecosystem can facilitate another ecosystems, however many people have facilitated my PhD. To these people I would like to extend my sincere gratitude.

I would like to thank my promoters and co-promoters Dr Tjeerd Bouma, Prof. Peter Herman and Prof. Alan Ziegler if it were not for their patience, encouragement, advice and knowledge this PhD would never have been possible. Even though they had busy schedules they always gave detailed and considerate input on endless manuscripts.

My gratitude also goes to the people of NIOZ-Yerseke for hosting me. The institute is a credit to science and scientists, studying and working there was a pleasure. There are too many people to thank individually but from the personnel departments to the analytical laboratory, everyone helped with this PhD in a direct or indirect way.

However, I would especially like to thank my department. Jim and Olivier - I'm still happy to start the "lego paper", the seagrass group was essential for help on logistics, inspiration, methodologies and papers (Yayu, Laura, Siti, Laura G, Wouter) and for the entire department thank you for creating a truly motivating working group especially for listening to presentations and giving excellent feedback during departmental meetings.

I spent many months in Singapore, and I would like to thank the welcome from the Singapore Water Delft Alliance, who looked after me when I was an orphan scientist and gave me a desk plus Friday afternoon refreshments. I would also like to extend my gratefulness to Claire Jeuken who provided support and administration for some of the worst aspects of the project, without her help it could have been impossible for us to concentrate on science.

The majority of my fieldwork was done in Thailand, many people helped with the running of the work. A huge thank you to all my MSc students (Tuan, Sam, J-W) and research assistants (Lucy, Mairi, Yaa, Nam, Jantima) you definitely kept me sane during periods of really tough fieldwork.

There are also many scientists who helped me with papers and were especially encouraging and patient to a young, inexperienced scientist. Many thanks go to Marieke van Katwijk, Clive G Jones, Ivan Negelkerken, Cecile Cathalot, Daphne van Wal, Dick van Oevelen, Wawan Kiswara and Peter Todd.

My family and friends have supported me for the last few years and I would never have completed this PhD without their encouragement. Roz and Francesco - you probably saw me at my worst moments and did not stop having faith in me. Eva, Sairah, Maike and Greg - for advice on coping with PhD's and post-docs! Dad and Alice - for keeping me updated on family news and distracting me from science. Thanks for my Edinburgh friends (Shelley, Ross, Tony, Anne) for giving me breaks from the madness of my PhD and always

listening. Eyu and Caroline – you were with me for my last year of my PhD although you weren't always sure what I was doing, you understood impact factors were important and finally Mum for having almost faith in me before, during and hopefully after my PhD.

Curriculum vitae

Lucy G. Gillis

Department of Spatial Ecology

Royal Netherlands Institute of Sea Research (NIOZ)

Korringaweg 7 • 4401 NT • Netherlands

Email: lucygwen.gillis@nioz.nl Phone +31 (0) 113 577 470



Education

Doctor of Philosophy, In Progress

2009-2014

The Royal Netherlands Institute of Sea Research (NIOZ).

University of Nijmegen, Netherlands.

Thesis: Are physical fluxes important in the tropical coastal seascape?

Masters of Science

2004-2005

Heriot-Watt University, Edinburgh, UK.

Thesis: Marine Resource Development and Protection

Bachelors of Science (Honours)

1998-2002

Bangor University of Wales, UK.

Specialization: Geological Oceanography

Publications

Lai S, Gillis LG, Mueller C, Bouma TB, Guest JR, Last KS, Zeigler A, Todd PA (2013) First experimental evidence of corals feeding on seagrass matter. *Coral Reefs* 32 (4): 1061-1064.

Gillis LG, Bouma TB, Kiswara W, Ziegler AD, Herman PMJ (2014) Leaf transport in mimic mangrove forests and seagrass beds. *Marine Ecology Progress Series* 498:95-102.

Gillis LG, Bouma TB, Jones CG, van Katwijk MM, Nagelkerken I, Jeuken CJL, Herman PMJ, Ziegler AD (2014) Potential for landscape-scale reciprocal facilitation among tropical marine ecosystems: A review. *Marine Ecology Progress Series* 503:289-303.

In Review

Gillis LG, Ziegler AD, van Oevelen D, Cathalot C, Herman PMJ, Bouma TB. Tiny is mighty: Seagrass bed influence of organic matter fluxes in the tropical coastal zone.

Paul M & **Gillis LG**. Let it flow: How does an underlaying current affect wave propagation over a natural seagrass meadow?

In preparation

Wolters JW, **Gillis LG**, Ziegler AD, van Katwijk MM, Bouma TB. Land use effects on mangrove nutrient status in Phang-Nga Bay, Thailand.

Gillis LG, Bouma TB, Ziegler AD, Cathalot C, Herman PMJ. Toward understanding the roles of mangrove and seagrass particulate matter as a nitrogen source in tropical coastal ecosystems.

Gillis LG, Jones CG, Ziegler AD, Bouma TB. Mind the Gap: Disjointed management in the tropical coastal seascape.

Gillis LG, Paul M, Bouma TB. No waves, no nutrients: How waves affect nutrient uptake in seagrass beds.

Supervisory Experience

2013 MSc student Sam Lai, National University of Singapore

Thesis: First experimental evidence of corals feeding on seagrass matter.

2012 MSc student Tuan Will, Heriot-Watt University, UK

Thesis: Antimicrobial properties of crude extracts from 2 species of scleractinian coral and 1 species of octocoral from Southern, Thailand.

2011 MSc student Jan-Willem Wolters, Radboud University, Netherlands

Thesis: Land use effects on mangrove nutrient status in Phang-Nga Bay, Thailand.

Presentations

Netherlands Annual Ecology Meeting, Lunteren, 2012.

Gillis LG, Bouma TB, Jones CG, van Katwijk MM, Nagelkerken I, Jeuken CJL, Herman PMJ, Ziegler AD. Potential for landscape-scale reciprocal facilitation among tropical marine ecosystems: A review.

Coastal and Estuarine Research Federation, San Diego, 2013.

Gillis LG, Bouma TB, Ziegler AD, Cathalot C, Herman PMJ. Toward understanding the roles of mangrove and seagrass particulate matter as a nitrogen source in tropical coastal ecosystems.

International Association of Ecology, London 2013.

Gillis LG, Bouma TB, Kiswara W, Ziegler AD, Herman PMJ. Leaf transport in mimic mangrove forests and seagrass beds.

Invited speaker

Naturalis Biodiversity Center, Leiden Central, 2013.

Lai S, **Gillis LG**, Mueller C, Bouma TJ, Guest JR, Last KS, Zeigler A, Todd PA. First experimental evidence of corals feeding on seagrass matter.

Makassar State University, Makassar. 2013.

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Singapore Water Delft Alliance, Singapore. 2012.

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