

The effect of invasive ecosystem engineers on ecosystem functioning

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Abstract

Invasive species can have drastic impacts on the functioning of ecosystems and thereby may threaten human use of these natural resources. However, invasive species can have positive effects also as creating refuges for other organisms. By modifying, creating and maintaining habitats invasive ecosystem engineers directly or indirectly influence their environment and may have a large impact on a habitat. Because of the increasing rate with which species settle in non-native habitats the importance of a framework that helps to predict the impact of invasive species on an ecosystem is increasing. The effects of three well known ecosystem engineers were compared, namely the Japanese oyster (*Crassostrea gigas*), a seaweed (*Caulerpa taxifolia*) and Eelgrass (*Zostera japonica*) on four physical and biological aspects of the invaded habitat: structural change, abiotic change (e.g. biochemical cycle, sedimentation), biotic change (e.g. species abundance, richness, effect on species interactions) and feedback of structural, abiotic and biotic changes on the engineer. I expected that most invasive engineers have a positive net effect on ecosystem functioning because they tend to increase the habitat complexity and thereby increase species abundance and diversity. This thesis showed that the impact of an invasive ecosystem engineer depends on the effect an engineer has on: the complexity of a system, on the native ecosystem engineer and the ecosystem services and that effects of an invasive ecosystem vary widely. For future research I would recommend to focus on functional groups because some generalisations can be made by comparing the effects different invasive ecosystem engineers species of the same functional group have. These generalisations can provide more insight in the effect possible new invasive ecosystem engineers may have on an ecosystem.

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1. Introduction

Invasive organisms

Invasive organisms are organisms that have settled beyond their natural biogeographical range to new regions, in which it did not exist in historical time (Carlton 1979, Rilov et al. 2012). Invasive species can have a large impact on the functioning of ecosystems. They can harm both natural resources in an ecosystem and thus threaten human use of these resources (Rilov et al. 2012). Invasive organisms can as well have positive effects such as stabilizing sediment or providing shelter for other organisms. An aquatic invasive species can be introduced to a new area via ballast water of oceangoing ships, attached to the hulls of ships, intentional or accidental releases of aquaculture species, aquarium specimens or bait, and by other means (Rilov et al.2012). Among the invasive organisms that have the largest impacts are those that directly or indirectly modify their environment, defined as “ecosystem engineers”, and thereby can cause a cascade effect (Crooks 2002).

Invasive ecosystem engineers

Ecosystem engineers modify create and maintain habitats by altering the physical state of abiotic or biotic factors in a habitat (Jones 1994). By doing so they change habitat structures, biochemical flows of nutrients, productivity and abundance of native organisms and alter the structure and functioning of an ecosystem (Crooks 2002). The concept of ecosystem engineers was first articulated by Jones et al. in 1994. Since that time it is widely used to gain more insight in the functioning of ecosystems (Wright and Jones 2006). Nevertheless, there is still some uncertainty about what it is, and some scepticism about the integration of the concept into a general understanding (Jones 2010). Jones et al. (2010) tried to create a framework to understand physical ecosystem engineering by organisms. This framework contains four general cause and effect relationships that link four components (fig. 1) “1. An engineer causes structural change; 2. Structural change causes abiotic change; 3. Structural and abiotic change cause biotic change; 4. Structural, abiotic, and biotic change can give a feedback to the engineer.” Because of the increasing rate with which species now traverse the globe and settle in non-native habitats (Ruiz et al. 1997) the importance of a framework that helps to predict the impact of invasive organisms on an ecosystem is increasing. The framework Jones et al. (2010) has

provided may have a guiding function in creating a more general framework. Invasive ecosystem engineers can have negative as well as positive effects on a variety of systems within an ecosystem. If we understand the various effects invasive ecosystem engineers have on ecosystem functioning we should be able to predict possible impacts of invasions in the future.

Aims

The introduction of non-native ecosystem engineers can be seen as a great opportunity to expend the knowledge about ecosystem functioning. Interactions among organisms, limitations and dominances that are otherwise invisible due to co-evolution and a long evolutionary history can be revealed (Padilla 2010). The purpose of this thesis is to gain more insight in the impacts invasive marine ecosystem engineers have on ecosystem functioning and tries to find some generality between them. The question that stands central during this thesis will be: *What is the impact of invasive marine ecosystem engineers on ecosystem functioning and what causes these impacts?* To answer this question and to create a framework I will perform case studies of three well known invasive marine ecosystem engineer species. Namely: The Japanese oyster (*Crassostrea gigas*), a seaweed (*Caulerpa taxifolia*) and a sea grass (*Zostera japonica*). These three engineers all influence a native ecosystem engineer. The Japanese oyster seems to take over the ecological function of the Blue mussel (*Mytilus edulis*) in the Wadden Sea. *Caulerpa Taxifolia* is associated with the decline of seagrasses (*Posidonia australis* and *Zostera capricorni*) in estuaries near Sydney in southeast Australia. *Zostera japonica* seems to have an influence on the native *Zostera marina* in estuaries of northwest America.

Framework

The framework of Jones et al. 2010 will be used as a guideline to examine the effects invasive engineers can have on ecosystem functioning and test its usefulness at the same time. The effects the different invasive species have on physical and biological aspects and thereby on the habitat complexity, the native ecosystem engineer and the ecosystem services of the invaded habitat will be compared. The framework of Jones et al. 2010 contains four components:

- Structural change
- Abiotic change (e.g. biochemical cycle, sedimentation)
- Biotic change (e.g. species abundance, richness, effect on species interactions)
- Feedback of structural, abiotic and biotic changes on the engineer.

After these four components the net effect on ecosystem functioning and the consequences for ecosystem services will be described. In the article of Jones et al. (2010) richness and biodiversity is not mentioned as a biotic response on structural or abiotic changes. On the other hand, species abundance is designated as an effect. Nevertheless, richness and biodiversity are often strongly influenced by engineers. In this thesis the changing species richness and biodiversity, resulting from structure and abiotic changes, will be assigned as a biotic response.

Hypothesis

All of the above mentioned aspects might be positively or negatively influenced by ecosystem engineers. My expectation is that the overall effect on ecosystem functioning depends on the influence an engineer has on habitat complexity and native ecosystem engineers. A habitat is considered complex if it has either a higher density or a greater diversity of structural elements than the habitat to which it was being compared (Crooks 2002). For example, a mixed forest is more complex than a monospecific forest. A higher habitat complexity generally implicates a higher species

diversity and abundance. A mixed forest creates contains more niches for different organism as a monospecific forest. I expect that most invasive engineers have a positive net effect on ecosystem functioning because they tend to increase the habitat complexity of a system and thereby increase the heterogeneity, species abundance and diversity.

2. Effects of Invasive ecosystem engineers

Successful invasive organisms

There are a lot of studies done to find some generality in the invasion ecology. There are three stages described for invasive organisms: 1) colonization of the receiving habitat, 2) establishment in the receiving habitat, 3) natural range expansion after establishment. Diseases, predation, unsuitable climate or competition can be reasons that an invasion fails. Successful invaders generally have a selection of characteristics that make invasion possible. Most of the time they have a r-selected life history strategy (rapid growth, rapid sexual maturation, high fecundity), they are generalists (ability to colonize wide range habitat types), they have a broad diet, they are tolerant to a wide range of environmental conditions and they are ecosystem engineers (Troost 2010).

Allogenic and Autogenic engineers

There are two different types of engineering based on the way they alter their environment. *Autogenic* engineers modify the environment with their own physical structures. For example, the shell of an oyster creates a suitable hard substrate where *Fucus* can grow on. When the oyster grows, the increasing shell causes more available space. *Allogenic* engineers modify their environment by mechanically transforming living or non-living materials into another physical state (Rilov et al. 2012). The classical example for allogenic engineers is the beaver. By building dams they alter the water current and create habitats for other organisms. In all cases the physical state transformations can have positive as well as negative ecological consequences for other species that live in the old or the new environment that is formed. This is because these other species depend on resources whose availability is directly or indirectly controlled by these physical state changes (Jones et al. 1997). A positive consequence is, for example, the hiding places the shells of the oysters or the dams of the beavers provide for other organisms. A possible negative consequence of a beaver dam could be that by changing the water flow the terrestrial organism that live there are flooded out. For some species it is hard to say if it is an allogenic or autogenic engineer. Sessile organisms are often autogenic species (e.g. trees and corals). However there are also sessile organisms that are allogenic (e.g. growing of leaves create shadow patches on the ground) or mobile species that are autogenic (e.g. shells of living crabs create epibiont habitat). Many organisms are simultaneously auto- and allogenic (Jones 2010).

Framework to examine effects of ecosystem engineers

The framework of Jones et al. (2010) contains four general cause and effect relationships that link four components (fig. 1) "1. An engineer causes structural change; 2. Structural change causes abiotic change; 3. Structural and abiotic change cause biotic change; 4. Structural, abiotic, and biotic change can feedback to the engineer."

Structural change is the structure created by an engineer minus the structure loss through decay. Decay can be caused by death (in case of autogenic engineers) or structure abandonment (in case of

allogenic engineers). The growing and dying of trees is an example of structural change. Structural change can cause abiotic change.

Abiotic change is a new abiotic state in comparison with a structurally unmodified abiotic state. Abiotic change is caused by kinetic energy and materials within an abiotic environment interacting with a structure. For example, coral reefs weaken wave action. These abiotic changes are often accompanied by changes in the distribution of material flows (e.g. sedimentation, water flows). The extent of these effects often depend on abiotic conditions (e.g. erosion, hydrology, sedimentation). In other words they are abiotic context dependent. For example, coastal erosion by burrowing marine isopods is affected by wave intensity (Talley and Crooks 2007).

Biotic change (excluding effects of the engineer itself) is a new biotic state in comparison to a structurally and abiotically unmodified biotic state. Biotic responses can often be addressed to structural and/or abiotic changes. Responses include effects on organismal growth and reproduction; species abundances and distributions; species interactions (e.g. competitive dominance); and ecosystem processes such as primary productivity. There are two different ways to generate this. 1. Structural change can have a direct effect on the biota. 2. Abiotic change caused by structural change can affect the biota. An example of pathway 1 is that the rough structure mussel beds have may provide living space for organisms (e.g. hiding places for predators, resting places). Changes in the physical structures of engineers, for example changed shape, size or dimension may adequately describe these kinds of effects. An example of pathway 2 is the structural change of growing corals that weakens the wave action and may cause appropriate habitats for animals on the coast. In the second pathway the abiotic variables that can be relevant includes consumable energy and materials (e.g. nutrients, water), constraining or enabling abiotic conditions (e.g. temperature, salinity, redox), and abiotic cues used by organisms (e.g. sound attenuation, temperature). Other important biotic factors are the species richness, abundance and diversity. As Jones et al. (1997) pointed out; there can be a positive, negative or no effect in a local area of an engineer on species richness. The direction of this effect is hard to predict. Nevertheless a comparison between an engineered habitat and an unengineered habitat suggest a positive net effect on the species richness because the habitat diversity increases (Jones et al. 1997, Wright et al. 2006). There are two conditions that must be met to have positive effects of an engineer on landscape-level species richness. 1. The engineered habitat must provide a resource that is not available in the unengineered environment. 2. There must be species of taking advantage of the resource(s) that exclusively occur in the engineered habitat (Wright et al. 2006).

These three components (structural, abiotic and biotic change) can have a feedback effect on the ecosystem engineer. This occurs when activity or density of the engineer are a function of the engineered structural, abiotic, or biotic states. Engineer activities include all things an engineer does that change the structure within an abiotic environment. Feedbacks can have a positive and/or a negative influence on the engineer. For example, a beaver dam provides shelter (abiotic positive) and prevents access of predator (biotic positive) but sometimes it can cause flooding that reduces the food supply (biotic negative). Studying possible feedbacks may provide more insight about why ecosystem engineers may engineer, when, how and where they might do so, and when structural maintenance or abandonment might be expected (Jones 2010).

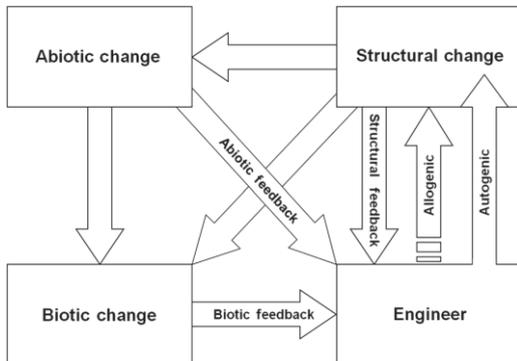


Fig 1. Physical ecosystem engineering by organisms. The cause/effect relationships representing an engineered system. (Jones 2010)

Effect of ecosystem engineers on habitat complexity

Autogenic engineers typically increase the habitat complexity (Crooks 2002) because they create new structures and thereby create more heterogeneity and more living space for different species. For example, Zebra mussels, which create dense beds on cobbles, had more individuals and species than the bare cobbles alone (Stewart and Haynes 1994). Allogenic engineers can also increase habitat complexity; the invasive cordgrass *Spartina alterniflora* alters the physical-chemical properties of sediment, which cause changes in macrofaunal community (Neira et al. 2007). In addition, invasive autogenic engineers can decrease the complexity by replacing organisms that create a higher heterogeneity. Allogenic species can have a negative influence on the complexity by changing, replacing or removal of a resource.

3. Case studies

In the next section, the effects of three well-studied invasive ecosystem engineers will be discussed. These being, *Crassostrea gigas* (Japanese oyster), *Caulerpa taxifolia* (seaweed) and *Zostera Japonica* (seagrass). By forming physical structures and altering biotic or abiotic materials they change the ecosystem structure and functioning. To get a good view on the possible effects these engineers could have on their environment the habitats before invasion and the habitats after invasion will be compared. Invasive ecosystem engineers often influence native ecosystem engineers.

Case study 1: *Crassostrea gigas*

General description *Crassostrea gigas*

The Japanese oyster, *Crassostrea gigas* is a suspension-feeding bivalve of the class Pelecypoda, or Bivalvia. *C. gigas* filters planktonic organisms and detritus from the surrounding water. Individual *C. gigas* filter larger volumes of water per time unite than other bivalve species in Dutch estuaries (Troost 2010). The shell of *C. gigas* is large (mature specimens can reach 80 mm to 400 mm) rounded, radial folded and often rough shaped and sharp. The colour of the shell varies but is usually

(e.g. shells of other species or rocks) it forms large reef structures on tidal flats (Diederich 2006). *C. gigas* is a spawner. The eggs and sperm are released into the water where the fertilization takes place. *C. gigas* is an invasive species in North America, Australia, Europe, and New Zealand. It is difficult to exactly outline the native distribution of the pacific oyster as it has been confused with other species over the years. But it seems to be a native species to Japan (Troost 2010).



Figure 2. Japanese oyster, *Crassostrea gigas*. Ref: <http://northislandexplorer.com/molluscs/giantpacificoyster.html>

Situation description

To get a better view of the effects *C. gigas* has on ecosystem functioning, Mussel beds (*Mytilus edulis*) will be compared on the intertidal of the Wadden Sea before and after invasion of *C. gigas*. Mussels play an important role as ecosystem engineer in the Wadden sea (e.g. stabilize sediment, clear water column, provide shelter for other organisms) (Rönnbäck et al. 2007). However the Japanese oyster is still steadily spreading and is increasingly found in mussel beds. In 2004 the total cover of the intertidal of the Wadden Sea was estimated at 4 km². In 2005 this was estimated at 5.5 km². (Troost 2010, Padilla 2010). Although Blue mussel beds have been replaced by Japanese oysters it is expected that mussels and oysters will coexist in compact reefs (Diederich 2006, Kochmann et al. 2008).

Structural change

Like *Mytilus edulis*, *C. gigas* lives attached to hard substrates in the intertidal and subtidal zones (Troost 2010). *C. gigas* larvae prefer settling on conspecifics (Arakawa 1990). However, they attach also to rocks, shells of other species and artificial materials such as chains and anchors in shallow or sheltered waters. When there is no hard substrate available oysters may also attach to muddy or sandy areas and create three-dimensional structures in an otherwise two-dimensional landscape (Padilla 2010). Oyster larvae often settle on the shell of adults and thereby create stable clusters of oysters. These clusters form a reef as the individuals stay cemented to the substrate of settlement (Markert et al. 2009). In the Wadden Sea oysters are often found in mussel beds (Kochmann et al. 2008). Because oysters have a different shape than mussels (bigger shells, sharper and lighter coloured) the beds get a different, more complex, structure (Markert et al. 2009).

Abiotic change

Like mussel beds, large oyster reefs can alter patterns of movement by sediments, thereby stabilizing sediments and raise the surface. However, mature oyster reefs seem to be more persistent than mussel beds and may therefore stabilize the sediments on a larger time scale (Troost 2010, Commito et al. 2008). Oyster reefs can have a positive influence on the saltmarsh by reducing erosion and increasing sediment rates (Padilla 2010). Furthermore, like mussels *C. gigas* enrich the sediment, excreting vast amounts of faeces and pseudo faeces and thereby alter the organic content and grain size of sediment (Commito et al. 2008). Oyster reefs do not only alter the sediment movements but they also alter the water flows. The roughness, caused by the sharp and large shells, enhance near-bed turbulence levels and thereby increase the food-flux, reducing refiltration of already filtered water (Gutiérrez 2003). *C. gigas* can filter a larger amount of water per time unit than *M. edulis*, (Troost 2010) increasing the water clarity, and thus, light penetration into the water column (Sousa 2009, Padilla 2010). Another engineering effect found by Padilla (2010) is the altering of the thermal

regime. According to this study the oysters were cooler than the surrounding rocks due to the lighter coloured shells.

Biotic change

The rapid spread of *C. gigas* and fast reduction of mussel beds had researchers worried about the future of *M. edulis* in the Wadden Sea. Several years after the first time *C. gigas* was found in the Wadden Sea the oyster still constitutes only a fraction of the total filter-feeder biomass in the Dutch Wadden Sea. However it is already the most dominant bivalve in the Oosterschelde estuary of the Netherlands (Troost et al. 2009a). Despite of the changes in structure and abiotic factors, due to the invasion of *C. gigas*, it is expected that mussels and oysters will coexist in compact reefs (Diederich 2006, Kochmann et al. 2008). Surprisingly the abundance of mussels seems to be even higher in beds with oysters than in beds without (Markert et al. 2009, own unpublished data). Markert et al. 2009 found a lower abundance of juvenile *M. edulis* in *C. gigas* dominated patches. This might be due to the low swimming velocity of *M. edulis* larvae and thereby the increasing chance of being filtered by *C. gigas*. However when the *M. edulis* larvae were successfully settled mortality seems to be lower in *C. gigas*-invaded areas than in *M. edulis*-dominated areas. An explanation for this can be that *C. gigas* may provide a refuge from predation. On the other hand, the mussels found in coexistence with oysters were smaller. Due to the higher filter capacity of oyster, the mussels may suffer from food shortage. The presence of oysters in mussel beds may have another advantage for mussels. It has been found that *C. gigas* can act as an alternate host and a sink for parasites of *M. edulis* (Thieltges et al. 2009). This suggests that the presence of *C. gigas* reduces the infection rate and load of parasites in *M. edulis*.

Oyster invasion in mussel beds provide a more heterogenic and more complex structure. This can enhance the local species richness and biodiversity (Kochmann et al. 2008, Markert et al. 2009, Troost 2010). Markert et al. (2009) and Kochmann et al. (2008) made a comparison between macrofaunal communities in mussel beds and oyster reefs. Both studies found a large similarity between the communities in mussel beds and oyster reefs. Markert et al. 2009 did not find species that had never been found in mussel beds. However, both studies showed a higher species richness in areas dominated by *C. gigas*. Markert et al. (2009) found an exclusive occurrence of *anthozoans* and a higher abundance and diversity of sessile suspension feeders, epibionts, epibenthic predators (*Carcinus maenas*, *Asterias rubens*, and *Harmothoe imbricata*) and infauna in *C. gigas* dominated areas. Kochmann et al. (2008) confirmed that *C. gigas* dominated beds harbour a higher abundance of sessile suspension feeders and found subtle differences in dominant associated infaunal species between oyster reefs and mussel beds. Both Markert et al. (2009) and Kochmann et al. (2008) concluded that *C. Gigas* reefs compensate for the conceivable loss of *M. edulis* beds in the intertidal of the Wadden Sea by replacing the ecological function of *M. edulis*.

Besides the more heterogenic and more complex structure there are other biotic impacts that can cause a higher species richness in *C. gigas* dominated areas. *C. gigas* is known to have a larger filtration capacity than *M. edulis*. The increasing water transparency, due to a decrease in plankton concentrations and other particles in suspension, can benefit light limited species (Padilla 2010). Besides a larger filter capacity, *C. gigas* probably affects near-bed turbulence levels more strongly than the native bivalves, due to the larger rough structures they create. This turbulence makes it more difficult for plankton to escape (Troost 2010). Eventually, *C. gigas* may exert a top-down

control on zooplankton communities and benthic communities through direct grazing on weak planktonic escapers and the filtration of pelagic larvae (Troost 2010, Markert et al. 2009, Sousa 2009).

The clearance rate corresponds with the biodeposit production. The biodeposit production depends on the size, respectively on the biomass of an organism. Because the biomass of *C.gigas* is on average higher than the biomass of *M. edulis*, *C. gigas* excretes more faeces and pseudo faeces. This gives rise to a higher nutrient concentration and favours colonization by endobenthic organisms (Markert et al. 2009).

Feedback on ecosystem engineer

The structural, biotic and abiotic changes cited in the previous paragraphs can have a feedback impact on *C. gigas*. The large three-dimensional structure may provide shelter against extreme environmental conditions (e.g. impact of waves or heat) (Gutiérrez et al. 2003), refuge from predation (e.g. birds that have difficulty reaching into the oyster bed) and provide food by altering the water current (Troost 2010). But these structures have also some disadvantages. Oysters growing at the edge of the reef suffer more from predation but grow faster and bigger. Oysters living in the middle of the reef are smaller and are often strangely formed. This is probably due to food competition between oysters and the oppression (Padilla 2010).

Net effect of invasive *Crassostrea gigas* in *Mytilus edulis* beds and ecosystem services

The Blue mussels in the Wadden Sea full fill an important role. The mussel beds provide important ecosystem services, for example, shelter for other organisms, stabilization of the sediment, clarity of the water column (Troost 2010, Padilla 2010, Diederich 2006) and mussels incorporate carbon produced in other systems into the food web. The mussels filter the plankton that would otherwise stay in suspension and deposited this as detritus on the bottom, where it provides energy input for invertebrates, which in turn improves the food base for fish (Rönnbäck 2007). In table 1 the effects of the invasion of *C. gigas* on ecosystem functioning in *M. edulis* beds are summarized. The invasion of oysters in mussel beds seems to have a net positive effect on the ecosystem functioning. The invasion by oysters provides a more complex habitat which ensures species richness, it stabilizes sediment on a larger time scale and because of a higher filtration capacity they provide higher water clarity than mussel beds uninvaded by *C. gigas*. The presence of the Japanese oysters in mussel beds provides more ecosystem services. A higher species richness in mussel beds improves the food base for fish and the fish stock gets larger. The stabilization of the sediment on a larger time scale prevents erosion which protects the shoreline (Grabowski 2012). A negative effect of the oysters is the oppression and the food competition with mussels which results in smaller and irregular-shaped mussels. This may have a negative influence on Blue mussel harvesting (Markert et al. 2009).

Table 1: Summary of effects *C. gigas* may have on *M. edulis* beds in the Wadden Sea. +: positive effect on ecosystem functioning, +/-: neutral effect on ecosystem functioning, -: negative effect on ecosystem functioning.

Aspect	Effect	Ecosystem functioning	Reference
Structural change	- Oysters and mussels coexist creating a more complex structure	+	Troost 2010 Padilla 2010 Diederich 2006
Abiotic change	- stabilize sediment on larger time scale - increasing water clarity - alter thermal regime (let it cool in darker environment) - stronger near-bed water turbulence - higher nutrient concentration	+ + +/- + +	Committo 2008 Gutiérrez 2003 Sousa 2009 Padilla 2010 Rönnbäck 2007
Biotic change	- higher abundance mussels - Smaller and misshapen mussels - Higher species richness - reduces the infection rate and load of parasites in mussels - compensate for loss of <i>M. edulis</i> Wadden sea - larger alteration of plankton community	+ - + + + +/-	Markert 2009 Thieltges et al. 2009 Markert et al. 2009 Kochmann et al. 2008 Sousa 2009
Feedback	- reefs provides shelter against extreme environmental conditions - provide refuge from predation - oyster at the edge of reef grow faster but are less protected against predation -oyster in middle of reef suffers from food and space competition	+ + + -	Gutiérrez et al. 2003 Padilla 2012

Case study 2: *Caulerpa taxifolia*

General description *Caulerpa taxifolia*

Caulerpa taxifolia is a green alga (or seaweed) of the class Chlorophyceae. The seaweed forms continuous dense meadows on many kinds of substrates such as rocks, sand, mud and dead rhizomes of seagrasses. *C. taxifolia* is more an allogenic ecosystem engineer than an autogenic engineer. *C. taxifolia* is particularly abundant in nitrogen-rich coastal waters (Williams and Smith 2007). It produces substances that are toxic to herbivores such as sea urchins and some fish. Reproduction occurs asexually by fragmentation. Small parts of algae will regrow into another algae (Glasby 2012). *C. taxifolia* has been easily carried over the world by anchors of ships and fishing nets. It is native to tropical oceans and seas, but it has invaded large areas of the Mediterranean sea and is also locally abundant in some estuaries of Southeast Australia that are outside of its native range (Bishop and Kelaher 2012). *C. taxifolia* has often been implicated with seagrass decline throughout the world (Glasby 2012).

Situation description

To get a better view of the effects *C. taxifolia* has on ecosystem functioning, seagrass meadows (*Posidonia australis* and *Zostera capricorni*) will be compared in estuaries near Sydney in SE Australia before and after invasion of *C. taxifolia*. Studies in the Mediterranean show that *Posidonia oceanica* seagrass beds have a positive effect on the growth of *C. taxifolia* and that beds of this seagrass are particularly vulnerable to invasion (Ceccherelli and Cinelli 1999). The effects of *C. taxifolia* on the native seagrasses in the estuaries of Australia are still not completely clear and form an interesting study site. Seagrasses form large meadows that are considered to be of high importance to the environmental conservation of the region as nursery grounds for many species of economically important fish and shellfish (NYS seagrass taskforce 2009).



Figure 3. *Caulerpa taxifolia*. Ref: http://cisr.ucr.edu/caulerpa_taxifolia.html

Structural change

While *P. australis* and *Z. capricorni* have long leaves, *C. taxifolia* has flat blades that give it a look of a fern. This morphological difference creates a difference in habitat structure. In southeast Australia *C. taxifolia* has been observed growing besides to and in seagrass beds, as well as in previously unvegetated sediments (Glasby et al. 2005). This may cause a patchiness structure of areas with only *C. taxifolia* or seagrass or areas where both species coexist, which may lead to an increase in habitat complexity. Like seagrasses *C. taxifolia* forms dense monospecific beds which contain almost no open areas. Like many other macroalgae, *C. taxifolia* has little structural defence. Consequently, it can decompose much faster than the seagrass litter. Whereas seagrasses contain phenolics in response to ecological pressures such as herbivory and pathogen, *C. taxifolia* contains the secondary metabolite caulerpenyne that can limit fouling and deter some herbivores and detritivores stressors (Bishop and Kelaher 2012).

Abiotic change

Because *C. taxifolia* decomposes more rapidly and has a lower C/N ratio than *P. australis* and *Z. capricorni* it can have a large impact on the sediment and the detrital material. Small quantities of slow decomposing species can enrich the habitat with useful nutrients. Large amounts of rapidly decomposing species, on the other hand, can cause anoxia of waterlogged sediments. The role of detrital material providing food and habits depends on the species and the volume (Bishop and Kelaher 2012). The changes in the supply and composition of detrital materials may have the potential to cause major changes to recipient ecosystems. The high decomposition rate of *C. taxifolia* can cause anoxia of sediment layers (Bishop and Kelaher 2012).

Biotic changes

Studies implicate that *C. Taxifolia* has a negative influence on the biomass of seagrasses in the Mediterranean Sea (Ceccherelli and Cinelli 1999). This negative effect has not yet been found in the estuaries of Australia. A study done by Glasby (2012) indicates that *C. taxifolia* is not having adverse impacts on the coverage of seagrasses in the estuaries of Australia. This study states that *C. taxifolia* is an opportunist. It persists longer and its coverage is greater in previously non-vegetated sediments than amongst seagrasses. *C. taxifolia* did not cause reductions in the cover of seagrasses, it co-existed with *P. australis*.

The fast decomposing rate of *C. taxifolia* can cause changes in the supply and composition of detrital materials. This can lead to major changes in recipient ecosystems. A study done by McKinnon et al. (2009) found a higher species richness in seagrass compared to *C. taxifolia*. They also found a significant lower abundance of infauna. Bishop and Kelaher (2012) tested the differences in the benthic communities supported by *C. taxifolia*, *Z. capricorni* and *P. australis* detritus on an intertidal mudflat in Australia. To do this they perform detrital enrichment experiments. They examined two factors: the detrital identity (from *C. taxifolia*, *P.australis*, *Z. capricorni*) and the supply (low [30 g dry weight] and high [60 g dry weight]). After four months they found that the detritus from *C. Taxifolia* had caused effects on the benthic communities that could not be replicated by detritus from *P. australis* or *Z. capricorni*. A loading of 30 gram dry weight detritus had a positive effect on macroinvertebrate abundance and richness. By contrast, the plots receiving 60g dry weight had a lower macroinvertebrate richness. This could be due to the anoxia created by the high decomposition rate of *C. taxifolia*. The abundance and species richness in the plots receiving detritus from the seagrasses was no different to the control. So, the effect of *C. taxifolia* on the species richness depends on the detrital supply and this depends on the biomass of *C. taxifolia*.

Seagrass meadows are known for their nursery function for many fish species. The invasion of *C. taxifolia* may have a large impact on the distribution and species richness of fish. A study done by York et al. (2006) showed that there is indeed a significant difference in fish assemblages among habitats dominated by *Z. capricorni*, *P. australis* or *C. taxifolia*. On several sites they found a lower species richness and abundance of fish in *C. taxifolia* than in seagrasses. On contrary, in the Mediterranean fish assemblages in *C. taxifolia* and seagrasses seems to be similar (Francour et al. 1995)

Feedback on ecosystem engineer

A high loading of detritus has a negative effect on the benthic community (Bishop and Kelaher 2012). The thick layer of detritus can cause an anoxic environment. This may also negatively influence *C. taxifolia*. The dense, large and toxic meadows provide protection against herbivores.

Net effect of invasive *Caulerpa taxifolia* in *Posidonia australis* and *Zostera capricorni* meadows and ecosystem services

Seagrasses are known for the high amount of ecosystem services they provide. Seagrasses play a large role in fish production because they function as nursery grounds for fish (York et al. 2006). The meadows control wave and current energy. This results in the protection against erosion of shorelines. Seagrass roots and rhizomes stabilize bottom sediments. In table 2 the effects of the invasion of *C. taxifolia* in *Posidonia australis* and *Zostera capricorni* meadows are summarized. The invasion of *C. taxifolia* in the habitat of *Posidonia australis* and *Zostera capricorni* seems to have a more negative net impact on ecosystem functioning as a positive net impact. The patchiness may enhance habitat complexity but this does not always lead to higher species richness. Nutrient enrichment may enhance invertebrate richness but when the biomass of *C. taxifolia* is high, anoxia may reduce invertebrate richness and may also have a negative influence on native seagrasses. The reduced oxygen levels and lowered food abundance affect higher trophic levels, including fish and thereby may have a negative effect on seafood production.

Table 2: Summary of effects *C. taxifolia* may have on *Posidonia australis* and *Zostera capricorni* in estuaries near Sydney in SE Australia. +: positive effect on ecosystem functioning, +/-: neutral effect on ecosystem functioning, -: negative effect on ecosystem functioning.

Aspect	Effect		Reference
Structural change	- patchiness structure may enhance habitat complexity	+	Bishop and Kelaher 2012
Abiotic change	- greater nutrient enrichment - causes anoxia of sediment	+ -	Bishop and Kelaher 2012
Biotic change	- lower invertebrate richness if there is anoxia - lower abundance infauna - higher invertebrate richness if there is nutrient enrichment - lower species richness and abundance of fish. - <i>C. taxifolia</i> did not cause reductions in the cover of seagrasses (in the Mediterranean sea <i>C. taxifolia</i> did influence seagrass cover negatively)	- - + - +	Glasby 2012 Ceccherelli and Cinelli 1999 McKinnon et al. Bishop and Kelaher 2012 York et al. 2006
Feedback	- meadows provide protection against herbivores - anoxia may lead to unfavourable habitat herbivores	+ -	...

Case study 3: *Zostera japonica*

General description *Zostera japonica*

Zostera japonica (also named Japanese or dwarf eelgrass) is a seagrass of the class *Liliopsida*. It is a flowering plant that reproduces sexually by seeds or asexually. *Z. japonica* forms dense patches in estuarine and intertidal zones. *Z. japonica* is more an allogenic engineer than an autogenic engineer. The meadows are a structure that provides hiding places and serves as a nursery ground for fish, which is a form of autogenic engineering. The rhizomes change sediment and thereby change the macrofaunal community which is an allogenic form of engineering. In the early mid-20th century it was first introduced from eastern Asia to Northwest America. By the 1980s it was found in several estuaries (Larned 2003).

Situation description

To get a better view of the effects *Z. japonica* has on ecosystem functioning, *Zostera marina* meadows will be compared in estuaries in the Northwest of the Pacific Ocean before and after invasion of *Z. japonica*. *Z. marina* is a native seagrass to the Northwest Pacific. *Z. japonica* and *Z. marina* can be found in close proximity and are closely related but they do not have overlapping distributions. Although found in the same area and functionally similar the two species exhibit large morphological differences and have distinct ecological niches in the intertidal zone. *Z. japonica* is traditionally found in the upper intertidal zone, but in absence of *Z. marina* can colonize into the lower intertidal zone. In addition, *Z. japonica* can exist in areas with much greater wave energy (Fong 1998) and exposure to the atmosphere. This suggests that *Z. japonica* is more fit as an invader than *Z. marina*. *Z. japonica* has narrower blades and has a shorter overall length (30 cm) (Hay 2011). Although *Z. japonica* and *Z. marina* are often found in close proximity, theory predicts that functional similarity increases the intensity of competition between native and invasive species (Bando 2005). There are concerns that *Z. japonica* will overgrow *Z. marina*, changing the habitat structure.

Structural change

Like *Z. marina*, *Z. japonica* forms dense meadows. As already mentioned, there is a large morphological difference between *Z. japonica* and *Z. marina*. *Z. japonica* is 30 cm long and has narrow blades of 1 mm (Haynes 2000a). *Z. marina* is respectively 100 cm long and has broader blades of 10 mm (Haynes 2000b). These differences result in large structural change when *Z. japonica* outcompetes *Z. marina*. Generally, the distributions of *Z. japonica* and *Z. marina* do not overlap. This can result in an area with patches of *Z. japonica* and *Z. marina*.

Abiotic change

Native seagrasses play a dominant role in nutrient cycles. The establishment of an invasive seagrass may alter the nutrient source sink patterns in the invaded habitats (Larned 2003). A study done by Larned (2003) compared the effects of *Z. japonica* and *Z. marina* on dissolved nutrient fluxes in Yaquina Bay, Oregon, USA. Based on patterns of influx or efflux, they determined both species work



as sinks for nitrate (NO_3), ammonium (NH_4) and dissolved reactive phosphorus (DRP). Influx and efflux is the nutrient removal and release from the water column. However, during the warm season, *Z. marina* patches were a larger DIN (dissolved inorganic nitrogen) sink than *Z. japonica*. The DIN influx was almost twice as high in *Z. marina* habitats. This could be caused by the differences in biomass, as the above-ground biomass of *Z. marina* was almost nearly three times higher than that of *Z. japonica*. Nevertheless, *Z. japonica* had a higher mean NO_3 influx rate per unit above-ground biomass. This would suggest that if the biomass levels of *Z. japonica* increase in the future, this can lead to an increased NO_3 flux and thereby a reduction in nutrient availability. Besides altering nutrient cycles Larned (2003) also found significantly higher mean sediment grain sizes, sediment heterogeneity and porewater NH_4 concentrations in *Z. japonica* habitats than in *Z. marina* habitats.

Biotic change

Because *Z. japonica* and *Z. marina* functionally resemble each other it is expected that there is a strong competition between those species. Bando (2006) tested this hypothesis. This study showed that both species experience reduction in above-ground biomass caused by interspecific competition rather than by intraspecific competition. However, *Z. marina* shows relative higher reduction in biomass when the species were subjected to disturbance than *Z. japonica* (Hay 2011). In addition, several studies found that in the presence of *Z. japonica*, *Z. marina* leaf and rhizome growth was inhibited. When isolated from competitive pressures placed on it by *Z. japonica*, *Z. marina* is capable of growing much more rapidly (Hay 2011). Remarkably, the productivity and fitness of *Z. japonica* improved in a more stressful area, suggesting that *Z. japonica* can be a threat to *Z. marina* biomass in stressful circumstances (Hay 2011). Estuarine mudflats are subject to high levels of natural and anthropogenic disturbance so *Z. japonica* is likely to become the dominate species.

Z. japonica alters the nutrient fluxes and thereby may affect pelagic productivity. DIN and DRP efflux has been shown to supply most of the nitrogen and phosphorus required for phytoplankton growth in estuaries (Bando 2006). An override of *Z. marina* by *Z. japonica* may result in a nutrient limitation due to reduced benthic efflux. This nutrient limitation may also affect the benthic fauna.

According to a study done by Thom et al. (1995) the community of epibenthic organisms in *Z. japonica* beds was not different from the community in *Z. marina* beds. However, more studies that compare the species richness in *Z. marina* beds and *Z. japonica* beds are not available. Studies that compared the species richness from *Z. japonica* with unvegetated areas were available. A study from Lee et al. (2001) showed that the macrofaunal species richness in a *Z. japonica* bed was greater than in an adjacent unvegetated area. But there are species that encounter disadvantages from the *Z. japonica*. For, example shellfish production is inhibited through the increase in sediment fallout by lowering of the water speed (Hay 2011).

Feedback on ecosystem engineer

The accumulation of sediment on the bottom has also a negative effect on *Z. japonica*. The rhizomes and stems can get covered so much as to kill the seagrass. The seagrass dies off, detach and floats to the surface (Hay 2011).

Net effect of invasive *Zostera japonica* in *Zostera marina* meadows and ecosystem services

As already mentioned in previous paragraphs, seagrasses provide a high amount of ecosystem services. They play a large role in seafood production, water health and protection of shorelines. *Z. japonica* and *Z. marina* are both seagrasses and many of their provide services are the same, nevertheless there are some differences. In table 3 the effects of the invasion of *Z. japonica* in the habitat of *Z. marina* is summarized and *Z. japonica* seems to have a negative net impact on the functioning of the ecosystem. Especially in stressful conditions *Z. japonica* has a tendency to overgrow *Z. marina*. How quickly this could happen is not clear. The distributions of *Z. japonica* and *Z. marina* do not overlap which may result in an area with patches that differ in morphology. On a larger space scale the habitat complexity will increase due to the two morphologic different seagrass patches. The habitat complexity of *Z. japonica* meadows compared with the habitat complexity of *Z. marina* meadows do not seem to differ. The reduction of nutrient availability in *Z. japonica* meadows may lead to a lower abundance and diversity of epibenthic which may result in a decline of fish species richness; however this is not confirmed by scientific research.

Table 3: A summary of the effects *Z. japonica* may have on *Z. marina* in estuaries in Northwest Pacific. +: positive effect on ecosystem functioning, +/-: neutral effect on ecosystem functioning, -: negative effect on ecosystem functioning.

Aspect	Effect	Ecosystem functioning	Reference
Structural change	- morphological different patches	+/-	Haynes 2000a, 2000b Hay 2011
Abiotic change	- higher mean NO ₃ influx rate per unit above-ground biomass can lead to an increased NO ₃ flux - reduction in nutrient availability - higher mean sediment grain sizes - higher sediment heterogeneity - higher porewater NH ₄ concentrations	- - +/- +/- +/-	Larned 2003
Biotic change	- inhibition of leaf and rhizome growth of <i>Z. marina</i> - overgrowing <i>Z. marina</i> in stressful environments - lower phytoplankton growth - epibenthic organisms show no differences (- species richness increases in comparison with unvegetated areas. No data available in comparison with <i>Z. marina</i>)	- - +/- +	Hay 2011 Hourdequin 1994 Bando 2006 Thom et al. 1995 Lee et al. 2001
Feedback	- rhizomes and stems get covered so much so that <i>Z. japonica</i> (partially) outcompete the <i>Z. marina</i>	+/-	Hay 2011

4. Comparison effects of case studies

The framework of Jones et al. 2010 is a useful tool to examine the effects ecosystem engineers can have. However, after this analysis factors other than mentioned in the framework appeared to be from great importance in relation with ecosystem functioning. First, as already expected, the effect an invasive ecosystem engineer has on habitat complexity is from great importance. In general the local biodiversity increases when the invasive ecosystem engineer enhances the habitat complexity. Second, the effects of invasive ecosystem engineers on native ecosystem engineers play an important role. The invasive ecosystem engineer may co-exist with native ecosystem engineer or may outcompete the native ecosystem engineer. Outcompetition in particular, may have catastrophic consequences on ecosystem functioning. Third, invasive ecosystem engineers can alter the ecosystem services an ecosystem provides which may have great consequences for humans.

Table 4. Summary of effects of case study ecosystem engineers on habitat complexity, competing with the native species, and ecosystem services. +: positive effect, +/-: neutral effect, -: negative effect.

Invasive ecosystem engineer	Habitat complexity	Native ecosystem engineer	Ecosystem services
<i>Crassostrea gigas</i>	+	+/-	+
<i>Caulerpa taxifolia</i>	+	+/-	-
<i>Zostera japonica</i>	+/-	-	+/-

C. gigas has an overall positive net effect on the Wadden Sea. The oysters and mussels coexist in mussel beds which increases the habitat complexity and higher species richness. The abundance of Blue mussels is higher in the presence of oysters but the biomass of the mussels is smaller. So the impact of the oysters on the mussels (a native ecosystem engineer in the Wadden Sea) can be seen as neutral. The presence of *C. gigas* seems to increase the amount of ecosystem services: the water clarity increases, sediment stability increases and the macrofauna species richness increases.

C. taxifolia on the other hand, has a more negative net impact on ecosystem functioning than *C. gigas*. This species does enhance the habitat complexity by providing a patchiness structure. In the estuaries of southeast Australia it seems to have no negative influences on the native seagrasses. However this can change when the species gets more abundant. A higher biomass of *C. taxifolia* may have a negative effect on the native seagrasses and the species richness by creating an anoxic environment. *C. taxifolia* does not provide the same ecosystem services as native seagrasses. *C. taxifolia* meadows have lower fish species richness.

Z. japonica has a negative impact on the ecosystem functioning. *Z. japonica* does not enhance the habitat complexity highly because the distributions of the two species do not overlap. It has a negative influence on the growth of the native seagrass (*Z. marina*) but provides the same ecosystem services as *Z. marina*.

5. Discussion

The net impact of invasive ecosystem engineers depend on many factors such as habitat type (e.g. soft bottom or hard bottom), native organisms and relative amount of stress in environment (Padilla 2010). In other words, as already pointed out by Jones et al. in 1994, the effect of ecosystem engineers is context depended. For example, the overall effect of *C. gigas* in the Wadden Sea can be seen as positive for the species richness and the maintenance of mudflats. However, the *C. gigas* population in the Oosterschelde of the Netherlands has a less positive effect. *C. gigas* is the dominant bivalve in the Oosterschelde and seems to overgrow the native mussel (*M. edulis*). *C. gigas* also seem to have a negative effect on eelgrass. Kelly and Volpe (2007) found a decrease in the growth of eelgrass due to *C. gigas* in Georgia, British Columbia.

Beside the context dependency the effect of invasive ecosystem engineers can also differ in time and space (Hastings et al. 2007). For example, *C. taxifolia* did not cause reductions in the cover of seagrasses in Australia but this can change when the biomass of *C. taxifolia* increases. The greater amount of detritus can cause an anoxic sediment layer. This can have a negative influence on species richness and diversity and on the ecosystem services.

Even though a complete generalisation of the effects of engineer perhaps can never be made, examining this concept can lead to a better understanding of ecosystem functioning and new insights. The framework of Jones et al. (2010) can be a useful tool to do this. It is a framework that is intended for the physical effects ecosystem engineer have, but the concepts are sometimes a little bit vague. For example, Jones et al. encounters the abundance of organisms as a biotic aspect but he says nothing about the effect engineers can have on the species richness or biodiversity.

6. Conclusion

The net effect of an invasive ecosystem engineer on ecosystem functioning depends on many factors. I hypothesised that in general ecosystem engineers may have a positive influence on ecosystem functioning because they enhance habitat complexity. In practice, the impact of engineers on an ecosystem can vary widely and is not always positive. The three invasive ecosystem engineers described in the previous case studies vary in their impacts on habitat complexity, the native ecosystem engineers and the ecosystem functioning.

These results show that a generalisation of the effects of invasive ecosystem engineers is difficult to make. However, an interesting study of invasive bivalves as ecosystem engineer shows that some generalisation in functional groups is possible (Sousa 2009). They found that bivalves in general have a great impact on ecosystem structure and ecosystem functioning. Bivalves provide changes in sediment grain size, and organic matter content due to bioturbation, increased light penetration into the water column due to filter feeding, changes in near bed flows, provision of colonisable substrate and refuges by shells. *C. gigas* is a bivalve and indeed provides these effects. So it is possible to make some generalisation within a functional group. These generalisations can provide more insight in the effect possible new invasive ecosystem engineers can have on an ecosystem.

This thesis shows that the impact of an invasive ecosystem engineer on ecosystem functioning depends on the effect the engineer has on: the complexity of a system, on the native ecosystem engineer and the ecosystem services. In addition, this thesis also shows that the context and space and time scale in which an engineer is examined of great importance is for the impact an invasive ecosystem engineer has.

7. References

- Arakawa, K. Y. 1990. Natural spat collecting in the Pacific oyster *Crassostrea gigas* (Thunberg). *Mar Behav Physiol* 17:95–128.
- Bando, J. K. 2006. The roles of competition and disturbance in a marine invasion. *Biol Invasions* 8:755–763.
- Bishop, M. J., Kelaher, B. P. 2013 Replacement of native seagrass with invasive algal detritus: impacts to estuarine sediment communities. *Biol Invasions* 15:45–59.
- Carlton, J. T. 1979. History, biogeography, and ecology of the introduced marine and estuarine invertebrates of the Pacific coast of North America. Ph.D. thesis, Univ. of California, Davis.
- Ceccherelli, G., Cinelli, F. 1998. Habitat effect on spatio-temporal variability in size and density of the introduced alga *Caulerpa taxifolia*. *Mar Ecol Prog Ser* 163:289–294.
- Comito, J. A., Como, S., Grupe, B.M., Dowa, W.E., 2008. Species diversity in the soft bottom intertidal zone: biogenic structure, sediment, and macrofauna across mussel bed spatial scales. *Journal of Experimental Marine Biology and Ecology* 366:70-81.
- Crooks, J. A. 2002. Characterizing ecosystem-level consequences of biological invasions: the role of ecosystem engineers. *Oikos* 97:153–166.
- Diederich, S., 2006. High survival and growth rates of introduced Pacific oysters may cause restrictions on habitat use by native mussels in the Wadden Sea. *Journal of Experimental Marine Biology and Ecology* 328:211–227.
- Francour, P., Harmelin-Vivien, M., Harmelin, J. G., Duclerc, J. 1995 Impact of *Caulerpa taxifolia* colonisation on the littoral ichthyofauna of north-western Mediterranean Sea: preliminary results. *Hydrobiologia* 300/301:345–353.
- Glasby, T. M. 2013. *Caulerpa taxifolia* in seagrass meadows: killer or opportunistic weed? *Biol Invasions* 15:1017–1035.
- Gutiérrez, J. L., Jones, C. G., Strayer, D. L., Iribarne, O. O., 2003. Mollusks as ecosystem engineers: the role of shell production in aquatic habitats. *Oikos* 101:79–90.
- Hay, L. 2011 Ecology of Japanese eelgrass, *Zostera japonica* and Impacts within the Pacific Northwest. Thesis, Univ. of Washington.
- Haynes, R. R. 2000a *Zostera japonica*. *Flora of North America*. North of Mexico Vol. 22. New York Publishing and Oxford.

Haynes, R. R. 2000b *Zostera marina*. Flora of North America. North of Mexico Vol. 22. New York Publishing and Oxford.

Jones, C. G., Gutiérrez, J. P., Byers, J. E., Crooks, J. A., Lambrinos, J. G., Talley, T. S. 2010. A framework for understanding physical ecosystem engineering by organisms. 119:1862–1869.

Jones, C. G., Lawton, J. H., Shachak, M. 1994. Organisms as ecosystem engineers. *Oikos* 689:373–386.

Jones, C. G., Lawton, J. H., Shachak, M. 1997b. Positive and negative effects of organisms as physical ecosystem engineers. *Ecology* 78: 1946–1957.

Glasby, T. M., Creese, R. G., Gibson, P. T. 2005. Experimental use of salt to control the invasive marine alga *Caulerpa taxifolia* in New South Wales, Australia. *Biol Conserv* 122:573–580.

Kelly, J.R., Volpe, J. R., 2007. Native eelgrass (*Zostera marina* L.) survival and growth adjacent to non-native oysters (*Crassostrea gigas* Thunberg) in the Strait of Georgia, British Columbia. *Botanica Marina* 50:143–50.

Kochmann, J., Buschbaum, C., Volkenborn, N., Reise, K. 2008. Shift from native mussels to alien oysters: differential effects of ecosystem engineers. *Exp Mar Biol Ecol* 364:1–10.

Larned, T. 2003. Effects of the invasive, nonindigenous seagrass *Zostera japonica* on nutrient fluxes between the water column and benthos in a NE Pacific estuary. *Marine Ecology Progress Series* 254: 69–80.

Lee, S. Y., Fong, C. W. Wu, R. S. S. 2001. The effects of seagrass (*Zostera japonica*) canopy structure on associated fauna: a study using artificial seagrass units and sampling of natural beds. *Journal Of Experimental Marine Biology And Ecology* 259:23-50.

Markert, A., Wehrmann, A., Kröncke, I. 2009. Recently established *Crassostrea*-reefs versus native *Mytilus*-beds: differences in ecosystem engineering affects the macrofaunal communities (Wadden Sea of Lower Saxony, southern German Bight). *Biological Invasions* 12:15–32.

McKinnon, J. G., Gribben, P. E., Davis, A. R., Jolley, D. F., Wright, J. T. 2009. Differences in soft-sediment macrobenthic assemblages invaded by *Caulerpa taxifolia* compared to uninvaded habitats. *Marine Ecology Progress Series* 380:59-71.

Neira, C., Levin, L. A., Grosholz, E. D., Mendoza, G. 2007 Influence of invasive *Spartina* growth stages on associated macrofaunal communities. *Biol Invasions* -.

Met opmaak: Engels
(Groot-Brittannië)

NYS seagrass taskforce 2009 Final Report of the New York State Seagrass Task Force: Recommendations to the New York State Governor and Legislature.

Padilla, D. K. 2010. Context-dependent Impacts of a Non-native Ecosystem engineer the Pacific Oyster *Crassostrea gigas*. *Integrative and Comparative Biology* 50:213–225.

- Rilov, et al. 2012. How strong is the effect of invasive ecosystem engineers on the distribution patterns of local species, the local and regional biodiversity and ecosystem functions? *Environmental Evidence* 1:10.
- Rodriguez, L. F. 2006. Can invasive species facilitate native species? Evidence of how, when, and why these impacts occur*. *Biol Invasions* 8:927–939.
- Rönnbäck, P., Kautsky, N., Pihl, L., Troell, M., Söderqvist, T., Wennhage, H. 2007. Ecosystem Goods and Services from Swedish Coastal Habitats: Identification, Valuation, and Implications of Ecosystem Shifts *A Journal of the Human Environment*. 36:534-544.
- Ruiz, G. M., Carlton, J. T., Grosholz, E. D., Hines, A. H. 1997. Global Invasions of Marine and Estuarine Habitats by Non-Indigenous Species: Mechanisms, Extent, and Consequences. *Amer. Zool.* 37:621-632.
- Sousa, R., Gutiérrez, J. L., Aldridge, D. C. 2009. Non-indigenous invasive bivalves as ecosystem engineers. *Biol Invasions*. 11:2367-2385.
- Stewart, T. W., Haynes, J. M. 1994. Benthic macroinvertebrate communities of southwestern Lake Ontario following invasion of *Dreissena*. *J. Great Lakes Res.* 20: 479–493.
- Talley, T. S. and Crooks, J. A. 2007. Habitat conversion associated with bioeroding marine isopods. In: Cuddington, K. et al. (eds), *Ecosystem engineers: plants to protests*. Elsevier. pp. 185 – 202.
- Thieltges, D. W., Reise, K., Prinz, K., Jensen, K. T., 2009. Invaders interfere with native parasite–host interactions. *Biol Invasions* 11:1421–9.
- Thom, R. M., Miller, B., Kennedy, M. 1995. Temporal patterns of grazers and vegetation in a temperate seagrass system. *Aq Bot* 50:201-205.
- Troost, K. 2010. Causes and effects of a highly successful marine invasion: Case-study of the introduced Pacific oyster *Crassostrea gigas* in continental NW European estuaries. *Journal of Sea Research* 64:145–165.
- Troost, K., Gelderman, E., Kamermans, P., Smaal, A.C., Wolff, W.J., 2009a. Effects of an increasing filter feeder stock on larval abundance in the Oosterschelde estuary (SW Netherlands). *Journal of Sea Research* 61:153–164.
- Williams, S. L., Smith, J. E. 2007. A global review of the distribution, taxonomy, and impacts of introduced seaweeds. *Annu Rev Ecol Syst* 38:327–359.
- Wright, J. P., Jones, C. G. 2006. The Concept of Organisms as Ecosystem Engineers Ten Years On: Progress, Limitations, and Challenges. *BioScience* 56:203-209.
- Wright, J. P., Jones, C. G., Boeken, B., Shachak, M. 2006. Predictability of ecosystem engineering effects on species richness across environmental variability and spatial scales. *Journal of Ecology* 94:815–824.

York, P. H., Booth, D. J., Glasby, T. M., Pease, B. C. 2006. Fish assemblages in habitats dominated by *Caulerpa taxifolia* and native seagrasses in south-eastern Australia. Marine Ecology Progress Series 312: 223–234.