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Biodiversity and food web indicators of community recovery in intertidal shellfish reefs

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ABSTRACT

In conservation strategies of marine ecosystems, priority is given to habitat-structuring foundation species (e.g. seagrasses, mangroves and reef-building corals, shellfish) with the implicit goal to protect or restore associated communities and their interactions. However, the number and accuracy of community level metrics to measure the success of these strategies are limited. Using intertidal shellfish reefs as a model, we tested to what extent foundation species alter community and food web structure, and explored whether basic metrics of food web structure are useful indicators of ecosystem complexity compared to other often-used indices. We found that shellfish reefs strongly modified community and food web structure by modifying habitat conditions (e.g. hydrodynamics, sediment grain size). Stable isotope-based food web reconstruction captured important differences between communities from bare mudflat and shellfish reefs that did not emerge from classic abundance or diversity measures. On shellfish reefs, link density and the number of top predators were consistently higher, while both connectance and the richness of intermediate species was lower. Species richness (+42%), species density (+79%) and total biomass of benthos, fish and birds (+41%) was also higher on shellfish reefs, but this did not affect the Shannon diversity or Evenness. Hence, our results showed that basic food web metrics such as link density and number of top consumers and intermediate species combined with traditional measures of species richness can provide a robust tool to measure conservation and restoration success. We therefore suggest that these metrics are included as Essential Biodiversity Variables (EBV), and implemented as ecosystem health indicators in legislative frameworks such as the Marine Strategy Framework Directive (MSFD).

1. Introduction

Coastal ecosystems are degrading at alarming rates worldwide (Lotze et al., 2006; Millennium Ecosystem Assessment, 2005). Human generated threats of overharvesting, habitat destruction, eutrophication, climate change and pollution have caused major declines of many coastal ecosystems, including those supported by foundation species, also described as ‘ecosystem engineers’ or ‘habitat modifiers’. For example, coral reefs have declined by at least 19% (Wilkinson, 2008), seagrasses by 29% (Waycott et al., 2009), mangroves by 35% (Millennium Ecosystem Assessment, 2005), oyster reefs by 90% (Beck et al., 2011) and Dutch intertidal mussel beds by 50% (Dankers et al., 2001). Numerous restoration and protection projects are attempted, motivated by the recognized high ecological and economical value of these ecosystems, including their role as carbon sinks (McLeod et al., 2011; Fourqurean et al., 2012; Macreadie et al., 2013), in flood protection (Christianen et al., 2013; Ferrario et al., 2014), for fisheries productivity (Moberg and Folke, 1999, Ronnback, 1999, Nagelkerken et al., 2002, Costanza et al., 1997) and as biodiversity hotspot (Roberts et al., 2002). Success rates of these attempts, however, are variable and so far have been quantified in different ways.

National and international conservation policies increasingly identify goals beyond the individual species' level such as the protection of functions and structure as well as “ecological completeness” of ecosystems (EU: European Commission, 2010; 2010/477/EU, NL: Ministry of Economic Affairs, 2014, USA; Raffaelli, 2004; Naiman et al., 2012; Thompson et al., 2012). To assess biodiversity worldwide and align biodiversity monitoring efforts, integrated and globally applicable indicators should be developed. Recently, Essential Biodiversity Variables (EBV) have been proposed as a general framework to reliably assess biodiversity change across ecosystems by combining variables that measure different aspects of biodiversity (e.g. genetic composition, species populations, community composition, ecosystem structure, ecosystem function) (Pereira et al., 2013). However, the identification and development of simple but effective indicators for the EBV framework is

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challenging. This is especially the case for food web functioning due to the highly dynamic and complex nature of these networks and the large variability in structure and functioning between separate ecosystems (McCann, 2007; Rombouts et al., 2013).

Multiple possible food web indicators have been proposed in the Marine Strategy Framework Directive (MSFD) in European territorial waters (EU, 2010) as well as other International legislation frameworks and commitments (e.g. Water Framework Directive (2000/60/EC), Habitat Directive (92/43/EC)) (Rombouts et al., 2013; Rogers et al., 2010). So far, the proposed food web indicators mostly focused on the structure of food webs, using traditional community-level parameters reported in ecological studies such as Shannon-Wiener diversity and species richness. However, these indicators do not include the functioning of food webs, the complexity of species interactions, and therefore only provide limited information on how the ecosystem functions (Schipper et al., 2016). This in turn may lead to a potential mismatch between goals of conservation policies and the ecological indicators used to measure policy success (McCann, 2007; Rombouts et al., 2013).

A large number of studies investigating food web structure have revealed that the type, strength and topology of trophic interactions, all adhere to a set of general defining rules, suggesting that changes in trophic network structure can be indicative of ecosystem health (e.g. Williams and Martinez, 2000; de Visser et al., 2011; van der Zee et al., 2016). In addition, a rapidly increasingly number of studies have recently demonstrated that non-trophic interactions play a key role in mediating food web structure and resilience (Compton et al., 2013; Kefi et al., 2015; van der Zee et al., 2016). The effects of habitat modifying species on their environment and biodiversity are well studied (Tylianakis et al., 2007; Lemieux and Cusson, 2014; van der Zee et al., 2015; Donadi et al., 2015), however to date only few studies have assessed the effects of these species on food web structure, function, and resilience (van der Zee et al., 2016; de Fouw et al., 2016).

In this study we explore how intertidal shellfish reefs – dominated by habitat-structuring blue mussels (*Mytilus edulis*) – affect community and food web structure in an intertidal ecosystem that is heavily impacted by human activity, the Wadden Sea. Similar to many temperate soft-bottom intertidal ecosystems, mussel beds in the Wadden Sea form reefs that increase benthic trophic diversity as shellfish provide shelter and settlement substrate for many species, reduce hydrodynamic stress, stabilize sediment and facilitate other connected ecosystems (Gutierrez et al., 2003; Donadi et al., 2013; Donker et al., 2013; van der Zee et al., 2012, 2015). Mirroring declines of coastal ecosystems worldwide (Lotze et al., 2006), however, the Dutch Wadden Sea lost virtually all (~4000 ha) its intertidal mussel beds around 1990 due to overfishing in combination with storms and recruitment failure. Re-establishment was slow and remained restricted to specific areas (Fig. 2) despite the implementation of protection measures (e.g. banning of mechanical shellfish fisheries) (Dankers et al., 2001, Piersma et al., 2001). Our objectives were to investigate how the local presence of shellfish reefs, intertidal mussel beds, under the same generic landscape conditions affects ecosystem structure, completeness, complexity and recovery, using various indicators of food web structure as proxies. Furthermore, we explore whether simple metrics of stable isotope-based food web structure, and biodiversity can be used to capture effects of foundation species on food webs, and on conservation and restoration success in general.

2. Methods

2.1. Sampling locations

Samples were collected at 6 locations spread across the highly impacted Dutch Wadden Sea (Fig. 1). At each location 2 sub-habitats were sampled; an intertidal shellfish reef dominated by mussels (also 'intertidal mussel bed') and a control site, an intertidal mudflat without mussels at ~500 m distance from the mussel bed, under the same generic landscape and abiotic conditions. The locations were at approximately the same depth and exposure time (~0.4–0.7 m below mean water level MWL; ~30% low water exposure time) and were all situated at the south side of one of the Dutch Wadden islands. Site locations were spread out over the Dutch Wadden Sea; 1) Texel (53°09′53″N; 4°53′31″E), 2) Vlieland (53°16′35″N; 5°01′58″E), 3) Terschelling (53°21′82″N; 5°17′52″E), 4) Ameland (53°26′05″N; 5°49′35″E), 5) Schiermonnikoog-west (53°27′08″N; 6°09′09″E), 6) Schiermonnikoog-east (53°28′05″N; 6°13′51″E). Because of the block design of our study, designed to control for site differences in generic conditions (Fig. 1), effects of the presence of mussel beds were expressed as relative magnitudes (on/off mussel bed). Therefore, differences in food web parameters could largely be attributed to the ecosystem engineering effects of the mussel beds (van der Zee et al., 2012).

2.2. Fauna sampling

For all 6 locations we pairwise compared habitat conditions, abundance and diversity of benthos, fish and birds between intertidal mussel beds and mudflats without mussel beds. Samples were collected between 12 August 2013 and 20 September 2013. Each location was sampled during 1 week and locations were alternated between the eastern and western part of the Dutch Wadden Sea. Environmental characteristics were measured in the same period. Different methods were used to

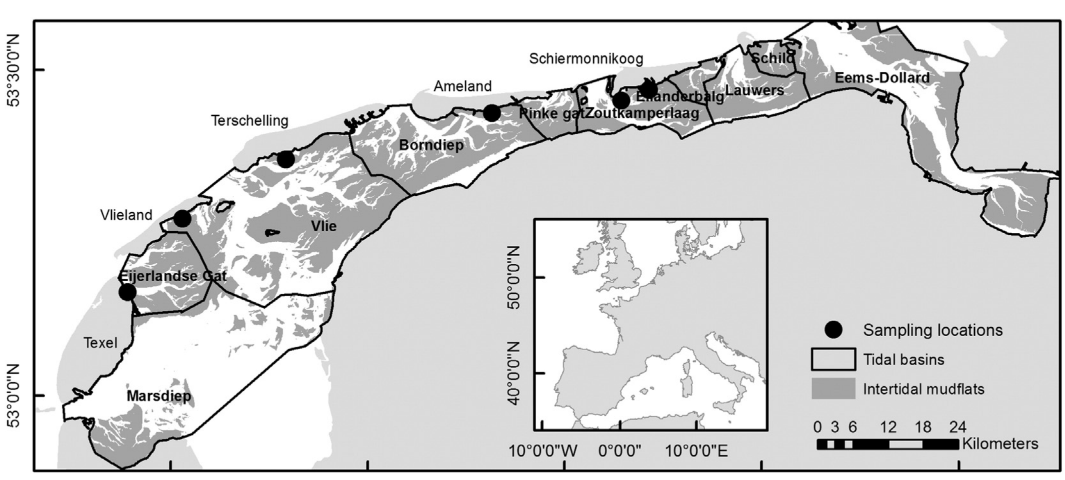

Fig. 1. Map of sampling locations spread across the Dutch Wadden Sea (black dots, $n = 6$), where at each location a paired comparison was made of food web structure on and off mussel beds (separated by 500 m). The intertidal flats (dark grey) are drawn in the main map. The inset shows the location of the Wadden Sea in Europe.

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