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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).

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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 increasing 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

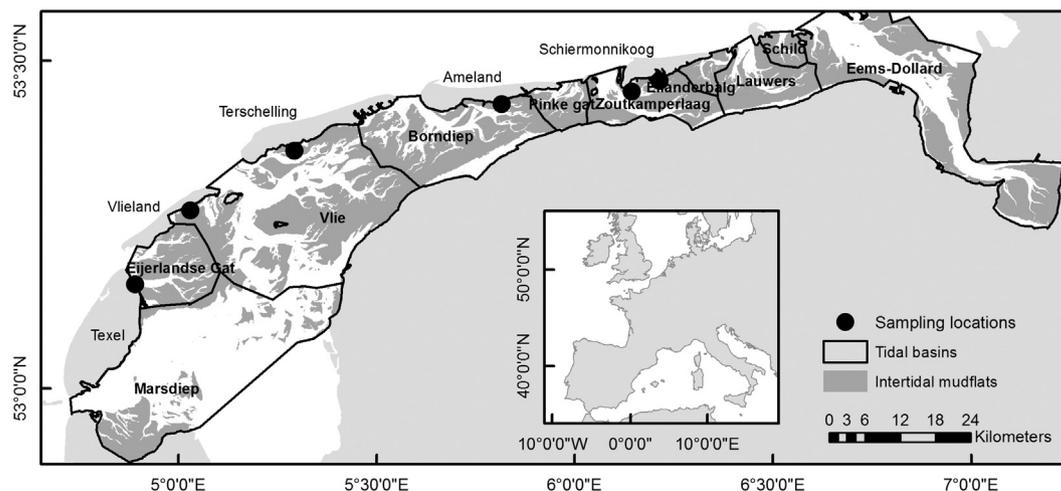


Fig. 1. Map of sampling locations spread across the Dutch Wadden Sea (black dots, $n = 6$), where at each location a paired comparison was made of food web structure on and off mussel beds (separated by 500 m). The intertidal flats (dark grey) are drawn in the main map. The inset shows the location of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

sample the biomass, density and food web structure of different communities (Fig. A.1 in Appendix).

Benthos samples were collected with a 15 cm² PVC corer at each habitat to a depth of ~25 cm after which samples were sieved over a 1 mm round mesh in the field. At the mussel bed habitat 5 cores were taken from mussel patches and 5 from mud patches in between mussel patches and at the control habitat 10 cores were taken. Demersal fish were collected using a pair of static unbaited fyke nets (entrance 0.6 m diameter, fyke mesh size 25 mm) of which the wings (~4.5 m) were connected in a straight line parallel to the water current and set up using steel pins (Fig. A.1).

Fish were collected from the fykes twice a day during low tide for 3 days, keeping the content of the 2 pens of one fyke pair separately yielding a total of 12 samples from each sub-habitat. The fykes at the 2 sub-habitats were set up to fish simultaneously. Samples of small fish and crustaceans were collected in shallow pools using five 5-m long hauls using a shrimp net (30 cm wide, mesh size 3 mm) at the control habitat. At the mussel bed, habitat pools were sampled with shorter hauls but also to a total haul length of ~25 m. All fauna was identified to species level in the laboratory.

Bird density at each sub-habitat was determined in a 50 * 50 m transect marked with PVC poles located at ~250 m from the observer. During one complete low tide cycle, the number of birds and their activity was scored every 10 min using a telescope (zoom ocular 20–60*; ATM 80 HD, Swarovski, Absam, Austria). Counting started when the water had retreated from the marked transect until the area was inundated again. For the analysis we selected birds that were active (i.e. not resting) during observations. Bird density and biomass was averaged per hour over 6 counts.

Additional samples for food web analysis were collected of macroalgae by handpicking and benthic diatoms were scraped from the sediment surface. After migration through a mesh (100 µm) into combusted sand, diatoms were collected in filtered seawater and filtered over a Whatman GF/F glass fiber filter (Eaton and Moss, 1966).

2.3. Environmental conditions

In order to quantify possible environmental effects in our study system we tested whether characteristics as bed level, hydrodynamic conditions, water turbidity, sediment properties and mussel bed characteristics differed between habitat types.

Habitat characterization: In the mussel bed habitat the area cover of mussels (*Mytilus edulis*), algae (*Fucus vesiculosus*), and oysters (*Crassostrea gigas*) was estimated inside a frame of 25 * 25 cm that was laid down every 5 m along two 50 m long lines ($n = 20$). These two lines were positioned north to south and east to west respectively and crossed each other in the middle. The same setup was used to count the number of lugworms at the control locations. Along these same lines bed level height (m MWL) was measured every meter using a RTK-GPS (Real Time Kinematic Global Positioning System. Small-scale spatial heterogeneity was measured every 5 m using “rugosity” ($n = 20$). To measure rugosity, we placed a stainless steel chain (ϕ 2 mm) in a straight line on the substrate surface in such a way that it followed all small-scale spatial variation (e.g. hummocks, hollows, crevices). Next, we noted that the length of the chain needed to cover 25 cm of distance as rugosity.

Water flow velocity: Hydrodynamics were measured using plaster dissolution sticks at both sub-habitats. Dissolution cylinders (length 6.3 cm; diameter 2.4 cm) from model plaster (Knauf Modelgips, Knauf B.V., Utrecht, Netherlands) were dried, weighted and placed in the field for two tidal cycles (about 23 h), after which they were retrieved and dried until constant weight. To account for difference in the exposure time between sites, plaster weight loss values were divided by the average tidal submersion time of each site estimated by means of Sensus Ultra pressure loggers (Reefnet, Mississauga, Canada).

Water turbidity: At neap tide 5 l of water was collected from the nearest gully and filtered over pre-combusted Whatman GF/F glass fiber filters. Filters were dried for 48 h at 60 °C and the obtained particulate organic matter (wPOM) was weighted to get a measure of water turbidity as weight per volume.

Sediment properties: Sediment samples were taken right next to the location of each benthos core using a centrifuge tube to a depth of 4 cm and then frozen at –20 °C. Sediment samples were freeze-dried for up to 96 h and then homogenized with a mortar and pestle. The grain size of homogenized samples was measured using a particle size analyzer (Coulter LS 13320, optical module ‘grey’, grain sizes from 0.04 to 2000 µm in 126 size classes). All sediments were analyzed according to the ‘biological approach’, i.e. the organic matter and calcium carbonate was not removed from the samples. Organic matter content in freeze-dried sediment samples was estimated as weight loss on ignition (LOI; 5 h, 550 °C). Silt content (% sediment fraction <63 µm) and clay content (% sediment fraction <2 µm) was determined by a Particle size Analyzer (Coulter LS 13320, optical module ‘grey’, grain sizes from 0.04 to 2000 µm in 126 size classes).

Mussel growth: Mussel production was measured by tagging 50 mussels (20–50 mm shell length) at each location on selected mussel beds, 3–4 months prior to sampling. Here, each individual was tagged with a polyethylene label (Hallprint glue-on shellfish tags, Australia) glued to the shell with cyanoacrylate glue. Shell length was measured to the nearest 0.01 mm with a vernier caliper during labeling and at retrieval of the mussels. The same mussels were collected to measure flesh:shell ratio using ash free dry mass (AFDM) determined by loss on ignition (5 h, 550 °C) after drying for 48 h at 60 °C.

2.4. Isotope analysis

$\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ stable isotopes analysis was performed on all collected species, sediment, sPOM and wPOM, using the tissue of 5 samples per species. Whenever possible muscle tissue was used of fish, crustacean and bivalves and soft tissue of invertebrates and macro-algae, however for smaller samples the whole organism was used. All material was rinsed with demineralized water, dried at 60 °C for 48 h, ground and sub-samples for the measurement of carbon were decalcified by adding HCl, if necessary. Homogenized samples were weighed into tin cups and analyzed for carbon and nitrogen stable isotope composition with a Flash 2000 elemental analyzer coupled online with a Delta V Advantage-isotope radiomonitoring mass spectrometer (irmMS, Thermo Scientific). Carbon and nitrogen isotope ratios were expressed in the δ notation ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) relative to Vienna PDB and atmospheric N_2 . Average reproducibility based on replicate measurements for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were ~0.18‰. In total we analyzed 375 fish, 876 invertebrates, 124 algae, 90 diatoms, 60 sPOM, 60 wPOM and 60 zooplankton samples for isotopic signatures.

2.5. Data analysis

2.5.1. Food web analyses

Food web structure was assessed on the basis of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotope values, of each species in combination with Bayesian SIAR models. Based on abundance and size data, literature, the WoRMS (World Register of Marine Species, Boxshall et al., 2016) database, and connected online databases, we determined potential trophic relations for each species and constructed a maximized interaction matrix for each site that included all potential trophic links. For example, we excluded trophic links between species if we did not find >3 individuals of a species on a sampling location, if the minimum local prey size of a species were physically too big to be eaten (except for scavengers), or if interaction between species was highly unlikely and never reported in previous databases. Next, we used $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ bi-plots, in combination with Bayesian SIAR models (R-package SIAR, Parnell et al., 2010) per site for each species, to estimate the relative contribution of potential

resources to the consumer's diet. A minimum average of 3 replicates measurements of (mostly >5) $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ was used in SIAR analysis and per consumer we did not include >10 different species as sources for each run. As data on bird diet was already available for the Dutch Wadden Sea, data on trophic links connecting birds was filled in using publications and expert knowledge. Based on these analyses, we removed trophic links where a resource contributed <5% to the diet of the consumer and recalculated the contributions of the remaining resources. Finally, we used the obtained interaction matrix to calculate commonly used measures of food web structure. We used species richness (number of species or food web nodes; *S*) as an indicator of diversity, link density (number of links per species; *L/S*) and connectance (realized fraction of all possible links; *C*; defined as L/S^2) as metrics of topological complexity of the food web. Additionally, we used the fraction of top (species without consumers), basal (species without resources), intermediate species, herbivores and cannibals as trophic distribution metrics (May, 1972; Williams and Martinez, 2000; Gross, 2009). Food web images presented in Fig. 3 were constructed using the software Network3D (Williams, 2010). We included additional food web parameters, in the online appendix (Table A.2). As previous research stress that non-trophic interactions should routinely be included in food web programs (Olf et al., 2009; Berlow et al., 2009) we also included a theoretical exercise on the effect of non-trophic facilitation (interactions outside the trophic network such as shelter) of the mussel beds on food web interactions. We used an alternative theoretical matrix where species were removed if it depended obligatory on non-trophic interaction with mussel beds as habitat modifier. Food web parameters of this matrix are also found in Table A.2.

2.5.2. Statistical analyses

Prior to model fitting, all data were checked for normality using Shapiro-Wilks tests ($P = 0.05$) and further confirmation by graphical validation of the final models. If the normality assumption was not met, data were transformed. All relevant transformations are mentioned in the figures or table legends. The difference in biodiversity, food web metrics, environmental and habitat characteristics between subhabitats were analyzed with a paired samples ANOVA, pairing two subhabitats from the same location. Mann-Whitney *U* tests were used to test for habitat characteristics in case of 0 values at one subhabitat (Table 1, i.e. no mussels at the control habitat). An overview of the statistical output from these analyses is provided in Tables 1, 2, A.1, A.2.

3. Results

Local habitat conditions differed significantly between intertidal mussel beds and control sites (Table 1). We found both an increase in space for shelter and attachment for organisms on mussel beds, which was indicated by an increase of small-scale landscape heterogeneity of 1.4 times ($P < 0.05$) and at a larger scale an increase of 2.7 ($P < 0.001$) times. Additionally, benthic production was 6.4 times ($P < 0.001$) higher on mussel beds and hydrodynamic activity was 1.7 times ($P < 0.001$) lower. Sediment conditions on mussel beds differed from control sites with a 1.3 times higher silt content ($P < 0.001$), and 6.4 times higher organic matter ($P < 0.05$) content on mussel beds (Table 1, also for details on other habitat parameters).

Various food web parameters showed pronounced responses to the presence of intertidal mussel beds (Figs. 4 & 5). Both link density (*L/S*) and the number of top predators were higher (1.1 times, $P < 0.05$ and 1.6 times, $P < 0.05$, respectively) on mussel beds than on control habitat. Connectance and the richness of intermediate species showed the opposite difference and were 0.7 ($P < 0.05$) and 0.8 ($P < 0.05$) times lower at mussel bed dominated habitats than at control sites (Fig. 3, Fig. 5, Table 2).

In contrast we did not find significant differences in the classic Shannon-Wiener diversity between habitats, both for all species together as per species group separately (Table A.1). In contrast, species richness

Table 1
Comparison of environmental conditions measured on both sub-habitats; intertidal mussel beds ($n = 6$) and nearby intertidal mudflats without mussels ("control").

Parameter	Musselbed	Control	F	p	
	Mean SE	Mean SE			
Variation of bed level (stdev)	0.08 ± 0.01	0.03 ± 0.01	23	**	a
Max variance bed level (max-min)	0.33 ± 0.02	0.12 ± 0.03	23	**	a
Small scale heterogeneity (m chain length)	29 ± 2.2	21 ± 2.2	5	*	a
Sediment grain size (d50, median)	79 ± 7.5	105 ± 9.2	17	*	a
Silt content (vol% <63 µm)	34 ± 2.9	27 ± 3.4	20	**	a
Clay content (vol% <2 µm)	3.0 ± 0.2	2.32 ± 0.2	35	**	a
Organic content (% loss AFDW)	5.8 ± 0.6	0.90 ± 0.04	32	**	a
Diatom biomass (g Chl a m ⁻²)	315 ± 18	98 ± 11	51	***	a
Hydrodynamics (% gypsum loss d-1)	25 ± 0.8	43 ± 0.9	70	***	a
Water turbidity (g/l)	0.08 ± 0.00	0.08 ± 0.00	0.5	ns	a
Bed level (m NAP)	-0.46 ± 0.00	-0.39 ± 0.00		*	m
Lugworm density (# m ⁻²)	0 ± 0	40.2 ± 3.3		*	m
Mussel cover (%) in mussel patches	44.0 ± 1.1	0 ± 0		*	m
Oyster cover (%) in mussel patches	16.1 ± 0.8	0 ± 0		*	m
Fucus biomass covering mussels (gDW m ⁻²)	452 ± 34	0 ± 0		*	m
Mussel production (growth; mm d ⁻¹)	0.04 ± 0.00	0 ± 0		*	m
Mussel flesh:shell ratio	0.01 ± 0.00	0 ± 0		*	m
Size mussel patches (m)	5.71 ± 0.47	0 ± 0		*	m

F-values and significance levels for sub-habitat are given from paired one-way ANOVAs ("a") or independent 2-group Mann-Whitney *U* Tests ("m"). ns; not significant.

* 0.01 ≤ P ≤ 0.05.

** 0.001 ≤ P ≤ 0.01.

*** 0.001 < P .

and density were strongly different for several groups: mussel beds enhanced species richness (1.8 times, $P < 0.001$, Fig. 3), species density (1.4 times, $P < 0.001$) and total biomass of benthos, fish and birds (1.4 times, $P < 0.05$) compared to control habitats (Fig. 2, Table A.1). When separated in different species groups the increase in biomass and species number accounts for all groups except Annelida, which were negatively impacted by mussel beds (Table A.1). The facilitation effect of intertidal mussel beds on the biomass per species is positive for the majority of species except for most endo-benthic species (species in the sediment) (Fig. A.2). Table A.3 shows a species list per location and sub-habitat. In addition, we found that apart from trophic-interactions, non-trophic interactions (e.g. the effect of increased space for shelter) were changing food web indicators. Removal of species from the interaction matrix that are obligatory dependent on habitat modification by mussel beds increased similarity to unmodified, control habitat (Table A.2). This was shown by the similarity between food web characteristics of control plots and plots without mussel bed habitat modification ('M') for link density, trophic links and other metrics based on *L* and *S* except for connectance, that was significantly lower in M' compared to control plots (Table A.2).

4. Discussion

Here, we demonstrate that intertidal shellfish reefs dominated by mussels not only enhance productivity, species diversity, and abundances of associated species, but that they also significantly changed trophic interactions among species and therefore the overall trophic network. Moreover, we found that topological changes in food web structure in our study system were well captured by simple food-web metrics such as connectivity, link density and the number of top predators. By including food web and ecosystem-level indicators, we captured differences in ecosystem complexity between mussel beds and adjacent intertidal mudflats without mussel beds that did not emerge from classic measures such as Shannon-Wiener diversity and evenness, but did emerge from the more crude measure of species richness.

Recent studies are increasingly linking topological food web parameters to dynamical properties of food webs such as robustness and

Table 2

Comparison of community- and food web-properties on intertidal mussel beds and control habitat (intertidal mudflat without mussels). Food web properties were obtained from a trophic interaction matrix in which potential trophic links were confirmed using SIAR analysis on $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ stable isotope data. F-values and significance levels for sub-habitat are given from paired one-way ANOVAs. The total number of species included in SIAR models differ from earlier presented averages as it does not include bird species and species that contributed <5% to the diet of the consumers (see Table A.2 for more metrics and values of mussel bed food webs without habitat modification; i.e. species dependent on non-trophic interactions).

Metric	Foodweb incl facilitation		M vs C			
	Average		ANOVA			
	Musselbed	Control	F	P	Description	
Shannon-Wiener index	H'	1.7 ± 0.20	1.8 ± 0.1877780434	0.174	ns	Weighted geometric mean of the proportional abundances of the species
Evenness	E'	0.40 ± 0.05	0.42 ± 0.0436280678	0.174	ns	Relative abundance of the different species making up the richness of an area
Species richness	S	34 ± 0.92	24 ± 1.2382783747	145	***	Number of species (nodes)
Trophic links	L	149 ± 7.20	101 ± 4.9	222	***	Number of links between species (lines)
Link density	L/S	4.4 ± 0.07	4.2 ± 0.1609863718	2.113	*	L/S, L is number of links, S is number of species
Connectance	C (L/S ²)	0.13 ± 0.00	0.18 ± 0.0095217092	26.01	**	L/S ² , L is number of links, S is number of species
Top species	Top	0.34 ± 0.03	0.21 ± 0.0259471433	13.8	*	Fraction of species that have no predators (top species)
Intermediate species	Int	0.51 ± 0.03	0.64 ± 0.0216036526	14.29	*	Fraction of species that have both predators and prey (intermediate species)
Basal species	Bas	0.15 ± 0.01	0.15 ± 0.0163828877	0.002	ns	Fraction of species that do not consume anything (basal species)
Herbivores	Herb	0.07 ± 0.02	0.10 ± 0.0152768051	4.23	ns	Fraction of species that are herbivores (only consume basal species)
Cannibals	Can	0.16 ± 0.02	0.22 ± 0.0138969752	6.341	ns	Fraction of species that are cannibals

* 0.01 ≤ P ≤ 0.05.
 ** 0.001 ≤ P ≤ 0.01.
 *** 0.001 < P.

resilience. In this study, we found evidence that foundation species such as intertidal mussel beds increase link density. Theoretical work suggests a positive relation between link density and robustness (Dunne et al., 2002; Gilbert, 2009), which would imply in our case that mussel beds promote food web robustness. Enhanced robustness supports food web integrity and may therefore increase ecosystem health, stability, and resilience to extinction (Coll et al., 2008; Gilbert, 2009; Dunne and Williams, 2009). However, the absolute value of topological parameters is dependent on species richness, sampling effort and type and scale of systems (Goldwasser and Roughgarden, 1997; Dunne et al., 2004; Banasek-Richter et al., 2009; Tyljanakis et al., 2007; Poisot and Gravel, 2014), making the comparison between systems of absolute metrics difficult. Nevertheless, a large number of studies from other marine food webs also showed that ecosystem degradation leads to simplified food webs (Fagan, 1997; Dunne et al., 2004; Tyljanakis et al., 2007; Coll et al., 2008; Mukherjee et al., 2015), which will likely have consequences for food web stability (Coll et al., 2008). The simple topological parameters described here can thus be linked to dynamical properties of food webs and ecosystem health, may help in assessing conservation success, and might help filling in the gap in tools and methods

(Kennish, 2002) in quantifying the anthropogenic impact of ecosystems.

The usefulness of food web topology parameters in capturing ecological restoration successes likely depends on the species richness of an ecosystem. Especially in relatively species-poor ecosystems such as the Wadden Sea, food web indices can provide additional information on interaction structure. For example, 4 species can be arranged in a variety of interaction structures (e.g. as a chain, diamond, 3 feeding on 1) that can be distinguished by food web metrics. Such variation in potential interaction structures increases exponentially with increasing species richness. Hence, in species rich ecosystems topological parameters are likely more useful as summary statistics or to reduce dimensionality of the problem of evaluating food webs (e.g., when the diversity of different species groups gives contrasting messages). Compared to species-rich ecosystems such as a coral reef, mussel beds in temperate areas harbor a relatively low number of species and therefore do not differ much between locations in terms of number of species, but do show large differences in the interaction structure of these species. The evaluation of species interactions; unraveling who eats who and how these interactions change therefore provides important additional information to classical measures as species richness. Hence, food web characterization can be an important additional tool to value ecosystem functioning, especially in relatively species-poor systems.

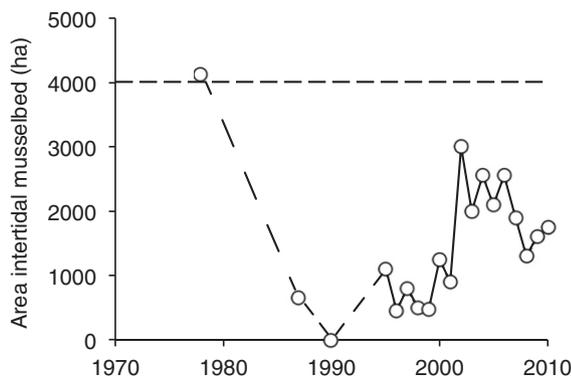


Fig. 2. Total area of intertidal mussel beds in the Dutch Wadden Sea (modified from Dankers and Fey-Hofstede, 2015, with additional data provided by N. Dankers, based on Dankers et al., 2001). The line defines the target area cover of stable intertidal mussel beds in the Dutch Wadden Sea as stated within the European water framework directive. Note that mussel bed recovery is slow and has not reached historical surface areas, even despite active conservation measures were taken to protect mussel beds. The line shows area cover of mussel beds solely and does not include the area covered by oyster beds (*Crassostrea gigas*) that has started to expand in The Dutch Wadden Sea since 2003.

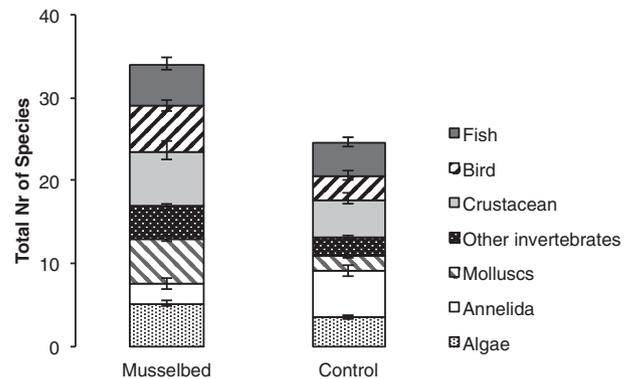


Fig. 3. Total number of species found on intertidal mussel beds and intertidal mudflat ("control") habitats. Error bars represent SE (n = 6). Species were observed using a combination of methods; transect counts (birds), fyke sampling (fish, crustaceans) and benthos cores (macrofauna, algae). For a comparison of the average number of species per method and statistics see Table A.1. For details on sampling effort see materials and methods.

A. Intertidal mussel bed

B. intertidal mudflat without mussels

("control")

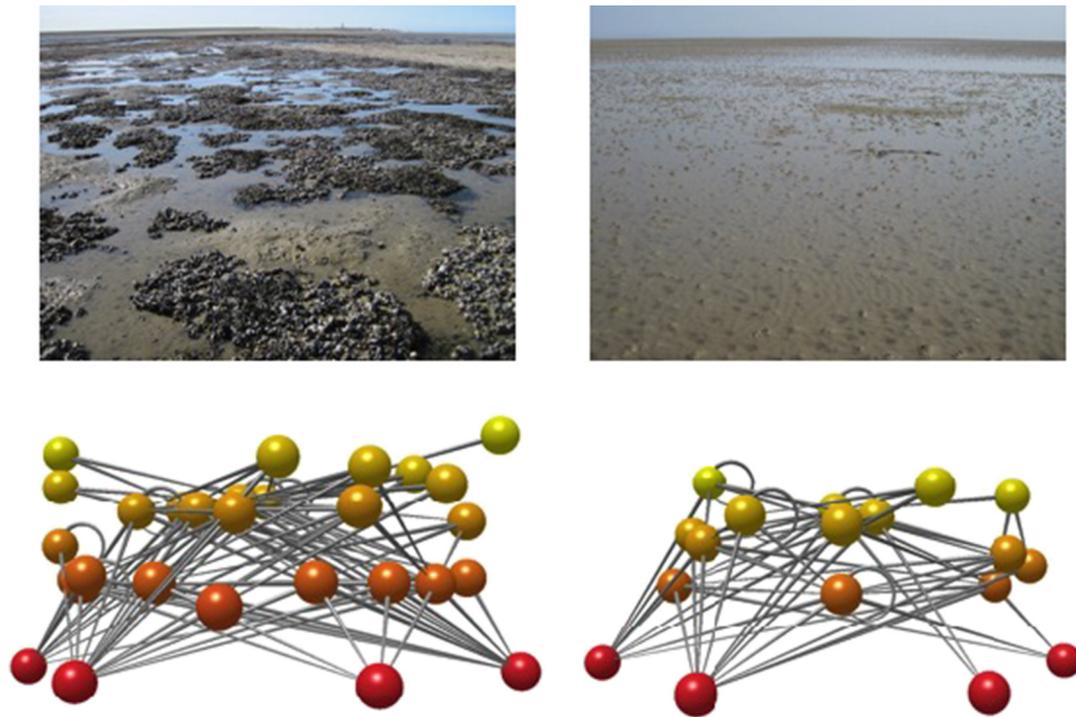


Fig. 4. Food webs of (A) intertidal mussel beds and (B) intertidal mudflats without mussel beds ("control"). The food web of a mudflat without mussel bed is typically simpler. Nodes represent species and lines links between species if a species is included in the diet of the species higher up in the food web. Node colors changes from red (basal species) to yellow with increasing trophic level. Note that the food web on mussel beds has a higher species richness (# nodes), link density (lines per node; L/S), but not a higher trophic level of top predators (node color). See Table 2 and Table A.2 for averages and statistics. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Our results show that conservation and restoration success can be measured by simple metrics of food web structure; link density, connectance, number of species at top of food chain, intermediate species, trophic links and species richness, thus providing a promising new set of metrics that could be included as Essential Biodiversity Variables (EBV). These simple food web metrics can directly be implemented as indicators in legislative frameworks such as the Marine Strategy Framework Directive (MSFD) in European territorial waters (European Commission, 2010) and other legislative commitments (e.g. Water Framework Directive (2000/60/EC), Habitat Directive (92/43/EC)). These frameworks increasingly include status of food web as one of the descriptors of a 'Good Environmental Status' (e.g. descriptor 4; food web, MSFD) but so far did not include information on how the ecosystem functioning. We show that the implementation of simple food web metrics such as connectance and link density may increase the inclusiveness, completeness and correct implementation not only as we found opposite trends in other metrics, but also as they capture the complexity of non-trophic interactions in food webs. Additionally, food web metrics allowed assessment of structure to species loss and ecosystem degradation (Fagan, 1997; Dunne et al., 2004; Tylianakis et al., 2007; Coll et al., 2008; Mukherjee et al., 2015).

Indeed, the food web metrics used here have been used in earlier work to study the topology of trophic interactions, the nature of trophic interactions, the effect of food web structure on its stability, and the effect of non-trophic species interactions on food web structure (Dunne et al., 2002; Williams and Martinez, 2000; Neutel et al., 2002; Bascompte et al., 2005; van der Zee et al., 2016). To our knowledge, however, this is the first study to investigate whether these simple metrics can also be used within an ecosystem conservation framework. We found that,

apart from their value a theoretical measures of food web structure, these metrics may provide a very useful addition to current approaches to assess anthropogenic impact on ecosystems and regional biodiversity (Kennish, 2002). For instance, we found opposing trends between food web metrics and classic community metrics, indicating that stable metrics of richness may occur in parallel with substantial degradation of food web structure. A similar contrasting pattern was observed for bird abundance and diversity in North America, with stable species richness patterns during a decrease of bird abundance. (Schipper et al., 2016). This supports the importance of including simple food web metrics (Table 2) as overall diversity indicators as possible EBVs (Pereira et al., 2013).

Similar to our recent work in seagrass and salt marsh ecosystems (Van der Zee et al., 2016), we found a very strong link between the presence of shellfish reefs, and community and food web structure. This implies that in ecosystems dominated by habitat-modifying foundations species, some biodiversity metrics may potentially be tracked by simply monitoring these key species. This can often be done at very large spatial and temporal scales, and in many cases even from space using satellite imagery. For example, the (change in) cover of seagrass, salt marshes, forests, and shellfish and coral reefs may potentially be tracked by satellite monitoring and translated to biodiversity metrics (Eakin et al., 2010; Skidmore et al., 2015; Nieuwhof et al., 2015; De Fouw et al., 2016). The spatial and temporal grain size in which monitoring of habitat modifying ecosystems from space is possible likely depend on multiple factors such as the size, fragmentation and heterogeneity of structures, seasonality (seagrasses leaf structures are absent in winter) and inundation time (Skidmore et al., 2015). Therefore, we stress that it is of key-importance to know how and to what extent such general

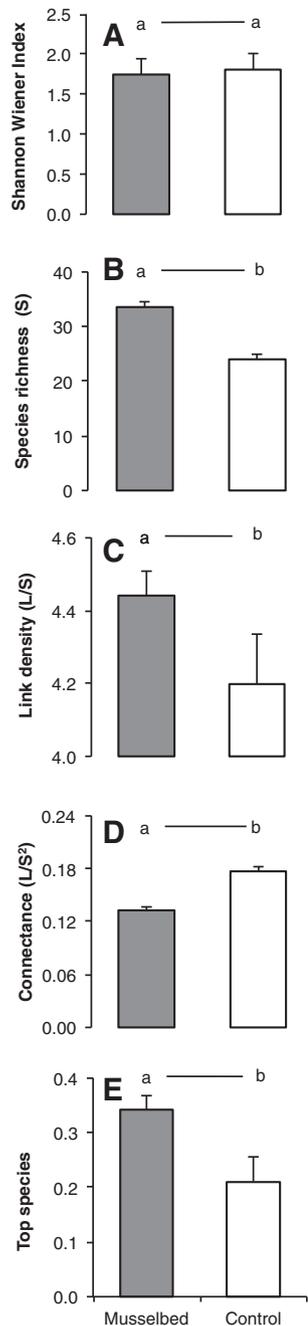


Fig. 5. Differences on mussel beds versus control habitat (nearby intertidal mudflat without mussels) nearby tidal flats without mussels in a range of community and food web structure indicators: (A) Shannon Wiener Index, (B) species richness, (C) food web link density, (D) food web connectance, (E) proportion of species at the top of the food chain ("top species"). Error bars represent SE ($n = 6$). Probability values of paired one-way ANOVAs are given; $*0.01 \leq P \leq 0.05$, $**0.001 \leq P \leq 0.01$, $***0.0001 < P$. The proportion top species and the link density are significantly higher in mussel bed habitats whereas connectance is lower. See Table 2 for more metrics and Table A.2 for values of mussel bed food webs where species dependent on habitat modification (i.e. non-trophic interactions) were removed.

and large-scale proxies can be used to assess the actual food web measures of interest such as top predator abundance or link density.

Our results emphasize the importance of non-trophic interactions as structuring component of food webs, as have been shown for other ecological interactions and ecosystems (Berlow et al., 2009; Olff et al., 2009; Kefi et al., 2015; Schipper et al., 2016). The mussel beds in our study clearly modified local habitat conditions by increasing space for shelter and attachment for organisms, and reducing the hydrodynamic stress for organisms (Table 1). Our results, combined with earlier work on

mussel beds demonstrate that habitat modification enhances species diversity and alters predator-prey interactions (Donadi et al., 2015; van der Zee et al., 2015). These findings support theoretical work (Olff et al., 2009; Kefi et al., 2012) and a thus far very limited number of recent empirical studies that show that trophic interactions are strongly controlled by non-trophic interactions in foundation species-dominated ecosystems (van der Zee et al., 2016; Kefi et al., 2015). Based on these combined results, we suggest that future indicators for ecological networks should not only deal with food webs but aim to assess trophic and non-trophic interactions in an integrated network approach.

5. Conclusion

We conclude that stable isotope-based food web construction is a promising method to evaluate conservation and restoration success of foundation species-dominated ecosystems. We observed opposing trends between food web metrics and classic community metrics. This indicates that stable metrics of diversity (Shannon Wiener index) may occur in parallel with substantial degradation of food web structure and supports the importance of food web metrics as an Essential Biodiversity Variable (Pereira et al., 2013). Nature managers may use these simple food web metrics; link density, connectance, number of top consumers, number of intermediate species, and number of trophic links, in concert with other EBVs, as a tool to gauge conservation progress and to trace which species in which areas need increasing conservation attention and protection. These tools become increasingly useful as the aim to restore more complete food webs is emerging in ecosystem restoration projects and international legislation. For example, our results serve the development of indicators to evaluate food web status in the legislative frameworks such as the European MSFD. The implementation is urgent with the growing general concerns on the worldwide decline of potentially ecologically important habitat-modifying species as mangroves, coral reefs, seagrasses and mussel beds.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.biocon.2016.09.028>.

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