Food web models reveal potential ecosystem effects of seagrass recovery in the northern Wadden Sea

Sabine Horn\textsuperscript{1,2} \textsuperscript{a}, Marta Coll\textsuperscript{3,4}, Harald Asmus\textsuperscript{1}, Tobias Dolch\textsuperscript{1}

In contrast to the global trend, seagrass beds have recovered in size and density in the northern part of the European Wadden Sea, but ecosystem effects of seagrass recovery and the impacts to ecosystem services are largely unknown. We used temporal-dynamic food web modeling Ecopath with Ecosim to assess potential ecosystem effects of seagrass recovery in the semi-enclosed Sylt-Rømø Bight at the German-Danish border. In addition to changes in the system’s structure and functioning over time, the model predicted changes in biomass of seagrass-associated species. For seagrass consumers, we projected an increase in biomass as a result of an increase in food supply. Likewise, the model predicted an increase in biomass of seagrass meadow inhabitants from decreased predation pressure. Correspondingly, the main predators of these inhabitants decreased in biomass according to model results. Proxies representing ecosystem services predicted an increase of tourism appeal of the site with increasing seagrass meadows. Indirect mediation effects of seagrass severely influenced the model output and are thus crucial to forecast potential effects of the recovery of habitat-forming species. Our study illustrates that holistic approaches such as food web models could provide a suitable basis for predicting ecosystem effects of changes in the biomass of habitat-forming species such as seagrasses.

**Key words:** Ecopath with Ecosim, ecosystem services, food webs, seagrass recovery, Wadden Sea, Zostera

**Implications for Practice**

- Seagrass recovery alters the structure and functioning of the food web and influences the biomass development of seagrass-associated fauna.
- Indirect mediation effects of seagrass strongly influence the food web model output and are crucial to include in models focusing on habitat-forming species.
- Food web models are promising tools to predict recovery and restoration effects of seagrass meadows on ecosystem scale by considering direct and indirect interactions in the system.

**Introduction**

In coastal waters worldwide, seagrass meadows are one of the most important systems providing habitat, shelter, food, and nursery grounds to a variety of species (Nacken & Reise 2000; Polte et al. 2005; Larkum et al. 2006), as well as essential ecosystem services such as nitrogen (Asmus & Asmus 2000; Aoki et al. 2019) and carbon sequestration (Greiner et al. 2013; Duarte 2017). However, seagrass meadows are declining globally as a result of decreasing water quality primarily induced by eutrophication, loss of habitats caused by sand extraction, embankment, or other coastal construction measures, and changing climatic conditions (Orth et al. 2006). About one-third of seagrass meadows worldwide have been lost since 1980, corresponding to a rate of 110 km\textsuperscript{2} per year, causing dramatic changes in ecological key features of coastal ecosystems (Waycott et al. 2009). In contrast to this dramatic, global trend, seagrass beds in the northern part of the European Wadden Sea have steadily recovered since the late 1990s. Intertidal seagrass beds were small and sparsely populated in the 1970s and 1980s due to high riverine nutrient loads that entered the Wadden Sea. A reduction in nutrient discharge since the mid-1980s has resulted in a seagrass recovery that started in the late 1990s. Today, intertidal seagrass beds cover a larger area in the northern Wadden Sea than in the 1930s (Dolch et al. 2013, 2017). The Wadden Sea is a shallow coastal sea stretching along the coastline of Denmark (DK), Germany (GER), and the Netherlands (NL) (Fig. 1). With a length of approximately 500 km and an uninterrupted belt of sand and mud flats of about 4,700 km\textsuperscript{2}, this World Heritage Site is the largest connected intertidal wetland in the world (Reise et al. 2010). Two species of seagrass grow in the Wadden Sea, the common eelgrass...
Zostera marina (Linnaeus, 1753) and the dwarf-eelgrass Zostera (Zosterella) noltei (Hornemann, 1832) (e.g. Dolch et al. 2017). In the past, Z. marina was the dominant species, forming wide meadows in the subtidal area of the Wadden Sea, but stocks of Z. marina collapsed in the 1930s due to the fungi-caused wasting disease. Z. marina has completely vanished from the subtidal area of the Wadden Sea and never fully recovered (den Hartog 1987; de Jonge & de Jong 1992). Since then, Z. noltei is the more common species, covering the intertidal flats of the Wadden Sea with dense beds during its growing season from May to October (Dolch et al. 2017). As habitat-forming species, seagrasses play a distinct role in ecosystem functioning (Larkum et al. 2006; Coll et al. 2011) and seagrass meadows change trophic interactions in marine communities (Jankowska et al. 2018). Therefore, their increase in the Wadden Sea might have caused further alterations in the system’s structure, in that seagrass-associated species may have also changed.

Food web models offer an appropriate tool to investigate complex interactions on an ecosystem level by providing a simplified representation of the ecosystem based on its trophic structure (Fath et al. 2019; Safi et al. 2019). The temporal-dynamic modeling approach Ecopath with Ecosim (EwE) (Christensen & Walters 2004; Heymans et al. 2016) is one of the most popular approaches to study dynamics of food webs by providing forecasts of future scenarios (e.g. Serpetti et al. 2017; Corrales et al. 2018). Thus, EwE is a promising tool to assess changes in food web properties of an ecosystem over time.

In this study, we used the Ecosim model of EwE to determine the potential ecosystem effects of seagrass recovery in a well-investigated tidal basin in the northern Wadden Sea, the Sylt-Rømø Bight (SRB). We focused on the following questions (1) How does the recovery of seagrass meadows influence the seagrass-associated fauna? (2) Does the seagrass recovery change the system’s structure and functioning represented by system attributes? (3) Are the potential effects generated by the model consistent with observed effects from current field studies? and (4) What is the impact of these effects on key ecosystem services?

Methods

Study Site

The SRB is an almost entirely enclosed tidal basin in the northern part of the Wadden Sea, located between the Danish island Rømø and the German island Sylt (Fig. 1). The bight covers a total area of 404 km² with an intertidal area of approximately 135 km² and connects to the open North Sea through a 2.8 km-wide channel, the Lister deep. The average water temperature is 9.0°C annually, with 5.3°C in winter (October to March) and 13.7°C in summer (April to September) (Backhaus et al. 1998). Salinity ranges from 30 to 32. The mean tidal range of the bight is about 2 m (Backhaus et al. 1998).

The intertidal area of the bight consists of different plant and animal communities structuring the tidal flats into a mosaic of different habitat types (i.e. Arenicola sand flats, sandy shoals, sandy beaches, mud flats, muddy sandy flats, blue mussel beds, and seagrass meadows). For each of these habitats, Baird et al. (2007) developed and analyzed a food web model based on empirical data. The food web model of the entire SRB (see Baird et al. 2004, 2012, 2019) considers the proportional contribution of each habitat to the entire intertidal area. These models provided the basis for our EwE approach.

Ecopath With Ecosim

We used the temporal-dynamic modeling approach Ecopath with Ecosim (EwE) beta version 6.6 for our analysis.
Effects of seagrass recovery

(Christensen & Walters 2004; Heymans et al. 2014). EwE combines the trophic mass-balanced food web model of the initial year (Ecopath) with a temporal-dynamic simulation approach (Ecosim) (Walters et al. 1997). Polovina (1984) developed the basis of Ecopath, which has been continuously improved upon since then. The temporal-dynamic component Ecosim was added in 1995 (Walters et al. 1997). The entire methodology is described in detail in Christensen and Walters (2004) and Heymans et al. (2016) and is only briefly summarized here.

The core routine Ecopath is based on two master equations. Equation (1) defines the production term of each component, i

\[ P_i = Y_i + B_i(M2) + E_i + BA_i + P_i(1-EE_i) \]  

(1)

where \( P \) is the production, \( Y \) is the total harvest, \( BA \) is the accumulation of biomass, \( B \) represents biomass, \( M2 \) is the predation mortality rate, \( E_i \) is the net migration rate and \( MO_i = P_i(1 - EE_i) \) is other mortality rate.

In addition, each system component needs to be balanced in its energy budget, defined in equation (2)

\[ C = P + R + E \]  

(2)

where \( C \) is the consumption of the component, \( P \) is the production, \( R \) is the Respiration, and \( E \) is the non-assimilated food. For a successful Ecopath model, both equations need to be balanced for each system component.

The Ecosim simulation predicts the biomass development of each system component over time subjected to changes in mortality rates and primary production. The biomass dynamics are expressed through a series of coupled differential equations defining the change of biomass through time and the amount of consumption by a predator on its prey. The change of biomass is calculated as described in equation (3)

\[ \frac{dBi}{dt} = g_i \sum_j Q_{ji} - \sum_j Q_{ij} + I_i - (MO_i + F_i + e_i)B_i \]  

(3)

where \( t \) is time in month, \( g \) is the gross food-conversion efficiency ratio, \( Q_{ij} \) is consumption of prey \( j \) by predator \( i \), \( Q_{ji} \) is consumption of prey \( i \) by predator \( j \), \( F \) is the fishing mortality rate, \( I_i \) is immigration rate, and \( e_i \) is emigration rate.

Food Web Data

We used the SRB model data of the time period 1990–1995 published in Baird et al. (2012) to create the initial mass-balanced Ecopath model with 59 compartments (Table S1; Fig. 2). We took biomass data directly from the publication, based on empirical data sampled in the SRB (Baird et al. 2004; Baird et al. 2012). We also used daily P/B and Q/B values of Baird et al. (2012) to calculate production and consumption. These values already consider seasonal variations at the study site and were extrapolated to represent a yearly average. We used the diet matrix of Baird et al. (2004) as a basis. If predation exceeded production of a prey compartment, we adapted the diet of the predator in order to mass-balance the model (Table S2).

The diet matrix represents initial species interactions, but changes its proportions as the dynamics of species change during temporal-dynamic modeling.

We used the Ecosim temporal-dynamic routine to model the development of the SRB ecosystem from 1990 to 2010. Using a Monte Carlo approach implemented in EwE, we ran 100 iterations to provide a representative development of system component biomass using the pedigree information of model inputs. We focused on changes of seagrass consumers, seagrass meadow inhabitants, and main predators of seagrass meadow inhabitants. We defined a system component as a seagrass meadow inhabitant if Baird et al. (2007) found the major contribution of the component’s total biomass (>55%) in seagrass meadows. Predation mortality rates in EwE defined the main predators of these inhabitants.

Given the fact that professional fishing is prohibited in the Wadden Sea, we did not include any fishing data in the model.

Seagrass Meadow Data

In the northern German Wadden Sea, the extension of seagrass meadows has been monitored annually since 1995. Dolch et al. (2017) describe the monitoring procedure in detail. The SRB is subdivided between Denmark in the north and Germany in the south. Unfortunately, seagrass monitoring approaches differ between the countries and are less frequent in the Danish part. Therefore, we could not generate a complete seagrass data set for the entire bight. Given the far more complete German dataset and availability of remote sensing data validated by direct field surveys, we opted to use the German dataset to assess the trend of seagrass extension in the study side assuming similarity in this trend in both parts of the bight. Seagrass spatial extent in the German part of the SRB increased by 505% from 1995 to 2010 (Fig. 1). The spatial extent percentage data were transformed to biomass data by using the seagrass biomass per m² in Baird et al. (2012) as reference data.

Time Series Data and Fitting Procedure

We fitted the temporal-dynamic simulation of Ecosim to time series data to specify the model output and included 11 time series of system components of different trophic levels in addition to seagrass time series data. At the base of the food web, we added phytoplankton time series data from the Sylt roads monitoring program, conducted weekly at the Alfred-Wege ner-Institut (AWI) Sylt (Rick et al. 2017).

In addition to seagrass, blue mussels (Mytilus edulis) and Pacific oysters (Magallana gigas) form important habitats for other species in the Wadden Sea. In contrast to native M. edulis, M. gigas was introduced to the Wadden Sea in the 1960s by aquaculture and caused crucial changes in the structure and functioning of the ecosystem (Troost 2010; Baird et al. 2012). Both bivalve species form dense beds that host diverse associated flora and fauna. During the modeled time period, the size of these bivalve beds, and biomass of M. edulis especially, declined steadily. Thus, we included time series data for M. edulis and M. gigas in order to represent the...
change of benthic composition in the model. We obtained data from both species from a regular monitoring program conducted by the Federal Administration for coastal and nature protection of the federal state of Schleswig-Holstein, Germany.

Fish represent major predators in the Wadden Sea, feeding on a variety of benthic invertebrates. In the SRB, monthly monitoring at the AWI Sylt has included fish abundances and composition since 2007 (Asmus et al. 2020). We used the fish data series of Pleuronectes platessa, Platichthys flesus, Clupea harengus, Merlangius merlangus, Gadus morhua, and Myoxocephalus scorpius in the model.

Herbivorous bids such as brent geese (Branta bernicla) or wigeons (Anas penelope) are the most important consumers of seagrass in the studied area (Nacken & Reise 2000). The Joint Monitoring of Migratory Birds (JMMB) program includes these species and is part of the framework of the Trilateral Monitoring and Assessment Program (TMAP) of the three countries bordering the Wadden Sea. Data of the two species were obtained from the Federal Administration for coastal and nature protection of the federal state of Schleswig-Holstein, Germany.

We fitted the Ecosim model to these data series by using the Ecosim routine "Fit to time series" and the application “vulnerability search by predator” to improve model fits with included time series. This procedure provides a more realistic model output of Ecosim considering intensities of interactions between changing system components.

Mediation Function

In addition to its function as a direct food source, seagrass indirectly influences the trophic interactions of prey species living in the seagrass meadow and their predators by providing protection and feeding grounds. Structures of submerged vegetation may influence predation efficiency by inhabiting movement of predators or by reducing the visibility of the prey (Stoner 1980; Savino & Stein 1982; Orth et al. 1984). For example, in experimental trials, Stoner (1982) and Orth and van Montfrans (1984) found that predation of pinfish (Lagodon rhomboids) and blue crabs (Callinectes sapidus) decreased with increasing seagrass density. Similarly, Nelson (1979) used blade density as a measure of structural complexity and found that predatory effectiveness of pinfish and the grass shrimp decreased in high blade density. Coen et al. (1981) found a decrease in predatory success of L. rhomboides in high densities of artificial seagrass. In addition, Heck Jr and Thoman (1981) observed decreased predatory success of the killifish Fundulus heteroclitus in high blade density of artificial seagrass. EwE can represent these effects by applying mediation functions of seagrass on the trophic relationships between seagrass meadow inhabitants and their prey and predators. Following previous studies focusing on habitat-forming species (e.g. Harvey 2014; Vilas et al. 2020), we applied two mediation functions to the model representing the effects of seagrass (Fig. 3). The first one followed Harvey (2014), in which a negative exponential function affected the vulnerabilities (v) of system components (Fig. 3A). This function was applied to all interactions between seagrass meadow inhabitants and their predators. The second mediating effect was a negative linear function influencing the search rate (a) of predators (Fig. 3B). It was applied to all interactions between seagrass meadow inhabitants and mobile predators (i.e. Carcinus maenus, Crangon crangon, fish, birds) and represented an increase in searching by predators as the seagrass meadow increased in biomass and complexity.

The mediating effect of seagrass increased with increasing seagrass biomass in the model. We assessed the mediating effect on seagrass consumers, seagrass meadow inhabitants, and on the main predators of seagrass inhabitants.

Figure 2. Schematic representation of the Sylt-Rømø Bight food web with exemplary icons of system components. The seagrass node is shown in green, numbers refer to group numbers in Table S1.
Network Analysis

EwE offers the option to calculate different network indices based on the theory of Ulanowicz (1986) describing the structure and functioning of a system (Christensen 1995; Fath et al. 2019; Safi et al. 2019). Some of these indices are candidates to assess the status of food webs in terms of the Marine Strategy Framework Directive (MSFD), which aims to achieve a good ecological status (Fath et al. 2019; Safi et al. 2019). However, we still lack knowledge on the sensitivity of these candidate indicators to changes on the scale of the ecosystem. In order to assess changes in network indices, we extracted Ecopath models for each year predicted in Ecosim using the “Ecopath from Ecosim” routine. We then analyzed the extracted Ecopath models (1990–2010) with EwE network analysis to determine changes in relation to seagrass recovery, focusing on three network indices:

1. The detritivory over herbivory (D/H) ratio represents the relationship between herbivorous and detritivorous trophic pathways, based on the tropho-dynamic calculations of Lindeman (1942). It expresses which of both food sources dominates. A system with an increasing importance of detritivorous pathways is considered more mature and stable than a system based on herbivorous pathways (Odum 1969).

2. The Finn cycling index (FCI) describes the recycled fraction of the system’s energy throughflow (Finn 1976) and quantifies the importance of cycling in the system by providing a percentage value of flows generated by cycling (Safi et al. 2019). A high FCI generally corresponds to a mature system (Christensen 1995).

3. The system omnivory index (SOI) represents the level of omnivory in an ecosystem. Omnivory describes organisms that feed on more than one type of food (e.g. detritus, primary producers, other organisms). A system increases in complexity with a higher level of omnivory because consumers feed on several different prey items leading to more connections and pathways in the system (Safi et al. 2019). Therefore, a high SOI presumably represents a more stable and well-connected system.

Attributes Representing Ecosystem Services

Seagrass meadows provide essential ecosystem services to humanity, but the measurement of these services in the field is often difficult and time consuming. Thus, we tested whether proxies from EwE models can be used to represent specific services and their changes in relation to seagrass recovery, selecting three attributes as a proxy for ecosystem services. The first attribute, the total net primary production in the system, represents the potential carbon sequestration of the SRB. The second attribute represents the potential impact of the fishing sector by measuring the total biomass of commercial fish species. The Wadden Sea is a protected area and fishing is strictly forbidden. However, most fish species migrate between the Wadden Sea and the adjacent North Sea, where significant fishing activity occurs. Thus, increasing fish biomass in the bight might result in larger fishing fleets outside of the Wadden Sea. The third attribute represents the importance of the Wadden Sea for the tourism sector. The intertidal flats are an important food source for a huge diversity of migrating and breeding birds and seagrass meadows have been shown to be favored foraging areas of coastal birds (Horn et al. 2017, 2020). Thus, these locations also attract bird watchers. We analyzed the development of bird biomass over time to represent the importance of the SRB for bird watchers and thus tourism.

Statistical Analysis

We used R Statistics version 3.6.1 for statistical analyses, evaluating correlations between modeled results (biomass development of seagrass-associated fauna; network indices; ecosystem service attributes) and time using Spearman’s rank correlation test (Corrales et al. 2017; Vilas et al. 2020).

Results

Effects on Seagrass-Associated Fauna

In the food web of the SRB, we characterized two components as seagrass consumers (i.e. Anas penelope and Branta bernicla). For both species, the model predicted an increase in biomass with increasing seagrass biomass. The highest change occurred in B. bernicla with a relative biomass increase of about 420%, followed by A. penelope with an increase of about 209% from 1990 to 2010 (Fig. 4). We observed only small differences in the results of food web models with and without mediation. Figure S1 shows the impact of both mediation functions on the model output.

The analyses established six of the food web groups as seagrass meadow inhabitants (i.e. Littorina littorea, Peringia ulvae,
Effects of seagrass recovery

Carcinus maenas, Capitellidae, Tharyx killariensis, and Pomatoschistus spp.). Predicted trends in these species differ with increasing seagrass biomass (Fig. 5). The relative biomass of L. littorea dropped by 38% from 1990 to 2010. In contrast, the relative biomass of P. ulvae increased by 159% during the modeled time period and the biomass of C. maenas increased by 272%. The polychaete groups Capitellidae and Tharyx killariensis both increased with increasing seagrass (11% and 58%, respectively). In contrast, the fish group Pomatoschistus spp. decreased in relative biomass by 29% from 1990 to 2010. In seagrass meadow inhabitants, most of the trends differed strongly between models with and without mediation indicating that indirect effects heavily influence the predicted development of relative biomass in seagrass inhabitants.

Based on predation mortality, we identified three main predators of seagrass meadow inhabitants. Nephtys hombergii caused the highest predation mortality in P. ulvae, Capitellidae, and T. killariensis. Merlangius merlangus was the main predator of Pomatoschistus spp. and Somateria mollissima caused the highest predation mortality in L. littorea and C. maenas. The biomass of these three main predators decreased over time with increasing seagrass biomass if mediation is included (Fig. 6). Biomass of N. hombergii dropped by 25% from 1990 to 2010. M. merlangus decreased by almost 100%. The smallest change occurred in S. mollissima with a decrease of 3%. These declines related to reduced access of predators to their prey with increasing seagrass biomass. Results differed strongly between models with and without mediation indicating that the mediating effect of seagrass severely impacts predator foraging behavior. Table S3 provides a complete list of yearly biomass changes of all system components.

Ecosystem Attributes and Services

The network indices differed in their response to increasing seagrass biomass in the system. The detritivory over herbivory (D/H) ratio increased from 1.43 to 1.47, the Finn cycling index (FCI) increased from 6.66% to 7.00%, and the System Omnivory Index (SOI) slightly decreased from 0.09 to 0.08 (Fig. 7). Spearman’s rank correlation test showed significant predicted development in all model indices projecting changes in structure and functioning with recovering seagrass meadows.

In addition, the model predicted changes in attributes used as proxies describing ecosystem services (Fig. 7). Biomass of commercial fish species decreased significantly by 94%. Total biomass of coastal birds representing tourism activities associated with bird watching increased significantly by 52%. The smallest change occurred in total net primary production representing carbon sequestration, which increased by about 6% and was not significant in Spearman’s rank correlation test.

Discussion

Effects of Seagrass Recovery

The modeled seagrass recovery in the SRB food web resulted in responses in seagrass consumers, seagrass meadow inhabitants, and the main predators of these inhabitants but influenced also other components of the system.

Seagrass consumers increased in biomass because of greater food availability to support larger populations of A. penelope and B. bernica. This contradicts results from the ongoing JMMB that show declining trends for A. penelope and stable status for B. bernica (Kleefstra et al. 2019). Birds are highly mobile and A. penelope and B. bernica are migrating species that spend only a few months of the year in the Wadden Sea (Nacken & Reise 2000). Declining trends in A. penelope probably reflect a population shift and decreased breeding success in northern Europe (Kleefstra et al. 2019). With larger seagrass meadows, the Wadden Sea could potentially host larger populations of herbivorous birds, but other factors outside of the Wadden Sea appear to be more important for actual population development than food supply during migration. In contrast to herbivorous birds, the model predicts declining biomass trends in several bentivorous bird species (i.e. Recurvirostra avosetta, Tadorna tadorna, Calidris alpina, Pluvialis apricaria) probably caused by decreased predation success. These declines align well with recent monitoring data from the area that show population decreases in all four species (Kleefstra et al. 2019). Generally, the negative trends presumably relate to eutrophication,
climate change, shellfish fisheries, disturbances associated with tourism, and habitat destruction, as well as changes in biological communities (van Roomen et al. 2012). Although the Ecosim model reflected some of the avian population decreases, reduced prey availability likely represents just one factor among many causing bird population declines in the Wadden Sea.

Predicted trends in seagrass meadow inhabitants differed among species. While most seagrass meadow inhabitants benefited from the protection of seagrass and increased in biomass (i.e. P. ulvae, Capitellidae, T. killariensis, C. maenas), L. littorea and Pomatoschistus spp. decreased with increasing seagrass biomass. These declines probably resulted from competition with other seagrass meadow inhabitants because the main predators of both system components (S. mollissima and M. merlangus, respectively) also decreased in biomass in the model over time. The periwinkle L. littorea feeds primarily on the microphytobenthos covering the sediment surface of the tidal flats. Microphytobenthos is also a major food source of the more abundant mud snail P. ulvae, which increased in biomass with seagrass recovery. Competition for the same food resource results in feedback reactions and cascading effects in the food web (Ulanowicz & Puccia 1990), which probably caused the decrease in L. littorea, because it appears to compete less effectively than P. ulvae. Likewise, Pomatoschistus spp.
decreased in biomass with recovering seagrass even though it presumably benefits from protection. Pomatoschistus spp. rely on the same benthic food sources as the shore crab C. maenas, which was projected to increase strongly from 1990 to 2010 and appears to be more competitive than Pomatoschistus spp. because of its more omnivorous diet. Thus, L. littorea and Pomatoschistus spp. suffer declines within the food web even though habitat conditions improved. Predicted trends in these invertebrate species and gobies are difficult to compare with field data given the absence of a regular benthic monitoring in the SRB. Studies from other parts of the Wadden Sea reveal stable trends in the entire macrozoobenthos community but no information on single species (Drent et al. 2017). However, inhabitants of seagrass meadows likely benefit from larger areas of suitable habitat. Previous studies demonstrate significantly higher abundances of C. maenas and C. crangon in Z. noltei beds than on bare sand flats (Polte & Asmus 2006b). We considered C. maenas to be a seagrass meadow inhabitant and the model predicted increased biomass over time. Indeed, Jung et al. (2017) and Meyer et al. (2016) reported increased abundance of C. maenas in the Balgzand area (the Netherlands) and Jade Bay (Germany), respectively, supporting an increasing trend. C. maenas might have benefited from mild winter temperatures in recent years (Beukema 1991; van Beusekom et al. 2012) and higher reproduction success (Meyer et al. 2016), but increasing seagrass meadow coverage potentially promoted this trend even more in the study site. Previous work already described high predation intensities of C. maenas in relation to seagrass meadows in the SRB system (Asmus & Asmus 2000).

The majority of fish species in our model decreased in biomass over time. This pattern aligns with time series data applied to the model (Asmus et al. 2020). Candidate factors for underlying mechanisms of these declines include pressure from fisheries outside of the SRB, climate change, habitat deterioration, or changes in nutrient dynamics (Tulp et al. 2017). Given observed declines in the entire Wadden Sea, it is unlikely that they link to increasing seagrass meadows because the positive seagrass trend is restricted to the northern part of the Wadden Sea. Indeed, seagrass meadows provide known spawning grounds (Polte & Asmus 2006a; Ford et al. 2010) and nursery habitats for juvenile fish (Nagelkerken et al. 2000; Bertelli & Unsworth 2014). Previous studies document spawning of Clupea harengus, Belone belone, and Gasterosteus aculeatus in Z. noltei beds in the Wadden Sea (Polte & Asmus 2006a). Furthermore, Polte et al. (2005) discovered higher abundances of juveniles of different fish species (Atherina presbyter, Platichthys flesus, Mugil chelo, Anguilla anguila, Belone belone) in Z. noltei beds than in surrounding habitats. Although these studies suggest an important role of Z. noltei beds for several fish species, the model predicts a decrease in biomass over time. This discrepancy highlights the need for continued research on the complex interactions within the benthic food web and the role of seagrass meadows in supporting biodiversity.
species, we lack comprehensive investigations of spawning behavior and juvenile abundance in comparison to the rest of the bight. In addition, the present model includes only two of the species using the *Z. noltei* beds either for spawning or as nursery ground (*C. harengus, P. flexus*) because of scarce abundance and biomass data for other species in the SRB. Thus, our EwE model excludes potential positive effects of seagrass recovery on fish species, requiring further investigations to improve model predictions for fish.

The biomass changes predicted by the Ecosim temporal-dynamic simulation differed among system components. Some benefited from seagrass recovery, others declined because of reduced access to prey or competition effects. The status of habitats such as seagrass meadows represents just one of many drivers forcing changes in the Wadden Sea ecosystem. For instance, climate change effects (e.g. increased water temperatures, sea-level rise, ocean acidification), invasive species, and pollution could induce large impacts on food web structure and functioning. In addition, stressors outside of the Wadden Sea might also affect migrating species. Thus, modeling results of seagrass recovery offer a first insight into potential effects, but to increase the reliability of predictions, future models should

Figure 7. Temporal development of the network indices and attributes representing ecosystem services; trend lines were inserted using smoothing procedure of the R package *ggplot2*, $p$-values and rho are obtained from Spearman’s rank correlation test.
consider additional drivers. Furthermore, our model focuses on species directly connected to seagrass meadows (e.g. consumers, inhabitants) and does not consider interactions with species or populations neighboring the seagrass meadow. Application of a spatial–temporal dynamic approach (e.g. Ecospace) could investigate these interactions in detail.

**Food Web Structure and Functioning**

The model predicted changes in the analyzed network indices over time indicating a change in food web structure and functioning. The increase in detritivory over herbivory (D/H) ratio and Finn cycling index (FCI) implies increased system dependency on detritivory pathways and recycling. Odum (1969) suggested that an ecosystem matures over time and develops from a food chain-structured system, more herbivorous system toward a web-like structured system increasingly dependent on detritivorous food sources and greater recycling. Thus, the increase in D/H ratio and FCI could indicate an increase in maturity of the SRB food web in relation to recovering seagrass meadows resulting in a more stable and resilient food web (Safi et al. 2019). However, higher recycling could also be a result of increasing ecosystem stress (Baird et al. 1991).

In contrast, the model projected a decrease in SOI over time with recovering seagrass. This decrease results from an increase in seagrass-related species with more specialized feeding behavior (e.g. herbivorous birds, detritivorous worms). Omnivory increases complexity of an ecological network and also its flexibility because systems with high omnivory absorb perturbations and recover quicker than systems with lower omnivory (Safi et al. 2019). Thus, the decrease in SOI indicates that the system loses complexity and flexibility, resulting in increased sensitivity to perturbations.

The results of the network indices remain inconclusive because the attributes partly contradict each other. Increase of D/H ratio and FCI indicate an increased stability of food web structure and increased system maturity (Odum 1969; Safi et al. 2019) but with decreasing system’s complexity (decreasing SOI) presumably resulting from more specialized feeding behavior in the food web.

**Ecosystem Services**

Seagrass meadows increase the complexity of ecosystems and provide ecosystem services (Larkum et al. 2006). Given the absence of field data on ecosystem services, we selected proxies for three ecosystem services to assess their changes with recovering seagrass.

We assessed potential carbon sequestration of the SRB by modeling total net primary production over time. Net primary production increased slightly, though not significantly. Seagrass meadows represent important carbon sinks (Greiner et al. 2013; Duarte 2017). In addition to carbon sequestered in primary production, significant carbon accumulates in the soil of seagrass meadows (Duarte et al. 2013; Greiner et al. 2013). Based on Duarte et al. (2013), belowground carbon sequestration might have increased from 30.0 t (1995) to 52.5 t (2010) in the German SRB over the study period. Thus, present models likely underestimate the potential carbon sequestration in the SRB by seagrass meadows. In addition to carbon, seagrasses provide important nitrogen sinks in coastal regions (Asmus & Asmus 2000; Aoki et al. 2019). Because we constructed our food web model based on carbon flows, we lacked an appropriate proxy for nitrogen sequestration. In addition, no local data exist on carbon and nitrogen sequestration by Z. noltei. More precise measurements would greatly improve future predictions and model results for these ecosystem services.

We used the total biomass of commercial fish species as a measure of fisheries potential and found that an increase in seagrass meadows does not result in a higher fish biomass. Generally, larger seagrass meadows could improve spawning and nursery habitats, but because our model excluded both services due to a lack of data on population sizes and abundances, we could not assess positive effects of seagrass on fish species.

In contrast, our model predicted total bird biomass would increase over time, representing a higher tourist attraction for bird watchers. However, the increase observed in our model links mainly to the predicted increase in herbivorous birds, a prediction not supported by field data.

Assessing ecosystem services remains challenging. Proxies taken from the model could be a valuable tool in future studies, but their application requires caution and results need careful consideration to avoid misleading conclusions. Model validation and ecosystem service assessment urgently require further studies to provide the necessary data.

**Potential Ecosystem Effects of Seagrass Restoration**

Human impacts can degrade seagrass meadows (Coll et al. 2011) and caused a global decline of about 30% of their known areal extent (Waycott et al. 2009). Widespread recognition of the importance of seagrass meadows for ecosystem structure and functioning have catalyzed attempts to restore degraded seagrass meadows all over the world (van Katwijk et al. 2009; Tanner 2014; Infantes & Moksnes 2018), but few studies have evaluated actual effects of seagrass restoration. Our model predictions point to general conclusions as to which effects can be expected when restoring seagrass beds. Overall, increased seagrass cover resulted in a potential increase in seagrass consumers because of increased food availability. In addition, expansion of suitable habitat and predation refuges might lead to an increase in seagrass meadow inhabitants. Furthermore, seagrass meadow restoration can change the system’s structure and functioning and contribute to a more stable and resistant food web. Ecosystem services such as tourism attraction could increase. Food web models could be used as valuable tools to predict unforeseen effects and indirect interactions when restoring habitats, such as seagrass meadows. Certainly, definitive effects of habitat restoration defy simple prediction. Feedback
reactions in the system and factors unrelated to the restoration site can play a distinct role and interfere with restoration efforts, as demonstrated for herbivorous birds. Our model provides a first approach in applying food web models to predict potential restoration effects. Inclusion of additional field data and information on further system drivers that influence the food web can improve predictions. An assessment approach of ecosystem services using model proxies appears promising, but requires support with additional empirical data to validate model results. Moreover, the study showed the importance of including indirect mediation effects in food web modeling (Vilas et al. 2020). Biomass development of seagrass meadow inhabitants and inhabitants’ predators differed strongly between models with and without mediation, implying that the mediating effect of seagrass heavily influences species development and the corresponding model output. This conclusion aligns with previous studies focusing on non-trophic interactions of habitat-forming species with the associated fauna (Harvey 2014; Vilas et al. 2020) and highlights the importance of including mediation in ecological models. Thus, studies must consider interactions between system components and mediating effects in order to effectively restore habitat-forming species and provide habitat for a distinct species. These effects are often only partially known and require further research to improve available modeling applications.

The SRB is a well-known system but data availability limited any straightforward assessment of recovery effects of habitats and ecosystem services. Thus, our study clarifies some model limitations and identifies a need for future studies to close gaps if food web models are used to eventually predict the success of restoration efforts. As a holistic ecological approach, food web models could help in evaluating the efficiency of expanding efforts in ecosystem restoration.

**Acknowledgments**

This study was funded by the project MERCES of the European Union’s Horizon 2020 research program (Grant agreement number 689518, www.merces-project.eu). The authors thank Kai Eskildsen, Ulrike Schückel, and Gabriele Müller of the National Park Authority, Schleswig-Holstein, for data provision, and Johannes Rick for assistance in collecting time series data from PANGAEA database. Further thanks to M. Nowicki for the productive EwE discussions. Open access funding enabled and organized by Projekt DEAL.

**LTURE CITED**

Aoki LR, Mcclatchey KJ, Oreska MPJ (2019) Seagrass restoration reestablishes the coastal nitrogen filter through enhanced burial. Limnology and Oceanography 65:1–12

Asmus H, Asmus R (2000) Material exchange and food web of seagrass beds in the Sylt-Rømø Bight: how significant are community changes at the ecosystem level? Helgoland Marine Research 54:137–150

Asmus H, Hassel B, Kadel P, Asmus R, Rick JJ, Wiltsone KH (2020) Fish monitoring in the Sylt Rømø bight (2007 et seq). Alford Wegener Institute - Wadden Sea Station Sylt; PANGAEA; https://doi.pangaea.de/10.1594/PANGAEA.911261

Backhaus J, Hartke D, Hübner U, Lohse H, Müller A (1998) Hydrographie und Klima im Lister Tidebecken. Pages 39–54. In: Gätje C, Reise K (eds) Ökosystem wattenmeer. Springer, Berlin, Germany

Baird D, Asmus H, Asmus R (2004) Energy flow of a boreal intertidal ecosystem, the Sylt-Rømø Bight. Marine Ecology Progress Series 279:45–61

Baird D, Asmus H, Asmus R (2007) Trophic dynamics of eight intertidal communities of the Sylt-Rømø Bight ecosystem, northern Wadden Sea. Marine Ecology Progress Series 351:25–41

Baird D, Asmus H, Asmus R (2012) Effect of invasive species on the structure and function of the Sylt-Rømø Bight ecosystem, northern Wadden Sea, over three time periods. Marine Ecology Progress Series 462:143–162

Baird D, Asmus H, Asmus R, Horn S, de la Vega C (2019) Ecosystem response to increasing ambient water temperatures due to climate warming in the Sylt-Rømø Bight, northern Wadden Sea, Germany. Estuarine, Coastal and Shelf 228:106322

Baird D, McGlade JM, Ulanowicz RE (1991) The comparative ecology of six marine ecosystems. Philosophical Transactions of the Royal Society of London Series B: Biological Sciences 333:15–29

Bertelli CM, Unsworth RKF (2014) Protecting the hand that feeds us: seagrass (*Zostera marina*) serves as commercial juvenile fish habitat. Marine Pollution Bulletin 83:425–429

Beukema JJ (1991) The abundance of shore crabs *Carcinus maenas* (L.) on a tidal flat in the Wadden Sea after cold and mild winters. Journal of Experimental Marine Biology and Ecology 153:97–113

Christensen V (1995) Ecosystem maturity—towards quantification. Ecological Modelling 77:3–32

Christensen V, Walters C (2004) Ecopath with Ecosim: methods, capabilities and limitations. Ecological Modelling 72:109–139

Cuen LD, Heck KL Jr, Abele LC (1981) Experiments on competition and predation among shrimps of seagrass meadows. Ecology 62:1484–1493

Coll M, Schmidt A, Romanuk T, Lotze HK (2011) Food-web structure of seagrass communities across different spatial scales and human impacts. PLoS One 6:e22591

Corrales X, Coll M, Ofrí E, Heymans JJ, Steenbeek J, Goren M, Edelst D, Gal G (2018) Future scenarios of marine resources and ecosystem conditions of the Eastern Mediterranean under impacts of fishing, alien species and sea warming. Scientific Reports 8:1–16

Corrales X, Coll M, Ofrí E, Pirollo C, Goren M, Edelst D, Heymans JJ, Steenbeek J, Christensen V, Gal G (2017) Hindcasting the dynamics of an Eastern Mediterranean marine ecosystem under the impacts of multiple stressors. Marine Ecology Progress Series 580:17–36

de Jonge VN, de Jong DJ (1992) Role of tide, light and fisheries in the decline of *Zostera marina* L. in the Dutch Wadden Sea. Netherlands Institute for Sea Research Publication Series 20:161–176

den Hartog C (1987) Wasting disease and other dynamic phenomena in Zostera marina L. in the Dutch Wadden Sea. Netherlands Institute for Sea Research Publication Series 20:161–176

Dolch T, Buschbaum C, Reise K (2013) Persisting intertidal seagrass beds in the northern Wadden Sea since the 1930s. Journal of Sea Research 82:134–141

Dolch T, Follmer EO, Frederiksen MS, Herlyn M, van Katwijk MM, Kolbe K, Krause-Jensen D, Schmedes P, Westerbeek EP (2017) Seagrass. In: Steenbeek J, Goren M, Edelst D, Heymans JJ, Christensen V, Gal G (eds) Hindcasting the dynamics of an Eastern Mediterranean marine ecosystem under the impacts of multiple stressors. Marine Ecology Progress Series 580:17–36

den Hartog C (1987) Wasting disease and other dynamic phenomena in *Zostera marina* L. in the Dutch Wadden Sea. Netherlands Institute for Sea Research Publication Series 20:161–176

den Hartog C (1987) Wasting disease and other dynamic phenomena in *Zostera marina* L. in the Dutch Wadden Sea. Netherlands Institute for Sea Research Publication Series 20:161–176

Drent J, Bijkerk R, Herlyn M, Goren M, Edelst D, Heymans JJ, Piroddi C, Goren M, Edelst D, Heymans JJ, Christensen V, Gal G (2017) Hindcasting the dynamics of an Eastern Mediterranean marine ecosystem under the impacts of multiple stressors. Marine Ecology Progress Series 580:17–36

den Hartog C (1987) Wasting disease and other dynamic phenomena in *Zostera marina* L. in the Dutch Wadden Sea. Netherlands Institute for Sea Research Publication Series 20:161–176

Duarte CM (2017) Reviews and syntheses: hidden forests, the role of vegetated coastal habitats in the ocean carbon budget. Biogeosciences 14:301–310

Duarte CM, Kennedy H, Marbá N, Hendriks I (2013) Assessing the capacity of seagrass meadows for carbon burial: current limitations and future strategies. Ocean and Coastal Management 83:32–38

Fath BD, Asmus H, Asmus R, Baird D, Borrett SR, de Jonge VN, et al. (2019) Ecological network analysis metrics: the need for an entire ecosystem approach in management and policy. Ocean and Coastal Management 174:1–14

June 2021 Restoration Ecology 11 of 13
Finn JT (1976) Measures of ecosystem structure and function derived from analysis of flows. Journal of Theoretical Biology 56:363–380
Ford JR, Williams RJ, Fowler AM, Cox DR, Suthers IM (2010) Identifying critical estuarine seagrass habitat for settlement of coastally spawned fish. Marine Ecology Progress Series 408:181–193
Greiner JT, McGlathery KJ, Gunnell J, McKee BA (2013) Seagrass restoration enhances “blue carbon” sequestration in coastal waters. PLoS One 8:1–8
Harvey CJ (2014) Mediation functions in Ecophyt with Ecosim: handle with care. Canadian Journal of Fisheries and aquatic Sciences 71:1020–1029
Heck KL Jr, Thoman TA (1981) Experiments on predator-prey interactions in vegetated aquatic habitats. Journal of Experimental Marine Biology and Ecology 53:125–134
Heymans JJ, Coll M, Libralato S, Morissette L, Christensen V (2014) Global patterns in ecological indicators of marine food webs: a modelling approach. PLoS One 9:e95845
Heymans JJ, Coll M, Link JS, Mackinson S, Stenbeek J, Christensen V (2016) Best practice in Ecophyt with Ecosim food-web models for ecosystem-based management. Ecological Modelling 331:173–184
Horn S, de La Vega C, Asmus R, Schwemmer P, Enners L, Garthe S, Binder K, Asmus H (2017) Interaction between birds and macrofauna within food webs of intertidal habitats of the Wadden Sea. PLoS One 12:e0176381
Horn S, Schwemmer P, Mercker M, Enners L, Asmus R, Garthe S, Asmus H (2020) Species composition of foraging birds in association with benthic fauna in four intertidal habitats of the Wadden Sea. Estuarine, Coastal and Shelf Science 233:106537
Hornemann, JW (1832) Flora danica fasciculus trigesmus quintus [fascicle 35]. pls MMXI-MMLX. Havniae. Copenhagen.
Infantes E, Moksnes PO (2018) Eelgrass seed harvesting: flowering shoots development and restoration on the Swedish west coast. Aquatic Botany 144:9–19
Jankowska E, de Troch M, Michel LN, Lejope G, Wlodarczak-Kowlczuk M (2018) Modification of benthic food web structure by recovering seagrass meadows, as revealed by trophic markers and mixing models. Ecological Indicators 90:28–37
Jung AS, Dekker I, Germain M, Philippart CJM, Witte JIJ, van der Veer HW (2013) Seagrass restoration in the northern Wadden Sea: a universally outstanding tidal wetland. Wadden Sea Ecosystem 29:7–24
Polte P, Asmus H (2005) The contribution of seagrass beds (Zostera noltii) to the function of tidal flats as a juvenile habitat for dominant, mobile epibenthos in the Wadden Sea. Marine Biology 147:813–822
Polte P, Schanz A, Asmus H (2006) Influence of seagrass beds (Zostera noltii) on the species composition of juvenile fishes temporarily visiting the intertidal zone of the Wadden Sea. Journal of Sea Research 55:244–252
Polte P, Asmus H (2006b) Influence of seagrass beds (Zostera noltii) on the function of tidal flats as a juvenile habitat for dominant, mobile epibenthos in the Wadden Sea. Marine Biology 147:813–822
Smit C (2010) The Wadden Sea system: structure, functioning and role in the mediating role of the North Sea in ecological processes: scaling up of ecological indicators of marine food webs as a juvenile habitat for dominant, mobile epibenthos in the Wadden Sea. Journal of Sea Research 55:244–252
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
Tanner JE (2014) Restoration of the seagrass Amphibolis antarctica—temporal variability and long-term success. Estuaries and Coasts 38:668–678
van Roomen M, Laursen K, van Turnhout C, van Winden E, Blew J, Eskildsen K, et al. (2012) Signals from the Wadden Sea: population declines dominate among waterbirds depending on intertidal mudflats. Ocean and Coastal Management 68:79–88
Vilas D, Coll M, Pedersen T, Corrales X, Filbee-Dexter K, Pedersen MF, Norderhaug KM, Fredriksen S, Wernberg T, Ramirez Llodra E (2020) Kelp-carbon uptake by Arctic deep-sea food webs plays a noticeable role
in maintaining ecosystem structural and functional traits. Journal of Marine Systems 203:103268

Walters C, Christensen V, Pauly D (1997) Structuring dynamic models of exploited ecosystems from trophic mass-balance assessments. Reviews in Fish Biology and Fisheries 7:139–172

Waycott M, Duarte CM, Carruthers TJ, Orth RJ, Dennison WC, Olyarnik S, et al. (2009) Accelerating loss of seagrasses across the globe threatens coastal ecosystems. Proceedings of the National Academy of Sciences of the United States of America 106:12377–12381

Supporting Information
The following information may be found in the online version of this article:

Figure S1. Relative biomass change of selected system components under different seagrass mediation scenarios.

Table S1. List of system components shown as groups included in the model with corresponding trophic level, biomass values as well as production and consumption ratios.

Table S2. Diet composition of system components.

Table S3. Predicted biomass development of system components from 1990 to 2010 assessed with Ecosim and extracted with Ecopath from Ecosim routine.

Guest Coordinating Editor: Paul Snelgrove

Received: 28 January, 2020; First decision: 5 May, 2020; Revised: 12 November, 2020; Accepted: 16 November, 2020