



Quantitative food web structure and ecosystem functions in a warm-temperate seagrass bed

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Received: 7 October 2020 / Accepted: 9 April 2021 / Published online: 24 April 2021
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Abstract

Seagrass beds are important habitats in coastal areas but increasingly decline in area and quality, thus conservation measures are urgently needed. Quantitative food webs, describing the biomass distribution and energy fluxes among trophic groups, reveal structural and functional aspects of ecosystems. Their knowledge can improve ecological conservation. For the recently discovered large warm-temperate seagrass (*Zostera japonica*) habitat in China's Yellow River Delta wetland, we used $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ measurements and a Bayesian isotope mixing model to construct its food web diagram with quantitative estimations of consumer diet compositions, comprising detritus and 14 living trophic groups from primary producers to fish. We then estimated the quantitative food web fluxes based on biomass measurements and calculated corresponding ecosystem functions. Pelagic producers were significantly ^{13}C -depleted compared to benthic sources. Consumers (except zooplankton) were increasingly ^{13}C -depleted with increasing trophic positions even though the consumed benthic production surpassed the pelagic one. Bivalves dominated consumer biomasses and fluxes and were the first to connect the pelagic and benthic pathways, whereas zooplankton and gastropods were specialized on the two pathways, respectively. We found flat biomass and production pyramids indicating low trophic transfer efficiencies. Generally, the energetic structure of the quantitative food web was consistent with the stable isotope analysis, and the estimated net primary production and most estimated production to biomass ratios of the trophic groups fell within literature ranges. This study provides a systematical understanding of the quantitative trophic ecology of a seagrass bed and facilitates synergistic knowledge on management, conservation, and restoration.

Introduction

Seagrass ecosystems form the foundation of one of the most important coastal wetlands due to their importance for blue carbon sequestration and other ecosystem services.

However, the habitat area and biodiversity in many of these ecosystems are declining due to multiple stressors, such as sediment runoff, species invasions, aquaculture and global warming (Duarte et al. 2008; Carmen et al. 2019). One of the most pressing challenges is, therefore, to counteract this ongoing loss of biodiversity and concomitant threats to ecosystem services and stability (Mori et al. 2013).

Quantitative food webs (QFWs) have been widely used to quantify the responses of ecosystem structure and functions to human-induced or other environmental changes (Boit et al. 2012; Boit and Gaedke 2014; Mehner et al. 2016). They reconcile the relationships among biodiversity, food web complexity, and ecosystem stability (de Ruiter et al. 1995; Thompson et al. 2012), and improve systematic ecological restoration strategies for fragile ecosystems (Bellmore et al. 2013; Cross et al. 2013).

Information on consumer diets is fundamentally important to establish such QFWs. Stable isotope analysis (mostly $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) constitutes a radical improvement to analyze diets that is now widely used to trace the pathways of matter

Responsible Editor: K. Bischof.

Reviewers: undisclosed experts.

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flows and determine the contributions of different sources to the nutrition of consumers (Vander Zanden et al. 1999; Schmidt et al. 2007; Christianen et al. 2017). The stable isotope signatures of a consumer reflect the isotopic values of the assimilated material and thus inform about the consumer's feeding over a period of time (Post 2002). Most previous studies achieved mass balance in QFWs (Gauzens et al. 2018), e.g. using an inverse matrix commonly referred to as ecological network analysis (Vézina and Platt 1988), the Ecopath model (Christensen and Pauly 1992), or the food web energetics approach (de Ruiter et al. 1995). In all of these mass balanced approaches, it is necessary to describe the major ecological processes for each living compartment, comprising ingestion, excretion, respiration, and production (Gaedke 1995). To achieve a mass balance, the production of each compartment has to offset losses from predation and from non-predatory mortality resulting from inadequate nutrition, constraints imposed by the organism's physical or chemical conditions, parasitism, or physiological death related to aging (Gaedke 2009).

According to a survey of seagrass habitats on Chinese coasts initiated in 2015, an unusually large discontinuous seagrass habitat (dwarf eelgrass, *Zostera japonica*), in total covering over 1000 ha, was discovered in the coastal shallow waters of the Yellow River Delta (YRD) wetland, northeastern China (Zhang et al. 2019). Increased attention is currently devoted to this seagrass habitat, in particular regarding the consequences of the increased turbidity resulting from the high sediment runoff of the Yellow River, the invasion of smooth cordgrass *Spartina alterniflora*, and the habitat loss recorded by National seagrass surveys due to river channel improvements, aquaculture, and harvesting activities, etc., (Zhang et al. 2019).

In the present study, we conducted system-wide biomass measurements and a stable isotope analysis that enabled to construct a QFW of a seagrass bed in the YRD wetland assessing its flux structure and ecosystem functions such as primary and consumer production. Specifically, our goals were (1) to identify the food web diagram showing the relative contribution of different prey to the diet of the numerous consumer groups via stable isotope analysis, (2) to construct a QFW model and estimate the flux structure, and (3) to compare the QFW flux structure and corresponding estimations of the trophic transfer efficiencies, the production to biomass ratio of each trophic group, and the net primary production with the literature. To the best of our knowledge, the present study provides the first QFW for a warm-temperate seagrass bed. Furthermore, we demonstrate that combining stable isotope analysis and QFW modelling is a powerful approach to analyse energetic patterns in food webs. It promotes understanding of complex interactions among trophic groups covering different trophic levels and the relative contributions of various trophic groups to the

whole food web. Such knowledge facilitates strategies of systematical ecosystem management and conservation.

Materials and methods

Study area

The Yellow River Delta wetland (37° 35' N to 38° 12' N, 118° 33' E to 119° 20' E) is located on the Pacific coast of northeastern China. Our studied seagrass bed (around 37° 51' 13" N, 119° 06' 10" E, Fig. 1a) within this wetland is ca. 20 km from the Yellow River mouth. The climate is warm-temperate, with an annual mean air temperature of 12.9 °C and monthly average air temperatures ranging from - 3 °C in January to 27 °C in July. Annual rainfall and evaporation is 552 and 1962 mm, respectively (He et al. 2009). Tidal fluctuation is irregularly semidiurnal, with the range of the two successive tides being unequal (He et al. 2009). The mean tidal range is between 0.73 and 1.77 m. The water depth and salinity averaged 1 m and 29‰, respectively.

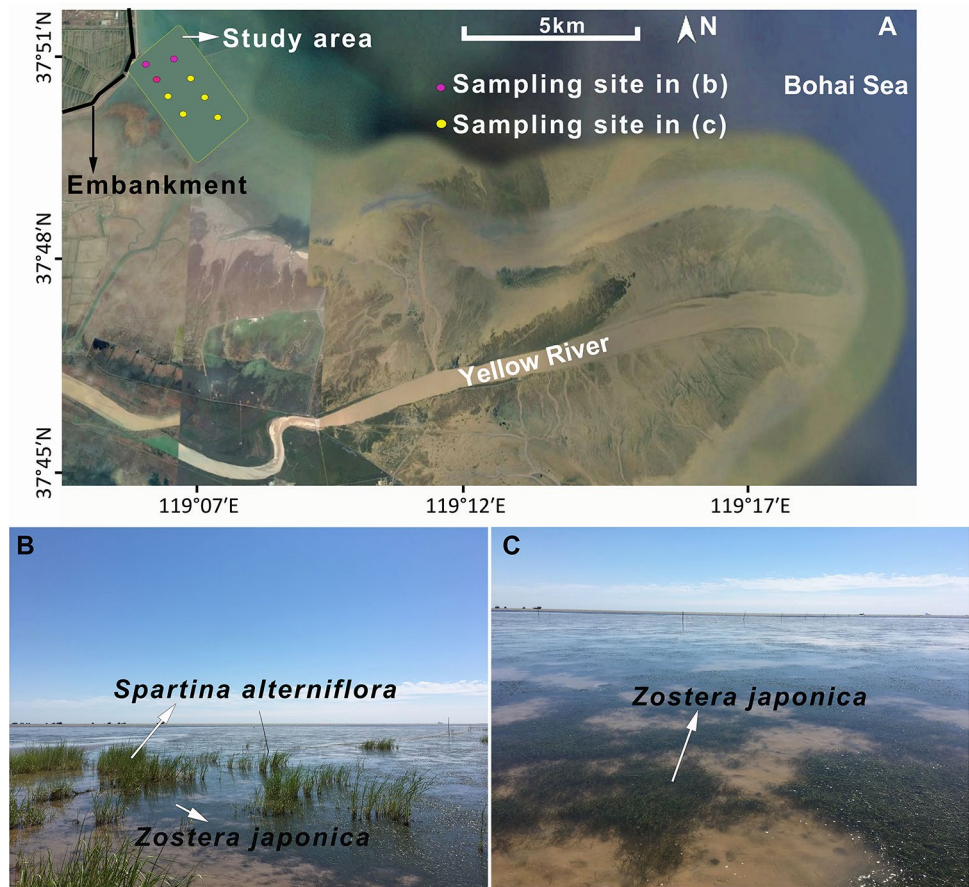
The study area was mainly covered by seagrass of *Zostera japonica*, and by the invading *Spartina alterniflora* leading to mixed communities in some areas near the embankment (Fig. 1b). Seagrass was still dominant at most study sites away from the embankment and close to the sea (Fig. 1c). *Z. japonica* is an annual submerged hydrophyte, with small-flattened stems, while *S. alterniflora* is a perennial herbaceous plant, with emerged tall and dense stems.

Samples for biomass determination

Biomass samples were taken at the end of May and the end of July 2017 to cover most of the growing season. We sampled suspended particulate matter (SPM), microphytobenthos, seagrass, *S. alterniflora*, and macroinvertebrates at eight sampling sites along two linear transects with 600 m intervals between sites from the embankment to the sea (Fig. 1). Phytoplankton and zooplankton were collected at six of the eight sampling sites, excluding the two sites nearest to the shore because of the low water level at low tide. Fish were collected in a tidal creek at six sampling points close to the phytoplankton and zooplankton sampling sites at the end of July 2017.

We acquired SPM by pre-filtering 1-L water samples from a Plexiglass water collector through a 200- μ m mesh to remove large detritus, rinsed on glass-fiber filters (0.45- μ m Whatman GF/F), and then dried in an oven for 72 h at 60 °C to obtain its dry weight. SPM was sampled during the tide going up when the sediments were easily suspended in the water column, thus, we did not sample benthic detritus independently but assume that it is included in our measurements of SPM.

Fig. 1 **a** Photograph of the studied area of a seagrass bed in China's Yellow River Delta coastal wetland, and locations of the eight sampling sites. Source: Google Earth. Photographs by the authors of representative vegetation communities **b** near the embankment and **c** close to the sea



Phytoplankton and zooplankton samples for biomass determination were collected from the Plexiglass water collector using 1 L for phytoplankton and 10 L for zooplankton, with no mesh used for phytoplankton and a 64- μm size mesh for zooplankton. We preserved the samples in Lugol's solution, transferred them to the laboratory, and identified the taxa under an Olympus CX31 optical microscope (Olympus, Tokyo, Japan). For each phytoplankton taxon, we used the geometric shape closest to the actual cell shape to calculate the mean cell volume, which we then transformed into a wet weight (Hillebrand et al. 1999). Zooplankton biomass equaled the abundance (mean number of individuals per sample) multiplied by the average wet weight of the individual zooplankton (Gaedke et al. 2002). For the microphytobenthos, we collected the surface sediment to a depth of 20 mm with a syringe and placed them on ice in a cooler for transferring to the laboratory in the dark. We determined the chlorophyll-a concentration in the surface sediment using high-performance liquid chromatography (Szymczak-Żyła et al. 2017), then estimated the microphytobenthos wet biomass assuming that the proportion of chlorophyll-a in the microphytobenthos wet weight is 0.5% (Kasprzak et al. 2008). The dry weight was assumed to be 15% of the wet weight for

phytoplankton and microphytobenthos, and 19% for zooplankton (Norland et al. 1987; Menden-Deuer and Lessard 2000; Madin et al. 2001).

Plant samples (seagrass and *S. alterniflora*) were collected at the eight sampling sites in three randomly chosen quadrats (50 cm \times 50 cm), respectively. Seagrass and *S. alterniflora* coexisted at three sites at the end of May and at four sites at the end of July, whereas only seagrass was found otherwise. Plant samples were dried in an oven for 72 h at 60 $^{\circ}\text{C}$ to obtain their dry weight. Macroinvertebrates were collected at three random locations at each sample site, and the collections were mixed to provide a single bulked sample for each site. We sampled the macroinvertebrate when the tide went down, which allowed us to dig holes with a size of 0.25 m \times 0.25 m \times 0.3 m (length \times width \times depth). Then, we collected all sediment in the hole and rinsed it with water to pass through a 0.5-mm mesh extracting the organisms $>$ 0.5 mm. The organisms were cleaned again in the laboratory and preserved in a plastic bottle with 75% alcohol until identification to the species level. We then counted the number of individuals per species, oven-dried, and weighed the samples per species to obtain their dry weight. Since we used a mesh of 0.5 mm, we excluded meiobenthos in our analysis.

Fish were collected employing fishing cages (length \times width \times depth: 4 m \times 20 cm \times 25 cm; mesh size 10 mm) in tidal creeks near the sampling sites. The creeks in our study area typically have a mean width and depth of ca. 2 and 1 m, respectively. The fishing cages were placed into the creek at an angle to increase the probability of catching under the guidance of the local fisherman. The fishing cages collect different sizes of fish through multiple entrances, and the captured fish could not escape from the cage. We counted the number of individuals per species in the field. Then we transferred three representative individuals of each fish species to the laboratory for oven-drying to determine the mean body dry weight to estimate the total dry weight per fishing cage.

We converted these values to biomass using the following equation (Li et al. 2020):

$$B = (C \times D) / (v \times t \times a \times q) \quad (1)$$

where B is the fish biomass (g DW m⁻², DW means dry weight), C is the total catch in dry weight per fishing cage (g DW), D is the mean water depth (here, 1 m), v is the current velocity (here, 1080 m h⁻¹; Zhang et al. 2016), t is the effective working time (here, 8 h), a is the opening area of the fishing cage (here, 0.4 m², designed so that fish could enter but not escape), and q is the capture efficiency. We used $q=0.5$ for *Lateolabrax japonicus* (Li et al. 2020), and for other fish species, q was scaled according to the ratios between their average body weight and the average body weight of *L. japonicus*. We acknowledge that this procedure may only deliver a rather rough estimation of fish biomasses, due to e.g. the variability in fish species occurrence, the mobility of fish, limited sampling time and uncertainties in the conversion factors.

Many food web studies adopted a ‘trophic groups’ approach, in which trophic groups are defined as groups of taxa that share the same set of prey and predators (Dunne et al. 2002). Following previous food web analyses for aquatic ecosystems (Mao et al. 2016; Iglesias et al. 2017; Lischke et al. 2017), we divided all collected taxa into 15 trophic groups (Table S1): SPM, phytoplankton (pelagic producers), microphytobenthos (benthic producers, BP), seagrass (BP), *S. alterniflora* (BP), zooplankton, gastropods (macroinvertebrates I, dominated by *Cerithidea sinensis*), bivalves (I, dominated by *Moerella hilaris*), crabs (I), polychaetes (I), shrimp (I), *Planiliza haematocheila* (fish, F), *Cynoglossus semilaevis* (F), *Synechogobius hasta* (F), and *L. japonicus* (F). We combined all gastropods and bivalves in two groups as they were both dominated by one component species (Table S1). We did so as well for polychaetes although there was no clear dominant species given the trade-off between food web complexity and

accuracy in diet compositions (Table S1, cf. Bayesian isotope mixing model and see below).

Samples for stable isotope determination

Stable isotope samples were collected in late July 2017 together with the biomass samples, but some isotope samples were treated differently from the biomass samples. Isotope samples from phytoplankton and zooplankton were collected by filtration through meshes with sizes of 64 μ m and 122 μ m, respectively. Isotope samples for the microphytobenthos were collected by scraping them from the surface of stones in the tidal creek and then transferring them into small amounts of distilled water with a soft toothbrush (O’Gorman et al. 2017). All isotope samples (SPM, microphytobenthos, phytoplankton, and zooplankton) were rinsed into pre-combusted (450 °C for 6 h) glass-fiber filters (0.45- μ m Whatman GF/F) for stable isotope determination (Mao et al. 2016). Leaves of seagrass and *S. alterniflora* were collected by hand and washed with distilled water, and all leaves (10–15 leaves) from a sample site were mixed to provide a single composite sample. Different pre-treatments were applied to different macroinvertebrates before the stable isotopic analysis. For snails and other organisms that live in a shell, we separated the viscera from the shell. Crab muscle tissue was extracted from the large claws. For shrimp, we removed the entire shell, as well as the head and tail, and analyzed the muscle tissue. For other small organisms, we used the entire body. For fish, we dissected white dorsal muscle tissue from three individuals per species for isotope detection.

In total, we collected 63 stable isotope samples ($n=3-10$ for each trophic group). The samples were oven-dried to constant weight at 60 °C and then ground into a fine powder using a mortar and pestle. Carbon and nitrogen isotopes were determined using a continuous-flow isotope-ratio mass spectrometer (Delta V Advantage, Thermo Scientific, Dreieich, Germany) coupled to an elemental analyzer (Flash EA1112 Thermo Scientific, Monza, Italy). The isotope values were compared with the Vienna PeeDee Belemnite (VPDB) standard and with atmospheric N₂ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively. Isotope ratios were expressed in the conventional δ notation as parts per thousand (‰):

$$\delta^{13}\text{C} = \left(\frac{{}^{13}\text{C}/{}^{12}\text{C}_{\text{sample}}}{{}^{13}\text{C}/{}^{12}\text{C}_{\text{VPDB}}} - 1 \right) \times 1000 \quad (2)$$

$$\delta^{15}\text{N} = \left(\frac{{}^{15}\text{N}/{}^{14}\text{N}_{\text{sample}}}{{}^{15}\text{N}/{}^{14}\text{N}_{\text{atmosphere}}} - 1 \right) \times 1000 \quad (3)$$

The analyzer was calibrated every 10 measurements, and the analytical precision of these measurements for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were 0.1‰ and 0.2‰, respectively.

We estimated consumer trophic positions according to their mean $\delta^{15}\text{N}$ values (hereafter, the trophic position based on stable isotopes, TP_{SI}) using the equation proposed by Vander Zanden et al. (1999)

$$TP_{\text{SI}} = (\delta^{15}\text{N}_{\text{consumer}} - \delta^{15}\text{N}_{\text{baseline}})/3.4 + 2 \quad (4)$$

where $\delta^{15}\text{N}_{\text{consumer}}$ is the $\delta^{15}\text{N}$ value of the consumer and $\delta^{15}\text{N}_{\text{baseline}}$ is the mean $\delta^{15}\text{N}$ value for zooplankton, gastropods, and bivalves in this study. The assumed trophic enrichment factor in $\delta^{15}\text{N}$ is 3.4‰ (Post 2002). The TP_{SI} of the basal sources were set to 1.

Bayesian isotope mixing model

We derived the potential prey groups for each consumer trophic group using published diet data based on gut content analysis or isotope signatures close to our study area (in Bohai Bay or the Bohai Sea) or more generally in estuary ecosystems and seagrass beds (see Table S1 and the Supplementary information for the diet literature). Zooplankton (dominated by Copepoda, Table S1) relies on phytoplankton (dominated by diatoms, Table S1). The gastropod *C. sinensis* is a typical deposit feeder (grazer); therefore, the potential dietary components include seagrass, *S. alterniflora*, and microphytobenthos. Filter-feeding bivalves (dominated by *M. hilaris*) may strongly control phytoplankton abundance by their feeding activities (Dame and Dankers 1988), but do not affect Copepoda due to their high mobility (Holzman et al. 2005). Thus, the potential prey for bivalves are SPM and phytoplankton. Crabs were represented by *Helice tientsinensis* and *Pyrhila pisum*; the former is an intertidal crab widely distributed in the Yellow River Delta wetland (Cui et al. 2011), and the latter usually occurs near the sea (Kobayashi and Archdale 2017). According to similar studies on the same crab species (Kanaya et al. 2008; Quan et al. 2012; Choi et al. 2017), we assumed that food sources for the crabs were seagrass, *S. alterniflora*, microphytobenthos, and bivalves. The observed polychaete species vary in their diet habits, e.g. deposit-feeding (e.g. Onuphidae, Capitellidae, Lumbrineridae) and predatory feeding (e.g. Nereididae) (Christian and Luczkovich 1999; Luczkovich et al. 2002). Gut analyses revealed that their main food resources include phytoplankton, SPM, bivalves, and gastropods (Christian and Luczkovich 1999). Shrimp were collected at large juvenile or adult stages, with potential food sources comprising SPM, phytoplankton, zooplankton, and bivalves. Previous gut content and stable isotope analysis for *P. haematocheila* both indicated that it is an omnivorous fish feeding mainly on the surface of sediments in estuarine wetlands (Quan

et al. 2010). Here, we considered microphytobenthos, seagrass, *S. alterniflora*, gastropods, bivalves, crabs, and polychaetes as its potential diet. We used data from gut content analysis conducted in the Bohai Sea for *C. semilaevis*, *S. hasta*, and *L. japonicus* (Zhang et al. 2018). *C. semilaevis* is a large, fast-growing but low-fecundity fish that inhabits the Bohai Sea, where it feeds on bivalves, crabs, shrimp, and *P. haematocheila*, *S. hasta* and *L. japonicus* are widely distributed around the Bohai Sea and coastal areas, where they feed on benthic organisms and fish (crabs, polychaetes, shrimp, and *P. haematocheila* for *S. hasta*; and crabs, shrimp, *P. haematocheila*, and *C. semilaevis* for *L. japonicus*).

Bayesian isotope mixing models were successfully used to assess the quantitative contribution of different food items to the target consumers (Phillips and Gregg 2003; Moore and Semmens 2008; Parnell et al. 2010). Therefore, we used the SIAR package (Parnell et al. 2010) implemented in version 3.6.1 of the R software. It describes the probability of the dietary proportion accounted for by each food resource using a Dirichlet prior distribution. We assumed a carbon trophic enrichment factor of $0.4 \pm 1.3\text{‰}$ and a nitrogen trophic enrichment factor of $3.4 \pm 1.0\text{‰}$ (Post 2002). We ran the SIAR model for 500,000 iterations for each consumer group to obtain the proportional contribution (%) of its potential food sources selected from literature. Based on the model's output, feeding links were assigned only when the lower limit of the 50% confidence interval ($\text{mean} \pm z \times \text{SE}$, where z is the z -score that has a confidence interval of 50%) for the contribution of one source to the target consumer diet exceeded 5% (Careddu et al. 2015; Bentivoglio et al. 2016). This ensured that the results included weak but statistically possible links in the food web. Following this procedure, we established a food web diagram that accounts for all consumers and their relevant food sources.

Based on the SIAR model output of diet relationships among trophic groups, we characterized the unweighted topology of the food web using 8 properties: link density, connectance, proportion of top species (that have no predators), proportion of intermediate species (that have both predators and prey), proportion of basal species (that do not consume other species), proportion of herbivores (that only consume basal species), proportion of omnivores (that feed on basal species and primary consumers), and proportion of carnivores (that feed on other consumers). We obtained these topological properties of the food web using the Network3D software (Williams 2010).

Quantitative food web model

We constructed the quantitative food web (QFW) by balancing the energy fluxes following de Ruiter et al. (1995), assuming that the steady-state production of each trophic group must balance its total loss:

$$P_j = F_j a_j p_j = M_j + d_j B_j \quad (5)$$

where P_j is the production of trophic group j (g DW $m^{-2} yr^{-1}$), F_j is the ingestion of group j (g DW $m^{-2} yr^{-1}$), a_j is the assimilation efficiency (the ratio between assimilation and ingestion, dimensionless), p_j is the production efficiency (the ratio between production and assimilation, dimensionless), M_j is the mortality caused by predation on group j (g DW $m^{-2} yr^{-1}$), d_j is the specific death rate resulting from non-predatory mortality (yr^{-1}) and B_j is the average biomass of group j (g DW m^{-2}) based on field sampling.

Since some predators feed on several prey groups, we considered the composition of the diet when calculating the ingestion by trophic group j on a particular food source i :

$$F_{ij} = f_{ij} F_j \quad (6)$$

where F_{ij} is the ingestion of trophic group j on prey i (g DW $m^{-2} yr^{-1}$) and f_{ij} is the mean diet proportion (dimensionless) for ingestion of food resource i by consumer j based on the SIAR model output. We assumed that the predation mortality (M_j) for top predators equaled zero, so we calculated F_j and F_{ij} starting from top predators and moving towards the lowest trophic level in the web.

Consumer trophic positions based on the QFW (TP_{QFW}) were quantified following the method of Gaedke (2009). This measure equals 1 plus the weighted average of the trophic positions of the prey species, where the weighting is given by the diet fractions:

$$TP_{QFW,j} = 1 + \sum_{i \in \Omega_j} TP_{QFW,i} f_{ij} \quad (7)$$

where Ω_j is the prey of consumer j .

The pyramids of biomass and production along trophic levels were derived from the QFW. Biomasses of SPM and primary producers were used to define the base of the pyramid, and the contribution of each consumer group to a particular trophic level was determined by its diet composition and that of their prey (Gaedke 2009). We used the same approach for the production pyramid. The trophic transfer efficiency (TTE , dimensionless) is defined as the ratio of the production at a given trophic level to the production at the next lower trophic level (Boit and Gaedke 2014).

We also calculated the production to biomass ratio (P/B , yr^{-1}) to assess the metabolic activity of each trophic group:

$$(P/B)_j = (F_j \times a_j \times p_j) / B_j = (M_j / B_j) + d_j \quad (8)$$

The QFW delivers an estimate of the net primary production (NPP) required to cover the ingestion of all consumers. In addition, a major fraction of the autotroph production is exported, decomposed or stored within the system. We estimated the total NPP required to cover all losses by assuming that 41%, 43%, 19%, and 31% of the phytoplankton,

microphytobenthos, seagrass, and *S. alterniflora*, respectively, is directly consumed (Duarte and Cebrián 1996). SPM was not considered in the NPP estimation. We then compared the total estimated NPP with literature values.

We first constructed a QFW (cf. Fig. S1) assuming consumer assimilation and production efficiencies as provided in Table S2 and a specific death rate of the two top predators resulting from non-predatory mortality of $0.33 yr^{-1}$ (Table S2) based on the measured maximum lifespan of these species (Randall and Minns 2000). The specific death rates of intermediate consumers were roughly estimated from published data for aquatic and soil food webs (Table S2; de Ruiter et al. 1995; Kuiper et al. 2015; van Altena et al. 2016). Subsequently, we evaluated the resulting TTE (cf. Fig. S3), P/B ratio of each group (cf. Table 1), and the NPP (cf. Table 2). Given the resulting rather high P/B ratios and NPP of the constructed QFW relative to literature values (cf. Tables 1, 2), we reduced the specific death rates of intermediate consumers to 50% of the literature values. After recalculating the QFW fluxes (cf. Figure 4) and corresponding production pyramid (cf. Figure 5), we found that reducing the specific death rates had little effect on the QFW flux structure and relative contributions to overall consumer production (comparing Fig. 4 with Fig. S1, and Fig. 5d with Fig. S3B). The resulting P/B ratios (cf. Table 1) and NPP (cf. Table 2) of the reconstructed QFW were more in line with published values (cf. Tables 1, 2), since the consumers require a lower energy input to balance the reduced specific death rates at equilibrium. Therefore, we focus subsequently on this QFW. All calculations were performed using the version 2019b of the MATLAB software.

Results

Stable carbon and nitrogen isotopes of trophic groups

We established the $\delta^{13}C$ and $\delta^{15}N$ values of 15 trophic groups from a seagrass bed in the Yellow River Delta wetland in late July 2017 (Fig. 2, Table S3). The $\delta^{13}C$ and $\delta^{15}N$ values of the basal sources (comprising suspended particulate matter (SPM) and four primary producers) varied significantly (Fig. 2a, one-way ANOVA, for $\delta^{13}C$, $F_{4,20} = 100$, $p < 0.001$; for $\delta^{15}N$, $F_{4,20} = 7$, $p = 0.002$). The most ^{13}C -depleted basal source was the only pelagic producer, phytoplankton ($-22.3 \pm 1.1\%$, mean \pm SD for the $\delta^{13}C$ values across all samples, Table S3), with a value significantly lower than that of all other sources (Tukey's HSD, $p < 0.001$; Table S3). SPM was the most ^{13}C -enriched group and its $\delta^{13}C$ value was very close to that of seagrass ($-11.7 \pm 0.4\%$ and $-11.5 \pm 1.2\%$, respectively), implying that the SPM mainly originates from the detritus of seagrass. Thus, we

Table 1 Comparison of the production to biomass (*P/B*) ratios of consumer trophic groups with previously published values

Trophic groups	<i>P/B</i> (yr^{-1})		Literature value
	50% of the literature values of consumer specific death rate (cf. Figure 4)	Literature values of consumer specific death rate (cf. Fig. S1)	
Phytoplankton	241	433	118 ^a ; 135 ^b ; 185 ^c ; 190 ^d ; 250 ^h ; 429 ^e
Microphytobenthos	147	250	33–35 ^b ; 37 ^e ; 40 ^b ; 100 ^j
Seagrass	0.80	1.39	2.5 ^b
<i>Spartina alterniflora</i>	0.70	1.18	–
Zooplankton	16	30	18 ^d ; 22 ^{bc} ; 25 ^{ag} ; 38–53 ^f
Gastropods	1.28	2.26	1.1–2.1 ^b ; 1.1 ^k ; 1.6–1.8 ^f ; 1.75 ^a ; 2 ^h ; 2.52 ^d
Bivalves	1.48	2.65	0.9–1 ^b ; 1–1.1 ^f ; 1.1 ^k ; 1.75 ^a ; 2 ^h ; 2.52 ^d
Crabs	1.49	2.42	2.1 ^a ; 2.5 ^e ; 2.4–3 ⁱ ; 4 ^d ; 4.9 ^h ;
Polychaetes	5.01	6.02	2.2–9.5 ^b ; 3.8 ^d ; 5.9 ^e
Shrimp	5.78	6.75	1.8 ^d ; 2.4–3 ⁱ ; 3.2 ^k ; 4.9 ^h ; 8.3 ^g
<i>Planiliza haematocheila</i>	6.35	6.50	0.9 ^g ; 2.3 ^d
<i>Cynoglossus semilaevis</i>	3.51	3.60	3.55 ^l
<i>Synechogobius hasta</i>	0.33	0.33	Table S2
<i>Lateolabrax japonicus</i>	0.33	0.33	

P/B ratios were derived from the two quantitative food webs (cf. Figures 4, S1) constructed using the specific death rate values of intermediate consumers from the literature and 50% of the values from the literature, respectively (cf. materials and methods and Table S2)

^aXu et al. (2011a)

^bBaeta et al. (2011)

^cPatrício and Marques (2006)

^dXu et al. (2011b)

^eMilessi et al. (2010)

^fTecchio et al. (2015)

^gZheng and You (2014)

^hJiang and Gibbs (2005)

ⁱde Mustsert et al. (2012)

^jHarvey et al. (2012)

^kColl et al. (2009)

^lDu et al. (2015)

Table 2 Comparison of our estimated net primary production (*NPP*) values with the range of most seagrass beds in the literature

System	<i>NPP</i> (only seagrass) (g DW m ⁻² yr ⁻¹)	<i>NPP</i> (g DW m ⁻² yr ⁻¹)	Source or derived from
50% of the literature values of consumer specific death rate (cf. Figure 4)	846	2237	Estimates from quantitative food web
Literature values of consumer specific death rate (cf. Fig. S1)	1471	3929	
Seagrass beds ^a	360–1460		Mateo et al. (2006)

Our *NPP* values were estimated by the two quantitative food webs (cf. Figures 4, S1) constructed using the specific death rate values of intermediate consumers from the literature and 50% of the values from the literature, respectively (cf. materials and methods and Table S2)

^aConverted from the range 0.5–2.0 gC m⁻² day⁻¹ for most seagrass beds with seagrass biomass > 50 g DW m⁻²

consider SPM as a basal source of the benthic pathways as well. The $\delta^{13}\text{C}$ value of seagrass did not differ significantly from that of microphytobenthos, but from that of *Spartina*

alterniflora (Tukey's HSD, $p = 0.001$). The $\delta^{15}\text{N}$ of the basal sources ranged from $2.5 \pm 0.04\text{‰}$ for phytoplankton to $5.3 \pm 1.2\text{‰}$ for SPM. Phytoplankton had a significantly

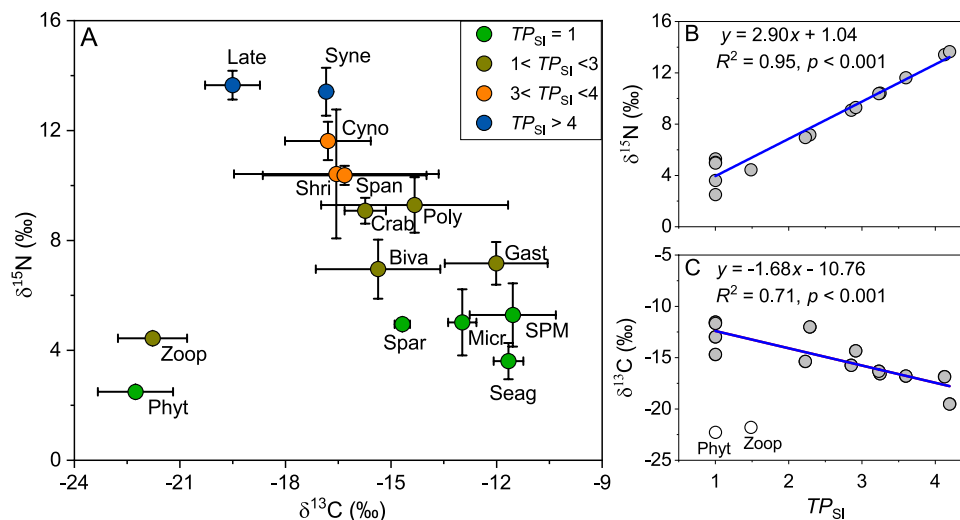


Fig. 2 a Stable isotope compositions ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, mean ± 1 SD) for the 15 trophic groups collected from a seagrass bed in China's Yellow River Delta coastal wetland. TP_{Si} is the trophic position based on the stable isotope ratio. b, c Linear regression of mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for all trophic groups against the corresponding TP_{Si} , except for the $\delta^{13}\text{C}$ values of phytoplankton (Phyt) and zooplankton (Zoop). Abbreviations of trophic groups from first trophic level to top

level: SPM suspended particulate matter, Phyt phytoplankton, Micro microphytobenthos, Seag seagrass, Spar *Spartina alterniflora*, Zoop zooplankton, Gast gastropods, Biva bivalves, Crab crabs, Poly polychaetes, Shri shrimp, Plan *Planiliza haematocheila*, Cyno *Cynoglossus semilaevis*, Syne *Synechogobius hasta*, Late *Lateolabrax japonicus*

lower value of $\delta^{15}\text{N}$ than SPM (Tukey's HSD, $p = 0.002$, Table S3), microphytobenthos (Tukey's HSD, $p = 0.02$), and *S. alterniflora* (Tukey's HSD, $p = 0.02$).

Consumers showed also a significant separation in $\delta^{13}\text{C}$ (Fig. 2a, one-way ANOVA, $F_{9,41} = 11$, $p < 0.001$), with zooplankton showing the most ^{13}C -depleted value ($-21.8 \pm 1.0\text{‰}$), close to the value for phytoplankton. The macroinvertebrates had values ranging from -16.6 ± 2.9 to $-12.0 \pm 1.5\text{‰}$, and the fish had values ranging from -19.5 ± 0.8 to $-16.3 \pm 2.3\text{‰}$. Zooplankton had a significantly lower $\delta^{13}\text{C}$ than the other consumer groups (Tukey's HSD, $p < 0.05$, Table S3), except for *Lateolabrax japonicus*. Gastropods were the most ^{13}C -enriched consumer in our study area, but did not differ significantly in $\delta^{13}\text{C}$ from crabs (Tukey's HSD, $p = 0.08$) and polychaetes (Tukey's HSD, $p = 0.5$). The consumer $\delta^{15}\text{N}$ values also differed significantly (Fig. 2a, one-way ANOVA, $F_{9,41} = 29$, $p < 0.001$), and covered a wide range, with values for the macroinvertebrates ranging from 7.0 to 10.4‰, and fish ranging from 10.4 to 13.6‰. Zooplankton was the most ^{15}N -depleted consumer ($p < 0.05$, Table S3). The predatory fish *L. japonicus* ($13.7 \pm 0.5\text{‰}$) and *Synechogobius hasta* ($13.4 \pm 0.9\text{‰}$) had significantly higher $\delta^{15}\text{N}$ values than the macroinvertebrates ($p < 0.05$).

The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures of the trophic groups showed a clear pattern along with their trophic positions based on stable isotopes (TP_{Si}) (Fig. 2b, c). As expected, the $\delta^{15}\text{N}$ values of the trophic groups increased significantly with increasing TP_{Si} (Fig. 2b). Furthermore, the $\delta^{13}\text{C}$ values

of the trophic groups decreased significantly with increasing TP_{Si} , except for phytoplankton and zooplankton (Fig. 2c). This correlation suggests that consumers (except zooplankton) gradually rely more on pelagic sources with increasing trophic position.

Food web diagram based on the Bayesian isotope mixing model

Based on the potential feeding links suggested by the literature (cf. materials and methods, Table S1) and the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ measurements evaluated with a Bayesian isotope mixing model (SIAR model), we constructed a food web diagram for the seagrass bed in which the links reflect the relative contributions of the various prey groups to each consumer's diet (Fig. 3). In total, we found 37 relevant links among the 15 trophic groups in the food web, with a linkage density of 2.47 and a connectance of 0.16 falling into the low and intermediate part of the normal range of 1.6–25.1 and 0.03–0.32 of empirical food webs, respectively (Dunne et al. 2002). Among the trophic groups, 33%, 54%, and 13% of them belonged to the basal, intermediate, and top species, respectively. Specifically, 20% of all trophic groups were herbivores, i.e. zooplankton, gastropods, and bivalves; 27% were omnivores, i.e. crabs, polychaetes, shrimp, and *Planiliza haematocheila*; and 20% were carnivores, i.e. the remaining 3 fish species. Overall, bivalves had the largest number of predator taxa ($n = 5$) and *P. haematocheila* had the largest number of prey taxa ($n = 7$) in the food web.

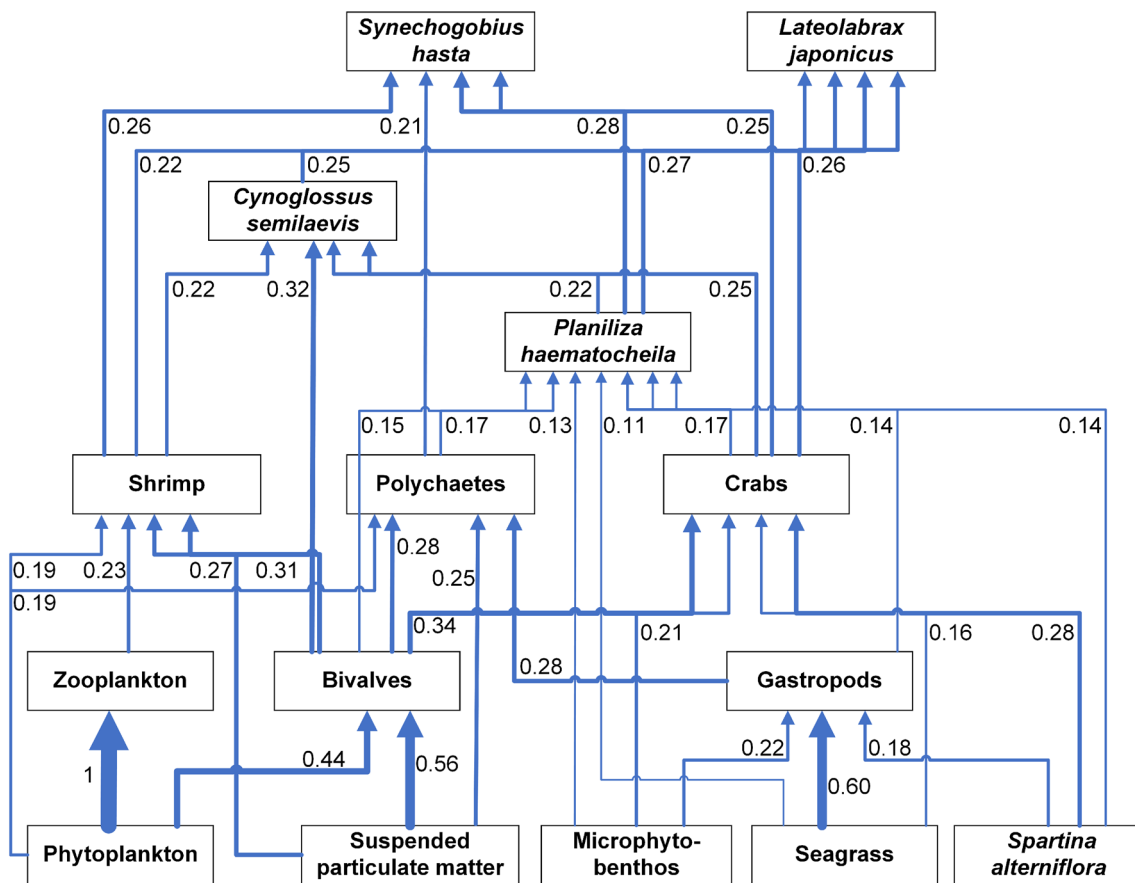


Fig. 3 Food web diagram for the seagrass bed in China's Yellow River Delta coastal wetland. The arrows represent the trophic feeding links from prey to predator, and are scaled according to the diet composition of the respective consumer (that is, thicker arrows repre-

sent greater proportions). The number near a link represents the relative contribution of the prey item to the target predator's consumption based on the Bayesian isotope mixing model

Most consumer groups relied on a broad and relatively evenly distributed diet composition, except for zooplankton, relying exclusively on phytoplankton, i.e. the pelagic pathway, and gastropods depending to 60% on seagrass and to another 40% on other benthic sources (Fig. 3).

The longest food chains were 6, arising either from two benthic or a pelagic food chain: microphytobenthos (or seagrass, or *S. alterniflora*) → gastropods → polychaetes → *P. haematocheila* → *C. semilaevis* → *L. japonicus* or SPM → bivalves → polychaetes → *P. haematocheila* → *C. semilaevis* → *L. japonicus*, or from the pelagic pathway: phytoplankton → bivalves → polychaetes → *P. haematocheila* → *C. semilaevis* → *L. japonicus*. Bivalves firstly connected the pelagic and benthic pathways by consuming both, phytoplankton and SPM (Fig. 3).

Observed biomasses and quantitative food web flux structure

Seagrass and *S. alterniflora* had high biomasses (201 ± 68 and 100 ± 122 g DW m⁻², respectively, mean \pm SD across all sampling sites sampled in late May and late July 2017), and together accounted for 93% of the basal biomass. Seagrass biomass was significantly higher than that of all other trophic groups (Tukey's HSD, $p < 0.001$, Table S4). Bivalves had the highest biomass among all consumers (76 ± 27 g DW m⁻²), followed by gastropods (30 ± 19 g DW m⁻²), which together accounted for 94% of all herbivore biomass and 89% of all consumer biomass. The biomasses of the other trophic groups were lower than 2 g DW m⁻², except for SPM (18 ± 3 g DW m⁻²) and crabs (10 ± 12 g DW m⁻²).

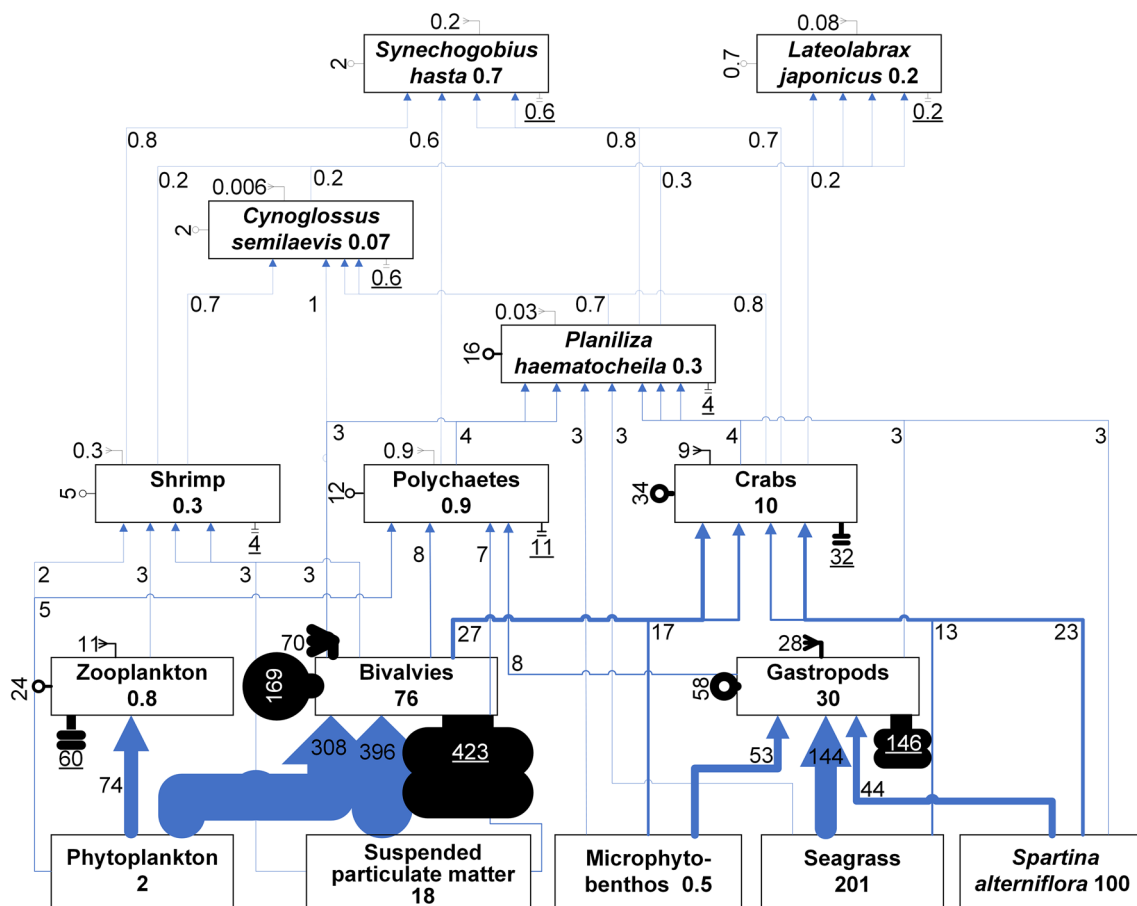


Fig. 4 Quantitative food web of a seagrass bed in China's Yellow River Delta coastal wetland, which was constructed by setting the specific death rate values of intermediate consumers at 50% of the values from the literature (cf. Table S2). Each trophic group is represented by a box and the number provides its biomass (g DW m⁻²). Blue arrows indicate the ingestion of a given prey by the predator,

and the numbers provide the quantity (g DW m⁻² yr⁻¹). Numbers at the left side of ○ indicate the respiration, underlined numbers under ≡ indicate the excretion, and numbers located at the left of ≧ indicate the non-predatory mortality of the trophic group (all in g DW m⁻² yr⁻¹). Widths of the blue arrows, ○, ≡, and ≧ are proportional to the values of the fluxes

The distribution of the fluxes in the QFW (Fig. 4) was non-random and followed a log-normal distribution (Fig. S2a). The majority of the ingested biomass was not converted into new production but mostly lost due to excretion (57%), followed by respiration (27%), and non-predatory mortality (10%) in the QFW. The total ingestion of each consumer group was highly predictable from its trophic position, as about 87% of the variation is explained by the TP_{QFW} (linear regression, $R^2 = 0.88$, $p < 0.001$, Fig. S2b). Accordingly, herbivores contributed 87% to the total consumer ingestion. Consumer ingestion was sustained to 36% by pelagic production (i.e. phytoplankton), and to 64% by benthic production originating from microphytobenthos, seagrass, *S. alterniflora*, and SPM which originated mostly from seagrass (Figs. 4, 5). Of the consumed pelagic production, 19% were used by zooplankton specialized on this food source, and 79% were taken up by bivalves which consumed additionally 56% of the benthic production. Thus, bivalves

linked the pelagic and benthic food chain already at a low trophic level and dominated the consumer fluxes in the entire food web. In contrast, gastropods representing the second quantitatively most important macroinvertebrate group, were specialized on benthic sources, consuming 34% of their edible production. Zooplankton production was either transferred to shrimp (21%) or lost by substantial non-predatory mortality. Bivalves were mainly consumed by crabs (64%), and gastropods by polychaetes (71%). The production available to fish originated similarly from the pelagic and benthic pathways (ca. 45% vs 55%) except for *P. haematocheila* relying to 79% on the benthic pathway.

Combining the observed biomasses with the trophic positions derived from the QFW results in a rather flat biomass pyramid, with the total biomass at trophic level 1 being 2.8 times that at trophic level 2, and 58 times that of all higher trophic levels (Fig. 5). The ingested production of basal sources in the corresponding production pyramids was 6

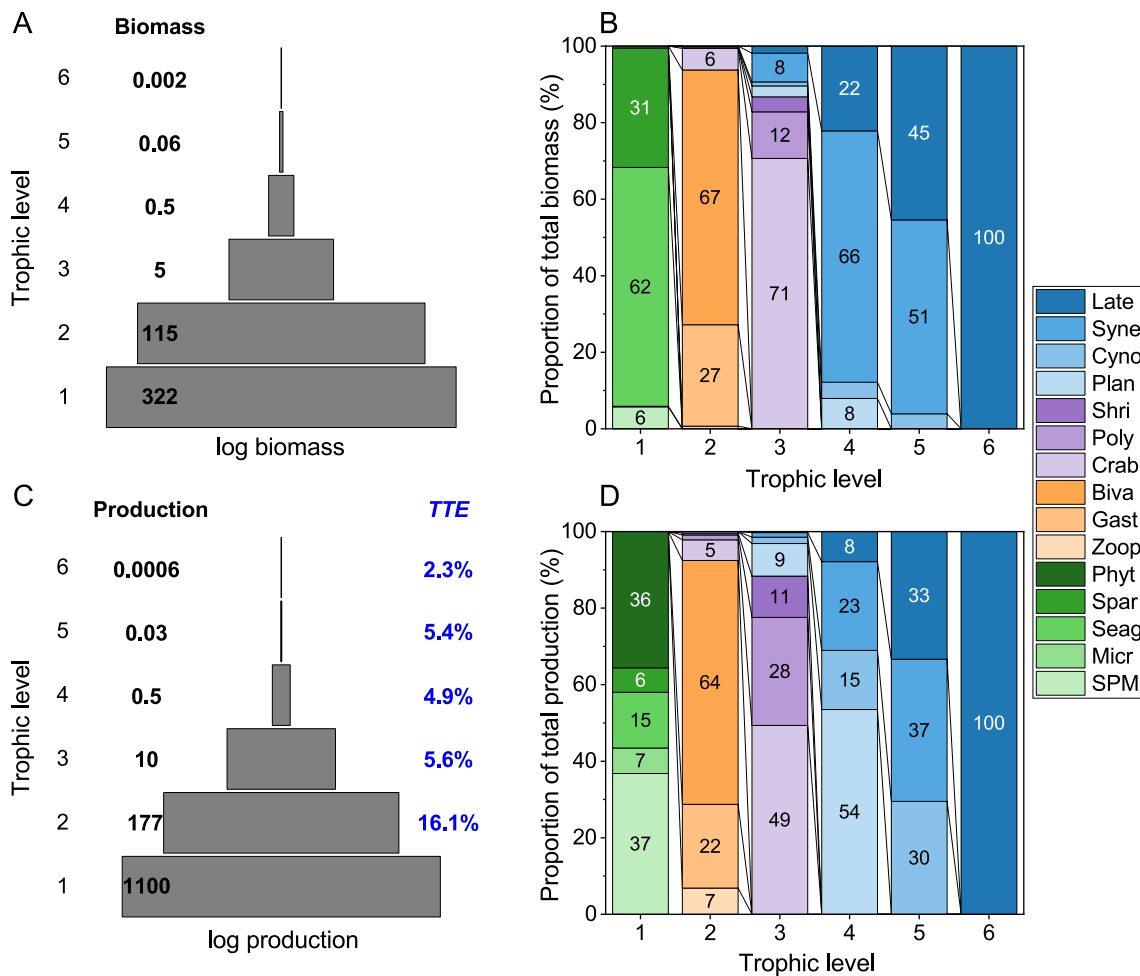


Fig. 5 **a** Biomass pyramid and **c** production pyramid with corresponding trophic transfer efficiencies (*TTE*) from a seagrass bed in China’s Yellow River Delta coastal wetland based on the quantitative food web (cf. Figure 4). Here, the production of each trophic group indicates the required production offsetting its predatory losses (if any) and its non-predatory loss. The horizontal bars are scaled log-

arithmically. Bold black numbers provide the non-transformed total **a** biomass (g DW m⁻²) and **c** production (g DW m⁻² yr⁻¹) at each trophic level. Bold blue numbers are the *TTE*. **b**, **d** Contribution of each trophic group to the total biomass and production at each trophic level, respectively. Proportions greater than 5% are labeled. For abbreviations of trophic groups, see Fig. 2

times the production at trophic level 2, and 106 times the production at all higher trophic levels (Fig. 5). Thus, the *TTE* decreased strongly with increasing trophic level, with values ranging from 16 to 2% (Fig. 5).

We obtained the production to biomass (*P/B*) ratios for all living trophic groups (Table 1). The calculated *P/B* value of phytoplankton was ca. 290 and ca. 320 times the values for seagrass and *S. alterniflora*, respectively, and ca. 1.5 times the value for microphytobenthos. The calculated *P/B* ratios of zooplankton, gastropods, bivalves, and crabs were similar to previous studies. The *P/B* values for polychaetes and shrimp were much higher than those for the other macroinvertebrates and generally higher than those in the literature due to a relatively high top-down effect of their predators and a relatively low bottom-up effect from their prey (Fig. 4). The relatively

high *P/B* values for *P. haematocheila* and *C. semilaevis* were due to predation by the top predators *S. hasta* and *L. japonicus*.

Our estimated *NPP* value based on the QFW specifically for seagrass (846 g DW m⁻² yr⁻¹) was within the range from 360 to 1460 g DW m⁻² yr⁻¹ suggested for most seagrass beds with seagrass biomass > 50 g DW m⁻² (Table 2; Mateo et al. 2006). The estimated *NPP* value of the QFW constructed using the specific death rate values of intermediates consumers from literature was slightly above the upper limit of the range (Table 2).

Discussion

Our measurements of organismal biomasses and their stable isotope signatures combined with establishing a quantitative food web (QFW) of a seagrass bed in the Yellow River Delta (YRD) wetland provides a whole food web study with reasonable quantitative estimates of consumer diet compositions and fluxes among trophic groups. The QFW reveals that the consumed benthic production surpassed the pelagic one (64% vs 36%). Zooplankton and gastropods were specialized grazers of the pelagic and benthic pathways, respectively, whereas all other groups relied on both pathways. Bivalves, dominating the entire fluxes, strongly connected the two pathways, and consumer groups (except zooplankton) at higher trophic positions gradually depended increasingly on pelagic sources. Whole food web studies are extremely data demanding and thus involve inevitably numerous assumptions for individual parameters. Subsequently, we compare our findings in respect to individual groups and the food web energetic as a whole with previous studies.

The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of our collected trophic groups fell within the ranges of previously reported values for seagrass beds or coastal wetlands (Moncreiff and Sullivan 2001; Vizzini et al. 2005; Vafeiadou et al. 2013). For example, our seagrass $\delta^{13}\text{C}$ value ($-11.7 \pm 0.4\text{‰}$) was close to the most frequently found values in 31 previous studies, ranging from -10 to -11‰ (Hemminga and Mateo 1996). It is well established that $\delta^{13}\text{C}$ values allow to distinguish between benthic and pelagic food sources for coastal consumers (France 1995; Bode et al. 2006; Fry et al. 2008; Bouillon et al. 2011). For example, the average $\delta^{13}\text{C}$ values for benthic microalgae were more ^{13}C -enriched than for phytoplankton, and this pattern was reflected in invertebrates and fish mainly feeding on either benthic or pelagic sources (France 1995). In line, we found ^{13}C -enriched values for microphytobenthos, plants, and benthic consumers and ^{13}C -depleted values for phytoplankton and zooplankton. Our bivalves were consistently ^{13}C -depleted relative to gastropods as reported by Mallela and Harrod (2008) and Docmac et al. (2017). Our increasingly ^{13}C -depleted values of consumer groups at higher trophic positions suggest lower trophic transfer efficiencies in benthic than pelagic pathways (Lischke et al. 2017), e.g. the production of gastropods, dominating benthic fluxes, might be transferred to higher trophic levels with low efficiency. The assumed high non-predatory mortality of zooplankton might indicate that we underestimated the predation pressure by zooplanktivores. In addition, the increasing ^{13}C -depletion of consumers at higher trophic levels (e.g. fish species) may also imply that a part of their food originates from the open sea, where phytoplankton

is the dominant primary producer (Martinetto et al. 2006; Christianen et al. 2017). In general, coastal seagrass ecosystems are generally influenced by imports and exports to and from marine and terrestrial habitats. Active movement and passive transport of nutrients, detritus, prey and consumers between the two habitats may have a major impact on food web productivity and energetics (Valentine et al. 2002; Melville and Connolly 2005).

Our measured seagrass biomass was higher than the annual average value of seagrass meadows in YRD reported by Zhang et al. (2019), presumably due to the seagrass bed being most extensive in summer (our sampling season). It was similar to the average biomass of 29 temperate seagrass beds sampled in summer (Olesen and Sand-Jensen 1994), higher than the average above-ground biomass of 16 eelgrass meadows along the Baltic Sea coastline (Boström et al. 2003) and lower than some tropical meadows (Carlo and Kenworthy 2008; Ávila et al. 2015). Microphytobenthos biomass was much lower than that in an intertidal seagrass bed along the French Atlantic coast due to the influence of the long duration of low tide (Lebreton et al. 2012). Presumably due to the relatively high turbidity in our study area, biomasses of phytoplankton and zooplankton were lower than that in the adjacent Bohai bay (Zheng and You 2014). Our measured biomasses of gastropods and bivalves were much higher than the biomass of Mollusca in the low marsh of YRD wetland (Qiu et al. 2019) likely due to the enhanced rates of recruitment within seagrass canopies and shelter from predators. Otherwise macroinvertebrates had similar biomasses except for the low biomass of polychaetes. The biomasses of our herbivorous and omnivorous macroinvertebrates were higher and lower, respectively, than that in *Zostera marina* meadows at the Swedish northwest coast (Baden et al. 2012). The sampled fish species are well represented in the fish community in the studied area (Liu et al. 2018). Our fish biomass was higher than that in the creeks closer to land in the YRD, i.e. the middle and high marsh wetland (Li et al. 2020), and lower than in some temperate and tropical seagrass beds (Pihl et al. 2006; Jelbart et al. 2007; Moussa et al. 2020).

The dominance of bivalves in respect to consumer biomasses and fluxes is consistent with many previous studies (Luczkovich et al. 2002; Schlacher and Connolly 2009; Atkinson et al. 2014). Their dense populations may strongly deplete phytoplankton biomass (Nielsen and Maar 2007). Thus, filter-feeding bivalves substantially link the pelagic and benthic pathways, by transferring phytoplankton production to predominantly benthic consumers (Gergs et al. 2009; Kathol et al. 2011; Basen et al. 2013) for which they represent a suitable food source (Roditi et al. 1997), e.g. crabs, polychaetes, and some fish. Thus, in our web pelagic–benthic coupling starts already at a low trophic level compared to some lake ecosystems, where only fish residing at least

at the third trophic level bridges substantially among both pathways (Vadeboncoeur et al. 2002; Lischke et al. 2017).

Gastropods, representing the second most important consumer group in respect to biomasses and consumer fluxes in our food web, strongly selected microphytobenthos, which contributed 22% to their diet despite its marginal biomass compared to the higher plants. This is in line with findings that the grazing activity of gastropods strongly suppresses epiphytes growing on seagrass leaves (Schanz et al. 2002; Boström et al. 2006). Given that we cleaned the seagrass leaves prior to stable isotope analysis, our results suggest that gastropods can also directly consume seagrass. This is in agreement with measurements revealing that seagrass-associated gastropods directly ingest and digest living leaf tissue (Holzer et al. 2011a), suggesting that the grazing can rupture plant cell walls, providing access to the more nutritious cell content (Holzer et al. 2011b). The grazing effect of herbivorous fish was low in our food web, which is in line with White et al. (2011). In contrast, high grazing rates of herbivorous fish were reported from some temperate or tropical seagrass meadows (Tomas et al. 2005; Valentine and Duffy 2006), e.g. *Scarus guacamaia* can graze heavily on *Thalassia testudinum* seagrass.

Previous studies showed that in relatively turbid seagrass beds, consumers relied on a combination of food sources including seagrass, microphytobenthos, phytoplankton, and plants (Abrantes and Sheaves, 2009), which also holds for our study. We estimated a low contribution of seagrass to the energy fluxes, compared to that of phytoplankton (14% vs 36%). This may appear counterintuitive for a seagrass ecosystem, but is consistent with comparable studies (Mateo et al. 2006; Heck Jr et al. 2008; Lebreton et al. 2012) and can be explained by the high edibility and production to biomass (*P/B*) ratio of phytoplankton (Duarte and Cebrián 1996). In contrast, a substantial proportion of vascular plant carbon enters coastal and estuarine food webs through the microbial decomposition of detritus (Kristensen et al. 2008). The invaded *Spartina alterniflora* did not play a critical role in the energy fluxes, except for the high contribution to the diet of crabs. Its tall and intense stands are thought to offer favorable refuge conditions and substantial food sources for the crabs (Wang et al. 2008; Cui et al. 2011). Epiphytes attached to seagrass leaves are consumed by most consumers in many temperate and tropical seagrass beds (e.g. Moncreiff and Sullivan 2001; Connolly et al. 2005; Jaschinski et al. 2008). Some studies highlighted the importance of microphytobenthos in intertidal seagrass beds due to its high resuspension by tidal fluctuations (Lebreton et al. 2012), which is in line with our study.

The energetic structure of our QFW was consistent with that inferred from the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, since the trophic positions of consumer groups based on $\delta^{15}\text{N}$ (TP_{SI}), using the average value for zooplankton, gastropods, and bivalves

as baseline, strongly correlated with the trophic positions based on the QFW (TP_{QFW}) (Fig. S4). The goodness of fit further increases if only gastropods and bivalves are used to calculate the baseline. They may provide a more suitable baseline than zooplankton, since they integrate temporal diet variation in the isotopic signatures due to their relatively long lifespan (Nilsen et al. 2008). The TP_{QFW} values of some consumer groups were slightly lower than their TP_{SI} values, especially for shrimp, suggesting that we occasionally overlooked organisms and thus their feeding relationships in the QFW. This might be relevant for the transfer of zooplankton production to higher trophic levels and potentially also for meiobenthos. Besides, the slight differences in trophic positions may also result from the variability in the trophic enrichment factor for different trophic groups, varying in body size and life span, and the type of tissue used for stable isotope detection (Nilsen et al. 2008).

The trophic transfer efficiency (*TTE*) averaged ca.7% across all trophic levels in our study, which is similar to the value of 8.6% for China's Yangtze River basin (Guo et al. 2013), but substantially lower than the values established for a planktonic food web in a large lake ranging from 20 to 33% (Boit and Gaedke 2014). The decrease of the *TTE* with increasing trophic levels from 16 to 2% in our study reflects the increasing share of fish with their relative high respiratory losses compared to invertebrates.

Our study considers the food web energetics during summer and can thus not inform about seasonal variations in food web properties highlighted by Ouisse et al. (2012). In addition, seagrass is accessible to birds during low tide (Bessey and Heithaus 2013), but we lack quantitative bird counts in our study. Including them in future studies is recommended, because, e.g., geese and ducks directly graze on temperate seagrass coinciding with a biomass decline in winter (Ganter 2000; Rivers and Short 2007). For example, at European seagrass meadows, the feeding activity of waterfowl reduced seagrass biomass by more than 50% during the winter (Nacken and Reise 2000).

Conclusion

Our analysis provides the first whole food web study with a robust food web structure and reasonable quantitative estimates of fluxes and ecosystem functions in a warm-temperate seagrass bed. Combining stable isotope analysis with a quantitative food web model yielded consistent energetic pattern, which provides an example of how biological communities are shaped and function in seagrass ecosystems. The complex predator–prey interactions among trophic groups and the resulting trophic transfer of energy determine which trophic groups and feeding interactions play a decisive role in the whole ecosystem. Such knowledge promotes

sustainable management and conservation strategies for seagrass beds under increasing anthropogenic stressors.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s00227-021-03878-z>.

Acknowledgements This study was supported by the National Key R&D Program of China (No. 2018YFC1406404 and No. 2017YFC0404505), the NSFC-Shandong Joint Fund (No. U1806217), and the Interdisciplinary Research Funds of Beijing Normal University. X.X. Li is grateful to the China Scholarship Council (CSC) for their financial support to study abroad (No. 201906040070). We are indebted to Jun Pei, Ziyue Zhang, and Xianting Fu for invaluable field assistance. We thank Peter C. de Ruiter and Laurie Wojcik for helpful comments on the manuscript. We also thank Geoffrey Hart for providing language help during the writing of this paper.

Author contributions All authors have reviewed the manuscript and approved its submission. XL, UG and WY conceived the study, and XL performed the field sampling and the model analyses under the joint supervision of UG, WY, and TS. The manuscript was written by XL in close cooperation with UG, and valuable comments from WY. All authors approved the final manuscript.

Data availability The dataset generated and analyzed in the current study are available from the corresponding author upon reasonable request.

Declarations

Conflict of interest The authors declare they have no conflict of interest.

Ethical approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

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