

Subsets of food webs cannot be used as a substitute to assess the functioning of entire ecosystems

Victor N. de Jonge^{1,*}, Ulrike Schückel², Dan Baird³

¹Institute of Estuarine and Coastal Studies, IECS, University of Hull, Hull HU6 7RX, United Kingdom

²Schleswig-Holstein Agency for Coastal Defence, National Park and Marine Conservation, National Park Authority, 25832 Tönning, Germany

³Department of Botany and Zoology, Stellenbosch University, Stellenbosch 7600, South Africa

ABSTRACT: The effects of selecting system compartments in the calculation of Ecological Network Analysis (ENA) indices were studied based on data collected in the 3 main reaches of the Ems estuary. For each reach, ENA was applied to (1) a set of carbon flow models in which only the living compartments were hand-balanced, and (2) a set in which living and non-living compartments were hand-balanced. The models considered represent a full food web at the highest species resolution level and 4 food web subsets representing benthic macrofauna, benthic macrofauna plus demersal fish and epifauna, all fish, and all birds. Each of the 30 models consist of 11 to 57 compartments (species, functional groups, C-pools). Results demonstrate that the food web subsets are predominantly responsible for the variation in the ENA indices (relative ascendancy: 15% of its maximum of 1; internal relative ascendancy: 21%). The use of food web subsets also leads to increased variation in the Finn cycling index, effective link density, trophic depth and robustness. The use of subsets is therefore discouraged. The added value of robustness as a practical index was explored in relation to ascendancy-related (i.e. information-related) indices, but its use could not be supported because its range was too limited. The results also indicate that incomplete food webs significantly influence the size of the 'window of vitality'. ENA works well when food web subsets include the full trophic biomass pyramid, but top-down studies focussing on so-called iconic species are not advisable for assessments. The closer to the full food web, the better the results of ENA correspond with those of a full food web.

KEY WORDS: Assessment · Ecosystem · Indicators · Carbon flows · enaR · ENA indices · Metrics

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1. INTRODUCTION

There is a strong general interest in ecosystem models as a means to understand the functioning of coastal ecosystems and to explore future developments, but there are relatively few studies available that incorporate—in detail—all of these systems' biotic and abiotic components in relation to the water column, intertidal flats and subtidal areas. Using the shallow international Wadden Sea area in northwestern Europe (see Fig. 1) as an example, it can be concluded that most studies either focus on subsystems of Wadden Sea ecosystems (Asmus & Asmus 1985,

Baird et al. 2004, 2007, Horn et al. 2017), and on parts of food webs or habitats (Schückel et al. 2015, Christianen et al. 2017), or that they study the functioning of specific groups of macrobenthic organisms (e.g. Beukema & Dekker 2014, Dekker & Beukema 2014), microphytobenthos (de Jonge et al. 2012), parasites (Thieltges et al. 2013), or trends in species populations such as fish and shrimps (Tulp et al. 2008, 2012).

A clear exception was the comprehensive ecosystem research program Biological Research Ems-Dollard Estuary (BOEDE), run from 1972 to 1985 (BOEDE 1985, Baretta & Ruardij 1988). This research program focused on the functioning of the Ems estu-

*Corresponding author: v.n.de.jonge@planet.nl

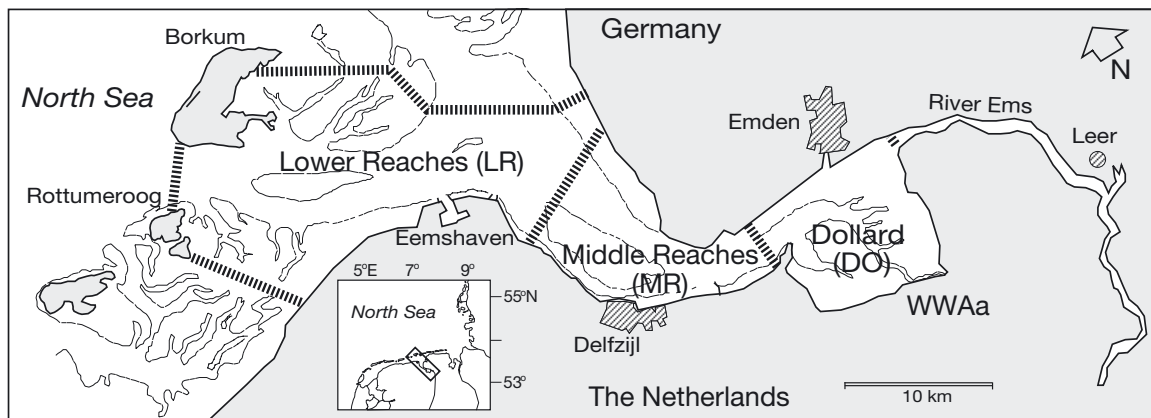


Fig. 1. Ems estuary with the 3 main reaches as used for the study. The inset shows the Dutch, German and Danish Wadden Sea and its coastline in north-western Europe, the barrier islands and the 3 main rivers of which the indicated Ems river is one. WWAa marks the point at which the River Westerwoldsche Aa enters the Dollard from the south. For system attributes and more details see Table 1 in de Jonge et al. (2019, this volume)

ary ecosystem, and its results were used to construct a dynamic simulation model (Baretta & Ruurdij 1988). This simulation model was quite detailed, and the majority of the underlying data of this model were published, while the unpublished data were traceable and accessibly documented so that they could be re-used. The basis of the present study was to apply Ecological Network Analysis (ENA) to the full BOEDE data set as reported by de Jonge et al. (2019, this volume), and to use exactly the same data set to explore the outcomes of ENA analyses when applied to 'food web subsets' instead of fully detailed species food webs. Therefore, the focus of the present study was set on specific parts of the larger system, e.g. a habitat such as intertidal flats, and specific benthic inhabitants or a food web subset, such as birds or fish. The direct motivation for this exercise is the consideration that experts on specific species groups and/or specific habitats easily base conclusions on the functioning and the quality status of entire ecosystems on their own narrowly focused—and thus potentially restricted (to a food web subset)—analyses. The same problem exists in some EU directives, such as the Water Framework Directive (WFD; EC 2000, 2005a) and the Marine Strategy Framework Directive (MSFD; EC 2005b, 2008). In the explanation of the directives the European Commission intended to assess the quality of full ecosystems, while for the implementation they requested the assessment of only specific species groups—and thus 'food web subsets'. Instead of taking the opportunity of more complete studies, the authorities of the EU member states just followed these requests, thus avoiding integrated ecosystem assessments. The question is whether it is possible to use food web sub-

sets as a substitute for an entire ecosystem. It is necessary to know if results obtained from any food web subset can be used as a reliable proxy for the entire ecosystem. If this is the case, it might save the authorities responsible for monitoring programs time, and thus money. But, if it is not the case, we need to know which alternative action should be taken with regards to ecosystem assessments (see de Jonge et al. 2006).

The main aim of this study is to test the hypothesis that it is possible to assess the functioning of entire ecosystems based on the analysis of food web subsets by means of ENA. Secondary questions are whether the 'window of vitality' is an applicable concept, whether the robustness indicator is useful for ecosystem management, and how the results of the analyses are affected when using carbon flow models for the analysis of food web subsets where only the living compartments were hand-balanced or where both the living and the non-living compartments were hand-balanced (see de Jonge et al. 2019).

2. MATERIALS AND METHODS

For the description of the study region (see Fig. 1), the data sources, the diet matrices, the process ratios P/B (production per unit biomass), C/B (consumption per unit biomass), E/B (egestion per unit biomass) and R/B (respiration per unit biomass), the carbon flow adjustments per compartment (based on the living organic material represented by the species compartments and the non-living organic material compartments as C-pools or detritus) and the description of Ecological Network Analysis (ENA), see de Jonge

et al. (2019). The biomass values are reproduced in the present study because the use of food web subsets leads to quite different biomass pyramids compared to the entire (or full) food web. ENA was performed by using the R (version 3.2.3; R Core Team 2015) package *enaR* (Borrett & Lau 2014, Lau et al. 2017). The software package can be downloaded from <https://CRAN.R-project.org/package=enaR>. In de Jonge et al. (2019) 4 different food webs were analysed: one for each of the 3 estuarine reaches indicated in Fig. 1, namely the Lower Reaches (LR), the Middle Reaches (MR), the Dollard (DO), and additionally one for the entire estuary. This was done for ‘all species’ and for aggregated ‘functional groups’ network models for each reach. The analyses were further applied to models where only the flows of the living compartments were hand-balanced (single hand-balanced models) and models where the flows of both the living and the non-living compartments were hand-balanced (double hand-balanced models).

In the present study, in addition to these previous analyses, 4 additional food web subsets were defined for each of the 3 reaches. To reduce the complexity of the present study, only parts of these analyses are presented. The model for the entire estuary (de Jonge et al. 2019) is omitted here, as are the ‘functional group’ models. The new subsets that were extracted from the base data set represent a benthic food web (Benthic FW; mainly based on macrozoobenthos), a full benthic food web (Full Benthic FW; macrozoobenthos plus epizoobenthos and demersal fish), a full fish food web (Full Fish FW; demersal and pelagic fish species) and a full birds food web (Full Birds FW; the total of bivalve feeders, worm feeders and mixed feeders—note that fish-feeding birds did not play a role during the study period). In the present study, as well as considering the main predator species, we also considered their prey. Table 1 presents the full overview of the species (living compartments) and the non-living compartments belonging to the full food webs and the food web subsets, plus the biomasses for each species and reach.

For all newly created data sets we performed exactly the same analyses as for the full food web (Full FW; all species) data sets (de Jonge et al. 2019). Assuming that the food web subsets can be considered as a ‘treatment’, we can further assume the following factor: spatial extent (LR, MR, DO) \times factor: balancing (single hand-balanced, double hand-balanced) \times factor: ecological boundary placement (Full FW, Benthic FW, Full Benthic FW, Full

Fish FW, Full Birds FW). This equates to $3 \times 2 \times 5 = 30$ treatments.

A number of ENA indices are of interest in this ecosystem study. The total system throughput (TSTp) expresses the sum of all flows in the system. The relative ascendancy (A/DC) is the ratio between the ascendancy (A), a measure of the size and flow organization (Ulanowicz 1986), and the developmental capacity (DC), i.e. the potential of the system to develop. A high A/DC indicates high efficiency of energy—or carbon—flowing through the system. The relative overhead (Φ /DC; based on the overhead Φ) is the counterpart of A/DC (since $A/DC + \Phi/DC = 1$). The Finn cycling index (FCI) represents a series of transfers between compartments, beginning and ending in the same compartment without passing through the same compartment twice (Baird et al. 2004). Robustness is also considered, which is related to the A/DC ratio as follows: $-(A/DC) \times \ln(A/DC)$.

Additional metrics (compared to de Jonge et al. 2019) are discussed to elucidate the effects of using either full food webs or food web subsets to assess complete ecosystems. These additional metrics are the internal relative ascendancy (A_i/DC_i), the internal relative overhead (Φ_i/DC_i), the trophic depth of the network (TD) and the effective link density of the network (ELD). The internal ascendancy (A_i) and the internal developmental capacity (DC_i) are metrics based only on internal exchanges, and thus exclude exogenous transfers. The ELD and TD are considered because a certain range of these values (TD: 2–5; ELD: 1–3.25) have been suggested to represent a ‘window of vitality’ (Zorach & Ulanowicz 2003). As this window is a potential food web indicator, it is useful to investigate how the present results fit the suggestions by Zorach & Ulanowicz (2003).

3. RESULTS

3.1. Output of ecological network analysis

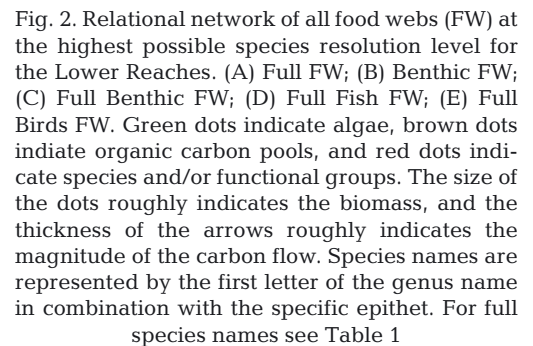
The results in Table 2 consist of a selection of the full set of metrics and indices (or dimensionless ratios) produced by the *enaR* package (Lau et al. 2017). This selection will suffice to answer to the main research questions of the present study. Table 2 is structured so that the single hand-balanced and the double hand-balanced models—as applied to the flow matrices of all 3 reaches—were grouped. The next treatment (see Section 2) was then the different reaches and then the type of food web (Full FW and the 4 food web subsets) per reach.

Table 1. Composition of different food webs (FW; see Section 2 for details). Ecological Network Analysis compartments, i.e. biological species and non-living carbon pools (DOC: dissolved organic carbon; POC: particulate organic carbon), the functional group the compartments belong to, and the biomass for each compartment for each reach are shown. 'X' indicates the presence of that species in the full food web or food web subset for each reach. LR: Lower Reaches, MR: Middle Reaches, DO: Dollard

ID no.	Species (ENA compartments)	Functional group	Biomass (mg C m ⁻²) in Full FW			Full FW			Benthic FW			Full Benthic FW			Full Fish FW			Full Birds FW		
			LR	MR	DO	LR	MR	DO	LR	MR	DO	LR	MR	DO	LR	MR	DO	LR	MR	DO
1	True phytoplankton	Phytoplankton	1027.000	895.000	67.000	X	X	X	X	X	X	X	X	X						
2	Resuspended microphytobenthos	Phytoplankton	416.000	346.000	501.000	X	X	X	X	X	X	X	X	X						
3	Microphytobenthos (0–2 cm)	Microphytobenthos	1905.000	1652.000	4378.000	X	X	X	X	X	X	X	X	X	X	X	X			
4	Free pelagic bacteria	Free pelagic bacteria	104.380	154.520	285.820	X	X	X	X	X	X	X	X	X						
5	Microzooplankton	Microzooplankton	251.200	177.400	100.100	X	X	X	X	X	X	X	X	X						
6	Mesozooplankton	Mesozooplankton	72.680	77.860	32.940	X	X	X	X	X	X	X	X	X						
7	Macrozooplankton	Macrozooplankton	0.150	3.580	2.330	X	X	X	X	X	X	X	X	X						
8	<i>Pleurobrachia pileus</i>	Pelagic invertebrate carnivores	0.156	0.063		X	X	X	X	X	X	X	X	X						
9	<i>Mya arenaria</i>	Benthic suspension feeders	437.200	1837.500	390.000	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
10	<i>Cerastoderma edule</i>	Benthic suspension feeders	203.100	41.900		X	X	X	X	X	X	X	X	X						
11	<i>Mytilus edulis</i>	Benthic suspension feeders	30.900	5.000		X	X	X	X	X	X	X	X	X						
12	<i>Arenicola marina</i>	Deposit feeder	220.800	227.900	27.800	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
13	<i>Heteromastus filiformis</i>	Deposit feeder	66.200	88.400	111.400	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
14	<i>Scoloplos armiger</i>	Deposit feeder	101.600	4.700		X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
15	<i>Hydrotia ulvae</i> (<i>Peringia ulvae</i>)	Grazers	30.900	69.800	20.800	X	X	X	X	X	X	X	X	X						
16	<i>Scrobicularia plana</i>	Interface feeders	8.800		48.700	X	X	X	X	X	X	X	X	X						
17	<i>Macoma balthica</i> (<i>Limecola balth.</i>)	Interface feeders	459.300	423.300	507.100	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
18	<i>Corophium volutator</i>	Interface feeders	13.250	144.200	149.400	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
19	<i>Nereis diversicolor</i> (<i>Hediste div.</i>)	Benthic invertebrate carnivores	154.600	74.400	584.600	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
20	<i>Cirratulus crangon</i>	Macro-epibenthos	125.740	149.380	63.280	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
21	<i>Carcinus maenas</i>	Macro-epibenthos	13.886	10.758	5.399	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
22	<i>Liocarcinus holatus</i>	Macro-epibenthos	3.567	0.331	0.065	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
23	<i>Eriocheir sinensis</i>	Macro-epibenthos	0.028	0.214	0.058	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
24	Meiofauna	Meiofauna	161.000	95.400	404.000	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
25	Benthic bacteria	Benthic bacteria	1152.300	945.000	1640.000	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
26	<i>Pleuromnecetes platessa</i>	Demersal fish	13.880	15.400	5.380	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
27	<i>Limanda limanda</i>	Demersal fish	6.000	5.850	0.088	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
28	<i>Solea solea</i>	Demersal fish	0.732	1.702	1.958	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
29	<i>Pleuronectes flesus</i> (<i>Platichthys fl.</i>)	Demersal fish	1.870	7.353	7.035	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
30	<i>Chelon labrosus</i>	Demersal fish	0.010	0.010	0.010	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
31	<i>Osmerus eperlanus</i>	Pelagic fish	3.425	15.140	30.690	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
32	<i>Pomatoschistus spec.</i>	Demersal fish	4.366	11.696	3.769	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
33	<i>Gasterosteus aculeatus</i>	Pelagic fish	2.058	2.042	0.171	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
34	<i>Clupea harengus</i>	Pelagic fish	0.985	87.500	8.730	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
35	<i>Sprattus sprattus</i>	Pelagic fish	9.372	14.950	13.144	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
36	<i>Zoarces viviparus</i>	Demersal fish	0.439	0.935	0.811	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
37	<i>Merlangius merlangus</i>	Demersal fish	2.013	1.046	0.054	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
38	<i>Gadus morhua</i>	Demersal fish	1.100	1.900	0.776	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
39	<i>Syngnathus rostellatus</i>	Demersal fish	2.348	0.753	0.308	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
40	<i>Agonus cataphractus</i>	Demersal fish	0.363	0.418	0.019	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
41	<i>Anguilla anguilla</i>	Demersal fish	0.050	0.309	0.814	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
42	<i>Liparis liparis</i>	Demersal fish	0.148	0.936	0.270	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
43	<i>Somateria mollissima</i>	Bivalve feeders	0.061	0.037	0.003	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
44	<i>Haematopus ostralegus</i>	Bivalve feeders	6.130	9.280	0.001	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
45	<i>Calidris alpina</i>	Bivalve feeders	0.146	0.199	2.248	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
46	<i>Recurvirostra avosetta</i>	Worm feeders	0.017	0.510	2.050	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
47	<i>Pluvialis squatarola</i>	Worm feeders	0.180	0.540	0.193	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
48	<i>Limosa lapponica</i>	Worm feeders	0.268	1.570	1.091	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
49	<i>Tadorna tadorna</i>	Mixed diet feeders	2.310	26.200	2.293	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
50	<i>Numenius arquata</i>	Mixed diet feeders	6.950	2.530	3.130	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
51	<i>Tringa totanus</i>	Mixed diet feeders	0.073	0.365	0.300	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
52	<i>Croicocephalus ridibundus</i>	Mixed diet feeders	0.419	2.470	1.030	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
53	<i>Phoca vitulina</i>	Mammals	1.321	0.617	0.722	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
54	<i>Phocoena phocoena</i>	Mammals	0.010	0.010	0.001	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
55	DOC	Labile DOC	150.419	109.865	483.201	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
56	Suspended POC (susPOC)	Labile POC	4886.8	12268.8	9061.6	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
57	Sediment POC (sedPOC)	Labile sediment POC	166350.2	179310.8	652003.8	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
		Number of living compartments	54	53	50	54	53	50	18	17	15	45	44	42	38	37	33	25	24	21

Table 2. Overview of the results of the Ecological Network Analysis for the full food webs (Full FW) and the food web subsets (Benthic FW, Full Benthic FW, Full Fish FW and Full Birds FW), applied to the food webs at the highest possible resolution level for the 3 investigated reaches and for carbon flow models where (a) the living compartments were hand-balanced (single hand-balanced models) or (b) both the living and the non-living compartments were hand-balanced (double hand-balanced models). LR: Lower Reaches, MR: Middle Reaches, DO: Dollard, TSTf: total system throughput, FCI: Finn cycling index, A: ascendancy, Φ : overhead, DC: development capacity, ELD: effective link density, TD: trophic depth, subscript i: internal, na: not applicable. Units are $\text{mg C m}^{-2} \text{ d}^{-1}$ or dimensionless ratios

Reach	Model	Total species	TSTf	TSTp	Sum input (boundary)	Sum export	FCI	A	Φ	DC	A/DC ratio	Φ /DC ratio	Robustness	ELD	TD	A_i	Φ_i	DC_i	A_i/DC_i ratio	Φ_i/DC_i ratio	Detritivory/ herbivory ratio	Redundancy/DC ratio
a) Living compartments hand-balanced																						
LR	Full FW	54	3914.2	5527.4	2070.4	1613.2	0.100	9952.7	14808.7	24761.3	0.402	0.598	0.366	2.531	3.484	4557.2	5799.7	10356.9	0.440	0.560	3.128	0.234
LR	Benthic FW	18	3896.6	5503.3	2091.4	1606.7	0.098	9942.9	14155.4	24098.4	0.413	0.587	0.365	2.439	3.498	4549.0	5225.4	9774.5	0.465	0.535	3.186	0.217
LR	Full benthic FW	45	3904.0	5517.3	2092.3	1613.3	0.097	10003.2	14321.8	24325.1	0.411	0.589	0.365	2.459	3.514	4587.5	5333.5	9921.0	0.462	0.538	3.171	0.219
LR	Full fish FW	38	1440.5	1922.7	915.2	482.2	0.108	2623.5	4872.1	7495.6	0.350	0.650	0.367	2.407	2.575	944.7	2183.1	3127.8	0.302	0.698	3.787	0.291
LR	Full birds FW	25	934.7	1356.5	770.0	421.8	0.043	1728.9	1864.2	3593.1	0.481	0.519	0.352	1.610	2.419	362.8	864.8	1227.6	0.296	0.704	na	0.241
MR	Full FW	53	3712.7	5433.7	2298.3	1721.0	0.082	9429.1	13798.2	23227.3	0.406	0.594	0.366	2.411	3.329	3740.5	4485.3	8225.7	0.455	0.545	4.331	0.193
MR	Benthic FW	17	3882.9	5592.7	2521.7	1709.8	0.073	9352.0	13735.5	23087.5	0.405	0.595	0.366	2.342	3.187	3554.5	4136.4	7690.9	0.462	0.538	4.496	0.179
MR	Full benthic FW	44	3896.5	5618.7	2526.2	1722.2	0.071	9463.1	13941.4	23404.5	0.404	0.596	0.366	2.363	3.214	3620.3	4261.4	7881.7	0.459	0.541	4.438	0.182
MR	Full fish FW	37	2238.0	3146.7	1847.9	908.8	0.048	3771.1	6727.6	10498.7	0.359	0.641	0.368	2.098	2.295	826.6	2000.0	2826.6	0.292	0.708	5.583	0.190
MR	Full birds FW	24	1478.1	2167.3	1345.8	689.3	0.023	2382.4	2354.5	4736.9	0.503	0.497	0.346	1.457	2.142	318.8	800.3	1119.1	0.285	0.715	na	0.169
DO	Full FW	50	4286.7	6137.8	2087.9	1851.1	0.154	11536.4	14936.8	26473.2	0.436	0.564	0.362	2.324	3.680	5260.0	5778.4	11038.5	0.477	0.523	9.027	0.218
DO	Benthic FW	15	4263.2	6111.0	2086.0	1847.7	0.154	11418.4	14704.8	26123.2	0.437	0.563	0.362	2.302	3.652	5168.4	5576.5	10744.9	0.481	0.519	9.228	0.213
DO	Full benthic FW	42	4267.4	6118.9	2086.8	1851.6	0.153	11448.4	14821.5	26269.8	0.436	0.564	0.362	2.315	3.658	5191.1	5641.7	10832.8	0.479	0.521	9.204	0.215
DO	Full fish FW	33	2433.3	3416.4	1847.6	983.1	0.043	4946.5	7716.7	12663.2	0.391	0.609	0.367	2.188	2.728	1371.2	2754.9	4126.0	0.332	0.668	2.206	0.218
DO	Full birds FW	21	1001.8	1456.7	626.9	454.9	0.082	2150.1	2514.6	4664.7	0.461	0.539	0.357	1.819	2.782	536.9	1450.6	1987.4	0.270	0.730	na	0.311
b) Living and non-living compartments hand-balanced																						
LR	Full FW	54	3914.2	5393.5	1479.0	1479.3	0.100	9762.6	15208.5	24971.1	0.390	0.610	0.370	2.660	3.510	5254.1	6923.4	12177.5	0.431	0.569	3.130	0.280
LR	Benthic FW	18	3877.9	5356.9	1479.0	1479.0	0.101	9755.0	14519.0	24274.0	0.402	0.598	0.366	2.558	3.533	5251.8	6336.6	11588.4	0.453	0.547	3.186	0.261
LR	Full benthic FW	45	3885.3	5364.3	1479.0	1479.0	0.100	9801.3	14676.0	24477.3	0.400	0.600	0.366	2.581	3.548	5298.7	6435.6	11734.4	0.452	0.548	3.171	0.263
LR	Full fish FW	38	1247.4	1842.6	595.4	595.2	0.128	2765.8	5020.1	7785.9	0.355	0.645	0.368	2.571	2.830	1026.1	2559.0	3585.1	0.286	0.714	3.787	0.329
LR	Full birds FW	25	741.7	1126.3	384.6	384.6	0.086	1482.6	1999.4	3461.9	0.422	0.578	0.364	1.850	2.460	461.7	1212.0	1673.8	0.276	0.724	na	0.350
MR	Full FW	53	3712.7	5348.2	1635.5	1635.6	0.084	9526.4	14228.8	23755.3	0.401	0.599	0.366	2.514	3.437	4555.6	5634.3	10189.9	0.447	0.553	4.331	0.237
MR	Benthic FW	17	3652.7	5288.2	1635.5	1635.5	0.083	9293.9	13702.7	22996.6	0.404	0.596	0.366	2.455	3.381	4360.9	5195.2	9556.1	0.456	0.544	4.496	0.226
MR	Full benthic FW	44	3666.3	5301.8	1635.5	1635.5	0.082	9381.4	13894.5	23275.9	0.403	0.597	0.366	2.480	3.409	4443.8	5307.9	9751.7	0.456	0.544	4.438	0.228
MR	Full fish FW	37	2007.9	3235.6	1227.6	1227.6	0.056	4707.8	6821.2	11529.0	0.408	0.592	0.366	2.076	2.742	1491.1	2541.9	4033.0	0.370	0.630	5.583	0.220
MR	Full birds FW	24	1247.8	1927.3	679.5	679.5	0.038	2467.4	2429.2	4896.6	0.504	0.496	0.345	1.548	2.429	761.2	1270.5	2031.7	0.375	0.625	na	0.259
DO	Full food web	50	4286.7	5930.9	1644.5	1644.2	0.166	11846.8	13594.1	25440.9	0.466	0.534	0.356	2.213	3.993	6031.3	6557.5	12588.8	0.479	0.521	9.027	0.258
DO	Benthic FW	15	4263.2	5907.7	1644.5	1644.5	0.166	11733.1	13375.9	25109.0	0.467	0.533	0.356	2.192	3.962	5939.0	6351.9	12290.9	0.483	0.517	9.228	0.253
DO	Full benthic FW	42	4267.4	5912.3	1644.9	1644.9	0.165	11762.0	13475.1	25237.0	0.466	0.534	0.356	2.203	3.971	5966.8	6411.3	12378.1	0.482	0.518	9.204	0.254
DO	Full fish FW	33	2433.3	3552.4	1550.7	1119.1	0.060	6037.3	6944.0	12981.2	0.465	0.535	0.356	1.969	3.248	2006.2	3216.0	5222.2	0.384	0.616	2.206	0.248
DO	Full birds FW	21	1001.8	1316.1	314.2	314.2	0.165	2047.7	2260.4	4308.1	0.475	0.525	0.354	1.813	2.940	796.3	1784.6	2580.8	0.309	0.691	na	0.414



3.2. Similarities and differences among structure and system attributes of food webs

Fig. 2, exemplifying the food webs of LR, was created to illustrate the structural differences among all the food webs as listed in Table 1. The food webs of the other reaches are roughly comparable. The figure illustrates that the selection of only a subset of the full food web easily leads to a strong simplification of the original Full FW structure. For Full Fish FW it is specifically the absence of all phytoplankton, bacteria, birds and mammals as food (prey) that strongly simplifies the results. Full Birds FW excludes all the benthic and pelagic primary producers. In addition, all zooplankton groups, bacteria, meiofauna, fish (fish-feeding birds did not play a role in this estuary) and mammals are also absent as food (prey). What remains is, as in Full Fish FW, a quite meagre remnant of Full FW. This obviously also affects the shape of the food pyramid (see Section 3.8). In the representative example of the LR (Fig. 2), the largest TSTp (see Table 2) is that of the 54 compartments of Full FW ($5527 \text{ mg C m}^{-2} \text{ d}^{-1}$) while the lowest TSTp values are those of the 25 compartments of Full Birds FW ($1356 \text{ mg C m}^{-2} \text{ d}^{-1}$) and of the 38 compartments of Full Fish ($1923 \text{ mg C m}^{-2} \text{ d}^{-1}$). Interestingly, the TSTp of Benthic FW, with only 18 compartments, is nearly as high ($5508 \text{ mg C m}^{-2} \text{ d}^{-1}$) as that of the highest value of Full FW for LR ($5527 \text{ mg C m}^{-2} \text{ d}^{-1}$). In Sections 3.3. to 3.8 the effect of choosing food web subsets on the food webs' construction and its indices — as compared to the full ecosystem — is shown.

3.3. Relative ascendancy

In Fig. 3 the relative ascendancy and relative overhead values (A/DC and Φ/DC), as well as the internal relative ascendancy and overhead values (A_i/DC_i and Φ_i/DC_i), are plotted against each other for all models and for single (Fig. 3A,C) as well as double (Fig. 3B,D) hand-balanced carbon flow models. A visual inspection shows (see Table 2) that the total ranges in A/DC (and Φ/DC) and A_i/DC_i (and Φ_i/DC_i) differ. For the single hand-balanced model the A/DC range is 0.35 to 0.50, or 15% of the full range of 1 (Fig. 3A), and for the double hand-balanced model, the A/DC range is 0.36 to 0.50 (14%) (Fig. 3B). The A_i/DC_i ranges are larger: 0.27 to 0.48 (21% of the full range) (Fig. 3C) for the single hand-balanced models, and 0.28 to 0.48 (20%) (Fig. 3D) for the double hand-balanced models. The plots demonstrate that in all cases double hand-balancing the carbon flows of the

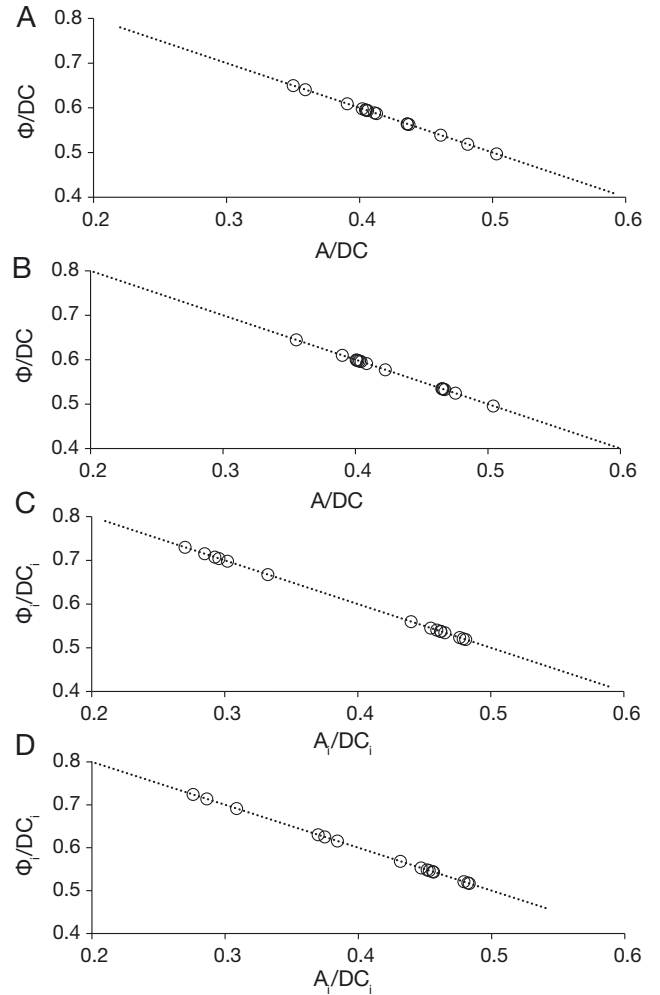


Fig. 3. Plot of the relative overhead (Φ/DC ; Φ : overhead; DC : developmental capacity) versus the relative ascendancy (A/DC ; A : ascendancy) and the relative internal overhead (Φ_i/DC_i) versus the relative internal ascendancy (A_i/DC_i) for the full food web plus the food web subsets of all 3 reaches (Lower Reaches, Middle Reaches, Dollard) together and for carbon flow models where (A,C) only the living compartments were hand-balanced and (B,D) for models where both the living and the non-living compartments were hand-balanced. The dotted lines connect the maximum values

models leads to a slightly narrower A/DC range, and thus slightly wider Φ/DC range.

When the A/DC and A_i/DC_i results in Fig. 3 are further detailed by plotting the values of all the food webs for each reach (Fig. 4), it becomes even clearer that the A/DC values (Fig. 4, panels indexed 1 and 3) of the Full Birds FW and the Full Fish FW markedly deviate from the rest of the values (Full FW, Benthic FW and Full Benthic FW). A comparable result emerges for the A_i/DC_i series (Fig. 4, panels indexed 2 and 4) where only the values of the Full FW, Ben-

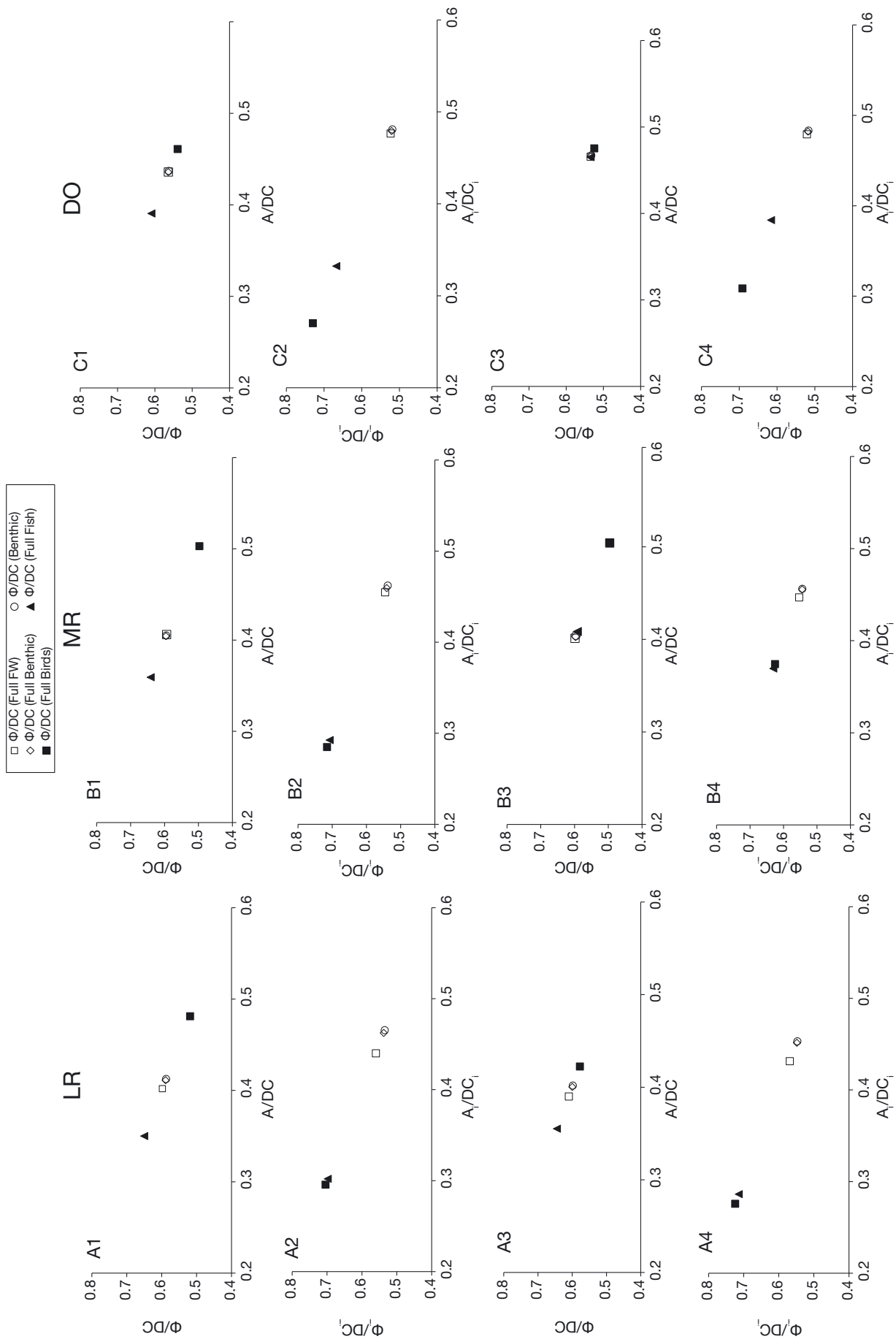


Fig. 4. Plot of the relative overhead (Φ/DC ; Φ : overhead; DC : developmental capacity) versus the relative ascendency (A_i/DC_i ; A : ascendency) and the relative internal overhead (Φ/DC_i) versus the relative internal ascendency (A_i/DC_i) for all the food web subsets per reach for carbon flow models where (A1, 2; B1, 2; C1, 2) only the living compartments were hand-balanced and (A3, 4; B3, 4; C3, 4) for models where both the living and the non-living compartments were hand-balanced. Panels A1–4 refer to Lower Reaches, B1–4 to Middle Reaches and C1–4 to Dollard. Panels indexed with 1 and 3 refer to A/DC and those with 2 and 4 refer to A_i/DC_i .

thick FW and Full Benthic FW tend to group together for both the unbalanced and balanced food web models.

It is further evident that the A_i/DC_i values for the Full FW, Benthic FW and Full Benthic FW are all systematically higher than the A/DC values (see A/DC and of A_i/DC_i in Table 2). For the Full Birds FW and the Full Fish FW the A_i/DC_i values are all systematically lower than those of the A/DC series. Since $\Phi_i/DC_i = 1 - A_i/DC_i$, the effect on Φ/DC is opposite that of A/DC . The main difference between the A/DC and the A_i/DC_i series is the inclusion (A/DC) or exclusion (A_i/DC_i) of input, output and respiration.

The A_i/DC_i ratios for the single hand-balanced Full Fish FW and the Full Birds FW (Fig. 4, panels indexed 2) group separately, which is not observed for the single hand-balanced A/DC series (Fig. 4, panels indexed 1). For the double hand-balanced series the results are nearly the same. The most remarkable change there is that, except the Full Birds FW in MR, all the values tend to group more (in DO) or less (in LR and MR). The A/DC range for DO is remarkably small compared to the rest. The largest

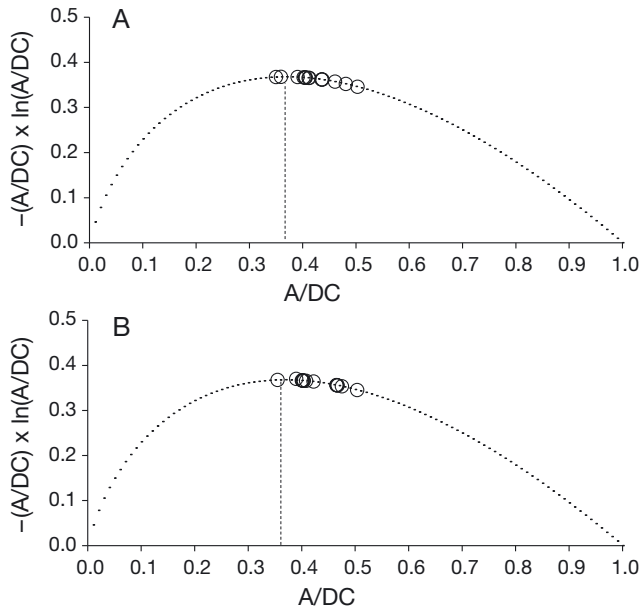


Fig. 5. Plot of the robustness $-(A/DC) \times \ln(A/DC)$ against the relative ascendancy (A/DC ; A: ascendancy; DC: developmental capacity) for carbon flow models where (A) only the living compartments were hand-balanced and (B) for models where both the living and the non-living compartments were hand-balanced. The dotted line represents the shape of the robustness curve for A/DC values between 0 and 1. The vertical dashed line shows the optimal A/DC , where the y-value is at its maximum. Note that all robustness values are situated on the calculated curve

differences in the output data thus occur due to the choice for either the A/DC or the A_i/DC_i ratio, and thus the choice for an ascendancy analysis that includes or excludes input, export and respiration.

3.4. Robustness

The relative distributions of the robustness values on the curves of Fig. 5 in relation to A/DC are similar to the distributions of the A/DC values presented in Fig. 3 because in both cases the x-axis (A/DC) is the same. It is clear that in Fig. 5 the robustness values for both the single hand-balanced (Fig. 5A) as well as the double hand-balanced (Fig. 5B) models are all quite close to their maximum (dashed vertical lines in the figures). The variation in the robustness values is very narrow (Table 2), ranging between 0.352 and 0.368 for the single hand-balanced A/DC series (Fig. 5A) and between 0.345 and 0.370 for the double

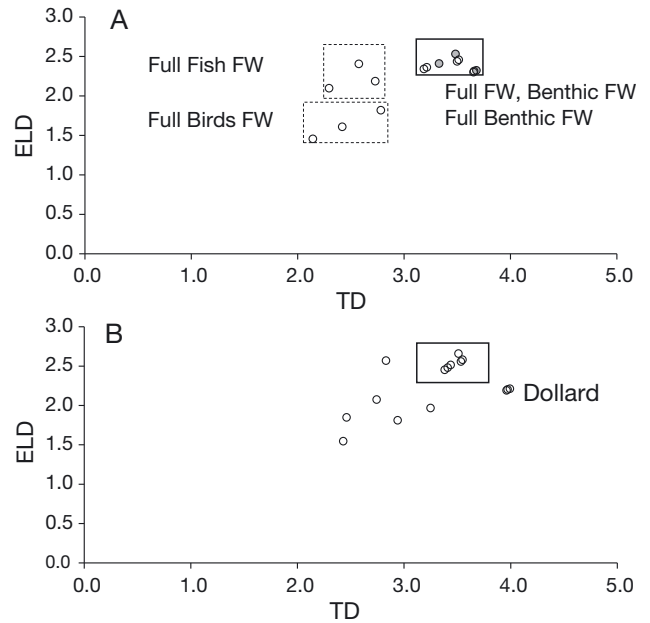


Fig. 6. Effective link density (ELD) plotted against the trophic density (TD) for carbon flow models where (A) only the living compartments were hand-balanced and (B) for models where both the living and the non-living compartments were hand-balanced. This figure was created to find a match with the 'window of vitality'. According to Zorach & Ulanowicz (2003) the 'window of vitality' covers the area between the TD range of 2 to 5 and the ELD range between 1 to 3.25 (see Fig. 9). Empty circles represent the FW subsets of LR, MR and DO. Filled grey circles represent the Full FW. Dashed outlines enclose values of the indicated FW subsets (Full Fish FW and Full Birds FW). Closed outline in panel A encloses the 3 values of the Full FW. This outline is copied to panel B to visualize the replacement of the values, specifically for DO

hand-balanced A/DC series (Fig. 5B). Thus, the full range in the values for the A/DC series lie between 0.345 and 0.370, a difference of only 0.025 (or ~7 % of the maximum). Such small differences between the calculated values and the optimal robustness value of 0.368 is not helpful when it comes to any application for practical use.

3.5. Window of vitality hypothesis

The 'window of vitality' is based on work by Zorach & Ulanowicz (2003) and is hypothesized by Ulanowicz et al. (2009) to represent the delimitation of a domain of robust balance that circumscribes sustainable behaviour in ecosystems. It is still a hypothesis and is thus missing a clear and widely accepted definition because of a lack of good field data. The present contribution to the ongoing discussion is the plotting of the effective link density (ELD; number of flows per ENA compartment) and trophic depth (TD; which is the number of ENA compartments divided by the 'connectivity' that can be calculated as the number of flows divided by the number of ENA compartments) presented in Fig. 6. The results are then compared with the findings of Ulanowicz et al. (2009, 2014). For further details see Ulanowicz et al. (2014). The aim was to find out if, and to what extent, variation in TD and ELD is caused by the use of the different food web subsets in combination with the single (Fig. 6A) and double (Fig. 6B) hand-balanced carbon flows. The distribution of the values in Fig. 6 shows some pattern. Some clear changes occur due to the double hand-balancing of the carbon flows. Most striking is that after further balancing the carbon flows of the group composed of Full FW, Benthic FW and Full Benthic FW—originally found in the small window—are now split into 2 groups. The new smaller group represents the food web subsets of only DO. The Full Fish FW and Full Birds FW remain separated. Both the range of ELD and TD increases somewhat (ELD: 0.038; TD: 0.026) due to balancing both the living and the non-living compartments (double hand-balancing). The conclusion from the ELD and TD analyses is thus that after having double hand-balanced all the food web subsets for the 3 reaches only, the subsets of Full FW, Benthic FW and Full Benthic FW group together. The differences are thus not only caused by having used different food web subsets, but the values related to the DO models are also moving away from the main cluster (see DO in Fig. 6B).

3.6. Finn cycling index

The FCI values (based on the total system through-flow [TSTf] of Finn 1976, 1980) of the different single and double hand-balanced full food webs and the food web subsets (Table 2) range in LR from 0.043 to 0.108 (a difference of 0.065), in MR from 0.023 to 0.082 (a difference of 0.059) and in DO from 0.043 to 0.154 (a difference of 0.111), indicating an increasing range in the FCI indices when moving upstream from LR and MR to DO. The values for the Full Fish FW and Full Birds FW deviate strongest from that of the other 3 food webs. The Full Fish FW values decrease upstream while the Full Birds FW values do not show a change in any particular direction. Most of the FCI values increase when double hand-balancing the carbon flows of all the models. The increases vary from 0 to over 100 %. The biggest changes are observed for the Full Birds FW in all 3 reaches. The second strongest changes are observed for the Full Fish FW of DO.

3.7. Food pyramid

The food web subset choices made here not only leads to differences in ENA metrics and indices but also, as illustrated in Fig. 7, to big changes in its related food pyramid. At the basis of all food pyramids are the primary producers. Contrary to what is generally visualised, for example in text books, the bacteria were also included in the food pyramids, one step above the primary producers, since bacteria are a primary food source for many organisms and are neither predator nor prey. The Full Fish FW (Fig. 7D) and the Full Birds FW (Fig. 7E) are very different from the results that represent the Full FW (Fig. 7A), Benthic FW (Fig. 7B) and Full Benthic FW (Fig. 7C).

3.8. Biomass pyramid

To be able to make the distinction between the classical food pyramid and the estuarine biomass pyramid, both pyramids are presented in Fig. 8. The reasoning is that the classical food pyramid (Fig. 8A) too often incorrectly ignores the importance of bacteria and detritus. Fig. 8A shows the distribution of all living compartments expressed in tons organic carbon, considering a sediment slice of maximally 2 cm. The thickness of the sediment slice is LR: 2.0 cm; MR: 1.54 cm; DO: 1.17 cm (for details see de Jonge et al.

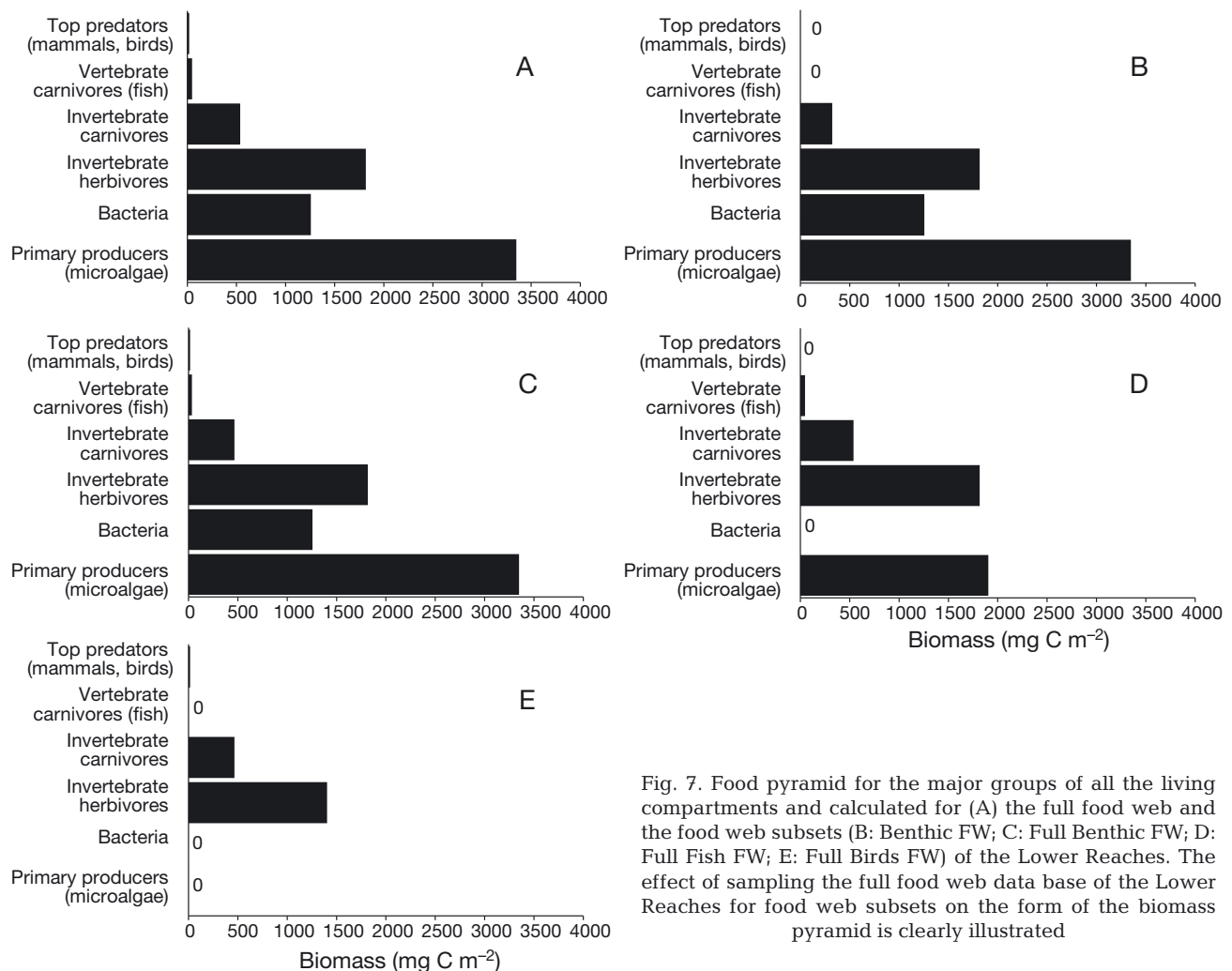


Fig. 7. Food pyramid for the major groups of all the living compartments and calculated for (A) the full food web and the food web subsets (B: Benthic FW; C: Full Benthic FW; D: Full Fish FW; E: Full Birds FW) of the Lower Reaches. The effect of sampling the full food web data base of the Lower Reaches for food web subsets on the form of the biomass pyramid is clearly illustrated

2019). Contrasting with Fig. 7, for the reason given above (their role as primary food source) the algae and the bacteria have been combined in Fig. 8. In Fig. 8B the suspended and sediment detrital carbon (dissolved organic carbon [DOC], suspended particulate organic carbon [POC] and sedimentary POC) have been added to the food pyramid. Notice that the considered sediment layer is again only 2 cm thick. Due to the addition of detritus, the total organic carbon biomass increased by a factor of ~40. Fig. 8C represents the relative distribution of the organic carbon as shown in Fig. 8B. The percentages here also refer to a sediment layer of 2 cm. It is evident that the detritus forms by far the most important carbon pool. With this sediment slice of only 2 cm, the detritus forms 97.4% of the total biomass. If the sediment layer is increased from 2 to 30 cm (the depth to which *Mya arenaria* and *Arenicola marina* are able to rework the sediment) the results further change in favour of the detrital carbon pool. With a 30 cm sediment layer,

99.68% of the total organic carbon of the ecosystem belongs to the detrital pool. This clearly illustrates the overwhelming importance of the detritus pool in the ecosystem, something that often is not taken into account at all.

The estuarine biomass pyramid for a sediment slice of 2 cm follows an exponential decrease from detritus, at its base, to mammals. It offers the possibility to estimate how much organic carbon in the system is needed to carry, for example, the present mammals or birds. For the Ems estuary ecosystem during the late 1970s, 1 kg of mammal organic carbon scales to a total basis of 250 000 kg organic carbon in the system. For 1 kg of bird organic carbon the value is much lower, averaging ~14 300 kg. The 2 perspectives, the food pyramid and the biomass pyramid, nicely illustrate the difference between biology and ecology. How large the magnitude of the absolute basis of ecosystems of tidal flat estuaries is can also be visualised by the simple symmetry of Fig. 8D.

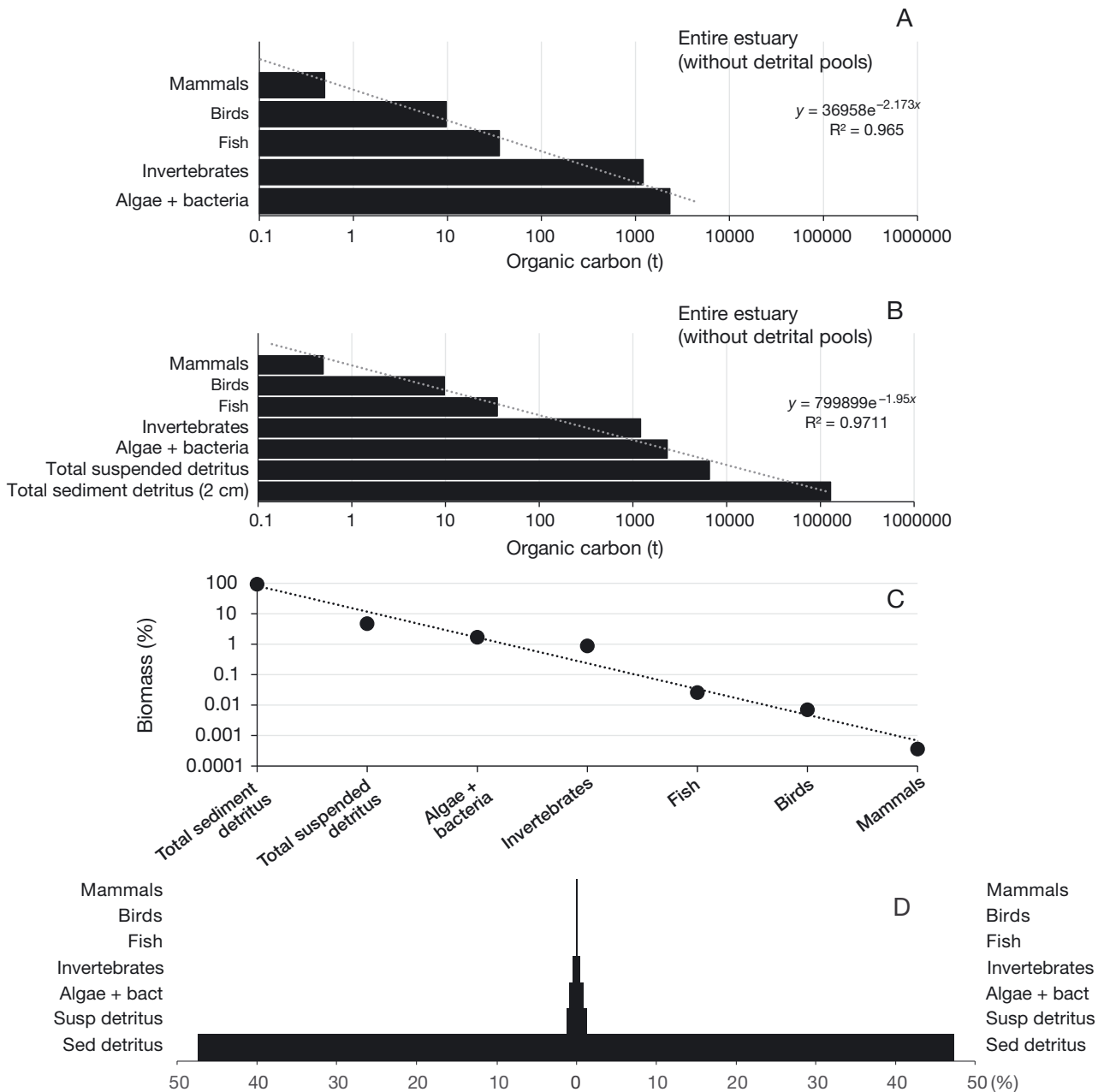


Fig. 8. (A) Ecological biomass pyramid (tons organic carbon for the entire estuary) for the main organism groups without the detrital carbon pools and (B) with the detrital carbon pools. (C) The absolute distribution of the biomasses of the biomass pyramid in (B), presented here in percentages. (D) The classical representation of the biomass pyramid, in percentages. Values represent the entire ecosystem (Lower Reaches + Middle Reaches + Dollard)

4. DISCUSSION

The trivial statement that the quality of the output of any study largely depends on the quality of the input becomes relevant when one attempts to make any comparison with the results of other network studies, of which the quality is sometimes unclear. Since comparisons have frequently been made

(Baird & Ulanowicz 1993), including the recent study by de la Vega et al. (2018), and with quite variable results, in the present study the focus will mainly be on the outcomes of our own results. The reason for this decision is that our basic data sets are consistent and have been thoroughly checked, value by value, and the models were run several times (see de Jonge et al. 2019). The only factor that can cause differ-

ences in the outcomes of the presented 30 models is the ‘treatment’ and thus the way the basic data sets were ‘subsampling’ to come to the present food web subsets. This means that the conclusions derived from the present study are one hand a bit restricted (mainly the present selected data sets) but are on the other hand even more valuable than just a general comparison with varying data from the literature because of the absence of any bias caused by unknown factors or issues beyond our control.

4.1. Selected ENA metrics and the structure of the studied food webs

Selection (subsampling) of compartments (species and functional groups) from the full food web not only simplifies the food web structure (Fig. 2) but may, as shown in Section 3, also significantly change the magnitude of TSTp of the food web subsets (Table 2). The detailed example of LR (Fig. 2, Table 1) indicates that the biggest differences between Full FW and Benthic FW is the absence of compartments with relatively weak connections between the nodes of the latter network (see Ulanowicz et al. 2014). Benthic FW misses many compartments but it includes all compartments with relatively high biomasses and large flows such as true phytoplankton, tycho-plankton (resuspended microphytobenthos), microphytobenthos, pelagic bacteria and benthic bacteria (and related substrate C-pools such as DOC, suspended POC and sedimentary POC). As soon as a food web subset misses one of the strong, and thus important, carbon flow related compartments, the TSTp value starts to decline along with related metrics and indices. The best examples are Full Fish FW, where part of the primary producers, the pelagic as well as the benthic bacteria are excluded, and Full Birds FW where all the primary producers and bacteria are not part of the food web subset. It is thus not just the number of compartments (nodes) that determines the network outcome, but it is the combination of the number of compartments and the related carbon flows. The low number of strong connections (primary producers and bacteria) is even more important than the presence of the many weaker connections represented by all the fauna together (see Ulanowicz et al. 2014). This phenomenon affects most of the results, since in ENA, TSTp is a crucial metric that many metrics and indices are directly related to. A consequence of the above is that, for instance, biodiversity on its own is not useful as an indicator to assess the status of any ecosystem unless a number of

function-related conditions is fulfilled. The most important such condition is that all primary producers and bacteria in the food web are—based on real field data—realistically represented as part of the functioning food web, so that the food web not only represents the complicated nodal network of species and C-pools, but also realistically represents the classical ecological biomass pyramid (Elton 1927, Bodenheim 1938, Lindeman 1942, Odum 1971). The differences that emerge from the use of food web subsets instead of Full FW can also be demonstrated by the data presented in Fig. 7, where the biological food web pyramid is shown as a bar diagram for all food web subsets of LR. This figure nicely illustrates how the original shape (Fig. 7A) of the biomass pyramid is deformed when groups of species are disconnected from the original network.

4.2. Estuarine biomass pyramid

The estuarine biomass pyramid (Fig. 8) roughly indicates the potential of the studied ecosystem to support megafauna such as mammals and birds. This potential is only roughly described by the exponential fit in Fig. 8, because real calculations with help of the given equation lead to unrealistically low values of the mammals and birds groups. The equation is based on the biomass distribution over groups of organisms and detritus (POC and DOC) and is also largely determined by the quality of the total non-living carbon pool-related data. The general biomass distribution and its exponential character (Fig. 8B,C) indicates that attention should be paid to the quality of the basis of this estuarine biomass pyramid and not only to bird and mammal species—and thus species-oriented policy making and management. If the quality of the detrital pool is sufficiently high (enough detritus substrate plus aerobic bacterial biomass) then the carrying capacity of the system under consideration can increase, since many of the estuarine species are able to feed on algae and bacteria, as well as other organic material that partly includes bacteria. During the late 1970s the carrying capacity of the Ems estuary ecosystem for harbour seals *Phoca vitulina* was <500 kg, less than 9 adult animals. During the balancing process of the living compartments, it was problematic to achieve results that allowed this number of harbour seals to be sustained. This can be seen as a clear indication that during that time the ecosystem was not very well able to feed them (without letting them feed at the North Sea, i.e. without permitting food import from the North Sea for the

seals). It has been shown (Lucke et al. 2013) that the average number of harbour seals in the Ems estuary during 2012 was roughly 400. The exact number is less relevant than the fact that in 2012 the seal biomass reached a level of >50 times that of the 1970s. Since the 1970s the total algal production has decreased (de Jonge & Schückel 2019) because of the increased turbidity of the Ems estuary (de Jonge et al. 2014). The challenging question with regard to the harbour seals is thus where they get their food from and how high the predation pressure of these mammals is on the local estuarine fish stocks and other food such as shrimps. Further detail of this issue is important but beyond the scope of the present study.

The construction of the food web and biomass pyramid was performed based on an entirely arbitrary classification of organism groups, but seems to perform quite well, as the concentration decrease from bottom to top follows an exponential biomass decrease.

There remain, apart from the above, some other intriguing issues that can be discussed with help of the present data sets, namely the usefulness of A/DC (and A_i/DC_i) and robustness as indicators for management purposes, and the possible added value of the hypothesized 'window of vitality'.

4.3. Ascendency analysis

Our A/DC data (Table 2, Figs. 3 & 4) enable the direct comparison of the A/DC among the different reaches and balancing modes as well as previously published results. A/DC values for the 30 single and double hand-balanced food webs (Table 2) show that the range in the A/DC data is, as mentioned in Section 3.3, mainly due to the creation of the Full Fish FW and Full Birds FW subsets that miss the few strong large flow compartments that are available in the other food webs (see Figs. 2 & 7).

A_i/DC_i reflects the systems functioning without taking into account respiration, inputs and outputs, and shows results that differs from that of A/DC . However, except for a broader range of A_i/DC_i values, it is not clear if the use of this index should be advocated above the A/DC . Strong arguments in favour of A/DC are the importance of external inputs and outputs of organic carbon related to the shallow estuarine and coastal systems (Postma 1967, de Jonge 1995), and the fact that—in the case of external pressures such as the turbidity changes due to dredging (de Jonge et al. 2014) and the changes in

eutrophication due to variations in nutrient supply and availability (de Jonge et al. 2002)—these are not covered by the internal indices because of an ignorance of inputs, outputs and respiration. The difference between A/DC and A_i/DC_i is important, however, because it provides an indication of the degree of dependence of the system on exogenous connections with the physical, geomorphological and hydraulic aspects of the estuary and adjacent systems which, once again, highlights the importance of measuring inputs and outputs correctly.

4.4. Robustness

The first issue to be discussed here is the effect of the use of food web subsets on the distribution of the robustness values as presented in Fig. 5. The second is related to the use of robustness as index to assess the state of the food web functioning. Just as in Figs. 3 & 4, in Fig. 5 (see Table 2) the use of food web subsets under single and double hand-balanced carbon flow conditions leads to an increase in the range of the obtained values and also here that range is mainly caused by the creation of Full Fish FW and Full Birds FW. This means that the use of any food web subset to assess the condition or state of the full ecosystem cannot be supported and should even be discouraged.

Recently, Goerner et al. (2009) suggested that the robustness concept and index that was developed by Ulanowicz et al. (2009) could be a good candidate to estimate whether the system's functioning is close to its optimum or not. We show the application of this concept in Fig. 5, showing how the different robustness values are distributed over the curve in comparison to its optimal A/DC (being $1/e$, or 0.368). The disadvantage of this presentation is that the robustness is defined as $-(A/DC) \times \ln(A/DC)$ and is thus plotted against its own basis of A/DC . The A/DC values for the 30 food web models (Table 2) range between 0.350 and 0.504, while the robustness values range between 0.345 and 0.370. The ranges are thus 0.154 for A/DC (or 15.4 % of the full range of 1) and 0.025 for robustness (6.8 % of the full range of 0.368). Since the robustness has been advocated as an indicator for 'vitality' (or an attractor of 'balanced development') (Goerner et al. 2009, Fath 2015), an important point of discussion is: Which indicator or index, out of the data we have generated, is the best to be recommended for practical application? Indicators need to be sensitive, which means that we expect them to change markedly under the influence

of varying factors that affect the studied ecosystems. In the present case we have 2 related indicators (robustness and A/DC). Considering the restricted variation in the robustness values (see Section 3.4) as compared to A/DC, the use of the A/DC ratio (or Φ /DC) should be recommended as a central indicator to assess systems flow order and disorder. Related indices such as average mutual information ($AMI = A/TSTp$) and flow diversity ($DC:TSTp$) are not investigated and discussed here because, as is proposed in EU Directives, we should favour non-correlated indices. Furthermore, the A/DC and Φ /DC are, to our current knowledge, by far the best candidates for the practical future application we wish to achieve. Future work will have to reach conclusive decisions, since the discussion on this topic has just begun (Fath et al. 2019, Safi et al. 2019). Despite the recent and current work, and the strong progress that is being made in this field, the present state-of-the-art is not yet enough to advocate assessments of the state of food web networks in relation to, for example, EU Directives such as the Water Framework Directive (EC 2000) and the Marine Strategy Framework Directive (EC 2008). We are preparing another study, based on the same data set as used in the present study, that will exclusively treat the issue of which indicator—or set of indicators—is most suited to meet the intended goals of the EU Directives WFD and MSFD (EC 2000, 2005a,b, 2008) and could potentially also serve other environmental EU Directive assessments.

4.5. Window of vitality

It is evident that the food web subsets with the weakest flow connections (Full Birds FW and Full Fish FW) are mainly responsible for the spread in ELD and TD values (Fig. 6A). Double hand-balancing leads to an increase in all ELD and TD values, except the ELD values for DO models. After double hand-balancing, values for Full FW, Benthic FW and Full Benthic FW models group together with DO values at the right side, while values of Full Fish FW and Full Birds FW are grouped at the left side. This distribution also resembles that of the divide between the values of DO and the values for LR and MR in Fig. 3 for the double hand-balanced mode. DO values in Fig. 3 are not labelled but their position in the figure can be determined with the aid of the A/DC values in Table 2. The spread of the values in Fig. 3 and 6 indicates that the grouping of the values in both figures is consistent.

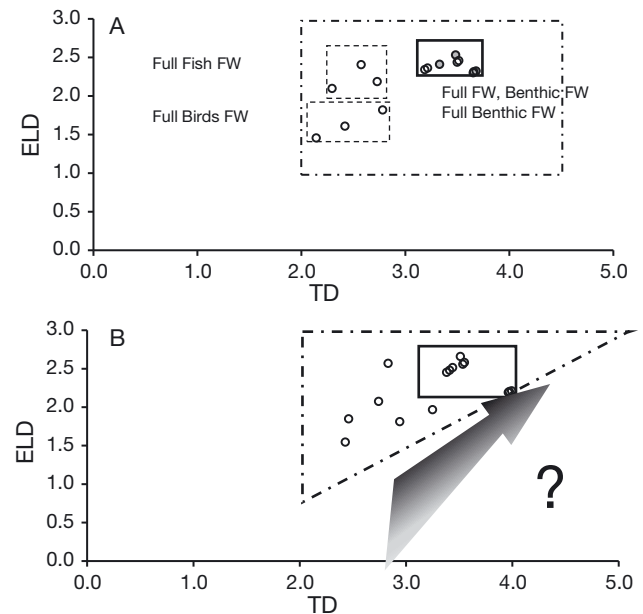


Fig. 9. Combination of the ‘window of vitality’ (dot-dash frames) (Zorach & Ulanowicz 2003) and the effective link density (ELD) and trophic depth (TD) values as obtained during the present study for (A) carbon flow models where only the living compartments were hand-balanced and (B) for models where both the living and the non-living compartments were hand-balanced. The values in the figures indicate that the food web subsets (Full Fish FW and Full Birds FW) that miss the direct connection with the primary producers and the bacteria are found in the left part of the proposed ‘window of vitality’, suggesting that more complex and more complete food webs tend to move to the top at the right hand side in the bigger window of Zorach & Ulanowicz (see arrow). Empty circles represent the FW subsets of LR, MR and DO. Filled grey circles represent the Full FW of LR, MR and DO. Dashed outlines enclose values of the indicated FW subsets (Full Fish FW and Full Birds FW). Closed outline in (A) encloses the 3 values of the Full FW. This outline is copied to (B) to visualize the replacement of the values, specifically for DO. Dashed-dotted frame in (A) represents the ‘window of vitality’ while the one in (B) suggests that, at best, only half the ‘window of vitality’ may be valid. For values see Table 2

Fig. 9A relates the results shown in Fig. 6 to the ‘window of vitality’ suggested by Zorach & Ulanowicz (2003) and Ulanowicz et al. (2009). Intriguingly, our data cover about half the ‘window of vitality’ frame (compare Fig. 9A and 9B). If the ELD/TD values of the Full Fish FW and the Full Birds FW are omitted, the remaining window based on the present data (solid outline in Fig. 9B) is ~10 times smaller than the Ulanowicz window (the big dashed frame in Fig. 9A). If food webs are incomplete (food web subsets, habitats or partial food webs), TD and ELD values of our indices decrease. This was previously noted by Ulanowicz et al. (2014) for sparser ecosys-

tems with fewer compartments, nodes and trophic levels.

If the differences between the ‘window of vitality’ as originally suggested by Zorach & Ulanowicz (2003) and the much smaller window we show in Fig. 9 have a more general validity, then the speculation is justified that not all data in the literature are of sufficient quality to reach useful conclusions about the functioning of ecosystems. If networks do not contain all the few but strong nodes (primary producers, decomposers, imports and exports) and related flows in an ENA analysis, these systems will group towards the left side of the suggested ‘window of vitality’ instead of the right hand top side (following the arrow in Fig. 9B). Thus, there may be reason for critically checking the structure of published food webs, as it is important to know which of the ENA-related indices are suitable for management purposes. This means that we can only accept data that can be compared based on the construction of full food webs. There is a need for standardization and for the creation of a manual on ENA applications.

The results here underpin the importance of the lower trophic levels in terms of connectivity, and also underpin the importance of their contributing flows to TSTp. More specifically this concerns the role of true phytoplankton, that of resuspended microalgae or microphytobenthos as tycho plankton (e.g. de Jonge 1985, 1995, de Jonge & van Beusekom 1992, 1995) and that of true microphytobenthos (Colijn & de Jonge 1984, de Jonge & Colijn 1994, de Jonge 1995). The quantitative role of both pelagic and benthic bacteria in the food web needs to be unravelled. The number of publications on bacteria is extremely low while their impact is extremely large. It is essential to also investigate whether it is necessary to include the anaerobic degradation and/or mineralisation of organic material by benthic bacteria in this type of analysis. The predator–prey and grazing interactions related to microzooplankton (often tintinnids, see Admiraal & Venekamp 1986) need much more attention than they have received so far. Finally, not only the processes need attention, but the determination of the biomass of different biological species, ENA compartments or groups needs to be more accurate. Specifically for bacteria, microzooplankton and macrozooplankton (Mees 1994) the current knowledge gaps are immense. Studies like the recent one by Christianen et al. (2017) are very important, but there are by far too few of these studies being performed to solve the problems indicated here.

4.6. Suitability of indices for policy making and management

The indices studied here form only part of what has been proposed so far. Safi et al. (2019) and Fath et al. (2019) propose a total of 13 indices, of which only the FCI and D/H (Table 2, and see de Jonge et al. 2019) are shared by both groups. The robustness indicator and the ‘window of vitality’ (related ELD and TD) are not part of either list. Information-based indices (e.g. A/DC and Φ /DC) are mentioned (Fath et al. 2019) but not discussed in depth in relation to policies and management. This exemplifies the difficulties scientists face in being clear in what they consider to be a suitable indicator for assessing ecosystem functioning. In a forthcoming study this specific issue will be discussed in further detail.

4.7. Required improvements in the application of ENA

As mentioned for TSTp in Section 4.1, a similar signal is observable for the differences in FCI between the full food webs and the food web subsets (Table 2). These differences also stress the importance of the lower trophic levels (see Section 4.1) in the carbon recycling. If lower trophic levels are lost in the ENA analysis due to grouping or due to the use of food web subsets, then—apart from the above indices—the magnitude of recycling may decrease relative to the original Full FW (see de Jonge et al. 2019). Pinnegar et al. (2005) showed that FCI tended to increase due to aggregation at the basis of the food web. In contrast to Johnson et al. (2009) and Allesina et al. (2005), the FCI values in the present study (see also de Jonge et al. 2019) changed slightly between full food webs and functional group based food webs (data not shown). This is attributed to the different aggregation schemes used, as Johnson et al. (2009) lumped, for example, detritus and bacteria into one large detritus group while we separated bacteria from the detritus as substrate.

5. CONCLUSIONS

The use of food web subsets leads to strongly increasing variation in all ENA metrics that were considered here (ELD, TD, robustness, A/DC, Φ /DC) and should therefore be discouraged.

Phytoplankton (resuspended microphytobenthos included), pelagic and benthic bacteria and external

flows related to inputs and outputs have a large impact on the ENA metrics of the Ems estuary ecosystem.

The added value of using robustness as an index instead of the more basic A/DC ratio, or its complement Φ/DC , is too small to be supported. The range of ELD and TD values increases strongly when analyses are performed on food web subsets.

ENA only works well when the flow matrices are hand-balanced for the living as well as the non-living compartments, and when the estuarine biomass pyramid is represented well, i.e. when all primary producers and all decomposers are reliably represented. There is consequently a strong need for realistic primary production values and decomposition values, and the need for proper input and output values of the relevant POC and DOC carbon pools for the system under consideration.

It is not advisable to only study ecosystems top-down, starting from iconic species like birds and mammals, and to then stop at the level of their prey or primary food sources, thus creating food web subsets. The present study demonstrated that the use of food web subsets results in loss of information, especially at the basis of the food web, and that this has huge consequences on the value of applying specific indicators, and for our understanding of the entire food web or ecosystem functioning.

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