

Linking long-term changes in trophic structure and function of an intertidal macrobenthic system to eutrophication and climate change using ecological network analysis

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ABSTRACT: Food web structure and function in benthic ecosystems are a reflection of environmental conditions and change in response to both anthropogenic and natural stressors. In Jade Bay (German Wadden Sea), the intertidal macrofauna communities have been intensively studied since the 1930s, and results have revealed pronounced temporal changes in species composition and community structure caused by climatic variability and anthropogenic impacts. Using ecological network analysis, we constructed 3 different food web models representing the status of the 1930s, 1970s and 2009 to assess system development and organization and how the system responded to changing environmental conditions. The biomasses, energetics and trophic exchanges of characteristic macrofauna species were estimated. The total biomass of the benthic communities increased by 70% from the 1930s to the 1970s but declined marginally from the 1970s to 2009. The size of the system in terms of flows through all its compartments increased over time, from 1756 to 2207 to 3464 mg C m⁻² d⁻¹ for the 1930s, 1970s and 2009, respectively. The amount of material that is recycled in the Jade Bay system declined between the 1930s and 1970s but increased in 2009, when we also found greater efficiency at retaining material within the food web until it leaves the system. The internal organization of the benthic ecosystem is characterized by short trophic pathways. Indices of system development and organization increased over time. There was a noticeable decline in parallel trophic pathways, indicating a reduction in the ability of the system to withstand perturbations.

KEY WORDS: Macrofauna · Temporal dynamics · Ecological network analysis · Energy flows · Ecosystem indices · Jade Bay · German Wadden Sea

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INTRODUCTION

Intertidal flats are highly productive, diverse, and ecologically and economically important coastal ecosystems (Kabat et al. 2012). These habitats harbour high standing stocks and densities of benthic macrofauna, which in turn provide an essential food source for higher trophic levels, such as epibenthic crustaceans, fishes and millions of migratory birds (Kabat et al. 2012).

In recent decades, the benthic fauna and flora of intertidal flats have been subject to increasing global warming, invasion of non-native species, sea level

rise and anthropogenic stresses, such as fisheries, eutrophication or pollution (Lotze 2005, Oost et al. 2009). Long-term and retrospective studies on benthic macrofauna are of great value as they use previous data as a baseline for comparison with more recent data to assess long-term changes and their underlying drivers. Macrofauna species are considered to be good indicators of environmental health as well as environmental changes and disturbances because macrofauna species are relatively sessile and consist of different species that exhibit different tolerances to stress (Dauer 1993, Schückel & Kröncke 2013).

Long-term changes in diversity, abundance and community structure of the intertidal macrofauna communities have been intensively studied in Jade Bay, a shallow bight in the German Wadden Sea, over the last 8 decades (Linke 1939, Michaelis 1987, Schückel et al. 2013, Schückel & Kröncke 2013). According to Schückel & Kröncke (2013) major changes that have occurred in Jade Bay are as follows. (1) Triggered by climate warming, a higher frequency of mild winters since 1997 led to recruitment failures and decreasing abundances of the common bivalve species populations (e.g. *Macoma balthica*, *Cerastoderma edule*) in 2009. Conversely, the opposite trend (i.e. an increase in the biomass of these species) was found between the 1930s and 1970s caused by a higher frequency of cold winters. (2) Species inventory increased between the 1930s and 2009 due to the increase of (i) non-native species introduced from overseas by shipping, and which were able to extend their distribution range due to increasing water temperatures, and (ii) cryptogenic species (species that are neither native nor introduced; Gollasch & Nehring 2006) immigrating into the Wadden Sea mainly in the 1970s. (3) Anthropogenic stresses, particularly eutrophication and pollution impacts. These mainly affected the macrofauna communities between the 1930s and 1970s (indicated by an increase in opportunistic deposit-feeding polychaetes and decreasing seagrass beds), whereas the opposite trend was observed between the 1970s and 2009. Short-lived opportunistic species, particularly annelids, are often characterized as dominating the community structure of disturbed or stressed habitats (Pearson & Rosenberg 1978, Dauer 1993). Eutrophication during the 1930s to 1970s resulted mainly from excess nutrient loads, which were drastically reduced in subsequent years. Furthermore, there is evidence that 2 different geomorphological regimes existed over time. In the 1970s, a high frequency of storm surges (Niemeyer 1987) resulted in the erosion of the intertidal flats in the eastern area of the Jade Bay. In contrast, extensive sedimentation processes together with a 13% increase in sediment volume import led to a silting-up and an increase in the average tidal elevation of 34 cm between 1999 and 2009, which is probably related to a concomitant rise in sea level (U. Schückel unpubl. data). As a result, there was an increase in abundance and range extension of deposit feeding macrofauna species well adapted to muddy sediments, in particular *Tubificoides benedii* (U. Schückel unpubl. data).

These comprehensive data on intertidal macrofauna species offer a unique opportunity to assess

changes in the ecological functioning based on energy flows of a trophic network. In the present study we used ecological network analysis (ENA). The construction and analyses of quantitative network models of coastal ecosystems is currently practiced on a global basis, and the assessments of trophic and biogeochemical flow models by means of ENA are one of the few tools available to ecologists to examine ecosystem structure and functioning. ENA methodology was developed to assess the complex interactions within an ecosystem (Fath et al. 2007), and consists essentially of a set of algorithms providing a holistic approach to ecosystem analysis from which several system properties can be derived.

Results from ENA include input-output, trophic and cycling analysis and the calculation of ecosystem indices describing the organizational and developmental state of the system. ENA requires a description of the flow structure, rates of flows and the magnitude of transfers between the living and non-living compartments, exports from and imports to the ecosystem, information on biomass, feeding ecology, predator-prey interactions, energy relationships as well as primary and secondary production are necessary (Ulanowicz & Kay 1991).

Information and knowledge gained from studying benthic trophic food webs can be used to understand how the system responds to changing environmental conditions as a whole and to make predictions of natural or human-induced impacts. Further, indices derived by ecological network analysis can be used

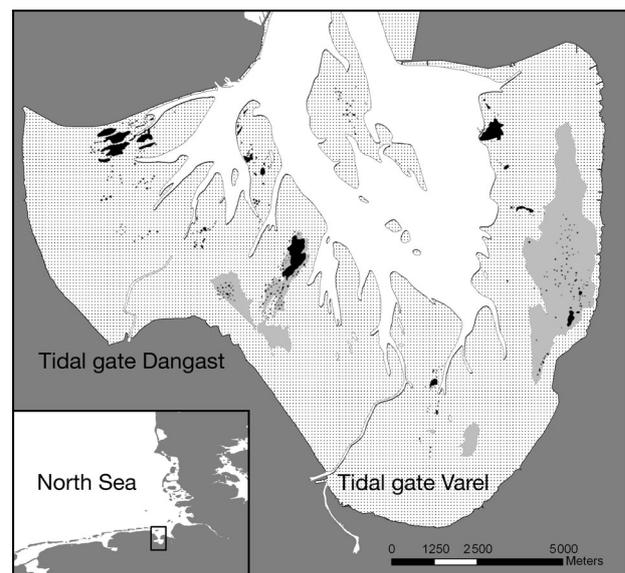


Fig. 1. Jade Bay in the German Wadden Sea (North Sea). Stippled: intertidal areas, black: mussel beds, light grey: seagrass beds

for management purposes as discussed in many studies which used outputs to assess system maturity, resilience, robustness and stress (e.g. Scharler 2012, Niquil et al. 2012, Saint-Béat et al. 2015).

In the present study, 3 carbon flow models representing a snapshot of the trophic flows occurring in Jade Bay in the 1930s, 1970s and 2009 were developed. The objective of this paper is to quantitatively assess changes in biomass, rates of flows between selected benthic living and non-living compartments as well as in the system-level properties in response to changing environmental conditions that have occurred in Jade Bay during the past 80 yr. Using ecological network analysis we evaluate and compare the resultant system properties and how these reflect on the functioning of Jade Bay at an ecosystem level over time.

MATERIALS AND METHODS

Study area

Jade Bay (53° 28' 42" N, 8° 12' 5" E) is a shallow tidal bay in the central part of the German North Sea coast and one of the largest tidal basins in the Wadden Sea (Fig. 1). It is part of the German National Park of Lower Saxony. Its present shape is a result of several storm floods in the Middle Ages (Behre 2004). Jade Bay is connected with the North Sea by the Inner and the Outer Jade through a narrow bottleneck east of Wilhelmshaven (Linke 1939). Upstream, Jade Bay branches into 3 main tidal channels draining into a system of tidal inlets and gullies far into a backswamp area. Due to tidal forcing, the water circulation pathways mainly follow a north-south direction (Schuster 1952). In the western area, the circulation is influenced by a 5.8 km-long training wall, which regulates the tidal currents. The mean water depths of the 3 channels vary between 8 and 10 m (BSH 2009). Mean ebb and flood current velocities are between 0.46 and 0.53 m s⁻¹ and the average tidal range is about 3.8 m (Götschenberg & Kahlfeld 2008). Salinity is fairly constant and nearly equal to that of the adjacent North Sea (S ≈ 29–30) (A. Bartholomä unpubl. data) except for the areas close to the tidal gates where it can occasionally decrease to 18 (Beck et al. 2013).

Data base and model construction

The spatial distribution of macrofauna species in Jade Bay was intensively studied from 1935–1937

(henceforth 1930s) (Linke 1939) and from 1975–1977 (henceforth 1970s) (Michaelis 1987) and reinvestigated in 2009 (Schückel & Kröncke 2013, Schückel et al. 2013). Quantitative samples were taken by using cylindrical corers to a depth of 30 cm and were sieved, in general, through a 0.5 mm mesh (a 1 mm mesh size was used for the sampling on mixed sediments and sandflats during the 1970s). The use of a 1 mm mesh sieve on the mixed sediments and sandflats in the 1970s, compared to the 1930s and 2009, may have underestimated densities of small cirratulid polychaetes and oligochaetes (*T. benedii*). However, the dominant species, such as tubicolous polychaetes (*P. elegans*), larger polychaetes (>10 cm) (*S. armiger*, *H. filiformis*; Hartmann-Schröder 1996) and more rigid species such as amphipods, gastropods and bivalves are expected to be less impacted (Degraer et al. 2007). Given the fact that, for example, oligochaetes generally occurred in low abundances, and thus had low biomass, on mixed sediments and sandflats in the 1970s (Schückel & Kröncke 2013), the impact of a smaller mesh size might be low. Organisms were identified to the lowest possible taxonomic level and counted. Biomass of each species was determined as ash-free dry weight (AFDW) per m². Samples taken in 2009 were dried for 24 h at 85°C and burned for 6 h at 485°C, whereas in the 1970s, samples were dried for 2 d at 60°C and burned for 3 h at 485°C (Michaelis 1987). Different drying and ashing temperatures can have an influence on biomass estimation (Wetzel et al. 2005). However, the drying and ashing temperatures used in the present study were in the range of recommended temperatures of 60 to 103°C for drying (Crisp 1971, Mason et al. 1983) and 450 to 550°C for ashing (Crisp 1971, Mason et al. 1983). For the 1930s, only abundance data were available, which we converted to biomass units by using individual wet weights of each macrofauna species from data of the same time period given in Thamdrupe (1935) and Smith (1951) for the Wadden Sea. Wet and ash-free dry weights of each species were converted to mg C m⁻². Values represent annual average conditions. Macrofauna species considered in the 3 models represent the numerically most abundant species, which significantly characterized the different communities found for each time period (Schückel & Kröncke 2013). The comprehensive biomass data on the intertidal macrofauna collected during the 1930s, 1970s and in 2009 form the basic information on which flow models were based for each of the time periods. No data are available on the concentration of suspended POC, pelagic phytoplankton, benthic microalgae and bacteria. However, the de-

mand by consumers of phytoplankton, benthic microalgae and free-living bacteria was considered as imports into Jade Bay from the adjacent North Sea. Modules for fish and birds were not included due to a current dearth of information on their numbers, although they are known predators of invertebrate prey in Jade Bay. Each model representing a specific time period consisted of 26 (1930s model), 30 (1970s model), and 31 (2009 model) living compartments. Each compartment represents a benthic species, or a community such as meiofauna, small polychaetes, and sediment bacteria, while 2 non-living compartments (suspended and sediment particulate organic carbon) were also included in the food networks. Not all species, or model compartments, were present in all 3 time periods (see Table 1). As mentioned in the introduction, several species immigrated into the Wadden Sea area in the 1970s (Michaelis 1987, Reise et al. 1998, Gollasch & Nehring 2006).

Energy budgets were calculated for each of the heterotrophic compartments. Consumption (C) was balanced by production (P) + respiration (R) + egestion (E). Rates of consumption, respiration and production of the different species as well as the dietary composition of the benthic compartments were obtained from literature or calculated using published conversion ratios (Warwick & Price 1975, Fauchald & Jumars 1979, Banse & Mosher 1980, Hartmann-Schröder 1996, Ysebaert et al. 2003, Baird et al. 2004a, 2007, Verdelhos et al. 2011). The biomasses for the different species/compartments used to construct the flow models, the respective ratios for each, and the production, respiration, egestion and consumption rates derived from them are given in Table 1. It should be noted that the calculated system properties, such as the total systems throughput, ascendancy, are sensitive to the derived rate functions (such as consumption, respiration, production). Here, comparable ecological ratios, assumptions and procedures were applied to each of the 3 food web models. Carbon was used as the flow currency to trace the interactions in the food webs. Biomass of each compartment is given in mg C m^{-2} and the rates (e.g. production, consumption, respiration) and flows between the compartments in $\text{mg C m}^{-2} \text{ d}^{-1}$. The Jade Bay intertidal benthic system was considered to be in a steady state during each of the time periods so that the input into each compartment was balanced by the output. Excess sediment POC (excretory products and organismal mortality) were not exported but assumed to become part of the detrital pool, an energy source for detritivores.

Ecological network analysis

The analytical methodology is described in detail by Kay et al. (1989) and reviewed by Ulanowicz (2004). The software package NETWRK 4.2a (Ulanowicz & Kay 1991) and supporting documentation can be downloaded from www.cbl.umces.edu/~ulan/ntwk/netwrk.zip. The outputs from network analysis provide many useful indices and system properties of natural ecosystems, as well as relevant information for the interpretation of energy and nutrient flows and how these affect the structure of the ecosystem. Outputs from network analysis were used to describe and assess changes in the food web dynamics in the intertidal Jade Bay ecosystem between the 3 time periods, and are briefly given below.

The Lindeman trophic analysis was used to assess temporal changes in the efficiency of carbon transfers over time. The Lindeman trophic analysis routine identifies the feeding pathways upon which any component within the network depends and calculates the effective trophic position of each. The mean trophic efficiency and the detritivory:herbivory (D:H) ratio are considered to be functional indicators of food web dynamics (Ulanowicz 1992). However, their use as operational metrics to assess the impact of disturbances or changes in biodiversity remains uncertain (Niquil et al. 2014). The mean trophic efficiency of an ecosystem is usually calculated from the geometric mean of the efficiency of energy transfer between discrete trophic levels (i.e. the Lindeman Spine) (Baird & Ulanowicz 1989). Primary producers and detritus together form the first trophic level when pooling primary producers and detritus (Miehls et al. 2009, Baird et al. 2012). Here we do not have information on the energetics or biomass of phytoplankton and benthic microphytobenthos (MPB), both essential food resources for many benthic invertebrate species, and these components were subsequently imported to satisfy consumer (herbivory) demand. It is thus not possible to calculate the trophic efficiency at trophic level 1 without having the values for respiration and primary production. However, the mean trophic efficiency has been considered for all levels from level 2 and higher as in the Ecopath routine (Coll et al. 2009, Heymans et al. 2012, Niquil et al. 2014), but unfortunately this prevents the comparison of trophic efficiencies with other systems where primary producers and detritus were considered as the first trophic level. The average number of benthic compartments and steps involved in passing a unit C through the system from its entry until it leaves (Christensen 1995) were

assessed by calculating the average path length (APL). The APL is expected to rise under normal succession and to decrease when the system encounters stress.

Various global system indices, based on information theory, describe the developmental and organizational state of the ecosystem (Ulanowicz 1986, 2004). For example, the measure of total systems throughput (TSTP) is defined as the sum of all flows in the systems, which is a surrogate for the total energy generated within the system (Odum 1969). The biogeochemical cycle routine of NETWRK assesses the structure and magnitude of the cycling of material in the system. The cycling index (CI) is derived from the fraction of the sum of flows that is devoted to cycling, and is an index of the retentiveness of the system (Baird & Ulanowicz 1989, Baird et al. 2004a,b). CI is equal to $T_{cyc}/TSTP$, where T_{cyc} is the amount recycled. The system ascendancy (A) reflects the functional attributes of the system. It incorporates both the size and organization of flows into a single index, and is formally expressed as the product of TSTP and the average mutual information (AMI) inherent in the flow network. It is sensitive to environmental changes, such as species richness (Chrystal & Scharler 2014) or eutrophication, which causes an increase of ascendancy due to the rise of TSTP (Saint-Béat et al. 2015). The AMI index, or normalized ascendancy ($A/TSTP$), is considered to be indicative of the developmental status of the ecosystem and corresponds to the degree of specialization of flows in the network (Ulanowicz 2004).

The development capacity (DC), the product of TSTP and the flow diversity, measures the potential for a system to develop and is the natural upper limit of A. The total system overheads Φ (i.e. sum of overheads on imports, exports, dissipation and redundancy) is a measure of the uncertainty associated with the presence of multiple or parallel pathways among the compartments of the network (Kay et al. 1989, Ulanowicz & Norden 1990) and is numerically represented by the difference $DC - A$, and represents that fraction of the DC that does not appear to be an organized structure (Bodini & Bondavalli 2002). Since $DC = A + \Phi$, the A/DC ratio provides a measure of the degree of system order, whereas Φ represents everything that is disordered, inchoate and dissipative in the same network. It follows that in a system with a low A/DC ratio, Φ then provides the opportunity for A to grow (Ulanowicz 2009). A system with low redundancy is postulated to be susceptible to external perturbations, which may impact on the trophic interactions between system compartments.

Parallel pathways of energy and material transfers, however, can act as a buffer or reserve should external perturbations or changes in biodiversity occur. Ascendancy measures the efficiency and definitiveness by which energy transfers are made, whereas the overheads quantify how inefficient and ambiguous the system performs on average. Higher indices of A reflect increased ecological succession characterized by, for example, species richness, decreased cost of overheads to the system, greater internalization of resources, and finer trophic specialization (Scharler & Baird 2005).

Internal ascendancy (A_i) and internal developmental capacity (DC_i) are functions of internal exchanges alone, and thus exclude exogenous transfers into and out of the system. The ratios A/C and A_i/DC_i have been used to compare the organizational status of ecosystems on temporal (Baird & Ulanowicz 1989, Baird & Heymans 1996, Baird et al. 1998, 2004b) and spatial (Baird et al. 1991, Baird & Ulanowicz 1993, Baird 1999, Baird et al. 2004a) scales. Baird & Ulanowicz (1993) speculated that a large decrease in the A_i/DC_i ratio in relation to the A/DC ratio could indicate a strong dependence of a system on dominant external connections, for example detritus coming from riverine or terrestrial outputs (Lobry et al. 2008). The magnitude of various attributes, particularly the DC, A, overheads and redundancy, are strongly influenced by the total activity or TSTP (cf. Ulanowicz 2004, Scharler & Baird 2005). By dividing these capacities (DC, A, and overheads) by TSTP, the resultant normalized values are scaled to eliminate the singular effect of TSTP (cf. Baird & Ulanowicz 1989, Baird et al. 1998). DC, A and R are expressed as 'bits' which refers to \log_2 used in the algorithms to calculate these metrics. Flow diversity, defined as $DC/TSTP$ (or normalized DC), measures both the number of interactions and the evenness of flows in the food web, and is thus a dynamic concept, more so than species diversity (Mann et al. 1989, Baird et al. 1998). Comparatively higher values of this index indicate an increase in interactions, a lower degree of unevenness and variability in the flow structure, and the greater ability of a system to cope with disturbances (Ulanowicz & Wulff 1991, Baird et al. 2004b). The overall connectance includes the effect of external transfers; the internal connectance index characterizes only internal exchanges, whereas the food web connectance index refers only to transfers among the living compartments in the system (Ulanowicz 2004). The calculation of system indices mentioned above is based on log-scaled measures; small percentage changes reflect much larger dispar-

ities and thus ecological changes (Ulanowicz 1986, Baird & Ulanowicz 1993).

RESULTS

Trophic structure and input-output analysis

The data used to construct food web models for each of the 3 periods (1930s, 1970s, and 2009) are given in Table 1. In addition to the biomass for each of the living compartments, rates of consumption, production, respiration and egestion were derived using the ecological ratios (P/B, P/R, and P/C) which were in turn obtained from the literature of similar species in comparable environments such as, for example, the Sylt-Rømø Bight, German Wadden Sea (Baird et al. 2004a,b). The diet composition of species was obtained from the literature and unpublished information from Senckenberg am Meer, Department for Marine Research, Wilhelmshaven, Germany. No information was available on the biomass or production of phytoplankton and benthic microphytobenthos or the concentration of suspended particulate organic carbon (suspended POC). The amounts consumed by consumers of these food items were considered as inputs into Jade Bay. The average demand for phytoplankton and microphytobenthos by consumers in the 3 models was $106.7 \text{ mg C m}^{-2} \text{ d}^{-1}$ (SD = 90.7, n = 3) and $214.25 \text{ mg C m}^{-2} \text{ d}^{-1}$ (SD = 47.6, n = 3) respectively. Production values for these 2 components were in range with primary production estimations from different estuaries ranging between 19 and $2397 \text{ mg C m}^{-2} \text{ d}^{-1}$ for phytoplankton, and those for microphytobenthos between 79 and $641 \text{ mg C m}^{-2} \text{ d}^{-1}$ (Underwood & Kromkamp 1999). Regarding the Wadden Sea, Baird et al. (2007) reported a phytoplanktonic and microphytobenthic primary production of $248 \text{ mg C m}^{-2} \text{ d}^{-1}$ and $972 \text{ mg C m}^{-2} \text{ d}^{-1}$ respectively on the mud flats of the Sylt-Rømø Bight. Cadée & Hegeman (1974) estimated a daily microphytobenthic primary production of 15 to $1120 \text{ mg C m}^{-2} \text{ d}^{-1}$ in the Dutch Wadden Sea. Values between 53 and $118 \text{ mg C m}^{-2} \text{ d}^{-1}$ were reported on the Lynher Estuary's (UK) mudflats (Warwick & Radford 1989).

The total intertidal area decreased by about 15 % between the 1930s and 1970s mainly due to a decrease in the mixed sed-

iment area and seagrass beds, but increased again by 16.4 % from the 1970s to 2009 (Table 2). The area covered by mudflats, however, increased by about 52 % (1930s–1970s) and 10 % (1970s–2009). Intertidal seagrass beds increased from 2.75 to 10.9 km^2 between the 1970s and 2009 (Table 2). The total standing stock of the macrobenthic fauna increased from 11.6 g C m^{-2} (1930s) to 19.7 g C m^{-2} (1970s), but then decreased marginally to 19.2 g C m^{-2} in 2009. The biomass of the individual macrofauna species/compartments incorporated in the network models fluctuated widely over the years since the 1930s (Table 1). The reasons for the temporal changes in macrofauna species composition, abundance and community structure are discussed in detail by Schückel & Kröncke (2013). The average daily production of the macrofaunal community, however, increased steadily from the 1930s to 2009, while the annual mean P/B ratio of the macrofauna declined by about 28 % during the years of eutrophication (1930s–1970s) but increased marginally (by about 5 %) during the warmer period to 2009 (Table 2).

The majority of the macrofauna species fell into trophic level 2 (Table 1), with the exception of *Eteone longa* (3.14) and *Crangon crangon* (3.07) which fell into trophic level 3. The results of the trophic aggregation routine of the 3 models were mapped into Lindeman spines as illustrated in Fig. 2. The detritus pool is separated from level 1, which represents the primary producers in the system. However, since information on the biomass and production of primary producers in Jade Bay was not available, the conventional trophic level 1 (TL1) was omitted from

Table 2. General system attributes of the intertidal Jade Bay, German Wadden Sea, for the time periods 1935–1937, 1975–1977 and 2009. Attributes involving area covered (in km^2) are approximates. R: respiration

Attribute	1935–1937	1975–1977	2009
Intertidal area (km^2)	137.4	116.8	136.0
Mudflats (km^2)	33	50	55
Mixed sediments (km^2)	57	22	31
Sandflats (km^2)	41	38	37
Seagrass beds (km^2)	5.30	2.75	10.9
Mussel beds (km^2)	1.07	4.03	2.07
Biomass (B) living compartments (mg C m^{-2})	11596.1	19709.0	19177.9
Production (P) living compartments ($\text{mg C m}^{-2} \text{ d}^{-1}$)	163.03	200.03	207.02
System P/B ratio (yr^{-1})	5.13	3.70	3.94
System R/B ratio (yr^{-1})	8.40	3.71	5.48
Tidal prism ($\text{m}^3 \times 10^6$)	396 ^a	400 ^b	400

^aLüders (1930); ^bvon Seggern (1980)

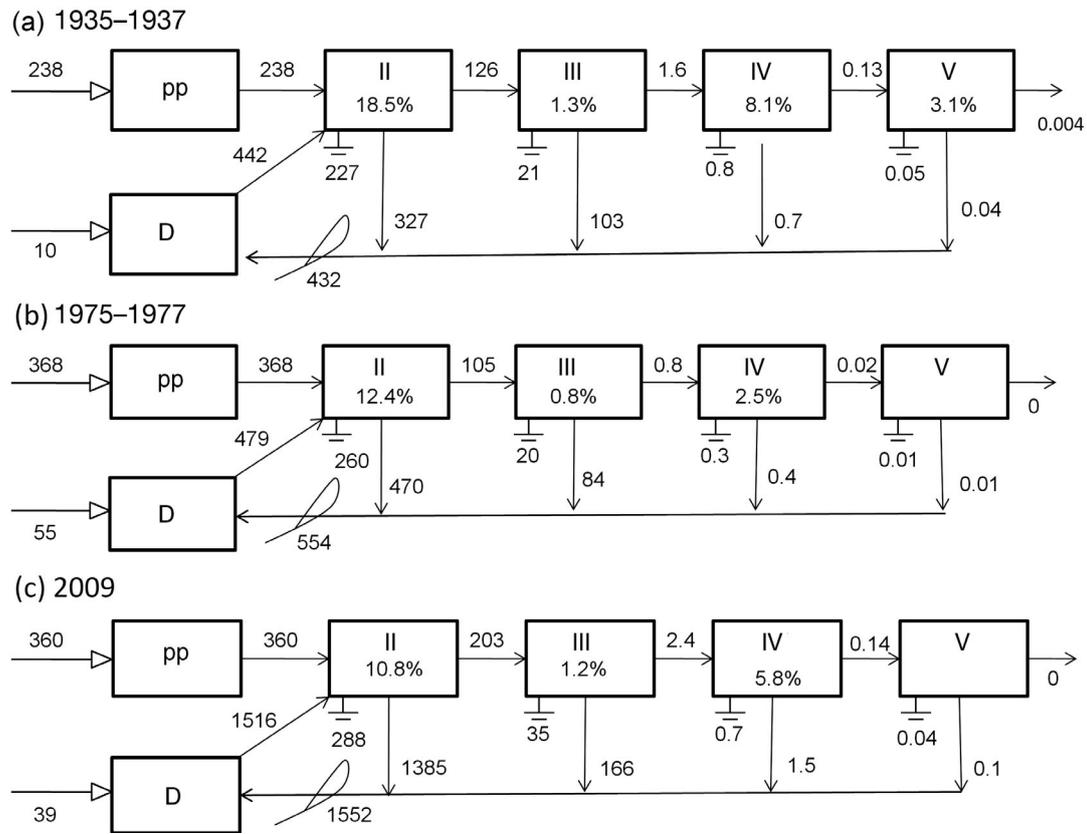


Fig. 2. Lindeman spines for each of the 3 models (a) 1930s, (b) 1970s, and (c) 2009. The percent value in each of the trophic level boxes gives the amount of input into that level that is passed on to the next higher trophic level. Numerals in each box indicate the different trophic levels. Shown are exogenous inputs, transfers between and from all trophic levels, and losses to the surrounding environment (exports and respiration) from each trophic level in $\text{mg C m}^{-2} \text{d}^{-1}$. pp: primary producers; D: detritus pool

the calculation of the trophic efficiency for the system. Detritivory exceeded herbivory by ratios of 1.8, 1.3 and 4.2 for the 3 respective time periods (1930s, 1970s and 2009). During the 1930s about 64% of the total energy intake at TL2 consisted of recycled material, while 98.5% of all detritus inputs into the detrital pool was derived from recycling within the system. It would appear that Jade Bay was, by the 1970s, and also in 2009, more dependent on intra-system recycling of detrital material than during the 1930s. Returns of detritus from the trophic levels 2 and higher as well as canonical exports and respirations leaving each trophic level are shown in Fig. 2. Five trophic levels were identified. The percentage value in each trophic level box indicates the efficiency by which energy is transferred from the lower to the next higher level. There is a progressive decline in trophic efficiencies from lower to higher levels in each spine (Fig. 2), with the exception of level 3, which showed a lower efficiency than levels 4 and 5 in all 3 periods. This anomaly is most probably due to the relatively high returns to the detrital pool from

level 3, when detrital return amounted to about 80% of the total intake of that level during all 3 time periods. The higher trophic efficiency at level 4 could also be ascribed to the ability of the system to transfer energy to predators at higher trophic levels. The high detritivory:herbivory ratio in 2009 is partly due to an increase in typical detritivore species such as *Tubificoides benedii*, *Scoloplos armiger*, *Arenicola marina* and *Capitella capitata*, and a decrease in suspension feeders such as *Cerastoderma edule*, *Macoma baltica*, *Scobicularia plana*, *Mya arenaria* and *Mytilus edulis*. The logarithmic mean of the trophic efficiencies (calculated over trophic level 2 and higher) of Jade Bay during the 3 time periods decreased from 4.96% in the 1930s to 2.92% in the 1970s, and increased again to 4.22% in 2009. Reasons for the fluctuation in efficiency values are that the drop in the 1970s efficiency is due to a much lower transfer efficiency at TL3 and TL4, which occurred during the time when eutrophication was high (Fig. 2). Two other system indices, namely the average path length (APL) and the average residence time (ART), are also

indicators of the trophic function of an ecosystem. The APLs for the 3 time periods fluctuated from 4.26 (1970s) to 7.69 (2009) with an APL of 6.1 in the 1930s. This means that energy was used over relatively more steps compared to other intertidal systems such as the Sylt-Rømø Bight, where the APL varied between 1.94 and 3.29 in 8 intertidal systems (Baird et al. 2007). The APL decreased from the 1930s to the 1970s (during eutrophication), while warmer water temperatures and mild winters caused a unit of energy to pass through more compartments. Material and energy appeared to reside for 43.6 d during the 1930s, 70.3 d in the 1970s, and for 65.3 d in 2009 (Table 3). These values fall within the range of ARTs (84 to 8 d) calculated for 8 intertidal systems in the Sylt-Rømø Bight (Baird et al. 2007).

Table 3. Global system indices and attributes derived from ecological network analysis of Jade Bay, German Wadden Sea, over 3 time periods: 1930s, 1970s and 2009. DC, A and R are expressed as 'bits' which refers to \log_2 used in the algorithms to calculate these metrics. Z: sum of all exogenous inputs

System attributes	1935–37	1975–77	2009
Number of compartments	28	32	33
Trophic efficiency over TL 2 and higher (logarithmic mean, %)	4.96	2.92	4.22
Number of cycles	101	85	92
Cycling index (CI; %)	43.16	28.94	31.04
Average path length (APL = TSTP – Z/Z)	6.10	4.26	7.69
Average residence time (ART; d)	43.64	70.3	65.32
Total system throughput (TSTP; mg C m ⁻² d ⁻¹)	1755.8	2206.6	3463.5
Development capacity (DC; mg C m ⁻² d ⁻¹ , bits)	8769.2	11415.0	14762
Ascendency (A; mg C m ⁻² d ⁻¹ , bits)	3061.9	4442.6	6189.4
Relative ascendency (A/DC; %)	34.92	38.92	41.93
Average mutual information (AMI) (A/TSTP, normalized A)	1.74	2.01	1.79
Flow diversity (DC/TSTP, normalized DC)	4.99	5.17	4.26
Overheads on imports (mg C m ⁻² d ⁻¹ , bits)	154.90	610.10	497.70
Overheads on exports (mg C m ⁻² d ⁻¹ , bits)	0	0	0
Dissipative overhead (mg C m ⁻² d ⁻¹ , bits)	1058.6	1180.4	1342.1
Redundancy (R; mg C m ⁻² d ⁻¹ , bits) (sum of overheads, mg C m ⁻² d ⁻¹ , bits)	4439.8	5182.1	6732.7
Relative ϕ (ϕ /DC; %)	5653.30	6972.60	8572.50
Relative redundancy (R/DC; %)	64.47	61.08	58.07
Normalized redundancy (R/TSTP)	50.63	45.40	45.61
Internal development capacity (DC _i ; mg C m ⁻² d ⁻¹ bits)	2.53	2.35	1.94
Internal ascendency (A _i ; mg C m ⁻² d ⁻¹ , bits)	6501.3	8166.5	11141.0
Relative internal ascendency (A _i /DC _i ; %)	2007.5	2984.4	4408.1
Average internal mutual information (AMI _i) (A _i /TSTP)	30.88	36.54	39.57
Internal redundancy (R _i ; mg C m ⁻² d ⁻¹ , bits)	1.14	1.35	1.27
Normalized internal redundancy (R _i /TSTP)	4493.8	5182.1	6732.7
Normalized ϕ (sum of overheads/TSTP)	2.56	2.35	1.94
Overall connectance	3.22	3.16	2.48
Intercompartmental connectance	2.81	2.55	2.17
Food web connectance (living compartments only)	3.23	3.08	2.23
Detrivory:herbivory ratio	2.82	2.35	2.43
	1.8:1	1.3:1	4.2:1

Structure and magnitude of cycling

Cycling in ecosystems occurs through a number of cycles of different path lengths, whilst the amount recycled is expressed by the CI (i.e. the amount of TSTP recycled). The number of cycles decreased from 101 (1930s) to 85 (1970s) then increased again to 92 (2009), while the CI declined from 43% in the 1930s to 29% in the 1970s and then increased marginally to 31% in 2009. The greater proportion of recycled carbon was cycled through nexuses containing only 1 cycle over the 3 time periods (Table 4). The increase in the number of cycles from the 1970s to 2009 is mainly due to 1 nexus containing 8 cycles, with the cycles beginning and ending in the crab *C. crangon*, but very little material was recycled over these pathways. Most of the carbon recycled was through loops of 2 and 3 path lengths during the 3 time periods (Table 5).

System level attributes

System-level attributes derived from network analysis for each of the 3 periods are given in Table 3. The TSTP, a metric on the total activity of the system, increased from the 1930s to the 1970s by 25.6% and from the 1970s to 2009 by 57% (see Table 3), indicating there was an increase in the amount of energy flowing through Jade Bay over time. The same trend can be observed in other metrics such as the development capacity, ascendency, and redundancy over time, as well as in the dimensionless ratios such as the relative ascendencies (A/DC and A_i/DC_i). However, other system properties, such as the AMI, AMI_i flow diversity, normalized redundancies and connectance indices increased from the 1930s to the 1970s during a period of eutrophication, but then decreased from the 1970s to 2009 under warmer climatic conditions. From this one can conclude that despite an increase in the system's activity (TSTP) most of the dimensionless ratios declined during the intervening years between the 1970s and 2009.

Table 4. Number (n) and percentage distribution of cycles per nexus in Jade Bay, German Wadden Sea, in the 1930s, 1970s, and 2009

Cycles per nexus	1935–37		1975–77		2009	
	n	%	n	%	n	%
1	29	28.7	36	42.4	40	43.5
2	20	19.8	20	23.5	14	15.2
3	0	0.0	9	10.6	12	13.0
4	12	11.9	8	9.4	12	13.0
5	0	0.0	0	0.0	0	0.0
6	12	11.9	12	14.1	6	6.5
7	14	13.9	0	0.0	0	0.0
8	0	0.0	0	0.0	8	8.7
14	14	13.9				
Total	101	100.0	85	100.0	92	100.0

Table 5. Amount of material (mg C m⁻² d⁻¹) recycled through loops of varying path length for the 1930s, 1970s and 2009 in Jade Bay, German Wadden Sea

Path length	1935–37		1975–77		2009	
	mg C m ⁻² d ⁻¹	%	mg C m ⁻² d ⁻¹	%	mg C m ⁻² d ⁻¹	%
2	397	52.39	378	59.18	559	51.99
3	327	43.15	256	40.08	510	47.43
4	33.60	4.43	4.2	0.66	4.98	0.46
5	0.20	0.03	0.5	0.08	1.21	0.11
Sum of cycled flow	757.80	100	638.70	100	1075.19	100

DISCUSSION

The 3 different network models constructed characterised the structure and trophic function of the intertidal benthic macrofaunal ecosystem of Jade Bay in the 1930s, 1970s and 2009. The intra-ecosystem comparison revealed differences and changes in biomass and trophic structure as well as system properties over time. Pronounced changes in the macrofaunal communities in terms of diversity, abundance and temporal variability of individual species, or groups of species were observed by Schückel & Kröncke (2013) over the 8 decades covered by their study. They ascribed community changes from the 1930s to the 1970s to increased nutrient enrichment in the Jade Bay area, evidenced in particular by an increase of small, opportunistic polychaetes. Major contributors to nutrient enrichment were the enhanced riverine inputs, local and regional discharges, as well as the import of organic matter from the North Sea, leading to increased eutrophication

during these years. However, eutrophication declined between the 1970s and 2009 due to reduced nutrient inputs, contributing to substantial seagrass recovery in Jade Bay (Table 2).

Furthermore, individual species fluctuated widely between the 3 time periods. For example, bivalve species populations (e.g. *Cerastoderma edule*, *Macoma balthica*, *Mya arenaria* and *Mytilus edulis*) increased from the 1930s to the 1970s following a series of cold winters which favoured recruitment success. These stocks declined by 2009, presumably caused by frequent recruitment failures caused by mild winter temperatures since 1997, a phenomenon also observed in the Wadden Sea proper (Diederich et al. 2005, Nehls et al. 2006) and in the Sylt Rømø Bight (Baird et al. 2012). Winter water surface temperatures have increased by about 1.5°C since the 1980s (van Aken 2008, van Beusekom et al. 2009). Such a temperature rise may have reduced bivalve populations due to declining growth rates, declining values of body mass index and lower reproductive output (Beukema et al. 2014).

In addition to changes in the community structure over time the total standing stocks of all species increased by about 70% from the 1930s to the 1970s, followed by a decrease in total biomass of about 3% between the 1970s and 2009 (see Table 1). It would thus appear that during a period of cold winters and increased eutrophication a general increase in biomass occurred, while decreased eutrophication and successive recruitment failures of bivalves (due to mild winters) contributed to the decline in biomass since the 1970s. Essink et al. (1998) also found that much of the temporal variability in mean total macrofauna biomass is caused by bivalves. However, the decline in biomass between the 1970s and 2009 was low due to increasing standing stocks of benthic grazers (*Hydrobia ulvae*), detritus feeders (*Tubificoides benedii*, *Arenicola marina*) and omnivores (*Hediste diversicolor*). In 2009, consumption, respiration and flow to detritus were dominated by *H. ulvae* and *A. marina*. *H. ulvae* appears to be one of the most important species in Jade Bay, probably due to the presence of extensive mudflats and *Zostera noltii* seagrass beds (Schückel et al. 2013). Its key role and relatively high overall effects on other benthic species inside a *Zostera* food web were similarly described for the Mondego estuarine ecosystem in Portugal (Baeta et al. 2011). In line with our study, the authors described an increase in opportunistic, deposit-feeding polychaetes and oligochaetes during a period of nutrient enrichment with *Heteromastus filiformis*, showing the highest value of keystone-ness

and relative overall effect (Baeta et al. 2011). Trends in community structure are clearly reflected in system properties derived from the analyses of the 3 network models representing each of the respective time periods. Between the 1930s and 1970s, the trophic efficiency (calculated over trophic levels 2 and higher) of the system declined from 4.96 to 2.92% (a decline of 41%). Niquil et al. (2014) reported trophic efficiencies ranging from 5.7 to 6.5% for a benthic invertebrate macrobenthic community in the Mondego estuary during a eutrophic period. These efficiencies were calculated on the trophic transfers from trophic level 2 and higher. During the eutrophication period (1930–1970), the CI declined by 33%, the amount of material recycled by 11% (Table 5), and the APL by 37%—in addition to declines observed in all connectance indices (Table 3). These same system properties (trophic efficiency, CI, APL, amount recycled) increased again from the 1970s to 2009, whilst all the connectance indices declined during this period (Table 3).

Important system metrics (Table 3) such as the TSTP, DC and DC_i , A and A_i , and Φ increased from the 1930s to 2009. To assess how data uncertainty influenced the results of network analysis, the coefficient of variation (CV) was calculated to compare system variability. The CV provides a measure of robustness of parameter uncertainty, and was calcu-

lated based on the results from ENA for the various metrics and ratios given in Table 3. The ratio-based indices had the lowest CV values compared to the CV for TSTP (Fig. 3) which indicate that they are more robust to uncertainty (Kaufman & Borrett 2010, Baird et al. 2011, 2012). In contrast, indicators such as DC, A and R, showed high CVs with larger variability, possibly due to data uncertainty. The CVs of the ratio-based indices with values below 12% are shown in Fig. 3. The relative ascendancy (A/DC) and relative internal ascendancy (A_i/DC_i) both increased over time indicating that the Jade Bay ecosystem has increased in maturity and organization over time.

However, when DC, A and R were normalized to eliminate the singular effect of TSTP, these ratios (namely the AMI and internal AMI, flow diversity and internal flow diversity) all showed an increase from the 1930s to the 1970s, but then a decrease from the 1970s to 2009. The AMIs, useful indices of the inherent organization of a system and the degree of specialization of flows in a network (Ulanowicz 2004, Baird et al. 2012), indicate an increase in system function during a period of eutrophication and cold winter temperatures, but a decline between 1970s and 2009, when eutrophication declined and during a period characteristic of warmer winters and indications of a gradual increase in the water temperature of the Wadden Sea (van Aken 2008, van Beusekom et

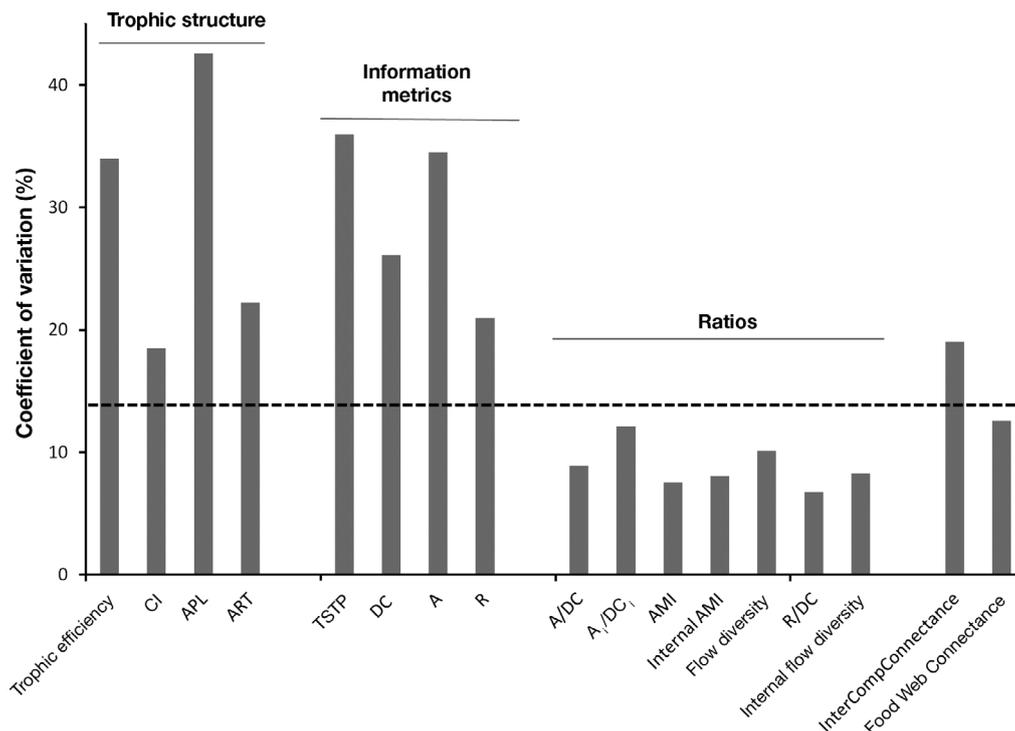


Fig. 3. Coefficient of variation (CV) of system properties derived from ecological network analysis. Dashed line indicates 12% CV level. For abbreviations see Table 3

al. 2009). Similarly, flow diversity (defined as DC/TSTP), which measures both the number of interactions and the evenness of flows in a food web network, and which is considered a much more dynamic concept than species diversity (Mann et al. 1989, Baird et al. 1998) increased from the 1930s to the 1970s, but then decreased between the 1970s and 2009. This implies an increase in interactions and a lower degree of unevenness and variability in the flow structure during the first period (1930s to 1970s), which is then reversed in the subsequent period (1970s to 2009). The normalized redundancy ratios and the normalized ϕ declined from the 1930s to 2009, pointing to a decrease in the strength in reserve (Baird et al. 2012). The general trend of these indices appears to be associated with firstly a period of increased eutrophication and colder winters (1930s to 1970s) and a concomitant increase in total system biomass, followed by warmer winters, declining levels of eutrophication, and in biomass (Table 3). It is also interesting to note that the amount of material recycled decreased during the years of increasing eutrophication and cold winters (as per the CI and Table 5) but increased during the subsequent years of reduced eutrophication and warmer winters. Of interest is also the detritivory:herbivory ratio in Jade Bay, which declined between the 1930s and 1970s, probably due to higher rates of phytoplankton consumption by bivalves. For 2009 it becomes apparent that Jade Bay relies more heavily on detritus, as detritivory exceeded herbivory by a factor of 4.2, thus reflecting the important consumption of detritus in Jade Bay (Rybarczyk et al. 2003). The high system APL value of 7.7 in 2009 indicates that a large proportion of the material is retained within the system (Monaco & Ulanowicz 1997), probably attributed to a higher production of feces caused by grazers (e.g. *H. ulvae*) and detritus feeders (e.g. *A. marina*) as well as to the higher net sediment import, both of which contribute to intensive benthic cycling.

Odum (1985) postulated 18 trends in ecosystem behaviour that can be expected when ecosystems are under stress, and listed a number of system function and structure characteristics that may occur over time. If we consider that the Jade Bay system was under eutrophication stress between the 1930s and the 1970s, then a few of these trends postulated by Odum can be identified from our ENA results. If Odum's suggestion that 'community respiration' increases under stress, then the increase in 'dissipative overheads' by 12.4% confirms his notion. Other indices that support Odum's trends are a decrease in the efficiency of resource use, reflected in the de-

crease in the trophic efficiency metric by 45%, a decrease in the cycling index by 27.4%, and a decline at the ecosystem level in relative and normalized redundancy by 5.5 and 7% respectively (Table 3). However, contrary to Odum's postulates, both the P/B and R/B ratios declined during the eutrophication period (1930s to 1970s) (Table 2). Few other studies considered the benthic macrofauna food network separately from an entire system including primary producers, fish and other higher level predators, so that comparisons between the Jade Bay macrofaunal system and other intertidal ecosystems are rather tenuous and thus not attempted here.

To conclude, although the present study only focused on macrofauna species, impacts of climatic variability and eutrophication on the ecological properties described by ENA indices become evident and provide a first insight into the ecosystem functioning of the Jade Bay system. From the 1930s to 1970s there were detectable increases in key indices (relative ascendancy, AMI, flow diversity) during a period of increased nutrient inputs, eutrophication and cold climatic conditions. In comparison, the same indices declined from the 1970s to 2009 when eutrophication decreased concomitant with warmer winters. Anthropogenic influences and environmental change thus controlled synergistically the functioning of the Jade Bay ecosystem. These impacts can be important for defining ecosystem indicators or coastal management decisions (Niquil et al. 2012). However, further research efforts and data including all ecological compartments and interactions are necessary to understand the ecosystem response as a whole.

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