

# Energy flow of a boreal intertidal ecosystem, the Sylt-Rømø Bight

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**ABSTRACT:** A detailed energy flow model consisting of 56 living and 3 non-living compartments was assembled for the intertidal area of the Sylt-Rømø Bight. The model depicts the biomass of each compartment, carbon flow between the components, imports and exports, as well as an energy budget for each. The food web was analysed by means of network analysis which showed that about 17% of the total daily flow through the system is recycled through a complex cycling structure consisting of 1197 cycles. The cycling network indicated that about 99% of the recycling involves 2 to 3 compartments, with sediment bacteria and particulate organic carbon (POC) participating in most instances. Input/output analyses indicated that phytoplankton production in the Bight does not satisfy the demands of filter-feeders on an annual average basis so that about  $160 \text{ mgC m}^{-2} \text{ d}^{-1}$  of phytoplankton have to be imported. We compared several dimensionless system level indices, such as internalised and normalised A/DC (ascendancy/development capacity) ratios, calculated for the Bight with those of other marine and estuarine ecosystems on a global basis. These comparisons showed that energy is rather inefficiently transferred within the Bight at a mean trophic efficiency index of 2.61%, and that most of the system level indices are lower than those of other coastal ecosystems. However, higher values were obtained for flow diversity and food web connectance compared to other systems. This study has revealed the Bight to be a highly complex system whose energy pathways appear to be sensitive to external perturbations.

**KEY WORDS:** Energy flow · Food web · Structure · Network analysis · System level properties · Coastal ecosystems · German Wadden Sea

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## INTRODUCTION

The Sylt-Rømø Bight is a large, shallow, tidal ecosystem in the German Wadden Sea comprising a mosaic of inter- and subtidal mussel beds, seagrass beds and sand flats. The Bight is rich in plant and animal species, some of which are commercially exploited. The productivity and diversity of the Bight result in a complex ecosystem with a multitude of interactions between the various living and non-living components of the system. The ecology of the Bight and its physical and chemical characteristics and processes have been studied for many decades, during which a comprehensive literature and database have been established. For example, Gätje & Reise (1998) provided detailed information and summaries of ecological data on virtually the entire ecologi-

cal spectrum from nutrient fluxes to the abundance of fish and bird communities. The flow of energy in a seagrass community in the Bight has been described by Asmus & Asmus (2000), as well as for the food web of the tidal flats (Asmus & Asmus 1985, Asmus 1994, H. Asmus et al. 1998). Sprung et al. (2001) reported on energy flow in the benthic assemblages of the intertidal area of the basin. Asmus & Asmus (1985) discussed the importance of the grazing food chain in selected sand-bottom communities, while Asmus & Asmus (1990) also reflected on the extent to which trophic relations in the tidal flats depend on imported energy. Apart from these aggregated and community-specific energy flow models, a detailed flow network of the Sylt-Rømø Bight ecosystem has yet to be produced. This paper is the first attempt to provide an energy flow model of the intertidal Bight.

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First we compiled a holistic description of the standing stocks of the major communities and species in the Bight and of the interactions between them by means of a quantitative food web model that illustrated the rate of energy uptake, dissipation and transfer between the components of the system. Second, we examined the functional processes (e.g. cycling of material, trophic efficiencies) and global ecosystem properties (e.g. total system activity, development capacity, ascendancy) by means of network analysis. Finally, we compared the output results derived from network analysis on the Sylt-Rømø Bight with those of other coastal ecosystems on a global basis.

Attempts to unravel the interactions between the living and non-living components of ecosystems and energy flow within them have resulted in the construction of food networks giving quantitative information on standing stocks of auto- and heterotrophic species and communities, their rates of consumption, production, respiration and egestion, their dietary composition, and the flow of energy and material between the system components (cf. Baird & Ulanowicz 1989, Baird et al. 1991). In many of these studies, network analysis, a set of algorithms derived from input/output analysis, trophic and cycle analysis, has been used to compute several ecosystem properties such as the structural complexity of the ecosystem, the structure and magnitude of the cycling of energy and material, the efficiency of energy transfer within the system, rates of energy assimilation and dissipation, trophic structure, system activity, growth and development (cf. Ulanowicz 1986, Baird & Ulanowicz 1989, Gaedke & Straile 1994, Baird et al. 1998, 2004, Heymans et al. 2002). Results from network analysis thus provide significant insight into the fundamental functioning of the ecosystem (Mann et al. 1989, Baird 1999). References to the basic concepts of network analysis and its application are given by Ulanowicz (1986), Kay et al. (1989), and Wulff et al. (1989).

## MATERIALS AND METHODS

**Study area.** The Sylt-Rømø Bight ( $54^{\circ}52'$  to  $55^{\circ}10' N$ ,  $8^{\circ}20'$  to  $8^{\circ}40' E$ ) is part of the Wadden Sea, a shallow coastal region of the North Sea, extending from the Netherlands to Denmark. The Bight is a semi-enclosed basin situated between the islands of Sylt, Germany, and Rømø, Denmark, and is connected to the North Sea by means of a 2.8 km wide channel between the islands (Fig. 1).

The Bight covers an area of  $404 \text{ km}^2$ , with an intertidal area of about  $135 \text{ km}^2$ . The salinity of Bight waters fluctuates between 28 and 32, and the water temperature between  $-1^{\circ}\text{C}$  in winter and  $20^{\circ}\text{C}$  in

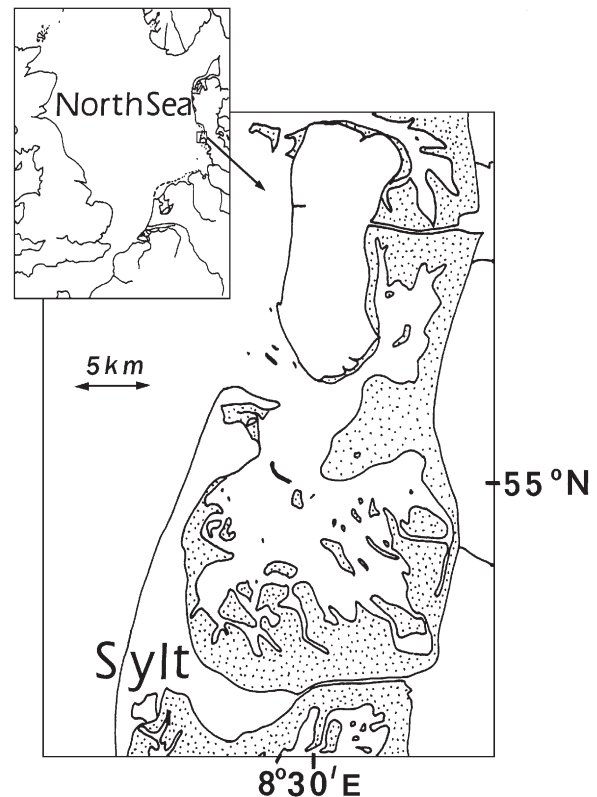


Fig. 1. Sylt-Rømø Bight situated between islands Sylt and Rømø in the northern Wadden Sea (eastern North Sea). Stippled area: intertidal areas

summer. The tidal range in the basin is, on average, 1.8 m, and the water residence time ranges between 19 and 29 d. The average depth of the Bight at mean high tide is approximately 4.2 m. Nutrient concentrations in the Bight and fluxes between the sediments, mussel beds, seagrass beds and the overlying waters have received considerable attention over the past few decades (cf. Asmus & Asmus 1993, Asmus et al. 1994, 1995, H. Asmus & R. Asmus 1998, 2000, R. Asmus & H. Asmus 1998).

Plant and animal communities occur in various proportions on the different substrate types and tidal reaches. Sandy substrates are dominant in the Bight and cover a total area (inter- and subtidally) of about  $360.5 \text{ km}^2$ , while muddy substrates, seagrass, and mussel beds cover approximately 17.1, 15.2 and  $10.8 \text{ km}^2$  respectively (R. Asmus & H. Asmus 1998, Bayerl et al. 1998). The deep subtidal area ( $>5 \text{ m}$  depth) of about  $40 \text{ km}^2$  consists of a sandy bottom, but is poor in macrofauna (H. Asmus & R. Asmus 1998).

**Data base and model construction.** Data and information for constructing a quantified food web, which consisted of 56 living and 3 non-living compartments, were obtained from the literature as well as from unpublished information deposited at the Alfred

Wegener Institute, Wadden Sea Station Sylt, Germany. None of the standing stocks, the diet of the various heterotrophs, or the rates of flow between the components in the Bight were derived from modelling estimates, but are based entirely on empirical data and results presented in the numerous publications and data sources cited in the text. The concentrations and standing stocks of the non-living compartments, i.e. suspended particular organic carbon (SuspPOC), sediment particular organic carbon (SedPOC), and dissolved organic carbon (DOC), were taken from the studies of Asmus & Asmus (1993, 1998, 2000) and R. Asmus & H. Asmus (1998). Data on the biomass of sediment and pelagic bacteria were obtained from Kirchman et al. (1986), Schulz (1990) and Rusch et al. (2001). The biomass, rates of gross primary (GPP) and net primary (NPP) production of the 3 primary producer communities, namely phytoplankton, microphytobenthos and macrophytes were given by Asmus & Bauerfeind (1994) and R. Asmus et al. (1998). Average annual biomass estimates for the various macrofaunal and fish species and communities were extracted from the published literature (cf. Asmus 1987, 1994, Asmus & Asmus 1990, 1993, R. Asmus & H. Asmus 1998, H. Asmus et al. 1998, Hermann et al. 1998) and from unpublished information (H. Asmus pers. comm.). Bird numbers were obtained from Scheiffarth & Nehls (1997) and Nehls & Scheiffarth (1998).

Energy budgets were determined for each of the 3 auto- and 53 heterotrophic compartments identified in the Bight ecosystem. For primary producers, GPP was assumed equal to the sum of NPP and respiration, and the values of GPP were entered as inputs into the system. Exudation by phytoplankton is considered to be an important source of DOC in aquatic systems (Valiela 1995). We assumed that about 25% of the net photosynthetic production of phytoplankton entered the DOC pool in the Bight (Vegter & De Visscher 1984, Baird & Ulanowicz 1989), and about 2% of the macrophyte NPP (Sieburth & Jensen 1969, Brylinski 1977, Valiela 1995). Inputs into DOC originated mainly from exudates from algae and served as the food source for free-living bacteria.

Energy budgets were constructed for each heterotrophic compartment according to the balanced energy equation: consumption of food (C) = production (P) + respiration (R) + egestion (E) (Crisp 1971). Rates of consumption, production and respiration were obtained from the relevant literature, or calculated using appropriate ecological efficiencies such as the P/B (where B = biomass), P/R, P/C, P/Ass (where assimilation Ass = P + R) ratios. Consumption of some invertebrate groups was obtained from the relationship C = assimilation/assimilation efficiency (Baird & Milne 1981). Fish consumption was either obtained from the

literature or estimated from the empirical relationship  $C = 1.25(P + 2R)$  (Winberg 1956, Mann 1965). The metabolic and feeding rates of birds in the field were derived from the allometric equations provided by Nagy (1987) and consumption by carnivorous birds from Scheiffarth & Nehls (1997).

Diet composition for each component was derived from synthesis of published literature and local expert knowledge (Plagmann 1939, Ehlert 1964, Jacobsen 1967, Höfmann & Hörschelmann 1969, Fenchel & Koefoed 1976, de Vlas 1979, Fauchald & Jumars 1979, Jensen & Siegismund 1980, Heip et al. 1984, Pihl & Rosenberg 1984, Pihl 1985, Zwarts & Blomert 1992) and sources in Gätje & Reise (1998). Excess production and egestion by water column organisms (bacteria, zooplankton) were assumed to remain in suspension as particulate POC. Egesta of benthic invertebrates and fishes, and all nonutilised production of the benthos, were assumed to become sediment POC, which was considered as the energy source for benthic bacteria.

A carbon flow network was constructed for the Sylt-Rømø Bight consisting of 56 living and 3 non-living compartments. Biomass of each compartment was given in  $\text{mg C m}^{-2}$ , and the flows in the system in  $\text{mg C m}^{-2} \text{ d}^{-1}$ . The model was assumed to represent a steady state condition in the sense that the inputs (GPP or consumption) into each compartment of the network were balanced by corresponding outputs (i.e. respiration and NPP for autotrophs, and respiration, secondary production and egestion for heterotrophs). All values represent annual average conditions.

The main energy inputs into the system were considered to be GPP of the 3 autotrophic compartments, while other imports into the system were assumed to occur in those compartments whose energy intake could not be met by prey production. Exports from the system consisted of the production of those compartments not fully utilised such as fish and bird production, SuspPOC and resuspended SedPOC. Export of shell- and fin fishes by commercial exploitation was not given separately but included in the sum of the exports from each of the relevant compartments.

**Network analysis.** Network analysis consists of methods for the systematic assessment of ecological flow networks. We used the software package NETWRK 4.2a (Ulanowicz & Kay 1991) to perform the following analyses:

(1) Input/output analysis which measures the importance of the direct or indirect effect of any particular transformation or flow to any other compartment (or species) (Hannon 1973), and allows one to quantify the interdependence of compartments. A matrix of 'dependency' coefficients (Szyrmer & Ulanowicz 1987) provides information on the fraction of the energy that leaves Compartment *i* that is eventually ingested by

Compartment  $j$  over all direct and indirect pathways. This analysis computes the extended diet of a species (or compartment) which gives the degree to which the diet of any particular component depends directly and indirectly on any other compartment in the system.

(2) The average path length (APL) is a system descriptor that measures the average number of compartments that a unit of carbon passes through from its entry into the system until it leaves the system. The APL is defined by  $(TST-Z)/Z$ , where TST is the total system throughput (see below) and Z equals the sum of all exogenous inputs (Kay et al. 1989, Baird et al. 1991). The path length is expected to be higher in systems with high degrees of flow diversity and cycling (Christensen 1995).

(3) The average residence time (ART) of energy in the system is the ratio between the total system biomass and the sum of all outputs (respiration and exports) (Christensen 1995).

(4) The Lindeman spine transforms each complex network of trophic transfers into a concatenated food chain with discrete trophic levels. The Lindeman spine illustrates the amount of carbon that each trophic level receives from the preceding level, as well as the amount leaving it through respiration, export, detritus and the net production passed on to the next higher level. It also represents the recycled pool of detritus, imported organic matter and autotrophs from the first trophic level. The Lindeman spine allows calculation of the trophic efficiency for each level, i.e. the efficiency of transfer from one level to the next. The system trophic efficiency is computed as the logarithmic mean of the integer level efficiencies.

(5) The structure and magnitude of the cycling of carbon in an ecosystem is given by the number and length of cycles within the system and the fraction of total systems activity that is devoted to cycling. The Finn Cycling Index (FCI) gives the proportion of the flow in a system that is recycled (Finn 1976). TST is the sum of all flows in the system. The FCI is equal to  $T_c/TST$ , where  $T_c$  is the amount of system activity devoted to cycling. The FCI measures the retentiveness of a system. Network analysis also describes the structure of biogeochemical cycling through identification and enumeration of all simple cycles in the system. A simple cycle represents a series of transfers between compartments beginning and ending in the same compartment without going through the same compartment twice. The fluxes between compartments in a cycle are not necessarily equal. The smallest flux represents the weakest link of the cycle (or weak arc), and all cycles that share the same weakest link are grouped into a nexus. By grouping cycles according to their weakest link, one defines the domain of influence of each weak arc. The flows associated with each cycle

and nexus of cycles are also quantified in this analysis (Baird & Ulanowicz 1989, Baird et al. 1998).

(6) Various global system properties, or indices, based on information theory, reflect the complexity of organisation of the system (Ulanowicz 1986, 1997). System ascendancy (A) is a single measure of the activity and organisation of an ecosystem and is the product of both the size (TST) and the average mutual information (AMI, i.e. the degree of specialisation of flows in the network) (Ulanowicz 1986). Complex trophic structure and high system productivity enhance ascendancy. The development capacity (DC) is the product of TST and the flow diversity and can be demonstrated to be the upper limit of A. System overhead (O) is numerically represented by the difference  $DC - A$ , and represents the fraction of the DC which has not yet been organised (Bondini & Bondavalli 2002). The sum of the overheads is the difference between the ascendancy and its upper boundary, DC (Ulanowicz & Norden 1990). Redundancies, or parallel flows in the imports, exports, dissipations and internal exchanges all contribute to the total overhead. Ascendancy measures the efficiency and definitiveness by which energy transfers are made, whereas the overhead quantifies how inefficient and ambiguous the system performs on average. Internal ascendancy ( $A_i$ ) and internal developmental capacity ( $DC_i$ ) are functions of internal exchanges alone, and thus exclude exogenous transfers. Flow diversity, defined as  $DC/TST$ , encompasses both the numbers of interactions and the evenness of flows in the food web (Mann et al. 1989, Baird et al. 2004). Connectance is the weighted average number of flows out of compartments, with weighting based on relative magnitudes of those flows. Overall connectance includes all transfers, internal connectance characterises only internal exchanges, whereas food web connectance refers only to transfers among the living compartments in the system (Ulanowicz 1997).

Results from these analyses were compared to similar system level indices of other marine ecosystems reported in the literature. However, comparisons of ecosystems are complicated at different degrees of aggregation (Mann et al. 1989, Baird 1998). To overcome this, species in the Sylt-Rømø Bight ecosystem having the same mode of feeding and which obtain their food from common prey resources were grouped together, and a model consisting of 18 compartments was constructed (using the AGGREGATION subroutine) and subjected to network analysis. In this paper, comparisons are made between systems comprising between 15 and 18 compartments, including 3 non-living ones in each. The same currency, carbon, was used for biomass and flows, and rates were expressed in  $\text{mgC m}^{-2} \text{d}^{-1}$  in all cases. The software routines (NETWRK 4.2a and AGGREGATION) that perform

all the above-mentioned analyses and its supporting documentation may be downloaded from [www.cbl.umces.edu/~ulan/ntwk/network.html](http://www.cbl.umces.edu/~ulan/ntwk/network.html).

## RESULTS

### Trophic structure and input/output analysis

The construction of the food web of the Sylt-Rømø Bight ecosystem is largely based on published and unpublished information on the energetics and biomass of the 56 living compartments and the standing stocks of the 3 non-living compartments (see Table 1) and on the diet composition of each living compartment (see Table 2). Where necessary, estimates of the amount of energy consumed, rates of respiration, production and egestion by heterotrophs were calculated using commonly used ecological efficiencies; none of the results were obtained through simulation modeling. The data in Table 1 are annual average values and show the energy demand of each compartment, that part of its production available to other consumers in the system, dissipative energy or respiration, and egesta which play an important role in the detrital food web. Excess production and egested material of the meio- and macrobenthos are largely retained within the system, recycled, and utilised as detritus. Fractions of the standing stocks of SuspPOC (57) and SedPOC (58) are exported by tidal action, whereas there appears to be a shortage of internally derived DOC. Phytoplankton production (Compartment 1) (Table 1) in the Bight, estimated at  $247 \text{ mgC m}^{-2} \text{ d}^{-1}$ , is too low to satisfy consumer demand and approximately  $160 \text{ mgC m}^{-2}$  of phytoplankton is assumed to be imported by tidal currents into the Bight on a daily annual average basis. Excess, or nonutilised, production of microphytobenthos (Compartment 2) and macrophytes are considered to be incorporated into the sediment POC pool and exported respectively. Similarly, very little zooplankton (Compartment 5) production is consumed and approximately 90% of zooplankton production is exported from the system. Birds have no predators in the Bight, while predation rates on fishes by top predators could not be quantified. We thus, for the purpose of this study, assumed their production to be exported. The diet composition of each component in the system are given in Table 2 together with the rates of flow from Prey  $i$  to Consumer  $j$ , the total amount of Prey  $i$  consumed by Predator  $j$ , as well as the imports to and exports from the relevant compartments.

The total standing stock in the system amounts to about  $35 \text{ gC m}^{-2}$ , and the total productivity (i.e. the sum of P of all living Compartments 1 to 56) to  $1266 \text{ mgC m}^{-2} \text{ d}^{-1}$ . Plants alone (Compartments 1, 2

and 3) contribute about 11.8% (i.e.  $4 \text{ gC m}^{-2}$ ) to the total standing stock and approximately 72.8% (i.e.  $921.31 \text{ mgC m}^{-2} \text{ d}^{-1}$ ) to the total productivity of the system. The biomass and secondary production of the benthos (Compartments 6 to 29, 55, 56) are  $30.6 \text{ gC m}^{-2}$  and  $266 \text{ mgC m}^{-2} \text{ d}^{-1}$  respectively, and comprise 87.6 and 21% of the total system biomass and production respectively. The biomass of fishes and birds (Compartments 30 to 54) is about  $178 \text{ mgC m}^{-2}$  (or 0.5% of the total) and their collective production approximately  $0.5 \text{ mgC m}^{-2} \text{ d}^{-1}$  (or 0.04% of the total system production). Biomass and production of free-living bacteria and zooplankton (Compartments 4 and 5 respectively) amount to  $21 \text{ mgC m}^{-2}$  (0.06% of total) and  $77.6 \text{ mgC m}^{-2} \text{ d}^{-1}$  (6.1% of total) respectively. The algal production in the Bight is dominated by microphytobenthos despite their relatively lower biomass than phytoplankton and macrophytes (see Table 1). Conversely, the high biomass of the benthos contributes only 21% to the total productivity of the system, compared to the high NPP rate of the autotrophs in the system.

The P/B ratio, considered to be a system attribute (Baird et al. 1991), was calculated for the whole system as  $0.036 \text{ d}^{-1}$ , which falls well within the range reported for various other bays and estuaries, and is very close the P/B ratio of 0.04 calculated for the Ems Estuary which has the same climatic environment as the Bight (cf. Baird et al. 1991, Baird 1998). The NNP efficiency (i.e. the fraction NPP directly consumed by herbivores) of 57.5% is relatively high compared to that in other systems, while the 1.4:1 ratio of herbivory to detritivory falls within the range reported by Baird et al. (1991) and Baird (1998).

The flow network provides information on the direct trophic interactions and, as such, reveals much about the way the system functions. However, NETWRK calculates a matrix of 'total dependency coefficients' which illustrates the indirect diet of each compartment or species (Szyrmer & Ulanowicz 1987). This routine uses the quantified biomasses and flows of the model and calculates the degree to which the diet of any one species depends, directly and indirectly, upon the production of any other component in the ecosystem. The matrix of 'dependency coefficients' (see Appendix 1: MEPS Electronic Supplement at [www.int-res.com/journals/suppl/baird\\_appendix.xls](http://www.int-res.com/journals/suppl/baird_appendix.xls)) shows the relationship of each prey item with each predator/consumer and can be interpreted in 2 ways: (1) the data in each row indicate the percentage of each predator's total intake that is dependent on any particular prey; (2) of more interest, each vertical column defines the extent of the diet of that consumer species. For example, Column 6 shows that 87% of *Hydrobia ulvae*'s diet comprises microphytobenthos (Compartment 2), 15%



Table 1. Biomass (mg C m<sup>-2</sup>) and energetics of all compartments in food web network. Nos. in parentheses: trophic position of each compartment/species. GPP: gross primary production; NPP: net primary production. Production, respiration, egestion and consumption of heterotrophs given in mg C m<sup>-2</sup> d<sup>-1</sup>; standing stocks of non-living compartments in mg C m<sup>-2</sup>

Compartment	Name	Parameter				
		Biomass	GPP	Respiration	NPP	
<b>Primary producers</b>						
1	Phytoplankton (1)	1040	437.34	190.14	247.29	
2	Microphytobenthos (1)	136.20	977.35	339.05	638.30	
3	Macrophytes (1)	2960	81.18	45.46	35.72	
<b>Heterotrophs</b>						
		Biomass	Production	Respiration	Egestion	Consumption
4	Free-living bacteria (2)	9.79	76.10	70.46	5.63	152.19
5	Zooplankton (2)	11.19	1.48	0.41	2.68	4.57
<b>Macrobenthos</b>						
6	<i>Hydrobia ulvae</i> (2.13)	1888	7.38	11.37	55.00	73.75
7	<i>Littorina littorea</i> (2.13)	67.90	0.14	0.42	0.84	1.40
8	<i>Arenicola marina</i> (2.45)	5913	42.37	39.42	200.66	282.45
9	<i>Scoloplos armiger</i> (2.45)	1030.23	0.98	7.48	19.51	27.97
10	Capitellidae (2.50)	25.70	0.14	0.59	1.46	2.19
11	Oligochaeta (2.50)	84.00	0.23	2.24	1.13	3.60
12	<i>Heteromastus filiformis</i> (2.50)	72.00	0.39	0.75	5.03	6.17
13	<i>Lanice conchilega</i> (2.01)	63.45	0.33	0.64	0.29	1.26
14	<i>Nereis diversicolor</i> (2.26)	193.48	0.56	2.27	5.93	8.76
15	<i>Pygospio elegans</i> (2.01)	127.71	0.47	2.18	0.93	3.58
16	<i>Corophium arenarium</i> (2.13)	52.05	0.14	0.33	0.05	0.52
17	<i>Corophium volutator</i> (2.13)	257.15	1.07	5.03	1.22	7.32
18	<i>Gammarus</i> spp. (2.21)	2.24	0.01	0.06	0.02	0.09
19	<i>Mytilus edulis</i> (2.01)	2030.00	2.00	11.01	1.84	14.85
20	<i>Cerastoderma edule</i> (2.01)	11400.00	56.80	17.81	209.39	284.00
21	<i>Mya arenaria</i> (2.01)	2076.81	4.54	10.56	7.60	22.70
22	Small polychaetes (2.51)	199.00	0.91	3.15	1.60	5.66
23	<i>Tharyx killariensis</i> (2.50)	24.00	0.13	0.25	0.26	0.64
24	<i>Macoma balthica</i> (2.13)	2652.00	21.86	4.07	115.40	141.33
25	Phyllodocidae (3.13)	10.00	0.03	0.30	0.04	0.37
26	Small crustaceans (2.24)	333.00	1.34	5.64	1.80	8.83
27	<i>Carcinus maenas</i> (2.37)	34.15	0.14	0.22	0.48	0.84
28	<i>Crangon crangon</i> (3.01)	30.96	0.340	1.170	0.340	1.850
29	<i>Nephtys</i> spp. (3.22)	484.28	5.34	5.07	18.39	28.80
<b>Fishes</b>						
30	<i>Pomatoschistus microps</i> (3.32)	3.17	0.03	0.07	0.61	0.71
31	<i>Pomatoschistus minutus</i> (3.11)	0.47	0.01	0.01	0.16	0.18
32	<i>Pleuronectes platessa</i> (3.16)	0.03	0.0002	0.0003	0.0009	0.0014
33	<i>Pleuronectes flesus</i> (3.37)	0.004	0.00206	0.0043	0.02414	0.0305
34	<i>Clupea harengus</i> (3.00)	0.0073	0.00006	0.00012	0.00006	0.00024
35	<i>Merlangius merlangus</i> (3.74)	0.53	0.003	0.008	0.014	0.025
36	<i>Gadus morrhua</i> (3.07)	0.02	0.00011	0.00031	0.00018	0.0006
37	<i>Myoxocephalus scorpio</i> (3.07)	0.02	0.00011	0.00023	0.00016	0.0005
<b>Birds</b>						
38	<i>Tadorna tadorna</i> (3.14)	18.60	0.05	1.92	0.49	2.46
39	<i>Somateria mollissima</i> (3.03)	48.00	0.13	5.09	1.30	6.52
40	<i>Haematopus ostralegus</i> (3.13)	10.90	0.04	1.46	0.37	1.87
41	<i>Recurvirostra avosetta</i> (3.14)	0.90	0.01	0.15	0.04	0.20
42	<i>Pluvialis apricaria</i> (3.28)	3.20	0.01	0.28	0.07	0.36
43	<i>Calidris canutus</i> (3.03)	2.70	0.01	0.53	0.14	0.68
44	<i>Calidris alpina</i> (3.13)	4.60	0.01	0.58	0.15	0.75
45	<i>Limosa lapponica</i> (3.17)	2.70	0.01	0.43	0.11	0.55
46	<i>Numenius arquata</i> (3.18)	4.90	0.01	0.30	0.08	0.39
47	<i>Larus ridibundus</i> (3.28)	2.10	0.01	0.23	0.06	0.30
48	<i>Larus canus</i> (3.05)	2.20	0.01	0.22	0.06	0.28
49	<i>Larus argentatus</i> (3.11)	7.70	0.02	0.60	0.16	0.78
50	Other birds [assumed					
51	intertidal benthic feeders] (3.15)	6.20	0.01	0.46	0.13	0.60
51	<i>Anas platyrhynchos</i> (3.37)	8.80	0.01	0.37	0.22	0.60
52	<i>Anas acuta</i> (2.00)	2.60	0.01	0.21	0.12	0.34
53	<i>Anas penelope</i> (2.00)	38.00	0.08	2.52	1.40	4.00
54	<i>Branta bernicla</i> (2.00)	10.00	0.02	0.50	0.28	0.80
55	Sediment bacteria (2.00)	625.00	98.10	109.00	38.15	245.25
56	Meiobenthos (2.00)	944.52	20.70	78.77	35.87	135.34
<b>Non-living compartments</b>						
57	Suspended POC (1)	167.44				
58	Sediment POC (1)	19000				
59	DOC (1)	62.02				

sediment bacteria (Compartment 55), and 21% Sed-POC (Compartment 58). However, it receives sustenance indirectly from virtually all other compartments, albeit a very small fraction in many cases. In fact, the matrix of 'dependency coefficients' (Appendix 1) shows that most species (with the exceptions of the autotrophs, free-living bacteria, zooplankton, 3 species of herbivorous birds and DOC) are indirectly dependent on most other species, illustrating the existence of a very complex and interdependent food web in the Bight. Because the same carbon may pass through several compartments before it is consumed by a particular consumer, the sum of any of the columns will usually exceed 100% (Ulanowicz & Kay 1991). According to Baird & Ulanowicz (1989), the sum of any column is related to the trophic position of that species.

The effective trophic position of each species is shown in Table 3. Knowing the dietary composition of the species in the ecosystem, the trophic analysis routine of network analysis yields the Lindeman transformation matrix in which each species or compartment is assigned to an average trophic position (Ulanowicz & Kemp 1979). The average, or effective, trophic level of each consumer is calculated from the distribution of the trophic levels of its prey. These trophic-position values have been defined by Levine (1980). For example, a population that obtains 60% of its energy from plants as a herbivore (at Trophic Level 2), and the balance (40%) as a primary carnivore (at Level 3) would have an effective trophic level of 2.4 ( $= 0.6 \times 2 + 0.4 \times 3$ ). The Lindeman trophic analysis keeps track of feeding pathways upon which any given population within the network depends, apportions species to trophic levels,

and maps the flow model into the simplified Lindeman spine consisting of discrete trophic levels (cf. Ulanowicz & Kemp 1979, Baird & Ulanowicz 1989, Kay et al. 1989, Heymans & Baird 2000). The results of the trophic aggregation of the Sylt-Rømø Bight carbon-flow model was mapped into the simplified Lindeman spine and is illustrated in Fig. 2. When the detritus pool is separated from the primary producers (top graph of Fig. 2) detritivory exceeds herbivory by a ratio of 1.44:1, about 60% of the total energy passed from the 1st to the 2nd trophic level comprises recycled material, and 94% of all detritus inputs into the detrital pool is derived from recycling within the system. Returns from all the trophic levels are shown in Fig. 2, as well as the contribution by plants to the detritus pool. The canonical exports and respirations values leaving each trophic level are also shown.

Primary producers and the detritus pool are combined in the lower graph of Fig. 2 in order to evaluate the trophic efficiencies, which are indicated in each box (representing an integer trophic level). We identified 8 trophic levels with a progressive decline in trophic efficiencies from lower to higher levels, with the exception of Level 3, which showed a lower efficiency than Levels 4 and 5. This anomaly can be ascribed to the relatively high returns to the detrital pool (77% of total intake at Level 3). Despite the extensive trophic chain, the highest effective trophic level of any species is 3.74 (for the whiting). However, very little energy is obtained from Level 4 and higher, so that the magnitude of such high-level carnivory is insignificant (Baird & Ulanowicz 1989). The trophic efficiency of the system, i.e. the efficiency with which

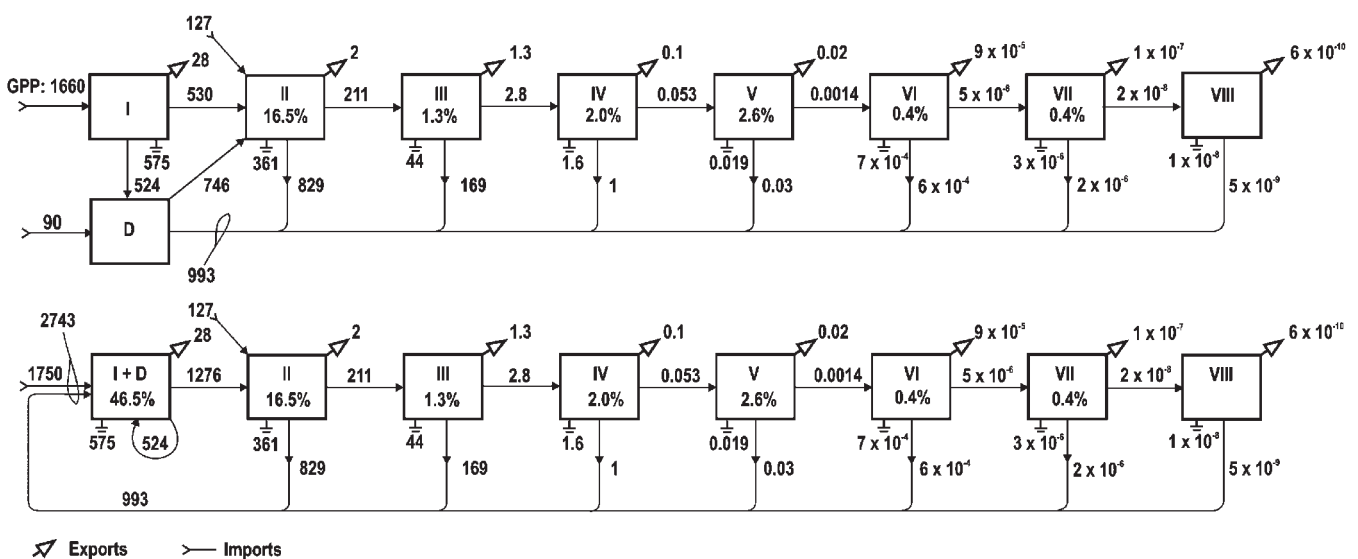


Fig. 2. Trophic aggregation of Sylt-Rømø network. GPP: gross primary production; roman numerals: trophic levels; D: detritus pool. Flow rates are in  $\text{mg C m}^{-2} \text{d}^{-1}$ . In top graph autotrophs and detritus are separated; in bottom graph autotrophs are combined with detritus pool

energy is transferred within the system, is 2.61%. There are 2 other indices which also reflect the trophic function of an ecosystem, average path length (APL) and average residence time (ART). Their respective annual averaged values were calculated to be 2.60 and 19.17 d respectively. This means that a unit of carbon is, on average, transferred by less than 3 steps before it exits the system, while the residence of biological energy in the Bight is approximately 19 d.

### Structure and magnitude of cycling

The cycling of energy and material in natural ecosystems is an inherent important process in ecosystem functions (Odum 1969), and contributes to their autonomous behaviour (Ulanowicz 1986). Below, we discuss 3 aspects of cycling (1) the cycling structure, i.e. the number of cycles and their distribution as a function of cycle length (Ulanowicz 1983), (2) the amount of material cycled over various path lengths, and (3) the amount of material recycled expressed by the FCI.

#### Cycling structure

We have identified in this analysis a total of 1197 cycles, through which 1162 mgC m<sup>-2</sup> d<sup>-1</sup> of the TST is recycled on a daily basis. Cycles sharing the same weak arc are grouped into nexus and the frequency of cycles per nexus are given in Table 4. The table shows, for example, that 170 cycles, or 14.2% of all cycles, occurred in 10 nexus each containing 17 cycles but sharing a different weak arc in each of them. The greatest proportion of cycles, i.e. >50%, are clustered in nexus containing 19 cycles or more (Table 4). A large nexus generally contains longer pathways involving a number of compartments and species occupying higher trophic positions (i.e. >3; Table 3). In contrast, a nexus containing fewer cycles invariably involves benthic compartments, particularly sediment bacteria (Compartment 55), meiobenthos (Compartment 56), and sediment POC (Compartment 58). The paucity of nexus with few cycles and the greater frequency occurrence of large-cycle nexus indicate the presence of a rather complex cycling structure in the Bight.

#### Amount cycled

Table 5 shows the amount of C cycled through cycles of different path lengths. It shows that cycles comprising 9 compartments are involved in cycling, although the amount cycled through pathways of more than 4

compartments is rather small at about 0.9 mgC m<sup>-2</sup> d<sup>-1</sup> (i.e. the sum of cycled flow through pathways >4). Much of the cycled material (54.8% or 637 mgC m<sup>-2</sup> d<sup>-1</sup>), however, is cycled through short cycles involving only 2 compartments, with either benthic bacteria (Compartment 55) or sediment POC (Compartment 58) participating in most of the cycling and linking with a benthic compartment (Compartments 6 to 29) to complete the cycle. Cycles with a path length of 3 compartments recycle 515 mgC m<sup>-2</sup> d<sup>-1</sup> (or 44.3% of all cycled material); they also involve compartments 55 and 58 to a large degree, and fishes and birds in addition to Benthic Compartments 6 to 29. The predominance of short path lengths over which 99% of the recycling take place indicates the importance of benthic interactions in the Bight. Short pathways are also indicative of fast rates of cycling (Baird & Ulanowicz 1993), in contrast to systems where cycling occurs over longer path ways (Baird et al. 1991).

#### Amount recycled

The FCI, calculated as 17.21%, indicates that about 17% of the total amount of energy flow in the system is recycled on a daily basis.

### System level properties

The system level properties of the Bight were derived from the network analysis, and are given in Table 6. The TST approximated 6752 mgC m<sup>-2</sup> d<sup>-1</sup>, the DC 32946 mgC m<sup>-2</sup> d<sup>-1</sup>, and A 12793 mgC m<sup>-2</sup> d<sup>-1</sup>. The difference between the realised structure (or A) of the system and its upper-bound DC, is the sum of the overheads of imports, exports, respiration and redundancy (Ulanowicz 1986, Heymans & Baird 2000). Overheads, according to Ulanowicz (1986), provide a limit to ascendancy and at the same time reflect the 'reserve strength' of the system to counter perturbations. The relative ascendancy (A/DC) and the relative internal ascendancy (A<sub>i</sub>/DC<sub>i</sub>) ratios, dimensionless ratios and suitable indices for comparing different ecosystems (Mann et al. 1989, Baird et al. 1991, 1998) were respectively calculated as 38.8 and 36.8%. Since A, DC and the overheads are strongly influenced by TST, normalised values of A, DC, and the overheads can be derived by dividing them by TST to remove the singular effect of TST (Baird & Ulanowicz 1989). The normalised A/DC ratio was calculated as 38.7% (Table 6) which did not differ significantly from either the A/DC or A<sub>i</sub>/DC<sub>i</sub> ratios. The internal redundancy ratio (R<sub>i</sub>/DC<sub>i</sub>), considered to be a measure of system stability (Rutledge et al. 1976, Baird et al. 1998), approximated 62.3%.



Other system level properties, e.g. connectance indices and flow diversity, are listed in Table 6. Of interest is the flow diversity index (DC/TST), a measure of the number and evenness of interactions in the system, calculated at a rather high value of 4.88 compared to other ecosystems in Table 7. The higher the value of this ratio, the larger the number of interactions in the flow network. There does not appear to be large differences between the overall connectance index (2.28) and food web connectance (2.20) (Table 6). The small differences between these connectance indices indicate the relatively important role of the non-living

compartments in carbon flow in the system. The higher inter-compartmental connectance index, which characterises only internal exchanges, points to high levels of internal connections, as also reflected in the complex cycling structure of the Bight.

The 2 other indices in Table 6, the average path length (APL) and the average residence time (ART), have been already explained in the first subsection of 'Results'.

The aggregated model of 18 compartments is illustrated in Fig. 3 showing which of the original 59 compartments grouped together using the AGGREGA-

Table 2. Dietary matrix for Sylt-Rømø Bight ecosystem. No.: Compartment no.; ETP: effective trophic position of each compartment/species; TPM: total predation mortality; I/E: import/export; Total consump.: total consumption of each consumer group. All flow units are in  $\text{mgC m}^{-2} \text{d}^{-1}$

No. Prey (i)	Consumers (j):		Macrobenthos																		
	ETP	Free-living bacteria 4	Zooplankton 5	<i>Hydrobia ulvae</i> 6	<i>Littorina littorea</i> 7	<i>Arenicola marina</i> 8	<i>Scoloplos armiger</i> 9	Capitellidae 10	Oligochaeta 11	<i>Heteromastus filiformis</i> 12	<i>Lanice conchilega</i> 13	<i>Nereis diversicolor</i> 14	<i>Pygospio elegans</i> 15	<i>Corophium arenarium</i> 16	<i>Corophium volutator</i> 17	<i>Gammarus</i> spp. 18	<i>Mytilus edulis</i> 19	<i>Cerastoderma edule</i> 20	<i>Mya arenaria</i> 21	Small polychaetes 22	
1 Phytoplankton	1.00		4.57								1.07	0.88	3.04					12.62	241.4	19.3	1.13
2 Microphytobenthos	1.00			55.31	1.05	28.25	2.80					0.88		0.39	5.48	0.02					0.28
3 Macrophytes	1.00															0.05					
4 Free-living bacteria	2.00										0.01		0.04				0.15	2.84	0.23		
5 Zooplankton	2.00																				
6 <i>Hydrobia ulvae</i>	2.13											0.15				0.01					1.13
7 <i>Littorina littorea</i>	2.13																				
8 <i>Arenicola marina</i>	2.45																				
9 <i>Scoloplos armiger</i>	2.45																				
10 Capitellidae	2.50																				
11 Oligochaeta	2.50																				
12 <i>Heteromastus filiformis</i>	2.50																				
13 <i>Lanice conchilega</i>	2.01																				
14 <i>Nereis diversicolor</i>	2.26																				
15 <i>Pygospio elegans</i>	2.01											0.07									
16 <i>Corophium arenarium</i>	2.13																				
17 <i>Corophium volutator</i>	2.13																				
18 <i>Gammarus</i> spp.	2.21																				
19 <i>Mytilus edulis</i>	2.01																				
20 <i>Cerastoderma edule</i>	2.01																				
21 <i>Mya arenaria</i>	2.01																				
22 Small polychaetes	2.51											0.20									
23 <i>Tharyx killariensis</i>	2.50																				
24 <i>Macoma balthica</i>	2.13																				
25 Phyllodocidae	3.13																				0.01
26 Small crustaceans	2.24																				
27 <i>Carcinus maenas</i>	2.37																				
28 <i>Crangon crangon</i>	3.01																				
29 <i>Nephtys</i> spp.	3.22																				
55 Sediment bacteria	2.00			9.22	0.18	127.50	12.59	1.09	1.80	3.08		0.88		0.07	0.92	0.01					1.30
56 Meiobenthos	2.00											0.88									0.28
57 Suspended POC	1.00										0.18	0.88	0.50				2.08	39.76	3.17		0.23
58 Sediment POC	1.00			9.22	0.18	127.10	12.59	1.10	1.80	3.09		3.94		0.06	0.92	0.01					1.30
59 DOC	1.00	152.19																			
Total consump.		152.19	4.57	73.75	1.41	282.85	27.98	2.19	3.60	6.17	1.26	8.76	3.58	0.52	7.32	0.10	14.85	284.00	22.70		5.66

(Table continued on next page)

Table 2 (continued)

Consumers (j):		Macrobenthos							Fishes							Birds			
No.	Prey (i)	ETP	<i>Tharyx killariensis</i>	<i>Macoma balthica</i>	Phyllodoctidae	Small crustaceans	<i>Carcinus maenas</i>	<i>Crangon crangon</i>	<i>Nephtys</i> spp.	<i>Pomatoschistus microps</i>	<i>Pomatoschistus minutus</i>	<i>Pleuronectes platessa</i>	<i>Pleuronectes l. flesus</i>	<i>Clupea harengus</i>	<i>Merlangius merlangus</i>	<i>Gadus morhua</i>	<i>Myoxocephalus scorpio</i>	<i>Tadorna tadorna</i>	<i>Somateria mollissima</i>
			23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39
1	Phytoplankton	1.00	60.80																
2	Microphytobenthos	1.00	35.33		2.65	0.17													
3	Macrophytes	1.00			1.94	0.38													
4	free-living bacteria	2.00																	
5	Zooplankton	2.00								0.11				0.0002					
6	<i>Hydrobia ulvae</i>	2.13		0.37		0.08	0.36						0.0001					1.96	
7	<i>Littorina littorea</i>	2.13																	0.03
8	<i>Arenicola marina</i>	2.45										0.0004	0.0002						
9	<i>Scoloplos armiger</i>	2.45					0.20	0.20	0.21	0.01									
10	Capitellidae	2.50						0.10											
11	Oligochaeta	2.50					0.13	0.15		0.01									
12	<i>Heteromastus filiformis</i>	2.50				0.03	0.05	0.05	0.01	0.01									
13	<i>Lanice conchilega</i>	2.01				0.05			0.01										0.03
14	<i>Nereis diversicolor</i>	2.26							0.04									0.20	
15	<i>Pygospio elegans</i>	2.01							0.03	0.02									
16	<i>Corophium arenarium</i>	2.13							0.01										
17	<i>Corophium volutator</i>	2.13							0.05	0.003								0.28	
18	<i>Gammarus</i> spp.	2.21																	
19	<i>Mytilus edulis</i>	2.01																	2.00
20	<i>Cerastoderma edule</i>	2.01					0.20				0.0007							0.02	3.80
21	<i>Mya arenaria</i>	2.01																	0.65
22	Small polychaetes	2.51						0.10		0.001									
23	<i>Tharyx killariensis</i>	2.50							0.01	0.02									
24	<i>Macoma balthica</i>	2.13					0.23				0.0002	0.0001							0.61
25	Phyllodoctidae	3.13																	
26	Small crustaceans	2.24							0.07			0.0001							
27	<i>Carcinus maenas</i>	2.37							0.04			0.03		0.011	0.0003	0.0003			0.10
28	<i>Crangon crangon</i>	3.01					0.03		0.07			0.0001		0.013	0.0003	0.0002			
29	<i>Nephtys</i> spp.	3.22																	
30	<i>Pomatoschistus microps</i>	3.32													0.001				
31	<i>Pomatoschistus minutus</i>	3.11													0.001				
32	<i>Pleuronectes platessa</i>	3.16																	
33	<i>Pleuronectes flesus</i>	3.37																	
34	<i>Clupea harengus</i>	3.00																	
35	<i>Merlangius merlangus</i>	3.74																	
36	<i>Gadus morhua</i>	3.07																	
37	<i>Myoxocephalus scorpio</i>	3.07																	
38	<i>Tadorna tadorna</i>	3.14																	
39	<i>Somateria mollissima</i>	3.03																	
40	<i>Haematopus ostralegus</i>	3.13																	
41	<i>Recurvirostra avosetta</i>	3.14																	
42	<i>Pluvialis apricaria</i>	3.28																	
43	<i>Calidris canutus</i>	3.03																	
44	<i>Calidris alpina</i>	3.13																	
45	<i>Limosa lapponica</i>	3.17																	
46	<i>Numenius arquata</i>	3.18																	
47	<i>Larus ridibundus</i>	3.28																	
48	<i>Larus canus</i>	3.05																	
49	<i>Larus argentatus</i>	3.11																	
50	Other birds	3.15																	
51	<i>Anas platyrhynchos</i>	3.37																	
52	<i>Anas acuta</i>	2.00																	
53	<i>Anas penelope</i>	2.00																	
54	<i>Branta bernicla</i>	2.00																	
55	Sediment Bacteria	2.00	0.32	17.67		2.12	0.08	0.28											
56	Meiobenthos	2.00						0.17	8.20	0.16	0.01								
57	Suspended POC	1.00		9.89															
58	Sediment POC	1.00	0.32	17.67		2.07	0.05	0.23	20.00										
59	DOC	1.00																	
	Total consump.		0.64	141.36	0.37	8.78	0.87	1.85	28.80	0.71	0.18	0.0014	0.03048	0.00024	0.025	0.0006	0.0005	2.46	7.22

<i>Haematopus ostralegus</i>	<i>Recurvirostra avosetta</i>	<i>Pluvialis apricaria</i>	<i>Calidris canutus</i>	<i>Calidris alpina</i>	<i>Limosa lapponica</i>	<i>Numenius arquata</i>	<i>Larus ridibundus</i>	<i>Larus canus</i>	<i>Larus argentatus</i>	Other birds	<i>Anas platyrhynchos</i>	<i>Anas acuta</i>	<i>Anas penelope</i>	<i>Branta bernicla</i>	Sediment Bacteria	Meiobenthos	Suspended POC	Sediment POC	DOC	TPM	I/E
40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59		
																			61.82	406.63	160 (I)
																44.68		461.03		638.32	
												0.34	4.00	0.80					0.71	8.22	27.5 (E)
																	72.83	5.83		81.93	
																	2.68			2.79	1.37 (E)
	0.16	0.17		0.52						0.05								57.42		62.38	
0.006									0.003									0.941		0.98	
0.48					0.15	0.114	0.16			0.16								241.97		243.04	
					0.026		0.03				0.20							19.63		20.50	
																		1.50		1.60	
																		1.07		1.36	
							0.0003				0.10							5.17		5.41	
				0.02	0.002		0.02											0.48		0.61	
	0.016				0.001			0.006	0.008		0.20							5.86		6.33	
				0.03														1.25		1.40	
				0.02													0.16			0.19	
	0.02			0.08				0.007	0.012	0.01								1.83		2.29	
																		0.03		0.03	
																		1.84		3.84	
1.32		0.55		0.29	0.204	0.03	0.212	0.15	0.30									258.89		265.97	
						0.05			0.06									11.24		12.00	
	0.12																	2.09		2.51	
																		0.36		0.39	
0.04		0.13		0.07	0.05	0.03	0.052	0.59										135.34		137.15	
																		0.06		0.07	
	0.03		0.09							0.01	0.05							2.89		3.14	
																		0.48		0.66	
0.002					0.0056			0.002										0.56		0.68	
	0.04			0.01	0.0136	0.02	0.013	0.015	0.01	0.05								23.58		23.76	
																		0.61		0.61	0.03 (E)
																		0.16		0.17	0.005 (E)
																		0.001			0.0002 (E)
																		0.02			0.00206 (E)
																		0.0001			0.00006 (E)
																		0.014			0.003 (E)
																		0.0002			0.00011 (E)
																		0.0002			0.00011 (E)
																		0.49			0.05 (E)
																		1.30			0.13 (E)
																		0.37			0.04 (E)
																		0.04			0.01 (E)
																		0.07			0.01 (E)
																		0.14			0.01 (E)
																		0.15			0.01 (E)
																		0.11			0.01 (E)
																		0.08			0.01 (E)
																		0.06			0.01 (E)
																		0.06			0.01 (E)
																		0.16			0.02 (E)
																		0.13			0.01 (E)
																		0.22			0.01 (E)
																		0.12			0.01 (E)
																		1.40			0.08 (E)
																		0.28			0.02 (E)
																		84.53		263.64	
																		46.83		56.36	
																				56.69	19 (E)
															245.00	90.68				537.33	841 (E)
																				152.19	0.47 (E)
1.85	0.20	0.36	0.68	0.76	0.55	0.39	0.34	0.29	0.78	0.60	0.60	0.34	4.00	0.80	245.00	135.36	75.67	1378.70	62.53		

Table 3. Effective trophic position of species or species groups in Sylt-Rømø Bight ecosystem. Trophic positions and compartments as in Table 1

Trophic position	Compartments
1	1, 2, 3, 57, 58, 59
2.0–2.19	4, 5, 6, 7, 13, 15, 16, 17, 19 20, 21, 24, 52, 53, 54, 55, 56
2.2–2.39	14, 18, 26, 27
2.4–2.59	8, 9, 10, 11, 12, 22, 23
2.6–2.79	
2.8–2.99	
3.0–3.19	25, 28, 31, 32, 34, 36, 37, 38 39, 40, 41, 43, 44, 45, 46, 48, 49, 50
3.2–3.39	29, 30, 33, 42, 47, 51
3.4–3.59	
3.6–3.79	35
3.8–3.99	

TION subroutine, as well as the main energy flow pathways in the system. Results from NETWRK based on the aggregated flow model pertaining to system level attributes were used for comparative purposes with other ecosystems. Network analysis results of the aggregated flow network showed that the TST of both the 59- and 18-compartment networks remained stable at  $6752 \text{ mg C m}^{-2} \text{ d}^{-1}$ , that DC and A were 5.8 and 2.6% less than for the 59 compartment model respectively,

Table 4. Percentage distribution of cycles per nexus in the Sylt-Rømø Bight network

Cycles/nexus	%	No. of cycles
1	2.84	34
2	9.36	112
3	0.25	3
4	3.01	36
5	0.42	5
9	1.50	18
6	0.50	6
10	2.51	30
11	0.92	11
12	4.01	48
13	1.09	13
16	1.34	16
17	14.20	170
18	7.52	90
19	1.59	19
20	3.34	40
22	1.84	22
25	2.09	25
30	2.51	30
40	3.34	40
46	3.84	46
48	8.02	96
39	3.26	39
76	6.35	76
77	6.43	77
95	7.94	95
Total	100	1197

Table 5. Amount of material ( $\text{mg C m}^{-2} \text{ d}^{-1}$ ) cycled through loops of varying path lengths (i.e. no. of compartments)

Path length	$\text{mg C m}^{-2} \text{ d}^{-1}$	%
1	0	–
2	637.0	54.82
3	515.0	44.32
4	9.2	0.79
5	0.5	0.04
6	0.3	0.03
7	7.60E-05	6.54E-06
8	5.50E-07	4.73E-08
9	9.90E-11	8.52E-12
Sum of cycled flow	1162.0	100.00

and that redundancy,  $DC_i$ , and  $A_i$  declined by 12.4, 9.4 and 4.2% respectively. The fact that the TST remained stable indicates that the aggregation procedure did not affect the calculated magnitude of the system's total activity. Considering that the DC of a network is derived from its TST multiplied by the diversity of its constituent exchanges, and that A represents the amount of capacity that appears as a coherent structure (Baird & Ulanowicz 1989), the slightly smaller values derived for the 18-compartment network are to be expected because of the lesser number of interactions in the smaller model. This is also the reason for the lower food web connectance and flow-diversity values between the 2 networks, as shown in Tables 6 & 7. Although the number of cycles identified in the 59-compartment model exceeds those in the aggregated model by 1090 as a result of fewer compartment and possible exchanges between them, the FCI index remained constant at 17.3%. Justification for the aggregation and comparison with other systems of approximately the same number of compartments thus exists.

## DISCUSSION

This study contributes to the growing interest and body of literature on ecosystem structure and function. One way of assessing the function of an ecosystem is to develop energy or material flow networks that depict not only the interactions between the components of the system, but also the magnitude of flows between them. Results from the analysis of these networks not only shed light on the behaviour of the system, but may also be used for comparative purposes over spatial and temporal scales. The flow-model developed for the Sylt-Rømø Bight includes only 7 conventional community guilds (Compartments 1, 2, 3, 4, 5, 55 and 56: Table 1), while the other 49 living compartments are treated and represented as species or genera levels. The model thus largely illustrates interactions between species at a resolution seldom reported in the literature.

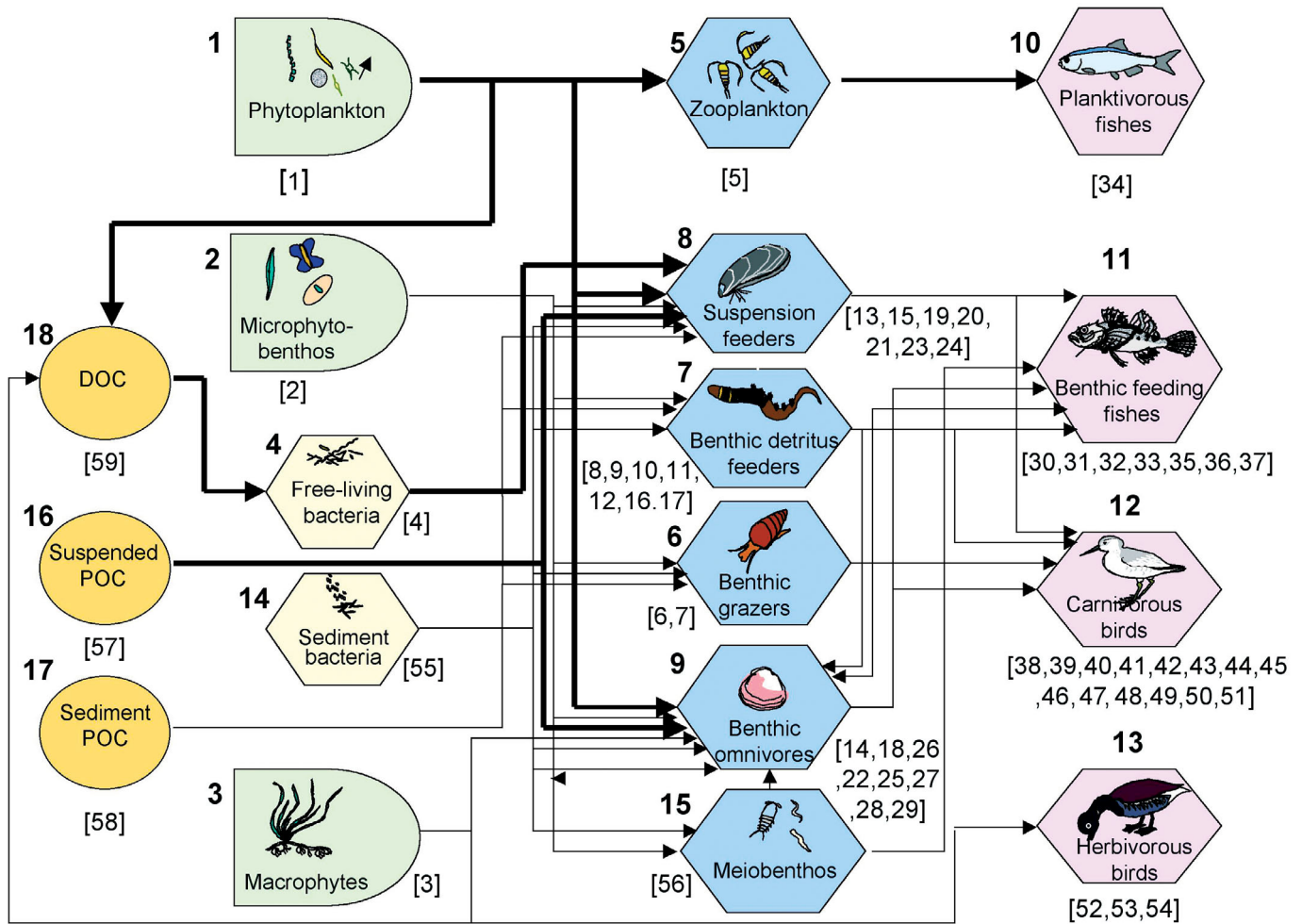


Fig. 3. Food web of Sylt-Rømø Bight, showing 59 compartments aggregated into an 18 compartments model. Numbers in bold face: aggregation numbers; numbers in brackets: original compartment numbers; thin arrows: interactions between compartments; thick arrows: pelagic interactions

Table 6. Global parameters of Sylt-Rømø Bight ecosystem

Attribute	Value	Attribute	Value
Model compartments	59	Overheads on imports, $O_i$ ( $\text{mg C m}^{-2} \text{d}^{-1}$ , bits)	3424
Total biomass ( $\text{mg C m}^{-2}$ )	34986.16	Overheads on exports, $O_e$ ( $\text{mg C m}^{-2} \text{d}^{-1}$ , bits)	1040
Total biomass autotrophs ( $\text{mg C m}^{-2}$ )	4163.20	Dissipative overheads, $O_d$ ( $\text{mg C m}^{-2} \text{d}^{-1}$ , bits)	4576
Net primary production, NPP ( $\text{mg C m}^{-2} \text{d}^{-1}$ )	921.31	Redundancy, $R$ ( $\text{mg C m}^{-2} \text{d}^{-1}$ , bits)	11112
Total biomass heterotrophs ( $\text{mg C m}^{-2}$ )	30819.96	Relative redundancy, $R/DC$ (%)	33.7
Total heterotrophic production ( $\text{mg C m}^{-2} \text{d}^{-1}$ )	344.49	Internal development capacity, $DC_i$ ( $\text{mg C m}^{-2} \text{d}^{-1}$ , bits)	17578
Total system production ( $\text{mg C m}^{-2} \text{d}^{-1}$ )	1265.79	Internal ascendancy, $A_i$ ( $\text{mg C m}^{-2} \text{d}^{-1}$ , bits)	6465
NNP efficiency (%)	57.5	Internal redundancy, $R_i$ ( $\text{mg C m}^{-2} \text{d}^{-1}$ , bits)	11112
Average path length, APL (trophic steps)	2.6	Relative internal ascendancy, $A_i/DC_i$ (%)	36.8
Average residence time, ART (residence time, d)	19.17	Relative internal redundancy ratio, $R_i/DC_i$ (%)	62.3
System P/B ratio ( $\text{d}^{-1}$ )	0.036	Normalised development capacity ( $\text{mg C m}^{-2} \text{d}^{-1}$ , bits)	4.88
Trophic efficiency of system (geometric mean, %)	2.61	Normalised ascendancy ( $\text{mg C m}^{-2} \text{d}^{-1}$ , bits)	1.89
Detrivore:herbivore ratio	1.44:1	Normalised A/DC ratio (%)	38.7
Number of cycles	1197	Overall connectance	2.28
Finn Cycling Index (%)	17.21	Intercompartmental connectance	2.84
Total system throughput, TST ( $\text{mg C m}^{-2} \text{d}^{-1}$ )	6752	Foodweb connectance	2.2
Development capacity, DC ( $\text{mg C m}^{-2} \text{d}^{-1}$ , bits)	32946	Flow diversity (DC/TST)	4.88
Ascendancy, A ( $\text{mg C m}^{-2} \text{d}^{-1}$ , bits)	12793		
A/TST ratio	1.89		
Relative ascendancy A/DC, (%)	38.8		



Table 7. System level properties of coastal ecosystems; adapted from Baird et al. (1991, 1998), Baird & Ulanowicz (1993), Baird (1998), Wilson & Parkes (1998). Values for Sylt-Rømø Bight derived from aggregated 18-compartment flow network. P/B: production/biomass; A: ascendancy; DC: development capacity;  $A_i$ : internal ascendancy;  $DC_i$ : internal development capacity; R: redundancy; TST: total system throughput. –: no data

Attribute	Ecosystem								
	Sylt-Rømø Bight	Chesapeake Bay	Dublin Bay	Baltic Sea	Southern Benguela	Northern Benguela	Ythan Estuary	Kromme Estuary	Swartkops Estuary
Daily system P/B	0.036	0.140	0.010	0.080	0.200	0.020	0.010	0.002	0.010
Mean trophic efficiency (%)	4.80	9.00	11.80	16.20	12.10	14.20	6.64	6.02	4.00
Relative ascendancy, A/DC (%)	40.20	49.50	42.20	55.60	50.60	48.10	34.40	33.70	28.00
Relative internal ascendancy, $A_i/DC_i$ (%)	38.90	35.00	43.80	39.70	45.00	43.90	33.80	29.40	30.40
Normalised A/DC ratio (%)	40.10	49.50	42.20	55.60	50.60	48.00	34.40	33.70	28.00
Relative redundancy R/DC (%)	31.40	65.00	26.80	60.30	55.30	56.40	33.60	34.00	69.60
Flow diversity, DC/TST	4.60	2.90	2.80	3.10	3.70	4.05	4.10	3.50	3.60
Finn Cycling Index (%)	17.28	29.70	31.90	22.80	0.01	7.12	22.50	25.90	43.80
Food web connectance	1.80	1.87	–	1.85	1.55	–	–	–	1.46

In an attempt to assess the functioning of the Bight in the context of other marine ecosystems, a number of dimensionless ratios were derived or obtained from published information. These ratios are listed together with a number of systems ranging from upwelling regions, to large shallow bays and seas, to small microtidal estuaries (Table 7). Comparison of the aggregated Bight ecosystem with the others in Table 7 revealed some interesting aspects.

The Bight's annual average daily P/B ratio is within the same magnitude as most listed in Table 7, but is considerably lower than that of Chesapeake Bay, the Baltic Sea and the Southern Benguela upwelling system. It is, however, higher than the average P/B ratios of Dublin Bay (Wilson & Parkes 1998) and of the 3 small estuaries Ythan, Kromme, & Swartkops (Baird & Ulanowicz 1993). Of interest is the rather low trophic efficiency of 4.8% calculated for the Bight (Table 7) which quantifies the efficiency by which energy is transferred within the system and derived from the Lindeman trophic analysis routine. A possible reason for this low efficiency could be that only a small fraction of the benthic primary production is transferred to the next trophic level, other reasons are a low phytoplankton production in the Bight, and that a considerable amount of phytoplankton is imported to satisfy the energy demands of suspension-feeders (Asmus & Asmus 1990).

It has been speculated that a decrease in the  $A_i/DC_i$  ratio in relation to the A/DC ratio could point to a strong dependency of such systems on external inputs (Baird & Heymans 1996). In the Bight, a decrease of 2% was observed between these ratios (Table 6), indicating some dependence on external connectance, although not as strong as that observed for Chesapeake Bay (14.5%) and the Baltic Sea (15%) (Baird et al. 1991) (Table 7).

Indices of relative ascendancy (A/DC and  $A_i/DC_i$ ) and the normalised A/DC ratio are lower for the Bight than for most systems in Table 7, but higher than those calculated for the 3 small estuaries. The relatively low values for the Bight indicate that the Bight is not well organised. High A/DC ratios are thought to reflect high degrees of organisation (Baird et al. 1991, Baird 1998), and therefore the Bight possesses no internal stability or resilience to perturbation (Baird et al. 1991, Wilson & Parkes 1998). The ratios are notably lower than similar bay-like systems such as the Chesapeake Bay, Dublin Bay, and the Baltic Sea, and are reflected in a low relative redundancy ratio (R/DC), which implies that energy pathways in the Bight exhibit low resistance or resilience to external forces and that broken pathways are not easily re-established. However, Dublin Bay, the Ythan and Kromme estuaries show similar redundancy characteristics in comparison to the other systems listed in Table 7. Furthermore, the FCI calculated for the Bight (17.3%) is much lower than the FCIs of other systems except for the Benguela upwelling ecosystems. Only a small fraction of the Bight's activity appears to be recycled on an annual average daily basis. Low A/DC and R/DC ratios coupled with a low FCI suggest that the Bight behaves as a coastal system (as opposed to upwelling regions where FCIs are <10%; Wilson & Parkes 1998), and also imply that the Bight is a relatively immature system (Mann et al. 1989, Baird et al. 1991), whose energy pathways could easily be disturbed.

On the other hand, high values for flow diversity and food web connectance were calculated for the Bight (Table 7). The Bight ecosystem thus appears to consist of a complex network of energy transfers, where detritivory exceeds herbivory by a factor of 1.44 (Table 6).

The characteristics discussed above, although in themselves unique to the Bight, reflect the annual average condition. However, large fluctuations in standing stocks and productivity of the living components are known to occur between seasons. Higher productivity and system activity are typical of spring and summer, whereas primary and secondary production is low during fall and winter (Asmus & Asmus 1985).

In addition, the Bight is characterised by different spatially aggregated plant and animal communities, each exhibiting different rates of consumption and production. For example, the secondary production of mussel beds was 10 times higher than in the other 3 communities, namely the *Nereis-Corophium* community, seagrass beds, and *Arenicola* flats (Asmus & Asmus 1990). Temporal changes in system activity have been reported for Chesapeake Bay and other systems, with these variabilities reflected in the system level properties (Baird & Ulanowicz 1989, Baird et al. 1995, 1998). The annual averages used in this study unquestionably mask seasonal variability, so that TST, DC and A values will most probably be higher in the biologically active seasons than during the colder, less productive ones. The FCI may also fluctuate seasonally, although Asmus et al. (1994) reported that seagrasses act as a sink for nitrogen and phosphorus which may dampen the magnitude of recycling of these elements. Baird & Ulanowicz (1989) have shown small variations in carbon cycling between seasons in Chesapeake Bay but, in contrast, the FCI revealed large differences in nitrogen recycling between seasons (Baird et al. 1995). Similar trends and patterns may well be present in the Sylt-Rømø Bight ecosystem.

This first attempt to analyse and assess the trophic function and interactions in the Sylt-Rømø Bight has revealed a complex, immature system whose energy pathways appear to be sensitive to perturbation. Networks representing the different assemblages over temporal scales are required for a deeper understanding of the functioning of this system.

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