Functioning of Intertidal Ecosystems of the Wadden Sea

Material exchange of the Sylt-Rømø Bight and its relation to habitat and species diversity

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Part 1
Synopsis

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Contents

1. Introduction

The analysis of community functions of a certain geographical unit requires an ecosystem approach tightly coupled with a larger spatial and temporal scale as can be covered by laboratory or most field experiments (Jax 2006; Post et al. 2007; Musacchio 2009). The various existing definitions of an ecosystem are able to describe the multifunctional nature of animal and plant communities only partially (Olff et al. 2009). Functions related to spatial and temporal variability, diversity and non-trophic interactions of organisms within a community are currently regarded separately from those functions focussing on the contribution of organisms to the material and energy flow (Jax 2006; Costello 2009).

An ecosystem is defined as a biological environment consisting of all the organisms living in a particular area, as well as all the abiotic, physical components of the environment with which the organisms interact. Based on this premise, definitions of ecosystems with a population dynamic approach are not sufficient to explain ecosystem function as a whole, because they only explain biotic variability by abiotic processes without integrating them into complex network models. Models of material or energy flow fit into this premise more easily, because they create abstractions from the species concept as a unit and consider mainly energy or the elemental constituents and its cycling between living and non living compartments (Lindeman 1942; Odum 1962; 1971). This approach facilitates a synopsis of abiotic and biotic processes, but generally includes only indirectly non-trophic relationships such as competition, resistance and symbiosis (MacArthur & Wilson 1967; Tilman 1982; Olff et al. 2009).

An ecosystem is also defined as a unit consisting of a community of organisms with the potential of self regulation and the space that is inhabited by them (Dahl 1908; Tansley 1935; Ramade 1978; Voronov et al. 2002; for review see Olenin & Ducrotoy 2006). A further problem is the often difficult separation of ecosystems (Jax 2006; Post et al. 2007; Yarrow & Marín 2007).

In marine environments, benthic coastal communities are difficult to separate from each other (Post et al. 2007), with the exception of those systems that are distinctly spatially separated or that can clearly be distinguished by their different habitat structure, such as mussel beds and seagrass beds. However, even these communities are interrelated to other ecosystems by numerous interactions and interconnections that the concept of self regulation is not entirely fulfilled in these systems.

From a global perspective a definition is easier, hence the ecosphere of the earth is a closed system and therefore a unit that can meet the preconditions required by the ecosystem definition (Ghilarov 1995). The first and second principles of thermodynamics form the basis for the energetic or energy approach to ecosystem behaviour and the steady state of abiotic and biotic processes (Hairston et al. 1960; Sellers 1969; Gallucci 1973; Hairston & Hairston

1993; Hedin et al. 1998). The subdivision of the ecosphere into ecosystems of equal importance is all the more indistinct as we diminish the spatial scale and further fragmentise the systems into smaller units.

The Wadden Sea is a landscape or a geographical unit including a mosaic of intertidal sand and mud flats as well as subtidal systems of inlets, channels and creeks characterising in this spatially extended form the coastal area of the southeastern North Sea. It can be seen as a transition region between land and sea or an ecotone (Kolasa & Zalewski 1995; Peters et al. 2006; Atrill & Rundle 2002; Hufkens et al. 2009), but it forms a marked morphological boundary both to the land and to the sea. The catchment area of a tidal inlet is the basis for a subdivision of the Wadden Sea into several systems and each inlet system exchanges its water with the North Sea separately, while the mixing of water bodies of adjacent tidal systems is spatially and temporally limited. The organisms living within a catchment area interact with each other much more frequently than they do with those of adjacent systems and they only leave their systems either actively by seasonal migration or passively by current drifting, or during episodic storms. The animal communities within a tidal basin are not fulfilling the premise of self regulation, but contribute to a network of interactions within a certain temporal and spatial frame that is built by biotic and abiotic structure of the particular tidal basin.

The Wadden Sea ecosystem is seldom considered from an holistic point of view, but some approaches to do so have been developed as well as in comparable systems worldwide. The first fundamental investigation of the Wadden Sea in this direction was already carried out at 1877 by Karl Möbius, who gave the first community concept using the example of an oyster bed of the Sylt-Rømø Bight. He stated that the system´s immanent mechanisms of self regulation guarantee the preservation and survival of this community. For an oyster bed this concept could not be further sustained (Reise 1990), although the biocoenosis or community as a scientific term has been defined at first time and this gave an important impulse for the further development of ecology as a scientific discipline. This scientific discipline subsequently developed rapidly through investigations in terrestrial, limnic and marine systems (e.g. Warming 1909; Elton 1927; Allee 1932; Allee et al. 1949). Only at a very much later stage ecology turned to intertidal systems (e.g. Connell 1961; Paine 1966; 1974). Odum & Hoskin (1958) analysed estuarine habitats at the American coast and used the holistic approach for ecosystems which was formulated some years earlier (Clements 1905; Gleason 1926) and has been debated controversially but found later large agreement in ecological concepts (e.g. Simberloff 1980; Wilson 1988; Liu et al. 2007). Subsequently in Europe scientists initiated investigations at the ecosystem level in different marine systems based upon the concepts of energy and material flow (e.g. Hughes 1970; van Es 1982; Warwick & Price 1975). In shallow water areas of the Baltic Sea many communities have been investigated, with the aim to assess the energy budget of the various subsystems of the Baltic (e.g. Jansson & Wulff 1977). In the North Sea in the late 70's and early 80's an energy budget has been developed for the Balgzand area in the Dutch Wadden Sea (Wolff & de

Wolf 1977; Wilde de 1980; Kuipers et al. 1981). Influenced by the rapid economic and industrial development in coastal areas and the assessment of consequences for the marine ecosystem, especially eutrophication, investigations of material flow gained importance, but focussed mainly on smaller sub-systems or sections thereof (e.g. Witte & Zijlstra 1984; Veldhuis et al. 1988; van der Veer 1989).

Only few analyses of whole ecosystems have been carried out in the German Wadden Sea. Between the two World Wars ecological research in the Sylt-Rømø Bight has been applied to aspects such as identifying and mapping coastal communities and their habitat requirements (e.g. sediments and tidal exposure) (Nienburg 1927). It was the aim to prove whether the Wadden Sea was a useful area for commercial fishing, especially shellfish (Hagmeier & Kändler 1927; Hagmeier 1941) and for land reclamation (Wohlenberg 1933; 1934; 1937). At the late 70ies to the beginning of the early 80ies research at the ecosystem level did start in earnest in the Wadden Sea. Following the paradigm of the American research (e.g. Paine 1966; 1974) exclusion/inclusion experiments of certain organisms have been used to investigate their interaction with adjacent communities (Reise 1978; 1981). Investigations of the energy flow following a holistic approach such as those used in North America (e.g. Teal 1962; Pamatmat 1968; Hargrave 1969; Pomeroy & Wiegert 1981; Dame 1996) and Sweden (Jansson & Wulff 1977) have been transferred to the Wadden Sea ecosystem (Asmus H 1982; Asmus R 1982; Asmus & Asmus 1985). In the Sylt-Rømø Bight ecological research has been carried out in one defined spatial area using both the organism approach (e.g. Reise 1998; Beusekom & Reise 2008; Reise & Beusekom 2008; Reise et al. 2008) and the material and energy flow approach (e.g. Asmus et al. 1998a,b,c; Asmus & Asmus 2000; Baird, Asmus, Asmus 2004; 2007; 2008; Baird et al. 2009) for a long period of time since 1978.

In the 90’s extended ecosystem analyses have been conducted, with results forming the base of a fundamental inventory of organism resources as well as of material and energy flow (Leuschner & Scherer 1989; Lindeboom et al. 1989). In the Sylt-Rømø Bight these investigations were limited to the intertidal area, but considered also for the first time fish, birds and marine mammals of the area (for summary see Gätje & Reise 1998). The outcome of these analyses was the development of nature conservation concepts, which has been scientifically. While the knowledge on Wadden Sea ecosystems was further complimented by this research, a total and common view on the interlinked dynamics of the material flow and the organisms was yet to be done. Even two dimensional hydrodynamic and numerical models that have been described during this period remained widely limited on abiotic processes such as currents and material transport (Stanev et al. 2003; Kohlmeyer & Ebenhöh 2009).

In the middle of the nineties research on biodiversity became a dominant discipline against the background of a drastic decrease in species numbers in various ecosystems of the world, apparently through anthropogenic activities (Chadwick & Furman 1992; Tilman 1999).

Concepts attempting to describe the relationship between biodiversity and ecosystem functioning were at the time rather elementary and rudimentary although many promising aspects have been published (Forster et al. 2006; Waldbusser & Marinelli 2006; Stachowicz & Byrnes 2006; Naeem 2006; Bulling et al. 2006; Duffy & Stachowicz 2006; Ruesink et al. 2006; Duffy 2006; Ieno et al. 2006; Raffaelli 2006; Heip et al. 2009).

During the last hundred years ecosystem research has developed along two routes. On one hand there is an approach that describes a community as the sum of its traits. Here spatial and temporal variabilities of abundances of species come to the fore, which are defined by their population dynamics (e.g. Turchin 2003; Geritz & Kisdi 2004) and their species diversity (Rosenzweig 1995) as well as the number of interactions between the organisms. This research focuses on ecosystem stability and resilience (e.g. Hughes 2003), on the occupation of niches by organisms, as well as the various effects that the organisms exert on each other (e.g. Bruno et al. 2003); these ideas were considered to impact on the development and structure of the community. Thus the community in an ecosystem is determined by the interplay between immigration and emigration, drift, recruitment, mortality as well as predator-prey interactions. By incorporating various community information an ecosystem model emerges which not only gives a qualitative image, but also quantitative information on the system as a whole. Within this quantitative ecosystem approach we are able to explain and describe the population dynamics of single species.

To characterise the function of an ecosystem a further approach is necessary which describes the material or energy budget of an ecosystem. Trophic dynamics and relationships are of prime importance in this context. The dynamics are defined by gross and net primary production for plants, while secondary production, consumption, as well as energy loss by respiration typifies that of an heterotroph (see Crisp 1984). Imports from outside the system and exports of material and energy from the system are some of the main controllers of the ecosystem behaviour and dynamics. The cross-linking of organisms in a food web describes an ecosystem through the availability of its resources and their efficient use from primary producer to top consumer. The mathematical formulation in form of vectors and matrices describe the interactions between donor and recipient within a food web and thus enables us to analyse not only single components but also imports, exports, recycling of material and common transformation tracks which are used by different ecological components. From this model system an array of indices can be derived which provides information on system characteristics which is greater than the information content of the sum of ecosystem parts. This approach describes the dynamics of ecosystem processes as well as the functioning of an ecosystem.

Both approaches indicate different directions. The population dynamic model illuminates primarily the qualitative changes within a system in the course of time, whereas the material and energy flow model illustrates a state description of the potential of an ecosystem on its sustainability, stability, maturity and the degree of development. To describe an ecosystem close to reality we have to consider the ability of change as well as the state of single and multiple functions. It is of special importance to note that certain key species can be able to influence the structure and dynamics of a system and are able to control material and energy flow in the system (e.g. Eriksson et al. 2010).

In the context of the above arguments, the main objective of this thesis is to propose a possible synthesis of different approaches of ecological research for a holistic description of ecosystems. This will be exemplified by comparing the exchange processes between the different communities and the overlying water column of a relatively separated large scale biotope, the Sylt-Rømø Bight, with its species configuration. This synthesis is based on my own work and on comparisons with literature data available.

2. Study site

The Sylt-Rømø Bight (SRB) situated east of the islands Sylt and Rømø is one of the large tidal basins of the Wadden Sea. A railway dam and a road causeway connect the mainland with the islands of Sylt and Rømø, respectively, separating the Bight from the other parts of the German and Danish Wadden Sea. This lagoon system is drained by three tidal inlets, the Rømø Dyb, the Høyer Dyb and the Lister Tief, all three meet within the Lister Ley basin which is connected to the North Sea by a narrow opening of 2.6 km between the islands. Two rivers, Vidå and Bredeå, open out into the bay draining a catchment area of about 1554 km² (1081 km² and 473 km², respectively).

a. Geological history

At the end of the last ice age the SRB developed from a sheltered sandy plain protected from a moraine chain in the west, forming now the islands of Sylt and Rømø and a sandur area at the mainland of Jutland/Denmark and Schleswig-Holstein/Germany in the east. When the sea level rose dramatically about 5000 years ago, sea water entered the swampy area that includes the river beds of Vidå and Bredeå and formed a marine bay. Due to intensive sedimentation processes especially at the mainland coast large marsh areas developed. At the western side of the moraine chain erosion and subsequent transport along the coastline leads to the formation of large dune areas which formed long spits in northern and southern directions.

b. Area

Today the SRB covers 404 km² (Backhaus et al. 1998) of which 160,5 km² (39%) is intertidal related to spring low tide line and the major part is formed by shallow subtidal areas up to 5 m below spring low tide line (205.0 km² or 51 %) (Fig.1). Based on mean low tide level 33% of the area is intertidal and 57% is occupied by the shallow subtidal. Deep tidal gullies below 5 m have an area of 38.1 km² or contribute 9.4% to the total bight. The deepest point is north of the Ellenbogen (Sylt) with 40.5 m related to NN. The supratidal region represents a transition between sandur at the mainland, moraine and dune landscape at the islands, and is composed by salt and brackish marsh areas and sandy beaches. The area of this region is in our days minute due to the forming of dikes, but originally includes the total marsh area under natural conditions.

c. Climate

The climate is cold temperate and oceanic with a mean average winter temperature (from October to March) of 5°C and a mean summer temperature (from April to September) of 13°C. Average amount of precipitation is about 750 mm a^{-1} (Lohse et al. 1995). Maximum rain fall is in August and the minimum is found in February. High wind speeds can be measured throughout the year with a yearly average of 7 m s^{-1} (Backhaus et al. 1998).

d. Hydrography

Tides: The hydrography of the SRB is formed by tides. Semidiurnal tides with a range of about 2 m characterise the area. At high tide the SRB has a volume of about 1 000 000 m^3, about 50% leave the Bight during ebb tide (Backhaus et al. 1998).

Currents: Largest current velocities can be measured at the surface of the tidal inlets with up to more than 1 m sec^{-1}. The current velocity decreases over the shallower, especially the intertidal parts of the bight. Here on average 5-10 cm sec^{-1} can be measured (Backhaus et al. 1998).

Salinity: Hence river discharge into the Sylt-Rømø Bight is only small, salinity changes are more influenced by precipitation and thus represent polyhaline conditions changing in the range of 28 to 32 psu.

e. Turbidity and light

Due to the low water depth of the bight and the windy climate, the water of the SRB is rich in particles generating high turbidity. This turbidity impacts the light climate, but only small rivers with a comparable small particle load enter the area and large estuaries are far away. Therefore the SRB has a mean transparency compared to most other tidal basins of the Wadden Sea (Asmus et al. 1998c).

f. Sediment properties

The sediment is mainly sandy but tends to be muddier towards the inner marginal and more sheltered parts of the bight. There has been observed a tendency that mudflats decrease within the bight whereas sand flats increase.

Sediment types have been described by Bayerl et al. (1998) in great detail.

For the purpose of the present thesis I divided the sediments roughly into sand flats and mud flats. The sand flats have been further divided due to the degree of exposure and tidal immergence into sandy shoals, sandy beaches, sand flats and muddy sands following the system after Bayerl et al. (1998) and the sediment maps drawn by the same author. These maps represent a snap-shot of the situation during the years 1992 -1996.

g. Communities

Each of the above mentioned sediment types is inhabited by a special community. In the following the names of the communities are those of the sediment types with the exception of the sand flat community which was described as *Arenicola* sand flat, due to the dominant faunal component in this community, the lugworm *Arenicola marina*. In addition those communities that could be easily distinguished from the sand flats by cover of visible epibenthic structures such as mussel beds and seagrass beds have been also considered as separate communities.

The coverage and share of the communities in the total intertidal area of the bight is indicated in Fig. 1.

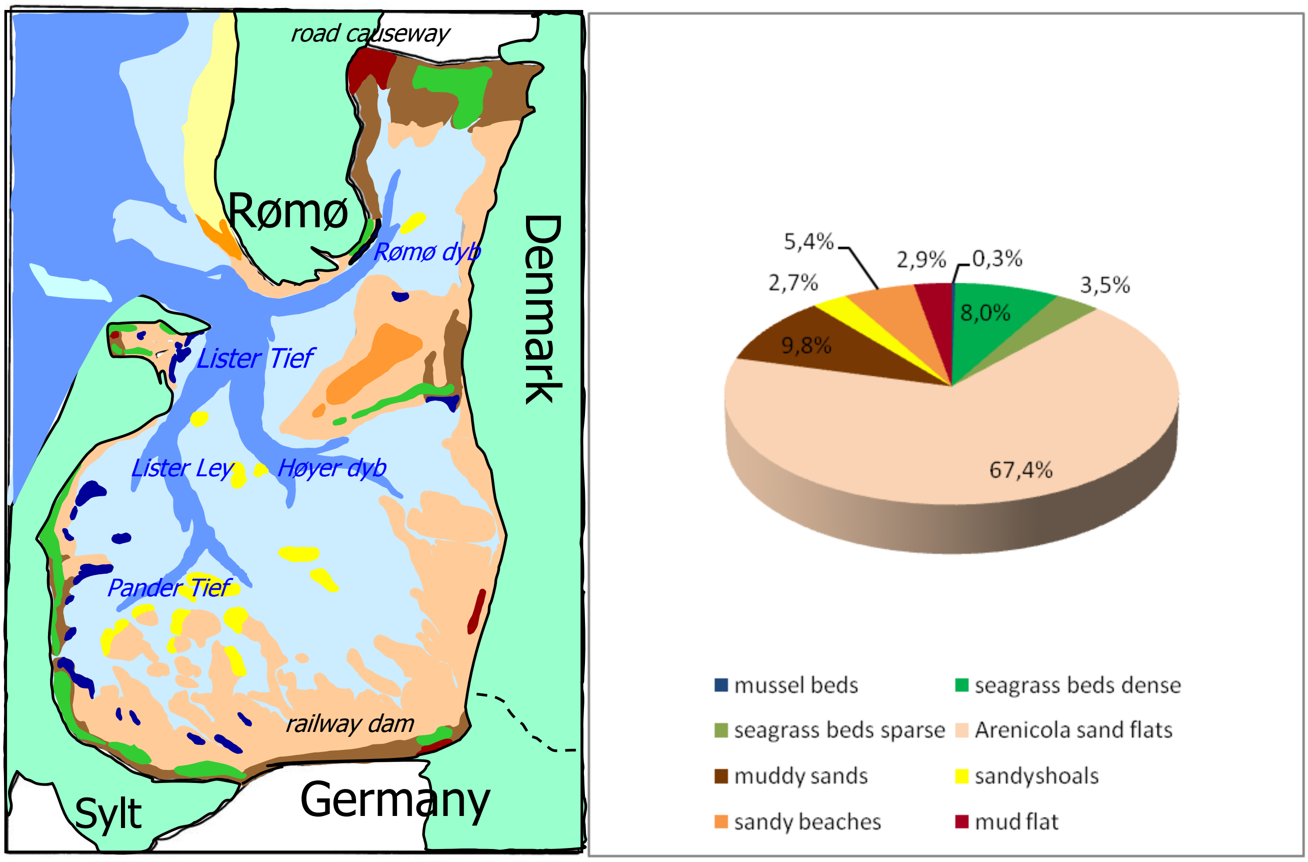


Fig. 1. Benthic communities of the Sylt-Rømø Bight showing areal distribution (left) and percentage cover (right) of the intertidal area (after Baird, Asmus & Asmus 2007). The distribution represents the situation from 1992-1996.

h. Present status

The system has changed in many aspects compared to the situation in 1992-1996. Sediment seems to show a tendency to become courser in exposed and subtidal areas while mudflats are decreasing (Dolch & Hass 2008). Due to the observed global climate change there have been significant changes in winter and annual average temperature within the area, that have probably lead to the spread of thermophile species such as Pacific oysters, cord grass and slipper limpets. Also Lusitanian fish invaded the area and became established populations. Some of these alterations may be visible at the ecosystem level, but they are not the subject of this thesis.

3. Materials and Methods

In the following section a short summary of the experimental methods is presented delivering data that are used for modeling the food web as well as to estimate material budgets.

Most of the general methods for determining biomass and productivity are already described in detail in Asmus 1984; 1987; Asmus & Asmus 1985; 1990; 1998,a,b, 2000. Methods used in the flume studies are described in Asmus & Asmus 1990; 1991; 1993; Asmus et al. 1992; 1994; 1995; 1998 a,b; 2000.
Methods for food web analysis by network analysis can be found by Baird, Asmus & Asmus 2004; 2007; 2008; 2009; 2011a, b.

a. Biomass and material flux measurements

i. Biomass

Phytoplankton: Phytoplankton biomass was estimated from cell counts in samples taken in the Sylt-Rømø Bight close to the Wadden Sea Station Sylt. Biomass of phytoplankton has been determined by converting individual cell size of the particular species into cell volume (for details see Asmus R 1984). Cell volume could be converted into individual carbon content after Edler (1979). Multiplying cell numbers and individual carbon content values resulted in species biomass. Biomass of total phytoplankton was estimated by summing up biomass of the different species in each sample separately.

Microphytobenthos: Microphytobenthos was estimated in the same way as described for phytoplankton (for details see Asmus R 1984). In each community eight replicate samples were taken monthly by small sediment corers (0.64 cm²) from the top 3 mm of the surface sediment during one year. Six of these sediment samples were cooked in a mixture of nitric and sulphuric acid (2:1) and rinsed with aqua dest (7-10 times) to clean the diatom shells and quantitative subsamples have been taken for species identification and cell counts. Two of the replicate samples were only fixed with formalin. In all samples cells have been counted and biomass has been estimated as described for phytoplankton. Epiphytes of seagrasses have been treated in the same way with acid as described for the sediment samples.

Macrophytes: Seagrass and macroalgae were collected from a defined area (12.5*12.5 cm) and the wet and dry weight has been determined (dry weight: 100°C for 2-3 days) by separating into above ground (leaves) and below ground biomass (roots and rhizoms).

Zooplankton: Zooplankton biomass data have been used from the long term monitoring programme for the particular years (Martens, personal communication).

Meiofauna: Biomass of meiofauna has been estimated using values from Xylander & Reise (1984) and Dittmann & Reise (1985) for turbellaria. Biomass of Nematoda was estimated after counts by own investigations (Asmus unpublished). For muddy sediments such as from mudflats, mussel beds, dense *Zostera* beds and muddy sands an average of total meiofauna biomass of 0.5 g C m^{-2} was estimated. In sandy sediments a higher value of 1 g C m^{-2} has been used as an annual mean for the total meiobenthic community.

Macrofauna: For the determination of biomass of macrobenthic organisms sediment cores were cut out by a box corer (10*10 cm, 15 cm depth). In total 6 different mussel beds were sampled monthly taking 6 replicates each (for details see Asmus 1987). The other communities have been sampled in the same way (for details see Asmus & Asmus 1985; 1990; 1998 a; 2000). Sediment cores were washed through a sieve of 1 mm mesh size already in the field. The remains (organisms, detritus and coarse sediment grains) have been transferred quantitatively into sampling devices and in the laboratory living animals or freshly dead animals were sorted out, separated into species and counted. Individuals of one species have been separated into size classes, when necessary, and after adherent water has been swabbed with wipes, the animals were put into aluminium crucibles. These samples were weighed freshly, after drying in an oven at 60-80°C (24 hours) and after subsequent cooling in a vacuum desiccator weighed to obtain the dry weight. After this procedure the dry and weighted samples have been ashed in a furnace at 450° C. From the difference between ash weight and dry weight, ash free dry weight has been estimated.

From very abundant specimen only 30-40 individuals representing the total size range have been sampled and both an easily measurable size parameter (depending on species i.e.: shell length, shell diameter in bivalves and molluscs or width of prostomium for polychaetes) per individual as well as individual weight was determined as mentioned above.

Fish: Biomasses of fishes are based on values taken during the SWAP (i.e. Sylter Wattenmeer Austausch-Prozesse)–Project (Herrman et al. 1998).

Birds: Bird biomass was based on measurements and observations during the SWAP-Project (Nehls & Scheiffahrt 1998).

ii. Productivity

Phytoplankton: For determination of phytoplankton primary production twice a month 8 light and 4 dark bottles (300 ml each) were filled with unfiltered seawater at low tide and incubated *in situ*, drifting in the middle of the water column. Production has been measured using the oxygen method (Asmus R 1984; Asmus R et al. 1998).

Microphytobenthos: Parallel to measurements of the community metabolism a thin surface sediment layer of 3 mm has been sieved through a 500 µ mesh to remove macrobenthic animals. This layer was taken by 9 – 16 small sediment corers covering the bottom area of 2 light and one dark sediment chambers of an area varying between 16.62 to 28.26 cm² or a volume of 100 to 300 ml. After pouring the sediment layer in, these chambers were filled with filtrated and equilibrated seawater of known oxygen content and incubated *in situ* for the total inundation period. At the end of the experiment oxygen concentration was estimated in the enclosed water body by oxygen electrodes. Gross primary production was estimated as

$GPP\ (mg\ C\ m^{-2}h^{-1}) = GPP\ (mmol\ O_2\ m^{-2}\ h^{-1})*12/0.8$

where 12 is the conversion for mmol CO_2 into mg C and 0.8 is the empirical photosynthetic quotient PQ measured for this study site (Asmus R et al. 1998).

Macrophytes: Primary production of macrophytes has been estimated in the seagrass bed and the mussel bed from community metabolism measurements. Oxygen production of macrophytes was estimated as the difference between total oxygen production and the oxygen production by phytoplankton and microphytobenthos. Oxygen consumption was estimated as the difference between total oxygen consumption, oxygen consumption of the water body, the sediment and the enclosed faunal components. After convertion of oxygen fluxes into carbon units, net primary production was computed as the difference between gross primary production and respiration.

Zooplankton: Secondary productivity data of zooplankton were computed from zooplankton biomass using a P/B ratio of 0.2 after Fransz (1981) for zooplankton of the Wadden Sea.

Meiofauna: Secondary production of meiofauna was computed from meiofauna biomass using a P/B-ratio of 8 after Witte & Zijlstra (1984).

Macrofauna: Secondary productivity of macrofauna was estimated after the method of Crisp (1971; 1984) using weight increments within a certain time period (months) using the following formula:

$$P = (N_{t1}*w_{t1}) + (N_{t2}*w_{t2})/ t_2-t_1$$

where P is production of a species or a size class per m^2 and $(t_2 - t_1)$ the time interval, N_{t1} is the average abundance of the particular species at time t_1, N_{t2} is the average abundance at time t_2. w_{t1} represents the mean individual weight at t_1, w_{t2} that at time t_2. Weight was given in ash free dry weight.

Estimation was based on the values of abundance and individual weights of organisms of the sediment cores. For organisms with only low biomass, production has been estimated after the method of Banse & Mosher (1980) using P/B-values.

Fish: Production of fish has been estimated from biomass data (Herrmann et al. 1998) using P/B-ratios.

Birds: Production of birds has been estimated from biomass data (Nehls & Scheiffahrt 1998) using P/B ratios.

iii. Respiration

Phytoplankton: Phytoplankton respiration was estimated from oxygen consumption in dark bottles, which was measured parallel to primary productivity. Oxygen fluxes were converted to carbon units using a respiratory quotient of 0.85.

Microphytobenthos: Microphytobenthos respiration was obtained from measurements of oxygen consumption in dark benthic chambers incubated parallel to the light benthic chambers for the production measurements. A RQ (CO_2/O_2) of 1.3 has been estimated empirically (Asmus R et al. 1998c).

Macrophytes: Respiration of macrophytes has been computed after the oxygen consumption within dark benthic chambers as the difference between total oxygen consumption and that of sediment and water including fauna and bacteria.

Zooplankton: Zooplankton respiration has been measured by annual R/B values of 13.3 (computed after Martens 1986)

Meiofauna: Meiofauna respiration has been estimated after Witte & Zijlstra (1984) using an average annual P/R value of 30.3.

Macrofauna: Measurements of respiration rates of dominant species have been carried out with individual macrobenthic animals in closed chambers at *in situ* temperatures due to the different seasons. Because respiration rate is dependent on the size of investigated animals, different size classes of a species have been considered, when necessary. For the measurements freshly caught organisms have been elected that represent the *in situ* nutritional stage and the level of metabolism of the particular species. Single laboratory experiments run over 12 to 24 hours. By choosing a sufficient ratio of animal to water volume it was ensured that oxygen saturation did not decrease below levels of 80% during this time to avoid adaptation of respiration rate to low oxygen levels. Oxygen content was measured with oxygen sensors at the beginning and end of the experiment. Respiration rate was given as mg O_2 per g ashfree dry weight and was estimated as follows:

mg O_2 /g asfdw /h = $(C_2-C_1)*V/(1000*W_{ind}*(t_2-t_1))$

where C_1 and C_2, represent oxygen concentration in mg L^{-1} at the beginning and end of the experiment, V is water volume of the respiration chamber in mL, W_{ind} is the individual weight of the incubated animal in g afdw, and t_1 and t_2 is the time at the beginning and the end of the experiment.

For the estimation of carbon fluxes respiration rates have been converted by an oxycaloric equivalent of 0.486 (Winberg 1971) in mg C $m^{-2}h^{-1}$.

Fish: Standard metabolic rates for fish were used to compute respiration rates. The allometric relationships were taken from the literature (Fonds et al. 1985; 1989; Panten 1995)**.**

Birds: The metabolic rates of birds in the field were derived from the allometric equations provided by Nagy (1987).

iv. Exudation, egestion and excretion

Phytoplankton, microphytobenthos and macrophytes: 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 and microphytobenthos entered the DOC pool in the Bight (Vegter & De Visscher 1984; Baird & Ulanowicz 1989), and about 2% of the macrophyte NPP (Sieburth 1969; Sieburth & Jensen 1969; Brylinski 1977; Valiela 1995).

Zooplankton: Zooplankton egestion was estimated as the difference between consumption by zooplankton and assimilation (ie. production + respiration) following the budgetary equation of C=P+R+E after Crisp (1971).

Meiofauna: As for zooplankton egestion by meiobenthos was estimated by the difference between consumption and assimilation.

Macrofauna: Egestion of some macrofauna species has been determined experimentally, where excretion of dissolved nitrogen and phosphorus has been measured (for details see Kürten 2006).

Determination of the egestion rate has been carried out parallel to measurements of respiration in closed chambers. Nutrients, such as ammonium, total nitrogen, ortho-phosphate and total phosphorus have been considered as egestion parameter.

Determination of concentration of this material was carried out following the recommendations of Graßhoff et al. (1983; 1999).

Excretion rate has been determined in mg N, P separated between dissolved and particulate components. Only for dissolved components:

mg dissolved (N,P,) /g asfdw /h = $(C_{N,P,2}-C_{N,P,1})*V/(1000*W_{ind}*(t_2-t_1))$

where $C_{N,P,1}$ and $C_{N,P,2}$, corresponds to nutrient concentration mg L^{-1} at the beginning and the end of the experiment, V is the water volume of the chamber in ml, W_{ind} is the weight of the incubated animal or animals in g afdw, and t_1 and t_2 is the time at start and end of the experiment.

Egestion of particulate matter (faeces) as well as excretion of dissolved carbon components have been estimated for the modelling by means of elemental analysis of faeces material or by literature values which have been related to the biomass of the particular component.

Fish and birds: Egestion of fish and birds has been computed by using the difference between consumption and assimilation.

v. Consumption

Consumption of heterotrophic organisms has been estimated as sum of production, respiration and egestion (Crisp 1971). In those cases, such as meiofauna, zooplankton, bacteria and some macrobenthic species, where egestion values were not available from own measurements, consumption (C) was computed from the equation $C= A/A_{eff}$ (Baird & Milne 1981), where A is assimilation and A_{eff} is assimilation efficiency. Values for assimilation efficiency were used from the literature for the particular species. In those cases where no information was available, assimilation efficiency was taken from species with a similar taxonomic range.

Fish consumption was either obtained from the literature or estimated from the empirical relationship $C = 1.25(P + 2R)$ (Winberg 1956; Mann 1965).

Consumption by carnivorous birds was taken from Scheiffarth & Nehls (1997).

Consumption by herbivorous birds was estimated using R/B values reported in Madsen et al. (1988).

b. Community – Metabolism

Methods for measuring community metabolism are described in Asmus H (1982), Asmus R (1982; 1986) and Asmus & Asmus (1985;1990).

Measurements were carried out in closed benthic chambers (bell jar technique) *in situ* (Fig. 2). For each community benthic chamber measurements were set up with a set of 6 dark and 6 light chambers to measure community respiration and net community production separately. Community measurements have been carried out monthly during one year.

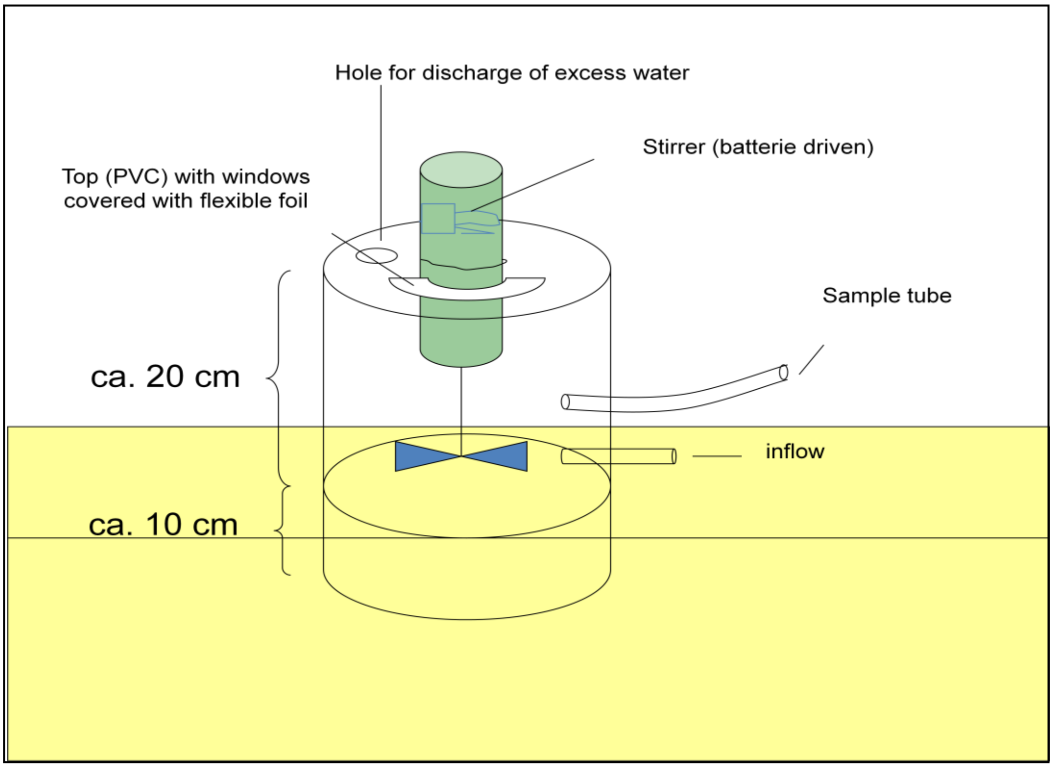


Fig. 2. Benthic chamber (bell jar) made from PVC for measuring metabolism rates of benthic organisms and communities *in situ*.

Oxygen concentration within the benthic chambers has been recorded with oxygen electrodes every hour. For analysis, only values higher than 80% saturation have been considered, to avoid alteration of respiration rates due to low ambient oxygen concentration.

c. Measurements of exchange processes

For measuring exchange processes *in situ*, the Sylt Flume was constructed. This large measuring facility was built in each of the investigated communities and measurements were carried out from 1989 to 1996. (Fig. 3, see also Asmus & Asmus (1991; 1993; 2000) and Asmus et al. (1992; 1995)).

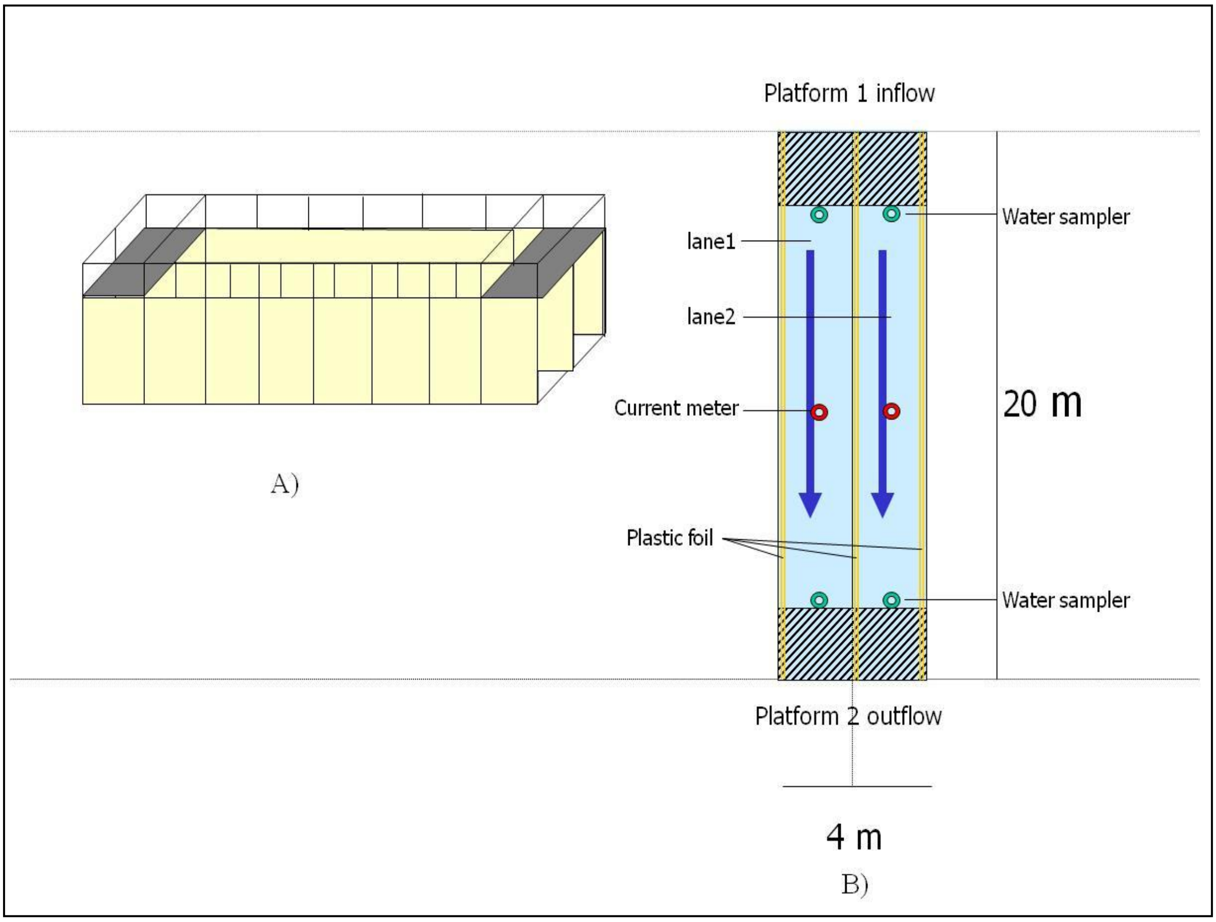


Fig. 3. Sylt Flume: A) Horizontal projection. B) Vertical Projection. Flume consists of a metal construction covered by 3 plastic foils (yellow) forming walls for two lanes. The flume is orientated parallel to the main current direction and its openings allow inflow and outflow of tidal water. Induction current meters are installed in the centre of each lane. Water samplers are positioned at each of the 2 platforms at the inflow and the outflow of the flume.

The Sylt Flume was constructed of a 20 m long and 2 m high steel frame system with two lanes 2 m wide each (Fig. 3). It was erected on a natural benthic community *in situ*. The flume is orientated parallel to the main flow direction. Plastic foils canalized the tidal waters and prevented lateral mixing. Heavy iron chains pressed the lower margin of the foils onto the bottom. When no measurements were taken, the foils could be rolled up and fastened to the frame. In one lane the natural benthic assemblage remained undisturbed, in the other lane, either mussels or seagrass were removed by hand or lugworms were displaced by burying a fine meshed net into the bottom of the lane. These manipulations were carried out four weeks before the experiments started, leaving in all cases a bare sediment. This lane served as a control. Every half an hour water samples were collected 15 cm above the bottom by electrical pumps at the inflow of the flume, and a corresponding set of samples was taken when the water had passed the flume. The parameters measured were particulate organic carbon, particulate organic nitrogen, ammonium, nitrate, nitrite, total nitrogen, total phosphorus, dissolved inorganic phosphorus, dissolved silicate (the data on silicate were not used for the synthesis in this thesis). The difference in concentration between inflow and outflow were used to estimate the material flux, considering the water volume passing in this time period. In the previous experiments current velocity was measured by drifting buoys as well as by induction current meters.

d. 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

Tc/TST, where Tc 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 ascendency (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 ascendency. 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. Ascendency 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 ascendency (Ai) and internal developmental capacity (DCi) 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, Asmus & Asmus 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 nonliving ones in each. The same currency, carbon, was used for biomass and flows, and rates were expressed in mgC $m^{-2}d^{-1}$ 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.hmtl.

e. Statistical analysis

For budgeting values were used from network analysis of the different communities described in recent papers based on our data set (Baird, Asmus & Asmus 2004; 2007; 2008; Baird, Fath, Ulanowicz, Asmus & Asmus 2009). Because the network analysis computes only average rates without showing a range of variability, it was not possible to give standard deviation for most of the values. This is a disadvantage of the current routine programme that is outweighed by the possibility to analyse and calculate complex interactions. Most statistics are described in the original papers (Part two of this thesis).

4. Exchange processes and food web of intertidal benthic communities - synthesis of results

The following chapter represents the body of data material derived from network models carried out in the last years (Baird, Asmus & Asmus 2004; 2007; 2008; 2011) and Baird , Fath, Ulanowicz, Asmus & Asmus (2009);. It includes also material of original flume and production measurements from earlier investigations which was discussed and published already in Asmus H (1982; 1984; 1987; 1994), Asmus & Asmus (1985; 1990; 1991; 1993; 1998a,b; 2000; 2005; 2011a; b) and Asmus et al. (1990; 1992; 1994; 1995; 1998;a;b,c; 2000). The scientific progress compared to earlier descriptions of the benthic-pelagic exchange processes of certain communities by the author is seen in the synthesis of exchange process data with the outcome of food web analysis, the higher resolution into partial processes and model results on a precise taxonomic level.

a. General description of exchange processes

Pelagic-benthic exchange processes: Interactions between the pelagic and benthic environments are related to a variety of abiotic and biotic processes that have a major influence on the structure and dynamics of marine ecosystems. Transport of particulate and dissolved material, gases, as well as living organisms, but also sedimentation and erosion are subsumed under these processes, that induce a shifting of material between benthic and pelagic material pools and vice versa. (Figs. 4, 5, 6). Imbalances in these transactions result in a change of the biotic structure and have far reaching consequences for the development of the communities. Exchange processes are either directed from the water (pelagic domain) to the bottom (benthic domain) (termed as pelagic-benthic) or reversed (termed as benthic-pelagic), and can impact on abiotic material pools as well as producers and consumers, or they can be related to the exchange between abiotic and biotic material components (Table 1).

Among the abiotic pelagic-benthic exchange processes are sedimentation and gas transport that includes oxygen transport which is of special ecological importance. Thus abiotic exchange processes not only take place on the biotope level but also at the interface between abiotic and biotic pools. While sedimentation decreases with increasing currents and turbulence, gas transport is accelerated by hydrodynamics. Physical factors have therefore promoting or inhibitory effects on exchange processes. Thus the abiotic inventory of a community or the determinative situation (Schwerdtfeger 1975) is modifying the exchange processes. Abiotic exchange processes coupled to physical factors exert indirectly on an ecosystem dimension, because hydrographic conditions and with this the determinative situation of the biotope can be changed by the community in certain limits (see also Massel 1999).

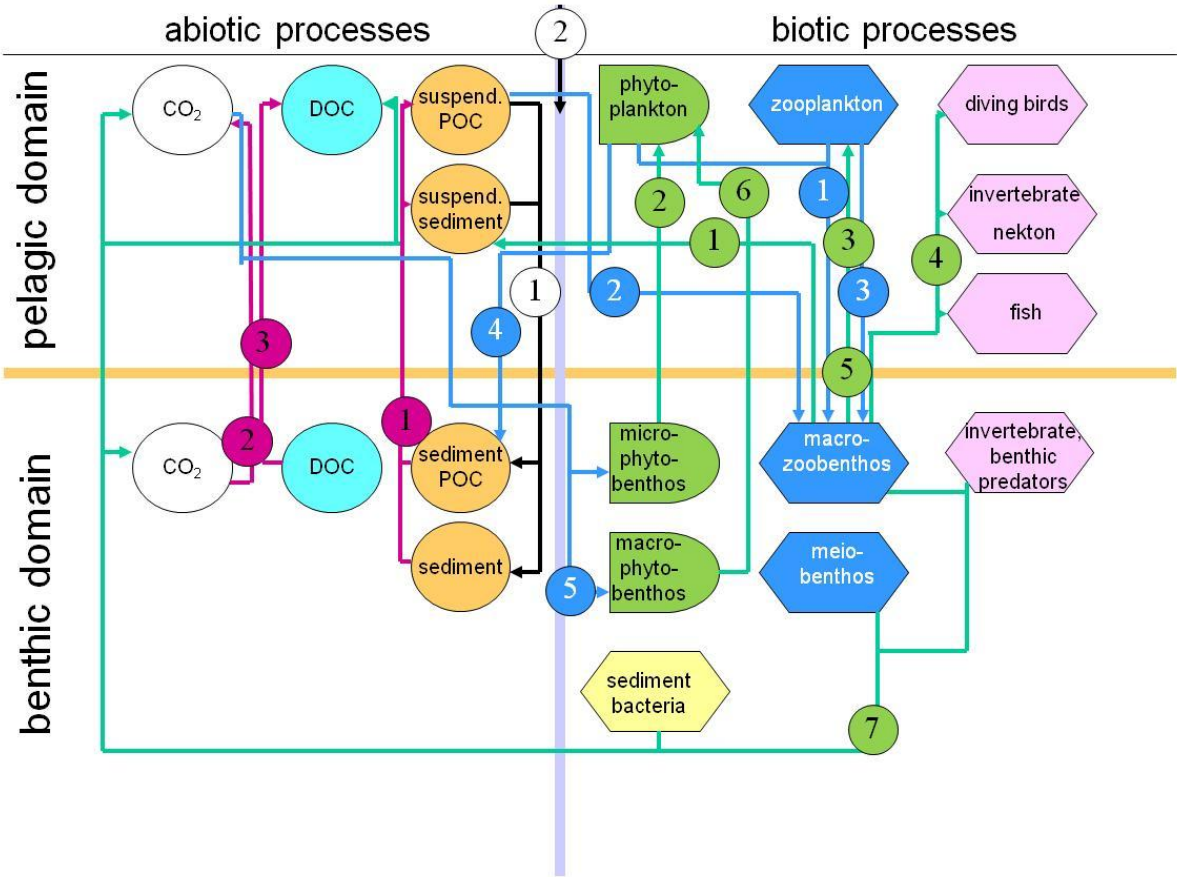


Fig. 4. Scheme of general pelagic-benthic and benthic-pelagic carbon exchange processes between an intertidal benthic community and the overlying pelagic domain.
Pelagic-benthic fluxes: abiotic: white: 1: sedimentation of organic material and sediments; 2: atmospheric CO_2 intake; biotic: blue: 1 phytoplankton uptake by macrobenthos; 2 suspended POC uptake by macrobenthos; 3 zooplankton uptake by macrobenthos; 4 sedimentation of phytoplankton; 5 CO_2-uptake by phytobenthos.
Benthic–pelagic fluxes: abiotic: red: 1 re-suspension and erosion of organic matter and sediments; 2 advection of pore water CO_2; 3 advection of dissolved organic carbon from pore water; biotic: green: 1 bioturbation of sediments and organic material; 2 resuspension of microphytobenthos; 3 release of macrobenthic spawn and recruits; 4 predation by birds, fish and invertebrate nekton. 5 macrozoobenthic drift; 6 macrophytobenthos drift; 7 CO_2 production by respiration of bottom fauna and bacteria.

Among exclusively biological exchange processes that are directed from the water body to the bottom are above all processes related to feeding and reproduction, particularly filtration of phytoplankton and the transition of larval recruits to the benthic phase, such as the primary settlement of postlarvae of many benthic organisms. These processes occur exclusively at the community level and are influenced by an array of different controlling factors (Dudas et al. 2009a, b; Kirby et al. 2008; Drent 2002), especially hydrographic conditions and temperature.

Many benthic-pelagic processes connect the abiotic biotope with its community and act therefore on the ecosystem level. These processes include the uptake of dissolved nutrients and CO_2 by

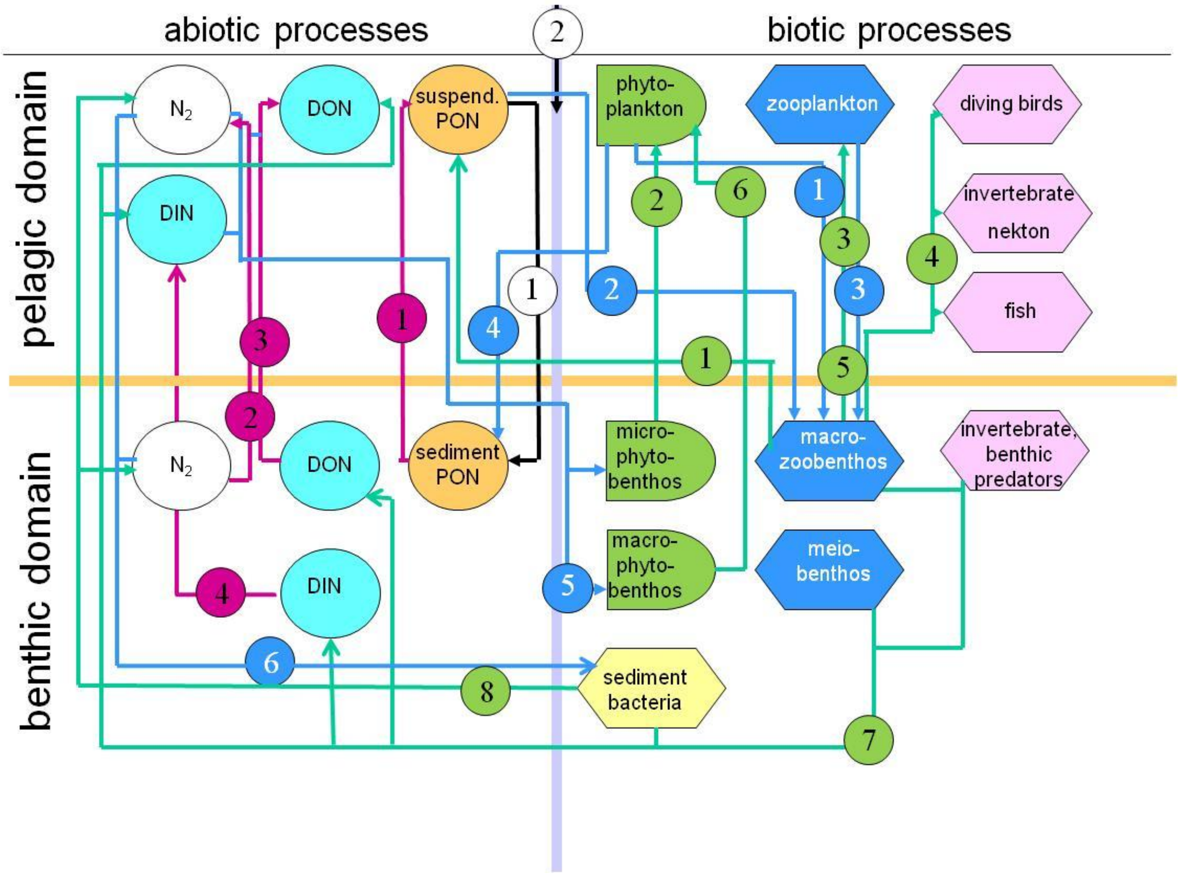


Fig. 5. Exchange processes scheme of general pelagic-benthic and benthic-pelagic nitrogen exchange between an intertidal benthic community and the overlying pelagic domain.

Pelagic-benthic fluxes: abiotic: white: 1: sedimentation of organic material; 2: atmospheric N_2 intake; biotic: blue: 1 phytoplankton uptake by macrobenthos; 2 suspended PON uptake by macrobenthos; 3 zooplankton uptake by macrobenthos; 4 sedimentation of phytoplankton; 5 DIN–uptake by phytobenthos; 6 nitrogen fixation by bacteria.

Benthic–pelagic fluxes: abiotic: red: 1 resuspension and erosion of organic matter; 2 advection of pore water N_2; 3 advection of dissolved organic nitrogen from pore water; 4 advection of dissolved inorganic nitrogen from pore water; biotic: green: 1 bioturbation of sediments and organic material; 2 resuspension of microphytobenthos; 3 release of macrobenthic spawn and recruits; 4 predation by birds, fish and invertebrate nekton; 5 macrozoobenthic drift; 6 macrophytobenthos drift; 7 DIN production by bottom fauna and bacteria; 8 denitrification.

phytobenthos, the oxygen uptake by benthic heterotrophs, filtration of detrital particles by suspension feeding macrobenthos, or the $CaCO_3$ uptake by benthic organisms for biogenic shell formation.

Benthic-pelagic exchange processes: Abiotic processes that transport material from the bottom to the water column are dependent on higher current velocities and turbulences. Due to increasing critical shear velocity sediment particles start to resuspend from small grain sizes to larger size fractions, and at high turbulences the total sediment surface layer can be removed. Transport of gaseous compounds such as CO_2 and N_2 will be intensified by water movement, but even a minor exchange will occur by diffusion as long as a concentration gradient exists between the benthic and pelagic pool of the particular compound.

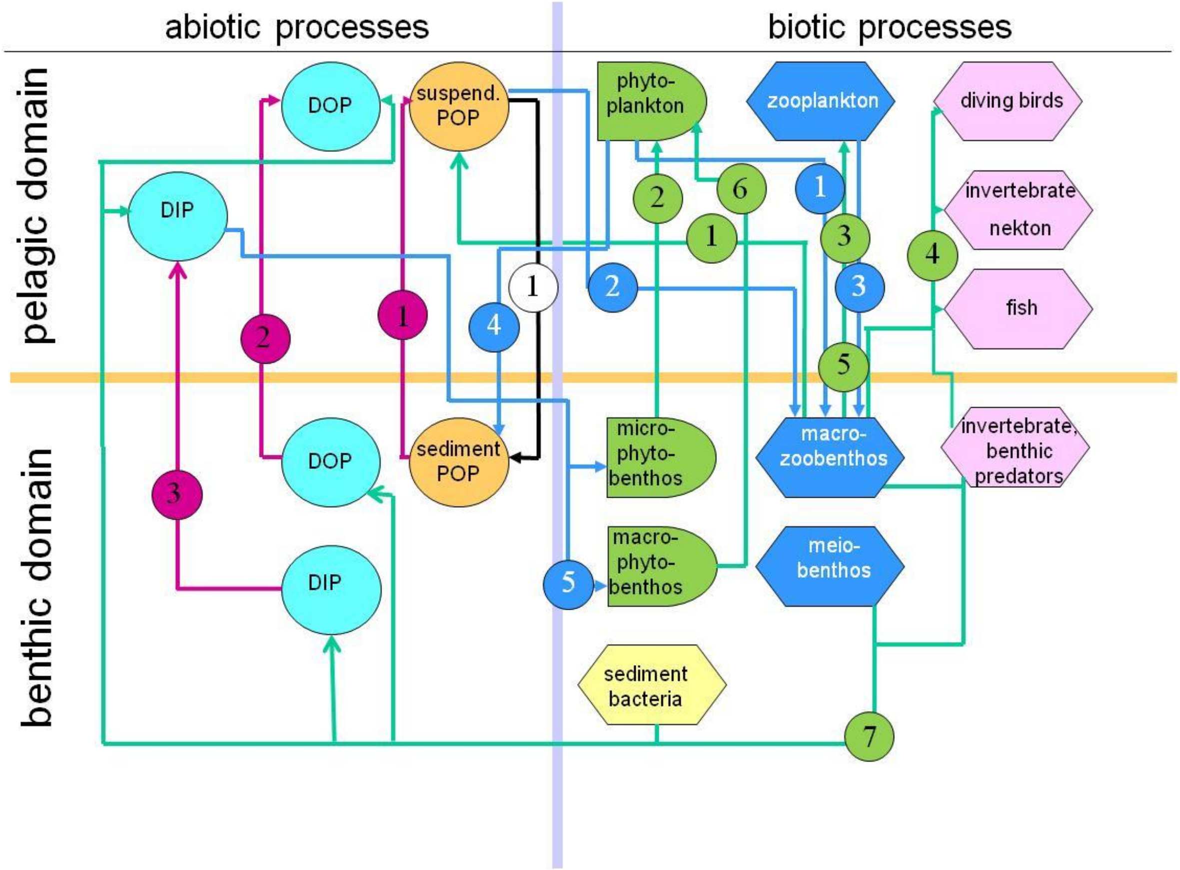


Fig. 6. Scheme of general pelagic-benthic and benthic-pelagic phosphorus exchange processes between an intertidal benthic community and the overlying pelagic domain.
Pelagic-benthic fluxes: abiotic: white: 1: sedimentation of organic material; biotic: blue: 1 phytoplankton uptake by macrobenthos; 2 suspended particulate organic phosphorus (POP) uptake by macrobenthos; 3 zooplankton uptake by macrobenthos; 4 sedimentation of phytoplankton; 5 uptake of dissolved inorganic phosphorus (DIP) by phytobenthos.
Benthic–pelagic fluxes: abiotic: red: 1 re-suspension and erosion of organic matter; 2 advection of dissolved organic phosphorus (DOP) from pore water; 3 advection of DIP from pore water; biotic: green: 1 bioturbation of sediments and organic material; 2 resuspension of microphytobenthos; 3 release of macrobenthic spawn and recruits; 4 predation by birds, fish and invertebrate nekton. 5 macrozoobenthic drift; 6 macrophytobenthos drift; 7 DIP production by bottom fauna and bacteria.

Beside passive drifting of benthic organisms and resuspension of microphytobenthos, vertical migrations and release of reproduction products by benthic organisms with a pelagic egg or larval phase are counted among the direct biological benthic-pelagic processes. In addition predation by pelagic predators on the community falls in this range of processes. The potential of such an interaction is specific for the species. Through biological benthic-pelagic processes energy and material as well as organisms are lost from the community steadily.

The abiotic and biotic material pool can be connected even by benthic–pelagic processes. Oxygen production through photosynthesis of benthic algae and seagrasses and the CO_2 production by respiration of heterotrophic components are examples of these processes at the ecosystem level.

While the exchange processes mentioned above represent single connections or interactions between two components, some interactions can be dependent on each other and form a process sequence such as the filtration of plankton and the subsequent excretion of dissolved nutrients or faecal material. In general such sequences consist of a pelagic-benthic and an antagonistic benthic-pelagic process, which are both connected by one or even more entire transformation processes such as digestion, defecation by macrobenthos and remineralisation by bacteria.

Pelagic-benthic exchange processes are exogenous material or energy imports as far as we consider the benthic system, but for the pelagic environment they are considered as exports. Correspondingly the reverse is happening regarding benthic-pelagic exchange processes. An overview of the order of magnitude of the pelagic-benthic and benthic-pelagic exchange processes is given in Table 1.

If the investigated ecosystem or community is characterised by a stable material pool, then pelagic-benthic as well as benthic-pelagic exchange processes must be in steady state equilibrium.

The depicted processes occur in intertidal systems only during immersion and can be brought to nearly a standstill during emersion. During this phase benthic communities are connected with the atmospheric environment, and thus other processes, especially gas exchange, desiccation and precipitation processes prevail, which can control settling structure and species composition of a community. Among the biotic processes predation by waders, geese and gulls is coupled to the low tide phase.

Exchange between two adjacent communities occurs mainly by interactions between the benthal and pelagial. Exceptions are sediment transports or migrations of mobile benthos or nekton at the bottom, such as those of snails and crabs migrating from one community into the adjacent one.

Because exchange processes depend to a large extent on the activity of single species, certain organisms within a community contribute more to the exchange than others. Thus material exchange processes are determined by the organism community and its species composition. They are distinct indicators of the activity of an ecosystem, because they express directly the interplay between abiotic and biotic processes.

Benthic-pelagic and pelagic-benthic processes are normally defined by the community where these processes happen and by its constituents. Both can be considered as a black box. In the Wadden Sea different communities contribute differently to this exchange due to the population density of plant and animal components and their species specific potential for exchange. Communities will be therefore regarded separately in the following text.

Exchange processes in single communities will be structured by their chemical components carbon, nitrogen and phosphorus (for an overview of carbon see Fig. 4, for nitrogen Fig. 5 and phosphorus Fig. 6.).

Table 1. Range of dominant pelagic-benthic and benthic-pelagic exchange processes (yearly average in mg m^{-2} h^{-1}), split into C, N, P, in intertidal communities of the Sylt-Rømø Bight.

Process	***Order of magnitude (in mg C, N and P m^{-2} h^{-1})***		
	C	***N***	***P***
Pelagic-benthic:			
Abiotic processes			
Sedimentation	0 - 320	0 - 71	0 - 17
Gas transport into the sediment	0 - 30	0 – 0.001	-
Biotic processes			
Filtration of phytoplankton	3 - 200	0.3 - 30	0.02- 2
Filtration of POC, PN	1 - 33	<0.1 - 3	0.01 - 0.8
Uptake of dissolved inorganic nutrients	-	3 - 34	0.23 – 2.08
Primary settlement of postlarval stages of benthic organisms	0.2 - 2	<0.01 – 0.39	0.003 – 0.04
Sedimentation of phytoplankton	not considered		
CO_2 Uptake by plants	38 - 220	-	-
Benthic-pelagic			
Abiotic processes			
Erosion	0 – 270	0 – 27	0 - 6
Gas transport into the water column (CO_2, N_2O)	0 - 20	0 - 0,025	-
Biotic processes			
Resuspension of faeces	0 – 56	0 – 6	0 - 3
Resuspension of microphytobenthos	low	low	low
Excretion dissolved matter			
inorganic:	-	1.6 -39	1 – 5.6
organic:	0 – 12.3	0 – 1,2	0 - 0.2
Drift of benthic organisms	39.4 – 194.9	8.7 – 42	0.6 – 3.4
Predation of benthos by nekton and diving birds	<0.01 – 43.7	<0.01 – 9.3	<0.01 – 0.6
Respiration /CO_2-Production	20 -307	-	-
Denitrification/ N_2 - production	-	0.07 – 0.1	-
Release of sexual products	0.06 – 14.8	0.002 – 3.4	0.001 - 0.3
Rupture of macrophytes and epifauna by storm and ice score	0 – 163.9	0 – 24.7	0 – 1.6

b. Exchange processes and food web organisation in intertidal mussel beds

i. Carbon exchange in mussel beds

Comparing both benthic-pelagic with pelagic-benthic processes leads to an estimation of the net fluxes which indicate the direction of the fluxes and characterise the mussel bed system either as a sink or a source for the exchange of material and organisms.

Table 2 summarises the main carbon fluxes due to their main constituents either organisms, particulate material, dissolved organic material or dissolved inorganic material.

Interestingly the loss of carbon due to living organisms by a mussel bed is higher than the import on an annual base. This loss is originated by loss of macroalgae by storms (39%) and by drift of organisms (47%), whereas loss by reproduction products is only 4%.

Predation by birds contributed also with 10% to total loss, whereas impact of fish was negligible. Counteracting organism import processes do not outweigh these losses. The main process is the uptake of phytoplankton by suspension feeders (196.94 $mgCm^{-2}h^{-1}$) representing 49% of total organism intake. Consumption of bacteria and zooplankton as well as settlement of postlarval stages is of minor quantitative significance for organism uptake. Mussel beds are therefore net sources of living organisms which have to be compensated by the entire production of the community.

The uptake of particles on the other hand is higher in mussel beds then its release. Organic material from detrital particles is therefore accumulating in the mussel bed or is processed by the community to support production and remineralisation. Even uptake of dissolved organic carbon prevails in mussel beds.

In total, a mussel bed is a sink for dissolved and particulate organic material, but a source for dissolved inorganic carbon and organisms. The total carbon balance characterises the mussel bed as a carbon sink where especially POC is taken up in excess at least on an annual base. This could lead to a burial of mussel beds with organic sediment, and indeed mussel beds show a distinct elevation by accumulating organic rich sediment below the living mussel carpet (Smaal & Haas 1997). However, after a certain elevation level is attained, mussel beds are sensitive to currents and turbulence especially during storms. These irregular events may regulate the carbon balance at a larger time scale.

Table 2. Budget of carbon fluxes through a mussel bed in mg C $m^{-2}h^{-1}$ based on annual means. The budget was computed as BP–PB, where PB = pelagic-benthic exchange and BP = benthic-pelagic exchange. Positive values indicate a net release and negative values a net uptake by the community.

	pelagic-benthic mg C $m^{-2}h^{-1}$	benthic-pelagic mg C $m^{-2}h^{-1}$	budget mg C $m^{-2}h^{-1}$	
C-exchange via organisms	399.75	417.37	17.62	release
C-exchange via particles	349.18	0.00	-349.18	uptake
C-exchange via dissolved organic carbon DOC	13.32	3.95	-9.37	uptake
C-exchange via dissolved inorganic carbon DIC	220.93	308.65	87.72	release
Σ Total	983.18	729.97	-253.21	uptake

ii. Nitrogen exchange in mussel beds

Similar to the benthic-pelagic C-flow, N-compounds are partly exported from the mussel bed system, but in total mussel beds are sinks for N. Nitrogen is imported by particle sedimentation as well as particle filtration. This N-input is the base for the high productivity and high metabolic activity of the mussel bed and thus DIN as well as nitrogen bound in living organisms leaves the system. The latter pathways hardly compensate for the high N-import. Thus mussel beds act as a sink for particulate N and a source for inorganic N or living organisms.

A net import of 109.39 mg N $m^{-2}h^{-1}$ (sum of net PON-exchange and net DON-exchange) has been measured for an intertidal mussel bed and this amount is allocated between particulate N import (68%) and dissolved organic N import (32%) (Table 3). A net export of 11.56 mg N $m^{-2}h^{-1}$ (sum of net organism exchange and net DIN exchange) has been measured to compensate for it, produced by export of organisms, especially the rupture of macroalgae (52%) and the export of ammonium (48%) due to remineralisation and excretion processes. In total 97.83 mg N $m^{-2}h^{-1}$ is accumulated in the mussel bed system, which can be compensated by irregular particle export due to strong winds or due to denitrification processes in the anoxic mud below the mussel layer within this community.

Table 3. Budget of nitrogen fluxes through a mussel bed in mg N $m^{-2}h^{-1}$ based on annual means.

	pelagic-benthic mg N $m^{-2}h^{-1}$	benthic-pelagic mg N $m^{-2}h^{-1}$	budget mg N $m^{-2}h^{-1}$	
N-exchange via organisms	73.41	79.43	6.01	release
N-exchange via particles	74.67	0.00	-74.67	uptake
N-exchange via dissolved organic nitrogen DON	34.82	0.09	-34.72	uptake
N- exchange via dissolved inorganic nitrogen DIN	33.80	39.35	5.55	release
Σ Total Exchange	216.70	118.88	-97.83	uptake

iii. Phosphorus exchange in mussel beds

Comparing the uptake and release rates of the different components in a mussel bed it becomes evident that mussel beds are distinct net sinks for P (Table 4). The reason for the sink function is the filtering potential of the community for particulate P and the uptake of dissolved organic P (Asmus et al. 1995). *Mytilus edulis* in particular contributes to this process by filtering detritus, bacteria and phytoplankton. However sedimentation is another important process.

In contrast to particulate P, inorganic P is released from a mussel bed at a net rate of 3.60 mg P $m^{-2}h^{-1}$ and has been confirmed by flume experiments (Asmus et al. 1995). The net release of P via living organisms is low.

Table 4. Phosphorus budget for intertidal mussel beds (mg P $m^{-2}h^{-1}$) based on annual means. Numbers in italics indicate fluxes under the assumption of immediate remineralisation of total faecal material.

	pelagic-benthic mg P $m^{-2}h^{-1}$	benthic-pelagic mg P $m^{-2}h^{-1}$	budget mg P $m^{-2}h^{-1}$	
P-exchange via organisms	5.48	5.79	0.31	release
P-exchange via particles	11.92	0.00	-11.92	uptake
P-exchange via dissolved organic phosphorus DOP	0.73	0.09	-0.64	uptake
P- exchange via dissolved inorganic phosphorus DIP	2.08	5.68	3.60	release
	2.08	*6.42*	*4.34*	
Σ Total Exchange	20.21	11.56	-8.16	uptake

iv. Ecological carbon transfer of mussel beds

Among the benthic communities in the Wadden Sea mussel beds are characterised by high consumption activity and secondary production per unit of area (Asmus 1987; Prins et al. 1994; 1996). The food requirement by the community exceeds autochthonous primary production due to the high density of suspension feeders and grazers. This imbalance is adjusted by the tidal plankton import from outside, by foraging migrations and probably by shifting to other food resources, i.e. microphytobenthos to juvenile balanids by *Littorina littorea* (Buschbaum 2002), or from phytoplankton to suspended detritus by suspension feeders (Smaal et al. 1986). High consumption rates of extended mussel beds may lead to diminishing resources within the community. The high accumulation of macrobenthic biomass attracts an array of predators and results in an increased predation pressure particularly on juvenile mussels and the associated fauna of mussel beds. The high predation by birds skims the main part of secondary production of this group.

Biomass of the dominant compartments: Mussel beds reveal the highest total biomass among the intertidal communities of the Sylt-Rømø Bight with 959.2 g C m^{-2}. A dense settlement of mussels as well as an extensive cover of macroalgae on top of the mussel aggregations result in the highest heterotrophic and autotrophic biomass within this community and within boreal intertidal areas (Table 5). The heterotrophic biomass is dominated by the biomass of *M. edulis* which occupy 79.8% of the total biomass and 94% of the heterotrophic biomass. The share of *Fucus vesiculosus* in total and autotrophic biomass is 15% and 99%, respectively.

Table 5. Biomass and energetics of all compartments in flow networks of the mussel bed subsystem of the Sylt-Rømø Bight. Biomass and standing stocks in mg C m^{-2}, gross primary production (GPP), net primary production (NPP), production (P), respiration (R), egestion (E) and consumption (C) in mg C m^{-2}d^{-1}.

Mussel bed	Biomass mg C m^{-2}	GPP mg C m^{-2} d^{-1}	NPP mg C m^{-2} d^{-1}	Respiration	
Autotrophic compartments					
Microphytobenthos	130.00	98.63	64.41	34.22	
Macroalgae (*Fucus* spp)	146236.00	5279.10	3933.70	1345.40	
Total autotrophs	146366.00	5377.73	3998.11	1379.62	
Heterotrophic compartments		Production mgC m^{-2} d^{-1}	Respiration mgC m^{-2} d^{-1}	Egestion mgC m^{-2} d^{-1}	Consumption mgC m^{-2} d^{-1}
Littorina littorea	19337.20	25.40	139.86	239.22	404.48
Capitellidae	1885.00	16.89	43.49	106.87	167.25
Oligochaeta	661.20	1.81	17.65	8.95	28.41
Heteromastus filiformis	806.00	4.42	8.41	56.29	69.11
Gammarus species	840.00	4.68	22.16	7.50	34.40
Mytilus edulis	761770.00	751.30	4132.30	690.00	5573.60
Macoma balthica	498.80	2.20	24.40	21.70	48.30
Balanus crenatus	1856.40	5.62	18.48	3.50	27.60
Semibalanus balanoides	2496.00	7.32	24.00	4.44	35.76
small crustaceans	1170.00	11.13	20.00	6.32	37.43
Carcinus maenas	6370.00	32.27	55.40	88.60	176.27
Crangon crangon	9.20	0.10	0.35	0.10	0.55
Pomatoschistus microps	1.79	0.02	0.04	0.34	0.40
Pomatoschistus minutus	0.47	0.005	0.01	0.16	0.175
Pleuronectes platessa	0.03	0.0002	0.0003	0.0009	0.0014
Merlangius merlangus	0.56	0.00	0.01	0.01	0.03
Gadus. morhua	7.5	0.04	0.12	0.07	0.23
Myoxocephalus scorpio	7.5	0.04	0.12	0.07	0.23
Somateria mollissima	9000.00	24.45	953.51	244.49	1222.45
Haematopus ostralegus	2043.75	7.00	273.15	70.04	350.19
Larus ridibundus	2.29	0.01	0.25	0.06	0.32
Larus canus	2.40	0.01	0.24	0.06	0.31
Larus argentatus	2887.50	7.50	225.00	60.00	292.50
Other birds	6.75	0.01	0.50	0.14	0.65
Sediment bacteria	625.00	121.53	192.60	67.41	381.54
Meiobenthos	500.00	10.96	41.70	19.01	71.67
Total heterotrophs	812785.34	1034.71	6193.74	1695.36	8923.85
Total	959151.34				

Primary production:

Gross primary production: About 5378 mg C m^{-2}d^{-1} is produced by the plants of a mussel bed (Table 5). The main part of this production (98%) is contributed by *Fucus vesiculosus*, and microphytobenthos has the balance of 2 %.

Net primary production: Approximately 3998 mg C m^{-2}d^{-1} is converted into plant biomass by primary production, which is about 74% of the gross primary production (Table 5). Grazing on macroalgae is low; only 5% of the available production is directly consumed by mainly crustaceans and most of plant production is stored in the system until winter when storms rupture the *Fucus* thalli and export the largest part of the plant production from the system to the beach. In contrast to grazing on macroalgae grazing on microphytobenthos is immense due to the high biomass of *Littorina littorea* in mussel beds. This leads to a shortage of microphytobenthos production in mussel beds in the order of about 300 mg C $m^{-2}d^{-1}$. To balance this carbon debt, *Littorina* uses other sources such as juvenile barnacles (Buschbaum 2002) or migrates from the entire mussel beds to adjacent sand flats during low tide to graze on microphythobenthos that is more abundant there (pers. observation).

Consumption: Approximately 8924 mg C $m^{-2}d^{-1}$ is consumed per day by the intertidal mussel bed. Suspension feeders consume about 5597.8 mg C $m^{-2}d^{-1}$ (Table 5). This is 63% of the total consumption of the community and shows the high dependency of mussel bed on the overlying water. The consumption exceeds also the production of the phytoplankton over a mussel bed by 4511 mg C $m^{-2}d^{-1}$ and demonstrates that mussel beds in the intertidal area are only supported with enough food when the tidal water imports rich phytoplankton biomass produced in the contiguous Wadden Sea or imported from the adjacent North Sea. The relation between consumption of imported pelagic material to total consumption of pelagic sources of 0.81 shows a high dependency of pelagic imports. The relation of total allochthonous food sources to total autochthonous food sources of 1.36 strengthen the importance of imported food for the mussel bed community. The autochthonous food consumption must be seen in relation to trophic levels and production of the heterotrophic organisms. However, the above mentioned ratios for consumption give us a quantitative parameter for the “openness” or “closeness” of an ecosystem.

Heterotrophic production: Heterotrophic production of a mussel bed community amounts to 1035 mg C $m^{-2}d^{-1}$. Most of the heterotrophic production is due to the second trophic level because of the prevalence of *M. edulis* and *Littorina littorea* in this system, which depends mainly on phytoplankton and detritus or microphytobenthos respectively. However, secondary production is high and reveals the highest values among all investigated intertidal communities (Asmus 1987). Predation pressure on *M. edulis*, *M. balthica* and *Carcinus maenas* is very high so that the production rates of these species were exceeded by 910 mg C $m^{-2}d^{-1}$, 93 mg C m^{-2} d^{-1} , and 55 mg C $m^{-2}d^{-1}$, respectively (Baird, Asmus & Asmus 2007). This could be a consequence of the relatively low areal extent of mussel beds which leads probably to an overexploitation by their predators.

Production to biomass ratio: Mussel beds show a very low production to biomass ratio of only 0.005 (on a daily basis) which is the lowest P/B- ratio found among the intertidal communities in the Sylt-Rømø Bight (Fig. 7). This is mainly because the main biomass is due to animals of older age groups showing low individual P/B ratios compared to juvenile specimens which have larger individual P/B ratios (Baird, Asmus & Asmus 2007)

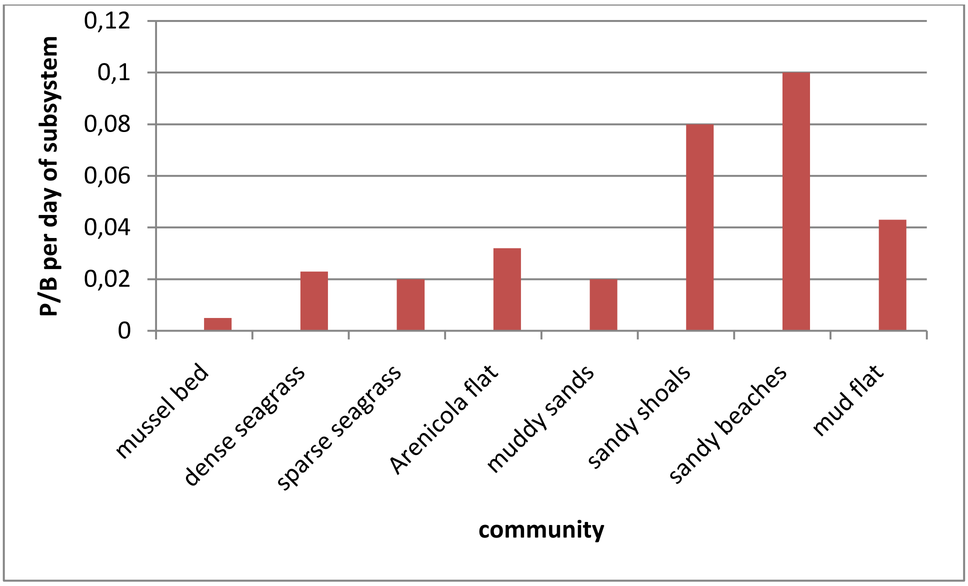


Fig. 7. P/B – ratio per day of the dominant intertidal communities of the Sylt-Rømø Bight.

Respiration: Community respiration of mussel beds amounts to about 7573.36 mg C $m^{-2}d^{-1}$ and is exported from the system. This process is considered within the budgets of exchange processes.

Egestion: Whether community egestion is an exchange process depends on the system and on the element the ecological transfer is based upon. In mussel beds C-egestion products like faeces are mainly accumulated between the mussels and lead to elevation of the community in relation to the adjacent sediment. Thus the egestion is accumulated within the detritus pool of the community. In total 1763 mg C $m^{-2}d^{-1}$ detritus is produced by a mussel bed (Baird, Asmus & Asmus 2007) (Fig. 8). Most of the egested C (86%) is recycled especially on the second trophic level.

v. Food web of mussel beds

(1) Trophic analysis of mussel beds

Diversity and biomass of trophic groups: Among the intertidal benthic communities of the Sylt-Rømø Bight, mussel beds reveal the highest diversity and biomass especially in macrobenthic species (Büttger et al. 2008). In mussel beds up to five trophic levels including the primary production level can be identified. The biomass of secondary producers consists mainly of *M. edulis* followed by *L. littorea*. The food web model constructed here includes 8 species that contribute mainly to this trophic group with biomasses higher than 0.1 g C m^{-2} species. Species other than *M. edulis., L. littorea, Capitella, Oligochaeta, Macoma* and *Jaera spec. (*included in small crustaceans*)* are using primary producers or detritus only partly as food but feed mainly at higher trophic levels. Bacteria and meiofauna species also contribute to the secondary producer level, but their diversity in mussel beds is unknown.

Within the secondary consumers, species diversity is higher and includes crustaceans, fish and birds. In the food web model 15 species were included with *Gammarus locusta* and

Carcinus maenas representing crustaceans, 7 fish species and 5 bird species including eider ducks, oystercatchers and herring gulls.

The tertiary consumers are mainly represented by predatory fish such as whiting (*Merlangius merlangus*), cod (*Gadus morhua*) and sea-scorpion (*Myoxocephalus scorpius)*. These three species were included in the model at this trophic level.

The consumers of the fourth level are mainly represented by the above mentioned predatory fish species feeding to a small degree on smaller specimens at the tertiary consumer level, even on their own species. In general seals, harbour porpoises and cormorants as well as terns should also appear partly in this trophic level but were not included because of the lack of empirical data. It is also unknown whether they prey on the mussel bed community.

Total system throughput (TST): The total system throughput is a measure of system size and represents the sum of all internal and exogenous inputs to the system compartments. Mussel beds contribute 41.5% to the daily production on a m^2 basis of all investigated intertidal communities (Baird, Asmus & Asmus 2007). They are thus areas of high activity indicated by the highest amount of C transported along the food web in a given time compared to the other communities. The total system throughput is estimated to be 33 571 mg C $m^{-2}d^{-1}$ (Table 6). The high rates of productivity of *Fucus vesiculosus* and the high activity of invertebrate and vertebrate predators are largely responsible for the high TST in mussel beds (Baird, Asmus & Asmus 2007).

Average path length (APL): The average path length of a food web of a community is a system descriptor that measures the average number of compartments that a unit of C passes through from its entry into the system before it leaves it. The APL is expected to be longer in systems with high degree of flow diversity and cycling (Christensen 1995; Thomas & Christian 2001). On average a unit of C passes 1.94 compartments before it leaves a mussel bed (Table 6). This means that short cycles prevail in a mussel bed in spite of the high flow diversity and the large number of cycles in this system.

Average residence time (ART): Although average path length is short, the material and energy appear to reside for a much longer time (ART= 84d) in a mussel bed compared to other systems (range 7 to 55d). The organic material deposited onto the mussel bed contributes to the long ART calculated for this system. This material is only removed during strong storms especially those from easterly directions.

Lindeman spine: The relation of production efficiencies between the trophic levels are shown in Table 6. The energy transfer can be computed by the Lindeman spine, which gives the food web as a concatenated flux through all trophic levels and allows to determine the actual number of trophic levels within the community as well as to estimate the energy transfer, loss and import from outside (Fig. 8). The highest efficiency of energy transfer among the heterotrophic compartments is in the second level. In the third trophic level energy transfer is very low with only 3.4% but at the fourth trophic level it increases again to 10%. This is due to better efficiencies of higher level predators such as birds and fish, compared with predators on lower level such as shore crabs, which may cause a bottleneck for the energy flow in this community.

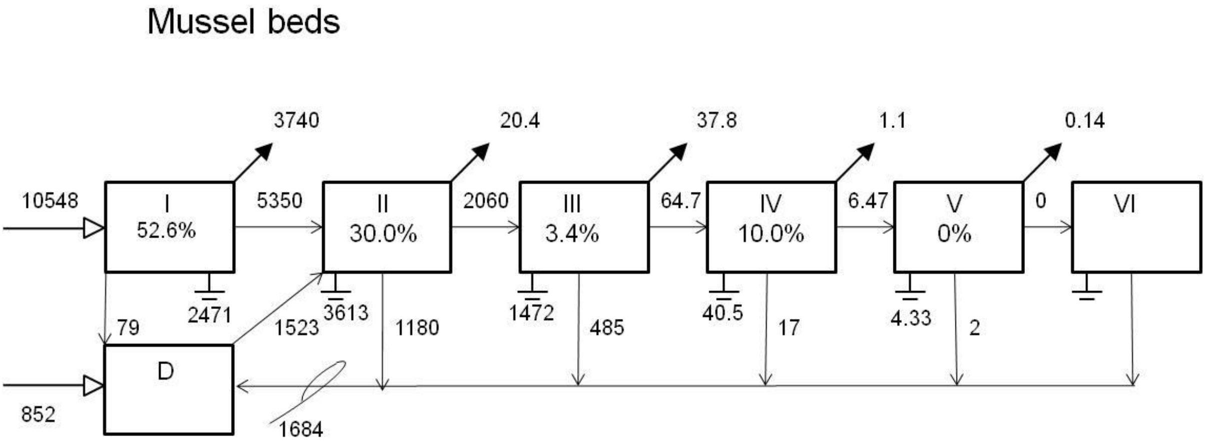


Fig. 8. Lindeman spine of an intertidal mussel bed of the Sylt-Rømø Bight. The box indicated D refers to the detrital pool, and the Roman numbers in the boxes of the Spine to discrete trophic levels. Percent values in Spine boxes refer to the efficiency of energy transfer between the integer trophic levels. Fluxes are given in mg $Cm^{-2}d^{-1}$.

Mean trophic efficiency: The logarithmic mean of the trophic efficiencies of the mussel bed is the highest (15%) among all intertidal communities investigated (Baird Asmus & Asmus. 2007). Mussels are the main secondary producers and also the main food for predators in this system. Thus the short food cycle from primary production of phytoplankton to mussels to birds is a dominating pathway within the food web and is responsible for the high trophic efficiency of the system.

(2) Structure and magnitude of cycling

The cycling of energy and material is an inherent and universal process in all natural ecosystems that contribute to their autonomous behaviour. Cycling occurs through a number of cycles of different path lengths.

Number of cycles: The number of cycles in the mussel beds is 173 (Baird, Asmus & Asmus 2007). Because of the dependency of mussel beds on phytoplankton input from outside the number of cycles is lower compared to communities were most of the community is based on detritus or microphytobenthos.

Cycle distribution: In mussel beds 11% of cycling takes place over longer pathways involving 4 to 6 compartments. Especially the important role of top predators (birds and cod, whiting and sea-scorpion) is reflected in these comparatively long cycles.

Finn Cycling Index: The amount of material cycled in each system is expressed as a fraction of the total system throughput in the Finn Cycling Index. The Finn Cycling Index is lowest in mussel beds. Little material is recycled in the mussel beds because of the high TST which can be ascribed to the high *Fucus vesiculosus* production, little utilisation of it and its subsequent export from this system.

(3) System level properties and system organization

Development capacity: The development capacity is a measure for the maximum number of potential fluxes and interactions which can be realized within a system. In the mussel bed DC is highest compared to other intertidal communities of the Sylt-Rømø Bight (Table 6). The development capacity splits up into ascendancy which gives the realized structure of a system and the system overhead which is the sum of the overheads of import, exports, respiration and redundancy. The system overhead reflects the reserve strength of a system to counter perturbations. The higher the overhead of export and import the more dependent is a system from external sources. In mussel beds about 13% of the system overhead is due to imports from outside which shows a high dependency from external sources compared to other communities of the Sylt-Rømø Bight (range 3% - 9.6%).

Table 6. Global system attributes derived from network analysis for the mussel bed subsystem of the Sylt-Rømø Bight. Values reflect results from network analysis where excess production and sediment POC were not exported from the subsystems. In compartments where predation exceeds production, no artificial imports were made to balance the compartment.

System Attributes	mussel beds
Trophic efficiency (logarithmic mean, %, Sed POC retained)	14.92
Detrivory (detritus pool to TL2, mg Cm^{-2}d^{-1}, Sed POC retained)	1523
Detrivory:herbivory ratio (D:)	0.3:1
Number of cycles (Sed POC retained)	173
Finn Cycling Index (%)	2.53
Average Path Lenght (APL=TST-Z/Z)	1.94
Ave Res Time (ART; days)(Sum Biomass/Sum Exports, Resp)	83.73
Total System Throughput (mg Cm^{-2}d^{-1})	33571
Total System Throughput (tonnesCarea^{-1}d^{-1})	12.1
Development Capacity (mg Cm-^{2}d^{-1}bits)	135620
Ascendency (mg Cm-^{2}d-1bits)	67521
Relative Ascendancy (A/DC, %)	49.8
Average Mutual Information (A/TST)(normalized A)	2.01
Average Internal Mutual Information (Ai/TST)	0.91
Overheads on imports (mgCm-^{2}d^{-1}bits)	17781
Overheads on exports (mgCm-^{2}d^{-1}bits)	2690
Dissipative Overheads (mgCm-^{2}d^{-1}bits)	23590
Redundancy (mgCm-^{2}d^{-1}bits)	24034
Relative Redundancy (R/DC, %)	17.7
Normalized Redundancy (R/TST)	0.72
Internal Development Capacity (mg Cm-^{2}d^{-1}bits)	54659
Internal Ascendency (mgCm-^{2}d^{-1}bits)	30624
Relative Internal Ascendency (Ai/DCi, %)	56.0
Internal Redundancy (mgCm-^{2}d^{-1}bits)	24034
Relative Internal Redundancy (Ri/DCi, %)	44.0
Flow Diversity DC (DC/TST, %)(normalized DC)	4.04
Φsum of overheads/TST (+#58)	2.23
Overall connectance	1.55
Intercompartmental connectance	1.78
Foodweb connectance (living compartments only)	1.29
GPP/TST	0.16

Redundancy: 18% of system overhead is due to redundancy. A system with low redundancy is considered to be susceptible to external perturbations which may affect the trophic interactions between system components. Parallel pathways of energy and material transfers on the other hand can act as a buffer or reserve should external perturbations occur and in changes in biodiversity. It is postulated that a sustainable system requires a balance between ascendancy and redundancy. In mussel beds the redundancy to ascendancy relation is 1:2.7 that shows that redundancy is too low for a sustainable and stable system probably because of the lack of parallel pathways. If both properties are balanced than the system can draw activity from the overhead to keep it in operation, but at a less organised state.

Ascendancy: 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. Higher indices of ascendancy reflect increased ecological succession characterised by for example species richness, decreased costs of overheads to the system, greater internalisation of resources and finer trophic specialisation. 50% of the development capacity (DC) is realized as ascendancy in intertidal mussel beds which thus can be interpreted as having well organised functions of energy transfers. The internal relative ascendency is a function of internal exchanges only. If this ratio decreases compared with the relative ascendancy, then the system becomes more dependent from external than internal sources. Although we have seen that mussel beds are largely dependent on external phytoplankton as food, the internal relative ascendancy increases compared with the relative ascendancy by 6.2%. The high *in situ* production of *Fucus vesiculosus* which uses internally produced nutrients for growth could explain this increase.

Average mutual information: AMI or normalized ascendancy is highest in the mussel bed subsystem at 2.01 compared to other communities of the Sylt-Rømø Bight. This index is indicative of the level of inherent organisation and the degree of specialisation. The high TST of mussel beds are mainly due to *F. vesiculosus*, which does not contribute much to flow structure since only few species feed on it. However, the high AMI as well as the high A/DC or Ai/DCi can be ascribed to an inflated ascendancy, which is enhanced by high system activity due to the size of flows associated with *F. vesiculosus*. The low value of the GPP to TST ratio in mussel beds of 0.16 demonstrates the influence of *F. vesiculosus* to the system, once its high system throughput is removed.

Flow diversity: Flow diversity or relative ascendancy measures both the number of interactions and the eveness of flows in the food web, and is thus a much more dynamic concept than species diversity. Comparatively higher values of this index indicate an increase in interactions and a lower degree of unevenness and variability in the flow structure. In intertidal mussel beds flow diversity is with 4.04 below the mean of all intertidal communities (4.33). This shows that most material is transported via pathways that are due to organisms such as *Fucus* and *Mytilus* which dominate the biomass of the system and create in this way an unevenness in flows.

Connectance indices: The effective number of connections between compartments is given by 3 connectance indices and is derived from the log averaged number of links calculated from the system overhead. The overall connectance includes the effect of external transfers whereas the internal connectance index characterises only internal exchanges, whereas the food web connectance index refers only to transfers among living compartments in the system. In mussel beds all 3 connectance indices are lowest compared with the other benthic communities. Connectance is higher when external sources as well as abiotic material is included in the considered web. The low food web connectance may be explained by the dominance of old mussels (storage compartment for C) linked only to the phytoplankton compartment and by a comparatively small “through flow” compartment consisting of younger mussels as well as associated fauna which is of less biomass and linked closely to birds and fish that exert a high predation and export of C from the system.

c. Exchange processes and food web organisation in intertidal seagrass beds

Seagrass beds have many functions such as being habitat, shelter and nursery for juvenile nekton and benthos species in the Wadden Sea (Asmus & Asmus 2000; Polte & Asmus 2006 a; b; Polte, Schanz & Asmus 2005 a; b). Biomass and production of seagrass communities is characterised by autotrophic plants and heterotrophic grazing macrobenthic animals. The high production of seagrasses and their epiphytes make this community ranking highest with respect to primary productivity among the communities of the intertidal Sylt-Rømø Bight. Internal primary productivity of microphytobenthos and seagrasses is sufficient to support secondary production of the entire community.

Since seagrasses tolerate a relatively broad spectrum of current velocities and water movement (Widdows et al. 2008), trophic interactions of seagrass beds of different sites are indirectly or directly determined by hydrodynamics (Schanz & Asmus 2003; Schanz et al. 2000; 2002). In the following chapter exchange processes of seagrass beds will be considered separately for a sheltered type of seagrass bed with dense vegetative coverage and an exposed one with scarce plant development.

i. Carbon exchange in dense seagrass beds

Dense seagrass beds are sinks for carbon. The main C-import is via organic particles which settle among the dense seagrass canopy. Material loss by drifting faeces of associated animals is too low to compensate for the intake of particles by sedimentation (Table 7).

DIC shows a net uptake by plant assimilation within this system. Respiration processes are distinctly lower. Thus the system is dependent on import of CO_2 from outside and this is a distinct hint that seagrass systems may be limited by dissolved C-components (Beer & Rehnberg 1997; Zimmerman et al. 1997) (Table 7).

Organisms show a net export of C from the seagrass bed (Table 7). To sustain the living biomass within the system, productivity is the main regulator. Larval stages with low biomass enter the system, they grow within the seagrass bed by using the C-resources (e. g. Moksnes 2002), especially detritus and microphytobenthos, and emigrating after achieving larger biomasses or being eaten especially by fish or crabs. Production and export of organisms is therefore the main counteracting process in a seagrass bed to the prevailing particle accumulation and CO_2 assimilation.

Information on exchange of DOC is poor. However, these components may show a low release which only contribute a little to the total export of C from the dense seagrass bed.

The surplus of assimilated C is stored within the system mainly as refractory organic substance within the sediment.

Table 7. Budget of carbon exchange processes in dense seagrass beds, based on annual means.

	pelagic-benthic mg C $m^{-2}h^{-1}$	benthic-pelagic mg C $m^{-2}h^{-1}$	net exchange mg C $m^{-2}h^{-1}$	
Carbon budget for organism exchange	267.51	99.31	-168.20	uptake
Carbon budget for particle exchange	261.08	57.29	-203.79	uptake
Carbon budget for DOC	33.36	6.93	-26.43	uptake
Carbon budget for DIC	75.79	57.39	-18.40	uptake
Σ Total	637.75	220.92	-416.82	uptake

ii. Nitrogen exchange in dense seagrass beds

Nitrogen is one of the major nutrients for plants in form of ammonia and nitrate which is assimilated by seagrasses as well as by microphytobenthos. Seagrasses can cover their supply of DIN from the water column as well as from the pore water. These two sources are normally used by the plant at equal parts but it may be dependent also from ammonium and nitrate availability. In addition to the uptake of dissolved N also particulate N is imported to the seagrass bed by particle sedimentation and by filtration of organisms.

Comparing the budget of pelagic-benthic with benthic-pelagic flux in dense intertidal seagrass beds it becomes evident that dense seagrass beds are net sinks for N (Table 8). Every component of the N-flux seems to be directed to this community. Nitrogen derived from organismal transport, from particle sedimentation as well as from the uptake of DON and DIN is accumulating in this community and may be released only during irregular processes such as storms. But also denitrification in the anoxic parts of the sediment may be a regulating process to balance the system. The N-exchange is controlled only by few dominant species in the seagrass bed, especially *Zostera noltii* and *Cerastoderma edule*. The activity of these two species explains already 37.1% of the N-flow into the system.

Table 8. Budget of nitrogen exchange processes in dense seagrass beds, based on annual means.

	pelagic-benthic mg N $m^{-2}h^{-1}$	benthic-pelagic mg N $m^{-2}h^{-1}$	net exchange mg N $m^{-2}h^{-1}$	
Nitrogen budget for organism exchange	47.03	21.63	-25.40	uptake
Nitrogen budget for particle exchange	17.74	5.70	-12.04	uptake
Nitrogen budget for DON	9.33	0.17	-9.17	uptake
Nitrogen budget for DIN	9.05	5.63	-3.42	uptake
Σ Total	83.15	33.13	-50.02	uptake

iii. Phosphorus exchange in dense seagrass beds

Comparing the counteracting pelagic-benthic and benthic-pelagic exchanges the uptake processes prevail for organismic and particle pathways as well as for dissolved organic phosphorus (Table 9). For dissolved inorganic P the dense seagrass bed is on average a source. This result was also found regarding the flume results. In the flume the dense seagrass bed acted as a sink for total P but also for DIP during calm weather situations. Including stormy days the seagrass bed turned to a source for DIP. The release of DIP is in contrast to the average uptake of DIN by the seagrass bed. This is a distinct hint that nitrogen is a limiting factor for the growth of seagrass beds, whereas phosphorus is not.

Table 9. Phosphorus budget for dense seagrass beds in the Sylt-Rømø Bight, based on annual means.

	pelagic-benthic mg P $m^{-2}h^{-1}$	benthic-pelagic mg P $m^{-2}h^{-1}$	net exchange mg P $m^{-2}h^{-1}$	
Phosphorus budget for organism exchange	2.99	1.40	-1.59	uptake
Phosphorus budget for particle exchange	4.03	1.00	-3.03	uptake
Budget for DOP	0.20	0.002	-0.19	uptake
Budget for DIP	0.48	1.96	1.48	release
Σ Total	7.70	4.36	-3.34	uptake

iv. Ecological carbon transfer of dense seagrass beds

Seagrass beds show a high primary as well as secondary production and biomass. The dense leaf carpet is a substrate for adhering microbiota, because it enlarges the substrate surface by up to a factor of 20 (Coutchman 1987). Seagrasses provide shelter for epibenthic animals such as crustaceans and fish and are a rich nutrition ground for benthic grazers such as snails. The increased sedimentation within a seagrass bed enriches the community with detrital components and enables a large guild of detritus feeders to develop. In contrast to mussel beds seagrass beds show a high primary production that is also used by the entire community. Even the primary production of the seagrass itself can be used by birds as food (e.g. brent geese and wigeons). Seagrass beds are less dependent from energy intake from outside and are based to a high degree on internal cycling.

Abundance, biomass of the dominant compartments: During this study period, dense seagrass beds occupied an area of 10.77 km^2 in the Sylt-Rømø Bight which represents about 7.89% of the total intertidal area. The community is ranking high with respect to total subsystem biomass of 76 020 mg C m^{-2} which consists of autotrophs and heterotrophs biomass at 31 010 mg C m^{-2} and 45 010 mg C m^{-2}, respectively (Table 10).

Among the autrophs the seagrasses *Zostera noltii* and *Z.marina* are the characteristic plants in dense seagrass beds of the Wadden Sea. The species composition varies between years and the present analysis refers to a situation found in the mid-nineties when most of the dense beds were composed by *Z. noltii* mixed with a high percentage of *Z.marina*. In 2005-2010 dense seagrass beds are mainly composed of only *Z. noltii* and this has consequences to the composition of benthic fauna. Especially *Hydrobia ulvae* and *Carcinus maenas* are recently more abundant than in the period of investigation. At present the species composition of benthic macrofauna in dense seagrass beds is more similar to the sparse seagrass bed of the former times.

Table 10. Biomass, productivity, respiration, egestion and consumption of compartments of the dense seagrass bed in the Sylt-Rømø Bight. Biomass and standing stocks in mg C m^{-2}, gross primary production (GPP), net primary production (NPP), production, respiration, egestion and consumption in mg C m^{-2} d^{-1}.

Dense seagrass bed	Biomass mg C m^{-2}	GPP mg C $m^{-2}d^{-1}$	NPP mg C $m^{-2}d^{-1}$	Respiration mg C $m^{-2}d^{-1}$	
Microphytobenthos	120.00	972.60	635.11	337.49	
Macrophytes	30890.00	846.30	372.37	473.93	
	Biomass mg C m^{-2}	Production mg C $m^{-2}d^{-1}$	Respiration mg C $m^{-2}d^{-1}$	Egestion mg C $m^{-2}d^{-1}$	Consumption mg C m^{-2} d^{-1}
Hydrobia ulvae	17475.40	77.50	72.77	509.04	659.31
Arenicola marina	12591.80	64.16	84.00	427.30	575.46
Oligochaeta	162.40	0.45	4.33	2.20	6.98
Heteromastus	87.00	0.48	0.90	6.09	7.47
Cerastoderma	7731.70	33.68	17.92	141.02	192.62
Mya arenaria	759.80	2.50	3.86	1.95	8.31
small polychaetes	208.80	1.14	4.81	1.75	7.70
Tharyx killariensis	226.20	1.23	4.91	2.50	8.64
Macoma balthica	3294.40	8.30	157.50	143.30	309.10
Phyllodocidae	92.80	0.25	2.74	0.35	3.34
small Crustacea	214.60	0.99	3.55	1.16	5.70
Crangon crangon	31.64	0.35	1.20	0.35	1.90
Nepthys spp.	550.00	5.97	5.70	21.04	32.71
Pomatoschistus microps	13.78	0.13	0.30	2.65	3.09
Pomatoschistus minutus	0.47	0.01	0.01	0.16	0.18
Pleuronectes platessa	0.03	0.00	0.00	0.00	0.00
Platichthys flesus	0.02	0.00	0.01	0.01	0.02
Merlangius merlangus	0.56	0.00	0.01	0.01	0.03
Pluvialis apricaria	3.50	0.01	0.30	0.08	0.39
Calidris canutus	2.95	0.01	0.58	0.15	0.74
Calidris alpina	5.02	0.02	0.64	0.16	0.82
Numenius arquata	5.35	0.01	0.33	0,08	0.42
Larus canus	2.40	0.01	0.24	0.06	0.31
Other birds	6.75	0.01	0.50	0.14	0.65
Anas penelpe	330.35	0.70	21.91	12.17	34.78
Branta bernicla	86.92	0.17	4.35	2.43	6.95
Sediment bacteria	625.00	305.93	192.60	67.41	566.94
Meiobenthos	500.00	10.96	41.70	19.01	71.67

Primary production:

Gross primary production: Gross primary production in dense seagrass beds is 1 818.9 mg C m^{-2} d^{-1} sharing into seagrass production and microphytobenthos production with 47% and 53% respectively (Table 10).

Net primary production: 1007.6 mg C $m^{-2}d^{-1}$ is converted into plant biomass. This net primary production is about 55% of the gross productivity and shows that the loss of C by respiration of plants is high (Table 10). Plant biomass is heavily grazed by birds for seagrasses and by macroinvertebrates especially *Hydrobia* for epiphytes and microphytobenthos. Birds, especially wigeons and brent geese remove 11% of the net primary production of seagrasses. Invertebrates remove 99.5% from the net primary production of benthic microalgae. The efficiency of net primary production is estimated at 42.1%.

Consumption: About 2506 mg C $m^{-2}d^{-1}$ is consumed by a dense seagrass bed community (Table 10). 357 mg C $m^{-2}d^{-1}$ is taken from the pelagic domain which is 14% of total consumption of the community. This shows that seagrass beds are less dependent on pelagic food sources than mussel beds. About 28% of the consumption is due to grazing of microphytobenthos and another 2% to direct grazing of seagrasses by birds. Detritus feeding accounts for the main part of consumption with 38%. Predation on heterotrophic animals is about 18% of the consumption. Therefore the community is dependent at 86% on material and organisms that are produced within the community and are therefore mainly dependent on autochthonous energy sources. The ratio of consumption of allochthonous to autochthonous sources is 0.17 and shows that seagrass beds are quite closed communities.

Heterotrophic production: Heterotrophic production amounts to 515 mg C $m^{-2}d^{-1}$ (Table 10). Most of the production appears at the second trophic level. Bacteria, *Arenicola marina, Cerastoderma edule, Hydrobia ulvae* and *Macoma balthica* dominate the heterotrophic production. 75 mg C $m^{-2}d^{-1}$ or 15% of the heterotrophic production is not used by predators of the community and is thus exported either by migration or drift or is available for changes in macrobenthic biomass. 86% of the heterotrophic production is consumed within the system which is a quite high value. Seagrass beds are typical nursery areas for juvenile fish and crustaceans and therefore are places of intense predation.

Production to biomass ratio: The production to biomass ratio of the dense seagrass bed subsystem is 0.023 which is higher when compared to mussel beds. This reflects the larger contribution of smaller and younger animals and the larger importance of plants in this community (Fig. 7).

Respiration: Community respiration of dense seagrass beds was estimated at 1 439 mg C $m^{-2}d^{-1}$ (Table 10). This is considered among the exchange processes.

Excretion: The rich community of intertidal dense seagrass beds produce a large amount of faeces in an order of magnitude of 1 362 mg C $m^{-2}d^{-1}$ (Table 10). Most of this material can be resuspended and is therefore considered among the exchange processes.

v. Food web of dense seagrass beds

(1) Trophic analysis

Diversity and biomass of trophic groups: In dense seagrass beds up to five trophic levels exist including producer and consumer levels. The biomass of secondary producers consists mainly of *Cerastoderma edule* followed by *Hydrobia ulvae.* The present food web includes 13 species contributing to this group. This trophic group can be divided into suspension feeders and benthic grazers both representing the same percentage of biomass. None of these species uses living plant material exclusively but also detritus. Small polychaetes, small crustaceans and *M. balthica* also feed on higher trophic levels (mainly bacteria). Species number of bacteria and meiobenthos is unknown for seagrass beds but they also contribute to secondary production. Birds have a significant part in biomass of secondary producers by the contribution of herbivorous brent geese and wigeons.

At the third trophic level 22 species of macrofauna, fish, and bird species are included. Macrofauna is represented mainly by *Nephthys* and *Crangon.* The gobies *Pomatoschistus microps* and *P. minutus* as well as the flatfish *Pleuronectes platessa* and *Plathichthys flesus* are the fish species at the third trophic level (5 species). Mallards, dunlins, golden plover, common gull and curlew are the dominant birds feeding in dense seagrass beds (5 species). Macrofauna dominate the biomass of tertiary producers followed by birds and fish.

At the fourth trophic level 10 species mainly consisting of predatory fish and birds contribute to biomass and production. These are whiting (*Merlangius merlangus*) in addition to both flatfish species and the goby *P. microps* while curlew and common gull represent the predatory birds.

Total System Throughput: Dense seagrass beds reveal the highest total system throughput next to mussel beds. 7 566 mg C $m^{-2}d^{-1}$ is passing the community in total (Table 11). The high rates of productivity of *Zostera noltii* and *Z. marina* as well as microphytobenthos together with a quite high predation activity due to fish in this system are the reason for this.

Average path length: Average path length in dense seagrass beds is estimated to 2.48 components per average food cycle which is higher than that of mussel beds (Table 11). Although food chains with much larger numbers of components occur in mussel beds the average path length is lower because of the dominance of mussels which cause an uneven distribution of different branches of material flow. In seagrass beds these food pathways are less uneven although some short pathways such as that of *Zostera* and herbivorous birds are dominant.

Average residence time: Material resides for much shorter time (46.54 d) in the dense *Zostera* bed as compared to the mussel beds (Table 11). Seagrass beds show a large input of organic material from outside which is stored within the community and is to a low degree resuspended and exported. The animal community consists more of younger animals and the ecological components show on average a higher turnover of material.

Lindeman spine: The Lindeman spine contracts the total food web into a simple food chain with discrete trophic levels. From the seagrass bed 6 different trophic levels can be identified (Fig. 9). The efficiency of energy transfer is highest within the first trophic level with 53.4%. Among the heterotrophic part of the food web efficiency of energy transfer is highest in the second trophic level with 20%. The third trophic level has only a very small efficiency with 0.6% but this is doubling in the fourth trophic level. As already observed in mussel beds the predators on a lower level such as *Crangon* or *Carcinus* have lower energy transfer efficiencies compared to higher level predators such as fish and birds. Predation is negligible but may be underrepresented because top predators such as gar fish *Belone belone* occur frequently over seagrass beds which they prefer as spawning grounds. They have not been included into the present model because of lack of biomass data on this species.

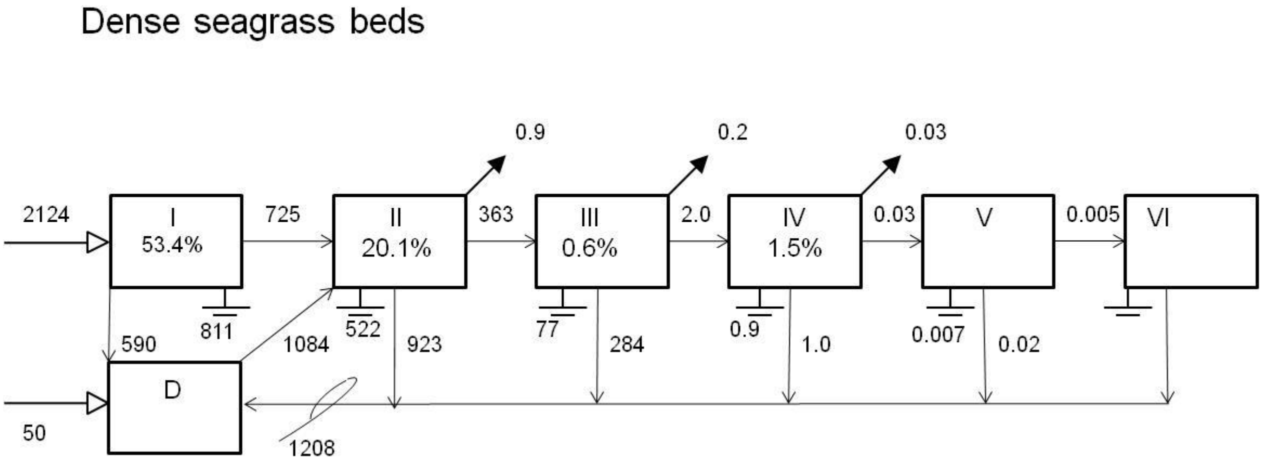


Fig. 9. Lindeman spine dense seagrass beds. The box indicated D refers to the detrital pool, and the Roman numbers in the boxes of the Spine to discrete trophic levels. Percent values in Spine boxes refer to the efficiency of energy transfer between the integer trophic levels. Fluxes are given in mg C $m^{-2}d^{-1}$.

Mean trophic efficiency: The mean trophic efficiency was estimated to be 5.58% and falls in the range of efficiencies reported for a seagrass bed with a comparable number of compartments in Florida (Baird, Asmus & Asmus 2007). Secondary production in dense seagrass beds is distributed among different macrofaunal species to equal parts thus the predation on these compartments is not straight by a short connection between the prey-predator compartments and this probably lowers the mean trophic efficiency of the system.

(2) Structure and magnitude of cycling

Number of cycles: The material within a dense seagrass bed is transported over 195 different cycles (Table 11).

Cycle distribution: Short cycles containing only two or three compartments are transporting 99.63% of the material in a dense seagrass bed. This implies a quick material turnover and explains also the relatively short residence time of carbon within the system. These short cycles invariably involve the sediment bacteria, meiobenthos and sediment POC as well as species that use detritus as well as sediment bacteria as a food source.

Finn Cycling Index: The Finn Cycling Index which gives the amount of material that is recycled within a dense seagrass bed was estimated to be 24.76% (Table 11). That means that a quarter of the material that is flowing through the present food web is recycled within this web. This is a further hint for the separate energy flow of a seagrass bed and for the relatively independent character of this system from external sources.

(3) System level properties and system organisation

Development capacity: A DC of 35 539 mg C $m^{-2}d^{-1}$ bits of intertidal dense seagrass beds ranges second among the different intertidal communities of the Sylt-Rømø Bight (Table 11). 36.7% of the DC is due to ascendancy of the system showing a lower level of organisation compared to mussel beds. Most of the system overhead (59%) is due to redundancy of the system. This gives a higher stability of the system to external perturbations.

Table 11. Global system attributes derived from network analysis for the dense *Zostera noltii* bed subsystem of the Sylt-Rømø Bight. Values reflect results from network models where excess production and sediment POC were not exported from the system. No artificial import was made to balance the compartments.

System Attributes	dense Z. noltii beds
Trophic efficiency (logarithmic mean. %. Sed POC retained)	5.58
Detrivory (detritus pool to TL2. mgCm-^{2}d-1. Sed POC retained)	1084
Detrivory:herbivory ratio (D:)	1.5:1
Number of cycles (Sed POC retained)	195
Finn Cycling Index (%)	24.76
Average Path Lenght (APL=TST-Z/Z)	2.48
Ave Res Time (ART; days)(Sum Biomass/Sum Exports. Resp)	46.54
Total System Throughput (mgCm-^{2}d-1)	7566
Total System Throughput (tonnesCarea-1d-1)	81.5
Development Capacity (mgCm-^{2}d-1bits)	35539
Ascendency (mgCm-^{2}d-1bits)	13027
Relative Ascendancy (A/DC. %)	36.7
Average Mutual Information (A/TST)(normalized A)	1.72
Average Internal Mutual Information (Ai/TST)	0.96
Overheads on imports (mgCm-^{2}d-1bits)	3440
Overheads on exports (mgCm-^{2}d-1bits)	12.4
Dissipative Overheads (mgCm-^{2}d-1bits)	5744
Redundancy (mgCm-^{2}d-1bits)	13315
Relative Redundancy (R/DC. %)	37.5
Normalized Redundancy (R/TST)	1.76
Internal Development Capacity (mgCm-^{2}d-1bits)	20830
Internal Ascendency (mgCm-^{2}d-1bits)	7515
Relative Internal Ascendency (Ai/DCi. %)	36.1
Internal Redundancy (mgCm-^{2}d-1bits)	13315
Relative Internal Redundancy (Ri/DCi. %)	63.9
Flow Diversity DC (DC/TST. %)(normalized DC)	4.70
Φsum of overheads/TST (+#58)	2.92
Overall connectance	2.189
Intercompartmental connectance	2.803
Foodweb connectance (living compartments only)	2.005
GPP/TST	0.24

Redundancy: Redundancy of the present seagrass system is 37.5% of the development capacity and this is double the value for intertidal mussel beds (Table 11). Seagrass beds seem to have more parallel cycles which act in a similar way and can thus stabilize the system. The material flow is not so dependent on only a single species as far as the heterotrophic part of the food web is considered.

Ascendency: The ascendancy (A) described the structure and organisation of the system and gives also some hints of the developmental state and maturity. Ascendency was estimated at 13 027 mg C $m^{-2}d^{-1}$ bits for dense seagrass beds and this shows that this system is on a much lower organisational level as a mussel bed (Table 11). However this community exhibits the second highest ascendancy value found among the intertidal systems of the Sylt-Rømø Bight. Ascendancy should be seen in relation to development capacity (DC) of the system and a ratio of 36.7% shows that dense seagrass beds fall at the lower end of the A/DC ratios among the intertidal systems. This community may not be at a mature developmental stage or is only in the state of early succession. The comparison between relative ascendency (A/DC) and relative internal ascendancy ($A_i//DC_i$) shows a decrease of only 0.1% which points to a low dependence of dense seagrass beds on exogenous material sources.

Average mutual information: The AMI ratio is 1.72 and represents compared to the other systems a medium level of inherent organisation and specialisation (Table 11). Although seagrass beds of the Sylt-Rømø Bight are less dependent on external sources they have not reached a degree of independence that they can be considered as specialised communities. Especially intertidal seagrass beds are considered to have a homogenous community which is only quantitatively different from the adjacent sand or mud flats. This is a strong difference to subtidal seagrass beds which are often highly specialised and contain many resident species which are strongly dependent on this community.

Flow diversity: Flow diversity is considered to reflect the variety of interrelations within a community in a more dynamic way as biodiversity and strengthen their functional aspects (Table 11). Flow diversity is higher in intertidal seagrass beds compared to mussel beds because the eveness of flows is higher. Flow diversity is lower as in unvegetated areas because some fluxes such as those directly dependent on the *Zostera* plants dominate.

Connectance indices: The difference of overall connectance to intercompartimental connectance shows that connectance is higher when external sources are excluded from the food web. The connectance is lower when one only focuses on the interactions within the living compartments of the system. This reveals on one hand that connectance is mainly provided within the community and the degree of independence of external sources is high. On the other hand abiotic compartments such as detritus play a large role for the connectance of the food web.

vi. Carbon exchange in sparse seagrass beds

Sparse seagrass beds are sources for carbon (Table 12). While in dense seagrass beds the C-budget is positive by dominating import processes, this is reversed when vegetation cover is thin. The main C-export is via POC. Particulate C-intake by suspension feeders such as *C. edule* and *M. balthica* is too low to compensate for the particle loss due to currents.

DIC shows a net uptake by plant assimilation within this system. Respiration processes are distinctly lower. Thus the system is dependent on import of CO_2 from outside.

Information on exchange of dissolved organic C is poor (Barron & Duarte 2009; van Engeland et al. 2010). However, this component may show an uptake which hardly counteracts the total export of C from the system. The permanent loss of assimilated C is reflected in the sediment becoming more and more sandy.

Table 12. Carbon budget for a sparse seagrass bed based on annual means.

	pelagic-benthic $mgC\ m^{-2}h^{-1}$	benthic-pelagic $mgC\ m^{-2}h^{-1}$	net exchange $mgC\ m^{-2}h^{-1}$	
Carbon budget for organism exchange	82.79	75.84	-6.95	uptake
Carbon budget for particle exchange	1.24	80.48	79.24	release
Carbon budget for DOC	44.20	6.27	-37,93	uptake
Carbon budget for DIC	66.97	38.01	-28.96	uptake
Σ Total	195,20	200.60	5,40	release

vii. Nitrogen exchange in sparse seagrass beds

In sparse seagrass beds the biomass of seagrass leaves is only half of that of a dense seagrass bed (see Tables 10 and 15). Currents and turbulence can reach the sediment surface of the meadow and also the movement of the floating leaves can induce the movement of particles and organisms. Thus a sparse seagrass bed acts as a source for particulate N (Table 13). The assimilation of dissolved inorganic N by plants cannot exceed the remineralisation processes that occur in the sediments of this seagrass bed. On the other hand nitrogen shows a net uptake in form of organisms and DON albeit at a low rate. However, uptake of DON can play a significant role (Vonk et al. 2008).

Table 13. Nitrogen budget for sparse seagrass beds based on annual means.

	pelagic-benthic $mg\ N\ m^{-2}\ h^{-1}$	benthic-pelagic $mg\ N\ m^{-2}\ h^{-1}$	net exchange $mg\ N\ m^{-2}\ h^{-1}$	
Nitrogen budget for organism exchange	17.65	16.52	-1.13	uptake
Nitrogen budget for particle exchange	0.12	7.85	7.73	release
Nitrogen budget for DON	1.59	0.63	-0.96	uptake
Nitrogen budget for DIN	8.12	9.63	1.51	release
Σ Total	27.48	34.62	7.14	release

viii. Phosphorus exchange in sparse seagrass beds

The phosphorus budget of sparse seagrass beds is dominated by release processes such as the net release of DIP as well as the net release of particles (Table 14). Phosphorus shows a net uptake for organisms as well as dissolved organic matter but at very low rates. In total, sparse seagrass beds are sources for P and resemble the behaviour of nitrogen exchange. The system releases 5.06 mg P $m^{-2}h^{-1}$ more than the half (3.01 mg P $m^{-2}\ h^{-1}$) is released as DIP and 2.64 mgP $m^{-2}h^{-1}$ via particles whereas counteracting uptake amounts to
0.1 mg P $m^{-2}h^{-1}$ as organisms and 0.31 mg P $m^{-2}h^{-1}$ as DOP. This phosphorus budget shows that the function of a seagrass bed whether it acts as a sink or a source for P is dependent on the seagrass biomass. If biomass decreases to one half of plant biomass of a dense

seagrass bed, the sink function is shifting to a source function by release of particles and a higher release of dissolved phosphate due to remineralisation.

Table 14. Phosphorus budget for a sparse seagrass bed based on annual means.

	pelagic-benthic mg P $m^{-2}h^{-1}$	benthic-pelagic mg P $m^{-2}h^{-1}$	net exchange mg P $m^{-2}h^{-1}$	
Phosphorus budget for organism exchange	1.68	1.57	-0.10	uptake
Phosphorus budget for particle exchange	0.03	2.67	2.64	release
Budget for DOP	0.49	0.01	-0.31	uptake
Budget for DIP	0.44	3.45	3.01	release
Σ Total	2.64	7.7	5.06	uptake

ix. Ecological carbon transfer of sparse seagrass beds

Sparse seagrass beds grow mainly on sandy bottoms with higher currents and turbulence of the tidal water. The reduced biomass of plants compared to dense seagrass beds characterises sparse seagrass beds as transitional habitats to intertidal sand flats. Species composition of the macrofauna community is continuously altered due to the decreasing seagrass biomass in the way that biomass of grazers, fish and predators decrease and biomass of endobenthic animals increases. At a certain threshold of maximum current velocity almost no grazers as *Hydrobia ulvae* are present because these small animals are easily flushed away (Schanz et al. 2002). However, the present sparse seagrass beds represent only a status of 50% reduction of seagrass biomass and this allows still a rich epibenthic community to live among the seagrass leaves. Nevertheless the function of this seagrass bed has already changed.

Biomass of the dominant compartments: Most of the macrobenthic invertebrate biomass (35%) is represented by the deposit feeding *Arenicola marina* and the suspension feeding bivalve *Cerastoderma edule* (22%) (Table 15). Grazing mud snails *Hydrobia ulvae* occupy 27% of macrobenthic biomass. Invertebrate predators such as *Carcinus maenas* and *Crangon crangon* have a lower biomass with only 1%. The remaining 15% of the macrobenthic biomass is shared between different species of polychaetes, oligochaetes, crustaceans and molluscs. In total 12 different macroinvertebrate species are regularly found in sparse seagrass beds.

Fish are dominated by the small goby *Pomatoschistus microps* which occupies 93% of fish biomass in this community. Other present fish species are young whiting 4%, sand gobies *P. minutus* (3%) and young flat fish (<1%).

Birds are represented by herbivorous wigeons and brent geese that have a share in total bird biomass of 75% and 20% respectively. Carnivorous birds are of minor importance but are represented mainly by curlews (1.2%) that feed on juvenile shore crabs and dunlins (1.1%) feeding mainly upon mud snails.

Table 15. Biomass, productivity respiration, egestion and consumption of compartments in a sparse seagrass bed of the Sylt-Rømø Bay. Biomass and standing stocks in mg C m^{-2}, GPP, NPP, P, R, E and C in mg C m^{-2} d^{-1}.

Sparse seagrass bed	Biomass	GPP	NPP	Respiration	
	mg C m^{-2}	mg C m^{-2} d^{-1}	mg C m^{-2} d^{-1}	mg C m^{-2} d^{-1}	
Microphytobenthos	120.00	901.37	588.59	312.78	
Macrophytes (*Zostera*)	14040.00	384.66	169.30	215.41	
	Biomass	Production	Egestion	Respiration	Consumption
	mg C m^{-2}	mg C m^{-2}d^{-1}	mg C m^{-2}d^{-1}	mg C m^{-2}d^{-1}	mg C m^{-2}d^{-1}
Hydrobia ulvae	7174.60	31.80	509.04	44.82	285.61
Littorina littorea	464.00	2.01	5.70	1.34	9.09
Arenicola marina	9135.00	64.16	427.30	84.00	575.46
Scoloplos armiger	545.20	0.52	10.32	3.96	14.80
Capitellidae	255.20	1.14	14.47	5.90	21.51
Oligochaeta	255.20	0.71	3.44	6.90	11.05
Cerastoderma edule	5805.80	25.33	106.65	9.00	140.98
Mya arenaria	922.20	4.00	2.40	4.70	11.10
Macoma balthica	1194.80	2.90	51.70	60.70	115.30
Phyllodocidae	81.20	0.22	0.31	2.40	2.93
Carcinus maenas	330.00	1.70	4.59	1.18	7.50
Crangon crangon	31.64	0.35	0.35	1.20	1.90
P. microps	13.38	0.13	2.65	0.30	3.09
P minutus	0.47	0.005	0.16	0.10	0.18
Pl platessa	0.03	0.002	0.00	0.00	0.00
Pl flesus	0.02	0.001	0.01	0.01	0.02
M. merlangus	0.56	0.003	0.02	0.01	0.03
Pl apricaria	3.50	0.01	0.08	0.30	0.39
C. canutus	2.95	0.01	0.15	0.58	0.74
C.alpina	5.02	0.02	0.16	0.64	0.82
N.arquata	5.35	0.01	0.08	0.33	0.42
L. ridibundus	2.29	0.01	0.25	0.06	0.32
L. canus	2.40	0.01	0.06	0.24	0.31
other birds	6.75	0.01	0.14	0.50	0.65
A. penelope	330.35	0.7	12.17	21.91	38.08
B. bernicla	86.92	0,17	2.43	4.35	6.95
Sediment bacteria	625.00	121.53	24.26	69.32	187.22
Meiofauna	1000.00	21.92	38.02	83.4	143.34

Primary production:

Gross primary production: Benthic gross primary productivity is 1286 mg C m^{-2}d^{-1}. Microphytobenthos contributes 70% and seagrass 30% to the primary production of sparse seagrass beds (Table 15).

Net primary production: About 758 mg C m^{-2}d^{-1} is converted into biomass of benthic plants (59% of gross primary production) (Table 15). Microphytobenthos has the major part of NPP (78%) and seagrasses have a share of only 22%. Efficiency of net primary production is the highest among the communities of the Sylt-Rømø Bight at 85%. Only microphytobenthos primary production plays an important direct role within the food web whereas most of the seagrass production has to be transferred to detritus before it is further used by consumers. From network analysis we computed that about 16% of NPP of seagrasses is decomposed to detritus within this system.

Consumption: Community consumption in sparse seagrass beds reaches a value of 1579.78 mg C $m^{-2}d^{-1}$ (Table 15) and is lower compared to dense seagrass beds. Benthic sources are dominantly consumed by the heterotrophic community of a seagrass bed. From the available carbon sources more than one third each is consumed in form of sediment particulate organic matter and microphytobenthos whereas pelagic sources such as phytoplankton and suspended POC contribute only 13% to the community consumption. Only 1% of consumed C flows to predators such as predatory invertebrates, fish and birds. Also in sparse seagrass beds the seagrass itself plays only a negligible role as food source. Only 3% of the consumption is based on seagrass material which is mainly due to herbivorous birds.

Heterotrophic production: Animals and bacteria together produce up to 279 mg C $m^{-2}d^{-1}$ (Table 15). Bacterial production contributes 34% followed by benthic grazers at 20% and deposit feeders at 12%, whereas suspension feeders have a share of only 11% in heterotrophic production. More than 70% of the production in sparse seagrass beds is thus based upon benthic carbon sources. However, seagrass itself contributes directly only at 0.02% to the heterotrophic production of the system. A larger amount of seagrass may be available to the food web after decomposition as detritus.

Total subsystem production: Although seagrass production is lowered and heterotrophic production is only half of that of dense seagrass beds, total system production ranges high among the different intertidal communities. About 73% of the total subsystem production is due to primary production indicating that sparse seagrass beds tend to be mainly autotrophic communities. The total community produces 4.9 t C per day and thus contributes at 3.8% to the total production of the intertidal area of the Sylt-Rømø Bay.

Production to biomass ratio: Although the autotrophic biomass in sparse seagrass beds is much lower than in dense seagrass beds, the heterotrophic biomass is in a similar range and thus the P/B ration of both communities ranges around 0.02 (Fig. 7). The P/B value of seagrass beds is one of the lowest among the intertidal communities of the Sylt-Rømø Bight but is in a comparable range with other estuaries and coastal systems.

Respiration: About 936 mg C $m^{-2}d^{-1}$ is lost from the system by respiration processes (Table 15). This is 73% of the total carbon entering the system by gross primary production. Community respiration is dominated by plant respiration whereas heterotrophic components only contribute by 44%. Plant respiration is dominated by microphytobenthos respiration. Bacteria have a share of only 7.5% in community respiration of sparse seagrass beds.

Egestion: Approximately 1392 mg C $m^{-2}d^{-1}$ is egested by the sparse seagrass community and is transferred to the detritus pool (Fig. 10). About 10% of this material is produced by the seagrass itself. In sparse seagrass beds the hydrodynamic activity is high and therefore this material does not accumulate in the sediment but is exported.

x. Food web of sparse seagrass beds

(1) Trophic analysis

The food web of the sparse seagrass beds includes bacterial and plant components as well as vertebrates such as fish and birds. Especially herbivorous birds are a dominant feature of seagrass beds and the high amount of epibenthic crustaceans and fish such as gobies contribute to the special character of this community.

Diversity and biomass of trophic groups: About 6 trophic levels have been distinguished in sparse seagrass beds. Biomass of primary consumers is less than in dense seagrass beds but consists of 13 species and thus has a comparable diversity. *Hydrobia ulvae* is the dominant secondary producer followed by *Cerastoderma edule* and *Macoma balthica* and some endobenthic polychaetes such as *Arenicola marina* and *Scoloplos intertidalis.* Wigeons and brent geese are also present.

Secondary consumers reach a higher diversity compared to dense seagrass beds especially due to the higher number of birds. In total 24 species build the third trophic level including 8 species of birds. Macrofauna is dominating biomass and production at the second and third trophic levels. At the fourth trophic level 4 fish and 4 bird species contribute to the carbon flow.

Total system throughput: TST in sparse seagrass beds is lower than that of dense seagrass beds and mussel beds: 5639 mg C $m^{-2}d^{-1}$ passes this community (Table 16). This characterises the community as having a quite high functional and trophic activity. The high rates of productivity of *Zostera* plants and microphytobenthos and the high invertebrate and vertebrate grazing are responsible for the high TST.

Average path length: APL within the food web of a sparse *Zostera* bed is quite low as found for most intertidal communities of the Sylt-Rømø Bight (Table 16). However, among these communities carbon is transported over relatively more steps compared to mussel beds and intertidal sand flats. This may be the result of a slightly higher flow diversity of sparse seagrass beds compared to the total intertidal area of the Sylt-Rømø Bight.

Average residence time: Compared to most communities the average residence time of a just imported carbon atom within a sparse seagrass bed system is surprisingly high at 56 days. This is only surpassed by the residence time for carbon within intertidal mussel beds (84d). The intense primary production of seagrass beds reveal an effective storage compartment and thus retard a quick passage.

Lindeman spine: Import of carbon into sparse seagrass beds is similar to that in bare sand or mudflats, but very much lower then that of dense seagrass beds. Comparable to most benthic communities within the Sylt-Rømø Bight 6 different trophic levels could be distinguished (Fig. 10), whereas the 5th and 6th trophic level is rather insignificant for the energy flow of the system.

The highest efficiency of trophic transfer is measured in the first trophic level at 52.9 % and this is only insignificantly lower as the trophic efficiency of dense seagrass beds. Trophic efficiency decreases as the trophic level increases. At the second trophic level 22.1% of the accumulated carbon is transferred to production but among the predator guild (3rd and 4th level) trophic efficiency rapidly decreases to only 0.7-0.8%. The main difference between the

Lindeman spines of both types of seagrass beds are the lower gross primary production in sparse seagrass beds which results in a decreased production of plant detritus. The detritus pool of this community has only a lowered input from outside and also detritus is used by primary consumers to a much lower degree compared to dense seagrass beds. Interestingly the export of carbon is higher in sparse than in dense seagrass beds, thereby this increased exports are mostly due to the predator level.

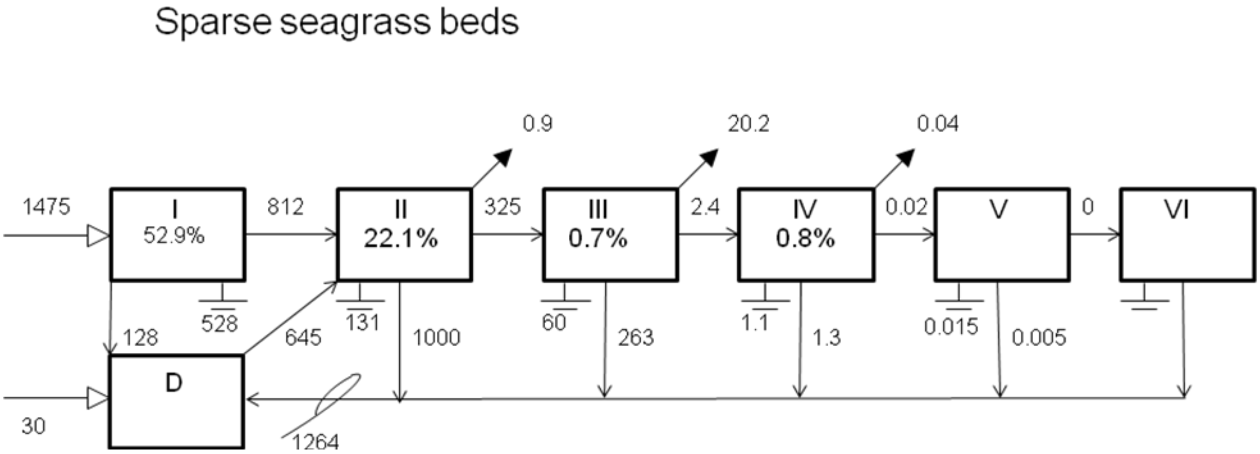


Fig. 10. Lindeman spine of sparse seagrass beds of the Sylt-Rømø Bight. The box indicated D refers to the detrital pool, and the Roman numbers in the boxes of the Spine to discrete trophic levels. Percent values in Spine boxes refer to the efficiency of energy transfer between the integer trophic levels. Fluxes are given in mg $Cm^{-2}d^{-1}$.

Mean trophic efficiency: With a value of 5.06% it is slightly lower than that of dense seagrass beds but higher than that of exposed sand flats. The value falls within the range reported for seagrass beds in Florida USA (Baird et al. 1998).

(2) Structure and magnitude of cycling

Number of cycles: The material flowing through a seagrass bed is cycled over 113 different cycles (Table 16).

Cycle distribution: Most of the material (59.4%) is transported over short cycles at only 2 elements. A similar dominance of short cycles with only 2 elements could be observed in sandy shoals and sandy beaches at 60.2% and at 87.1%, respectively, whereas in dense seagrass beds most of the material is cycled over cycles with 3 elements. The dominance of short cycles with only 2 elements could be a characteristic for exposed communities.

Finn Cycling Index: The FC index of sparse seagrass beds of 22.6% is between the low FC index of sandy communities of 16.2 - 20.3% and that of muddy communities ranging from 24.76 – 27.53%. Thus, sparse seagrass beds are transitional regions between sand flats and mud flats where recycling of material plays obviously a larger role.

Table 16. Global system attributes derived from network analysis for the sparse *Zostera noltii* bed subsystem of the Sylt-Rømø Bight. Values reflect results from network models where excess production and sediment POC were not exported from the system. No artificial import was made to balance the compartments.

System Attributes	sparse *Z. noltii* beds
Trophic efficiency (logarithmic mean, %,)	5.06
Detrivory (detritus pool to TL2, mgCm-^{2}d-1,	645
Detrivory:herbivory ratio (D:)	0,8:1
Number of cycles	113
Finn Cycling Index (%)	22.62
Average Path Lenght (APL=TST-Z/Z)	2.74
Ave Res Time (ART; days)(Sum Biomass/Sum Exports, Resp)	55.52
Total System Throughput (mgCm-^{2}d-1)	5639
Total System Throughput (tonnesCarea-1d-1)	26.8
Development Capacity (mgCm-^{2}d-1bits)	26124
Ascendency (mgCm-^{2}d-1bits)	10331
Relative Ascendancy (A/DC, %)	39.5
Average Mutual Information (A/TST)(normalized A)	1.83
Average Internal Mutual Information (Ai/TST)	1.12
Overheads on imports (mgCm-^{2}d-1bits)	2152
Overheads on exports (mgCm-^{2}d-1bits)	11.7
Dissipative Overheads (mgCm-^{2}d-1bits)	4175
Redundancy (mgCm-^{2}d-1bits)	9454
Relative Redundancy (R/DC, %)	34.5
Normalized Redundancy (R/TST)	1.68
Internal Development Capacity (mgCm-^{2}d-1bits)	15898
Internal Ascendency (mgCm-^{2}d-1bits)	6444
Relative Internal Ascendency (Ai/DCi, %)	40.5
Internal Redundancy (mgCm-^{2}d-1bits)	9454
Relative Internal Redundancy (Ri/DCi, %)	59.5
Flow Diversity DC (DC/TST, %)(normalized DC)	4.63
Φsum of overheads/TST (+#58)	2.68
Overall connectance	2.139
Intercompartmental connectance	2.498
Foodweb connectance (living compartments only)	1.832
GPP/TST	0.23

(3) System level properties and system organisation

Development capacity: The DC of 26124 mg C $m^{-2}d^{-1}$ bits is lower than that of dense seagrass beds and muddy sand flats but higher than that of mudflats. It surpasses all sandy bottom communities distinctly. A large share of DC (39.5%) is due to ascendancy and shows a slightly higher percentage of organised flows compared to dense seagrass beds. However, 60% of the flow is due to system overhead.

Redundancy: The redundancy of the system (9454 mg C $m^{-2}d^{-1}$ bits) is much lower compared to dense seagrass beds. However, the relative redundancy R/DC amounts to 34.5% of the development capacity and is only slightly lower than that of dense seagrass beds. This can be interpreted as lower stability of the system that is more comparable to *Arenicola* sand flats and bare mudflats.

Ascendency: The ascendancy of 10331 shows a similar degree of organisation as the muddy sand flats. The relative ascendancy A/DC of 39.5% shows a slightly increased degree of system organisation as for dense seagrass beds. The internal relative ascendancy increases compared to the relative ascendancy by 1%. This shows a relative independency of the sparse seagrass beds on exogenous connections which could be also observed at a lower degree for dense seagrass beds.

Average mutual information: Next to mussel beds, sparse seagrass beds showed the highest value for average mutual information of 1.83. This parameter is an indicative value of inherent organisation and specialisation. Thus sparse seagrass beds have beside mussel beds the highest value of specialisation among the intertidal communities.

Flow diversity: The value of flow diversity (4.63) is only slightly lower in sparse than in dense seagrass beds. This may reflect a lower number of interactions between the compartments as well as a more uneven distribution of single flows.

Connectance indices: Both CI´s (overall: 2.14, intercompartmental: 2.50) are slightly lower compared to dense seagrass beds showing a lower number of interactions. However, a comparison of the difference between overall and intercompartmental connectance shows that sparse seagrass beds are more dependent on external inputs than dense seagrass beds. The food web connectance (1.83) includes only living elements that are connected. Because food web connectance is lower than intercompartmental connectance, this points out the significance of detritus feeders that increase the number of flows between dead and living compartments.

d. Exchange processes and food web organisation in intertidal sand flats

Intertidal sand flats are inhabited by communities showing a large variety of biomass and production due to exposure of the particular site. Sandy tidal flats of medium exposure (currents of 1 to 10 cm s^{-1}) are dominated by dense settlement of lugworms (*A. marina*). In these *Arenicola* flats the different trophic groups vary seasonally and between years and this variability is crucial for the importance of the particular groups for material cycling. Suspension feeders are mainly represented by the cockle *Cerastoderma edule*, forming stocks which fluctuate strongly between years. This species is largely absent after hard winters, whereas after mild winters a high standing stock can be developed and suspension feeders become the dominant trophic guild within the food web of sand flats. Next to suspension feeders detritus feeders are important and after hard winters this guild becomes the dominant group. Most of the detritus feeders belong to the infauna and they play an important role in recycling of material by bioturbation and bioirrigation (Volkenborn et al. 2007). In sandy shoals and sandy beaches at the high tide line biomass of macrofauna is low. In sand flat areas sheltered from currents and waves organic content of the sediment is increasing, providing a rich food source for the animal community and therefore they are the richest intertidal habitats next to mussel beds within the Wadden Sea. Detritus feeders and omnivorous animals are dominating the energy flow in those places. Because of this different character, I discuss the different types of sand flats separately dividing them into the following groups: 1) *Arenicola* flats, 2) muddy sands, 3) sandy shoals, and 4) sandy beaches.

i. Carbon exchange in *Arenicola* sand flats

Arenicola sand flats are sinks for carbon (Table 17). On average 252 mg C $m^{-2}h^{-1}$ is taken up. Most carbon (84%) is taken up in form of particles, whereas only 7% is taken up by the assimilation of CO_2 by plant activity in this community. At a similar amount carbon enters the sand flat system via living organisms, but 8% is due to dissolved organic material. As already shown for the pelagic-benthic processes the total C-budget is thus characterised by sedimentation of particles and is determined by physical processes.

The amount of material exchanged between benthal and pelagial is lower per square meter in *Arenicola* sand flats compared to seagrass beds and mussel beds. However, this community determines the fluxes within the total area of the Sylt-Rømø Bight especially by the large extent of the *Arenicola* sand flats.

Table 17. Budget of carbon for an *Arenicola* sand flat based on annual means.

	pelagic-benthic mgC $m^{-2}h^{-1}$	benthic-pelagic mgC $m^{-2}h^{-1}$	net exchange mgC $m^{-2}h^{-1}$	
Carbon budget for organism exchange	57.21	40.25	-16.96	uptake
Carbon budget for particle exchange	254.16	56.68	-197.48	uptake
Carbon budget for DOC	27.42	6.75	-20,67	uptake
Carbon budget for DIC	41.33	24.40	-16.93	uptake
Σ Total	380.13	128.08	-252.04	uptake

ii. Nitrogen exchange in *Arenicola* sand flats

Nitrogen input from the water column to the *Arenicola* flat is about 3 times higher than the release of nitrogen compounds by the community (Table 18). Because N-loss and N-gain due to drifting is almost balanced, the net uptake of organisms can be mainly related to filtration of phytoplankton by suspension feeders of the community especially by *C. edule*. Sedimentation of detrital particles during high tide leads to a distinct uptake of nitrogen by the community. The release of DIN via remineralisation is a little higher than the uptake by phototrophic organisms so that DIN is distinctly released into the water column. However, this N-source is not balancing the import of nitrogen and thus an *Arenicola* sand flat acts in total as a sink for nitrogen.

Table 18. Nitrogen budget for *Arenicola* sand flats based on annual means.

	pelagic-benthic mg N $m^{-2}h^{-1}$	benthic-pelagic mg N $m^{-2}h^{-1}$	net exchange mg N $m^{-2}h^{-1}$	
Nitrogen budget for organism exchange	11.44	8.86	-2.56	uptake
Nitrogen budget for particle exchange	45.80	5.22	-40.58	uptake
Nitrogen budget for DON	4.46	0.16	-4.30	uptake
Nitrogen budget for DIN	3.44	3.83	0.39	release
Σ Total	65.14	18.07	-47.07	uptake

iii. Phosphorus exchange in *Arenicola* sand flats

The import from the water column into the sediment of an *Arenicola* sand flat amounts to 7.48 mg P $m^{-2}h^{-1}$ (Table 19). The counteracting release is about 5.85 mg P $m^{-2}h^{-1}$. In total an *Arenicola* sand flat acts as a net sink for phosphorus. However, the different P-compounds behave differently. For organisms (uptake by 0.17 mg P $m^{-2}h^{-1}$), particles (uptake 3.26 mg P $m^{-2}h^{-1}$) and dissolved organic material (uptake 0.18 mg P $m^{-2}h^{-1}$) an *Arenicola* sand flat acts as a sink. For DIP the release is higher than the uptake resulting in a source function for DIP (release of 1.98 mg P $m^{-2}h^{-1}$).

Table 19. Phosphorus budget for an *Arenicola* sand flat based on annual means.

	pelagic-benthic mg P $m^{-2}h^{-1}$	benthic-pelagic mg P $m^{-2}h^{-1}$	net exchange mg P $m^{-2}h^{-1}$	
Phosphorus budget for organism exchange	0.92	0.75	-0.17	uptake
Phosphorus budget for particle exchange	5.93	2.67	-3.26	uptake
Budget for DOP	0.24	0.06	-0.18	uptake
Budget for DIP	0.39	2.37	1.98	release
Σ Total	7.48	5.85	-1.63	uptake

iv. Ecological carbon transfer in *Arenicola* sand flats

Arenicola sand flats show a lower biomass and abundance of organisms compared to mussel beds and seagrass beds but they play a significant role within the total Sylt-Rømø Bight mainly by their large extention. A total biomass of 28606 mg C m^{-2} is estimated on average for an *Arenicola* sand flat situated close to the mean water level of the tidal flat. Because macrophytes are missing in this community, 94 % of the benthic biomass is due to macrobenthic animals.

Biomass of the dominant compartments:

Total biomass autotrophs: Autotrophic compartments build up about 130 mg C m^{-2} or 0.5 % of the total biomass in the *Arenicola* flat (Table 20). This is significantly lower than the autotrophic biomass of mussel beds and seagrass beds where macrophytes play an important role. Autotrophic organisms are restricted to microphytonbenthos, mainly diatoms.

Total biomass heterotrophs: Heterotrophs are dominating the biomass of the *Arenicola* sand flat and attain 28 476 mg C m^{-2}. Macrobenthos is the dominant part with 94% of the heterotrophic biomass. Most important are *C. edule* with 54% followed by *A. marina* with

18%. Much lower in biomass are other species such as *M. balthica* (9%), *Scoloplos intertidalis* (5%), *M. arenaria* (3%) and *Nephthys spec.* (2%). Most other species have shares less than 1% in heterotrophic biomass. Bacteria (2% in total biomass) and meiobenthos (3%) are more significant. The biomass of fish and birds is lower than 1%. Fish biomass is dominated by gobies, the common goby *Pomatoschistus microps* (63%) and the sand goby *P. minutus* (17%). From the other fish species only whiting *Merlangius merlangus* (19% fish biomass) and plaice *Pleuronectes platessa* (1%) attain significant shares.

Bird biomass is estimated at 76 mg C m^{-2} with highest shares of the eider duck (46%) and oystercatcher (11%). Dunlins and curlews contribute both with 7% to total bird biomass, followed by bar tailed godwits and golden plovers with 5 % each. Gulls and other birds are less abundant.

Table 20. Biomass and production of *Arenicola* sand flats.

Arenicola sand flat	Biomass mg Cm^{-2}	GPP mg C $m^{-2}d^{-1}$	NPP mg C $m^{-2}d^{-1}$	Respiration mg C $m^{-2}d^{-1}$	
Microphytobenthos	130.00	991.78	647,63	344,15	
		Production mg C m^{-2} d^{-1}	Egestion mg C m^{-2} d^{-1}		Consumption mg C m^{-2} d^{-1}
Hydrobia ulvae	40.60	0.12	1.18	0.30	1.60
Arenicola marina	5330.20	41.30	180.33	35.54	257.17
Scoloplos intertidalis	1450.00	1.38	27.46	10.53	39.37
Capitellidae	17.40	0.08	1.00	0.40	1.48
Lanice conchilega	80.00	0.42	0.37	0.80	1.59
Pygospio elegans	60.00	0.33	0.43	0.60	1.40
Cerastoderma	15578.80	78.38	286.12	23.64	388.14
Mya arenaria	846.80	1.76	3.10	4.31	9.17
small polychaetes	58.00	0.32	0.49	1.34	2.15
Macoma balthica	2639.00	23.80	114.80	116.80	255.40
Crangon	31.64	0.35	0.35	1.20	1.89
Nepthys spp.	640.00	7.07	24.30	6.71	38.08
P. microps	1.79	0.02	0.34	0.04	0.40
P. minutus	0.47	0.01	0.16	0.01	0.18
P. platessa	0.03	0.00	0.00	0.00	0.00
M. merlangus	0.56	0.00	0.01	0.01	0.03
Eider	35.61	0.10	0.97	3.77	4.84
Oystercatcher	8.10	0.03	0.28	1.08	1.39
Golden Plover	3.50	0.01	0.08	0.30	0.39
Knot	2.95	0.01	0.15	0.58	0.74
Dunlin	5.02	0.02	0.16	0.64	0.82
Bar-tailed Godwit	4.01	0.02	0.16	0.63	0.81
Curlew	5.35	0.01	0.08	0.33	0.42
Black-headed Gull	2.29	0.01	0.06	0.25	0.32
Common Gull	2.40	0.01	0.06	0.24	0.31
Other birds	6.75	0.01	0.14	0.50	0.65
Sediment bacteria	625.00	93.60	24.26	69.32	187.20
Meiobenthos	1000.00	21.92	38.02	83.40	143.34

Primary production:

Gross primary production: Microphytobenthos produces 992 mg C m^{-2} in *Arenicola* sand flats (Table 20).

Net primary production: 647.6 mg C $m^{-2}d^{-1}$ is converted into plant biomass (Table 20). 37% of this net primary production is consumed by herbivores, such as *Hydrobia ulvae.* Most of the net primary production (63%) enters the food chain via detritus.

Consumption: 1339 mg C $m^{-2}d^{-1}$ is consumed by the *Arenicola* sand flat community. 74 % of this is required by macrobenthos and 25 % is flowing into the microbial part of the food web. The share of bacteria in total consumption is 14 %, that of meiobenthos 11 %.

Heterotrophic production: 271 mg C $m^{-2}d^{-1}$ is produced by the heterotrophic part of the food web and 57 % is produced by macrobenthos, particularly *C. edule*, *A. marina* and *M. balthica.* Other macrobenthic animals are of lower importance. Bacteria contribute 35% to the heterotrophic production. Meiobenthos is estimated to have a share of 8 % on total heterotrophic production. The share of fish and birds is below 1%.

Total subsystem production: 918.7 mg C $m^{-2}d^{-1}$ is produced by an *Arenicola* sand flat community. 70 % is due to net primary productivity of microphytobenthos, 30 % is due to heterotrophic production. Production is dominated by autotrophic processes, and primary production has a similar share as sparse seagrass beds although macrophytes are absent.

The total community produces 83.6 t C per day and contributes with 65.1 % to the total production of the Sylt-Rømø Bay.

Production to biomass ratio: The production to biomass ratio of 0.032 is higher compared to mussel beds and seagrass beds, where heterotrophic components are more important for productivity. The P/B-ratio of the *Arenicola* sand flat is very close to the P/B-ratio of the total Sylt- Rømø Bay.

Respiration: 707 mg C $m^{-2}d^{-1}$ is lost by respiration processes from the community. 344.2 mg C $m^{-2}d^{-1}$ or 49 % of total community respiration is shared by microphytobenthos and 202.1 or 29% is estimated to be respired from macrobenthic components. Bacteria contribute with 10% meiobenthos with 12% to total community production. Fish and birds have small shares of 0.01 and 1%, respectively.

Excretion: About 705 mg C $m^{-2}d^{-1}$ enters the detritus pool from excretion processes of the community. 91% of this detritus is produced by macrofauna, 5% by meiofauna and 3% by bacteria. Fish and birds together have a share of about 1% in total faecal production. Most of the faecal material does not stay in the sediment, but is lost by resuspension after bioturbation by endofauna.

v. Food web of *Arenicola* flats

(1) Trophic analysis

Diversity and biomass of trophic groups: About five trophic levels could be distinguished in an *Arenicola* sand flat community. However, only four trophic levels contributed significantly to the energy flow.

Among secondary producers 11 species were included in the present food web. Biomass of secondary producers is dominated by macrobenthos, followed by bacteria and meiobenthos.

Macrobenthos biomass was dominated by *C. edule* and *A. marina,* while *M. balthica, M. arenaria, H. ulvae* and *L. conchilega* as well as small endobenthic polychaetes such as *S. intertidalis* and *P. elegans* contributed less to biomass.

At the third trophic level species number increased to 25, but biomass was only 1/6 of that of the secondary producers. The feeding guild at this trophic level was dominated by macrobenthos, especially those species that depend partly on bacterial diet, but feed to the main part at the second trophic level on detritus and microphytobenthos. Invertebrate predators such as *Nephthys* and *Crangon* contribute also to the biomass at this level. Birds and fish contributed at 10 and at 4 species respectively to the diversity at the third trophic level.

About 10 species contribute to the biomass of quarternary producers which is lower than biomass of the tertiary producers. *Nephthys* is the only invertebrate predator in this group while 3 fish species (*P. microps*, *P. platessa* and *M. merlangus*) and 6 bird species (*P. apricaria, Haemantopus ostralegus, Numenius arcuata, Limosa lapponica, Larus ridibundus* and *L. canus*) belong to this group.

Total system throughput: TST is lower than in most other communities of the intertidal part of the Bay, but surpasses that of sandy shoals and sandy beaches. 4928 mg $Cm^{-2}d^{-1}$ passes the community. Functional and trophic activity of the community are lower compared to seagrass beds and mussel beds.

Average path length: Within the food web of an *Arenicola* sand flat material is transported only over 2.24 steps on average. This shows that the food web of an *Arenicola* sand flat is of low complexity and is composed by small cycles that mostly include bacteria and sediment particulate organic matter. Also flow diversity is less compared to other communities, it is dominated by single simple structured flows connecting only few trophic steps.

Average residence time: Although average path length is short, the average residence time is higher compared with other sand flat communities such as sandy beaches and sandy shoales. The rich biomass of large infauna such as *A. marina* and *C. edule* store carbon and reduce the material turnover and the average residence time compared to those communities where bacteria, meiofauna and small macrofauna are the dominant compartments.

Lindeman spine: 1442 mg C $m^{-2}d^{-1}$ is fixed by gross primary production by the first trophic level (autotrophs) that consists exclusively of microphytobenthos (Fig. 11). 344 mg C $m^{-2}d^{-1}$ are lossed by respiration. 48.3% of the net production is used for growth of microphytobenthos and can be consumed by the next trophic level, the benthic grazers and deposit feeders. The excess production, not consumed by heterotrophic organisms enters the detritus pool from which additionally 550 mg C $m^{-2}d^{-1}$ are consumed by primary consumers. Primary consumers or secondary producers use 16.5% of the consumed detritus and plant material. 244 mg C $m^{-2}d^{-1}$ are lossed by respiration from this level and 716 mg C $m^{-2}d^{-1}$ flows back to the detritus pool. From the production of the benthic secondary producers only 0.9 % is used on the third trophic level, the predators and almost the same percentage is used on the fourth level. The top carnivory level 5 has still significant conversion rates of 0.7% that is directed to the next higher trophic level.

Mean trophic efficiency: Mean trophic efficiency of 3.47 is among the lowest of all investigated communities and is in the same order of magnitude as that found for sandy shoals. This is a consequence of the low average path length, indicating that cycling among compartments having a low trophic position dominate the material cycling within the food web.

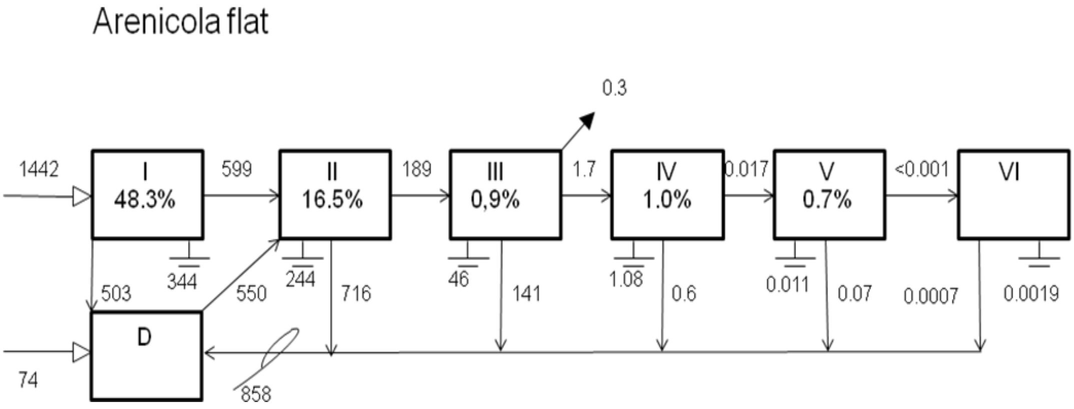


Fig. 11. Lindeman spine of an *Arenicola* sand flat in the Sylt-Rømø Bight. The box indicated D refers to the detrital pool, and the Roman numbers in the boxes of the Spine to discrete trophic levels. Percent values in Spine boxes refer to the efficiency of energy transfer between the integer trophic levels. Fluxes are given in mg Cm^{-2}d^{-1}.

(2) Structure and magnitude of cycling

Number of cycles: Material flow through an intertidal *Arenicola* sand flat is transported over 202 different cycles (Table 21).

Cycle distribution: 1000.59 mg C m^{-2}d^{-1} is transported over cycles within the food web of the *Arenicola* sand flat (Baird, Asmus & Asmus 2007). Through cycles consisting of 2 or 3 compartments 51% and 49% is transported, respectively. This is very similar to sparse seagrass beds, sandy shoals and sandy beaches. *Arenicola* sand flats are thus among the more exposed communities.

Finn Cycling Index: In *Arenicola* sand flats the Finn Cycling Index is the highest of the typical sand flat communities, 20.3% of the material turnover is recycled within this community.

(3) System level properties and system organization

Development capacity: The DC of 21275.0 mg C m^{-2}d^{-1} bits is lower than that of sparse seagrass beds but higher than that of other more exposed sand flat communities.

Ascendency: An ascendency of 8508 mg C m^{-2}d^{-1} bits is estimated for *Arenicola* sand flats. This shows a similar degree of organisation as mud flats and muddy sands. The relative ascendency of 40% is in the same range as that of sparse seagrass beds but shows a slightly higher level of organisation than dense seagrass beds, mud flats and muddy sand flats. The internal relative ascendency (38%) is a function of internal exchanges only. In the *Arenicola* sand flat it shows a decrease compared to relative ascendency and thus indicates some degree of dependence of this system on exogenous connections with adjacent systems which reflect the dependence from the pelagic input into this system and thus the intensity of pelagic-benthic coupling.

Average mutual information: AMI is an index of the level of inherent organisation and of the degree of specialisation in a community. In an *Arenicola* sand flat the AMI is with 1.73 in the same range as for dense seagrass beds and muddy sand flats and therefore shows a comparable degree of organisation and specialisation.

Redundancy: The redundancy of the system (8224.00 mg C $m^{-2}d^{-1}$ bits) is much lower than that of seagrass beds and mud and muddy sand flats but higher than exposed sandy shoales and sandy beaches. However. the relative redundancy is together with mud and muddy sand flats among the highest of the investigated communities in the Sylt-Rømø Bight. 38.7 % of the developmental capacity amounts to redundancy. A high redundancy indicates the presence of many parallel cycles acting in the same way. This strengthens the stability of a system.

Flow diversity: Flow diversity (4.32%) is slightly lower as for seagrass beds but higher as for sandy shoals, sandy beaches and mussel beds. This means that the number of interactions is higher as for exposed systems and the eveness of flows is higher as for mussel beds.

Connectance indices: Overall connectance (2.08) was in the medium range of the communities compared. It was lower than in seagrass beds, mudflats and muddy sands but higher than in sandy shoals, sandy beaches and mussel beds. Intercompartimental connectance (2.60) is higher than overall connectance and shows that internal transfers are of higher significance to the system than external transfers. The large difference between intercompartimental connectance and food web connectance (1.85) reflects the high importance of detritus feeders in the system that therefore depends to a large extent on the exchange between dead and living material.

Table 21. Global system attributes derived from network analysis for the *Arenicola* sand flat subsystem of the Sylt-Rømø Bight. Values reflect results from network models where excess production and sediment POC were not exported from the system. No artificial import was made to balance the compartments.

System Attributes	*Arenicola* flats
Trophic efficiency (logarithmic mean. %. Sed POC retained)	3.47
Detrivory (detritus pool to TL2. mgCm-^{2}d-1. Sed POC retained)	550.0
Detrivory:herbivory ratio (D:)	0.9:1
Number of cycles (Sed POC retained)	202
Finn Cycling Index (%)	20.3
Average Path Lenght (APL=TST-Z/Z)	2.24
Ave Res Time (ART; days)(Sum Biomass/Sum Exports. Resp)	48.06
Total System Throughput (mgCm-^{2}d-1)	4928
Total System Throughput (tonnesCarea-1d-1)	448.4
Development Capacity (mgCm-^{2}d-1bits)	21275
Ascendency (mgCm-^{2}d-1bits)	8508
Relative Ascendancy (A/DC. %)	40.0
Average Mutual Information (A/TST)(normalized A)	1.73
Average Internal Mutual Information (Ai/TST)	1.01
Overheads on imports (mg Cm-^{2}d-1bits)	1758
Overheads on exports (mg Cm-^{2}d-1bits)	2.2
Dissipative Overheads (mg Cm-^{2}d-1bits)	2783
Redundancy (mg Cm-^{2}d-1bits)	8224
Relative Redundancy (R/DC. %)	38.7
Normalized Redundancy (R/TST)	1.67
Internal Development Capacity (mgCm-^{2}d-1bits)	13269
Internal Ascendency (mgCm-^{2}d-1bits)	5046
Relative Internal Ascendency (Ai/DCi. %)	38
Internal Redundancy (mg Cm-^{2}d-1bits)	8224
Relative Internal Redundancy (Ri/DCi. %)	62
Flow Diversity DC (DC/TST. %)(normalized DC)	4.32
Φsum of overheads/TST (+#58)	2.42
Overall connectance	2.082
Intercompartmental connectance	2.594
Foodweb connectance (living compartments only)	1.85
GPP/TST	0.20

vi. Carbon exchange processes of muddy sands

Muddy sand flats are distinct sinks for carbon. However, the sink function is lower (180 mg C m^{-2}h^{-1}) (Table 22) compared to *Arenicola* sand flats (252 mg C m^{-2}h^{-1}). In muddy sands only detritus components are accumulated. Living organisms and dissolved carbon show a net release which is in contrast to *Arenicola* sand flats. This is because the high density and production of infaunal bivalves and gastropods and the removal by larval migration as well as by predators is quite high. But also the remineralisation of the imported high detrital load leads to a surplus of heterotrophic activity and thus a net export of CO$_2$. Although muddy sands are sources for living organisms as well as for dissolved C-components they are a distinct sink for particulate organic material. This sink function exceeds the counteracting processes by far. Thus muddy sands show the classical function of intertidal sand and mud flats by accumulating high amounts of particulate material and releasing living organisms and dissolved substances due to the high productivity and remineralisation, respectively.

Table 22. Carbon budget for muddy sand flats based on annual means.

	pelagic-benthic mgC $m^{-2}h^{-1}$	benthic-pelagic mgC $m^{-2}h^{-1}$	net exchange mgC $m^{-2}h^{-1}$	
Carbon budget for organism exchange	128.76	189.91	61.15	release
Carbon budget for particle exchange	254.01	23.59	-230.42	uptake
Carbon budget for DOC	21.96	6.62	-15.34	release
Carbon budget for DIC	40.53	45.41	4.88	release
Σ Total	445.26	265.53	-179.73	uptake

vii. Nitrogen exchange in muddy sands

Import of N into a muddy sand flat is much higher than the concurrent export. A net import of 48.2 mg N $m^{-2}h^{-1}$ characterises this community (Table 23). Most of this import is due to particle sedimentation and a smaller part is due to uptake of phytoplankton by filter feeders and settling processes as well as dissolved organic N. Although the community acts as a sink for N, it is a distinct source for dissolved inorganic N showing a net release of 1.04 mg N $m^{-2}h^{-1}$.

Table 23. Nitrogen budget for muddy sand flats based on annual means.

	pelagic-benthic mg N $m^{-2}h^{-1}$	benthic-pelagic mg N $m^{-2}h^{-1}$	net exchange mg N $m^{-2}h^{-1}$	
Nitrogen budget for organism exchange	27.38	25.41	-1.97	uptake
Nitrogen budget for particle exchange	45.85	2.50	-43.35	uptake
Nitrogen budget for DON	4.11	0.19	-3.92	uptake
Nitrogen budget for DIN	3.83	4.87	1.04	release
Σ Total	81.17	32.97	-48.20	uptake

viii. Phosphorus exchange in muddy sands

The total input of phosphorus into a muddy sand flat is slightly higher than its export (Table 24). Especially for living organisms and particulate organic P a muddy sand flat acts as a sink whereas inorganic P is distinctly released. The budget for dissolved organic phosphorus is balanced. Because particle uptake dominates the P flux, the total system acts as a sink for P taking up 4.41 mg P $m^{-2}h^{-1}$ on average.

Table 24. Phosphorus budget for muddy sand flats based on annual means.

	pelagic-benthic mg P $m^{-2}h^{-1}$	benthic-pelagic mg P $m^{-2}h^{-1}$	net exchange mg P $m^{-2}h^{-1}$	
Phosphorus budget for organism exchange	2.05	1.91	-0.14	uptake
Phosphorus budget for particle exchange	5.93	0.47	-5.46	uptake
Budget for DOP	0.12	0.12	0.00	
Budget for DIP	0.25	1.44	1.19	release
Σ Total	8.35	3.94	-4.41	uptake

ix. Ecological carbon transfer in muddy sands

Biomass of the dominant compartments: About 95% of the total biomass is due to macrobenthos, while bacteria and meiofauna occupy only 2% each. Fish are of minor importance for the biomass of the system (<1%) and also birds have comparable low biomass values compared to macrobenthos (<1%). In contrast to their high activity is the biomass of autotrophs only low at 0.3%. Biomass in muddy sands is dominated by macrobenthos, because this group is represented by some large animals such as *Mya arenaria* and *Arenicola marina* that contribute to total biomass at 21% and 35%, respectively. Also *Hydrobia ulvae* and *Macoma balthica* reach high biomasses in this community (Table 25).

Primary production: Gross primary production is about 972.6 mg C $m^{-2}d^{-1}$ in muddy sand flats. Microphytobenthos is the only compartment that contributes to this process. Net primary production amounts to 635.1 mg C $m^{-2}d^{-1}$ and this is indicating 65% net primary production efficiency.

Consumption: On average 1925 mg C $m^{-2}d^{-1}$ is consumed by the heterotrophic community of a muddy sand flat. Macrofauna contributes largely to community consumption with 73%, whereas only 27% of the food resources are consumed by the microbial food web. Among macrofauna most of the food is consumed by *A. marina* (21%), *Macoma balthica* (20%), *Hydrobia ulvae* (9%) and *Mya arenaria* (8%). Bacteria contribute largely to consumption by 19%. 81% of the resources are taken up from benthic sources within the community and 19% is taken up from the pelagic domain. Therefore most material that is consumed originated from autochthonous (81%) and only 19% from allochthonous sources.

Heterotrophic production: Approximately 535 mg C $m^{-2}d^{-1}$ is produced by heterotrophs. Bacteria have the largest share in heterotrophic production (315 mg C $m^{-2}d^{-1}$) of a muddy sand flat, followed by macrobenthos (177 mg C $m^{-2}d^{-1}$) and meiobenthos (43 mg C $m^{-2}d^{-1}$). The most productive macrobenthic species are *A. marina*, *M. balthica*, *Mya arenaria* and *Hydrobia ulvae.* 83% of the heterotrophic production is performed at the second trophic level, whereas the higher trophic levels are less productive. Fish and birds have only a share of 0.004 and 0.05%, respectively.

Table 25. Biomass, production, respiration, egestion and consumption of the compartments in a muddy sand flat of the Sylt-Rømø Bight. Values represent annual means used for network analysis.

Muddy sands	Biomass mg C m^{-2}	GPP mg C m^{-2} d^{-1}	NPP mg C m^{-2} d^{-1}	Respiration mg C m^{-2} d^{-1}	
Microphytobenthos	130.00	972.60	635.11	337.49	
	Biomass mg C m^{-2}	Production mg C m^{-2} d^{-1}	Respiration mg C m^{-2} d^{-1}	Egestion mg C m^{-2} d^{-1}	Consumption mg C m^{-2} d^{-1}
Hydrobia ulvae	4524.00	13.59	33.78	131.78	179.20
Arenicola marina	8537.60	66.29	56.90	289.70	412.90
Oligochaeta	307.40	0.84	8.21	4.15	13.20
Heteromastus	475.60	2.61	4.95	33.30	40.86
Nereis diversicolor	1090.00	3.12	13.23	33.40	49.80
Corophium volutator	2620.00	10.88	51.30	12.40	74.58
Mya arenaria	14372.40	29.90	73.10	52.60	155.60
small polychaetes	394.40	2.16	9.10	3.30	14.60
Macoma balthica	4048.40	36.50	179.20	176.10	391.80
small Crustaceans	2621.60	10.88	44.80	14.17	69.90
Carcinus maenas	60.00	0.25	0.38	0.83	1.46
Crangon	31.64	0.35	1.20	0.35	1.90
P. microps	0.40	0.00	0.01	0.08	0.09
P. minutus	0.47	0.01	0.01	0.16	0.18
P. platessa	0.03	0.00	0.00	0.00	0.00
P. flesus	0.02	0.00	0.01	0.01	0.02
M. merlangus	0.56	0.00	0.01	0.01	0.03
Golden Plover	3.50	0.01	0.30	0.08	0.39
Knot	2.95	0.01	0.58	0.15	0.74
Dunlin	5.02	0.02	0.64	0.16	0.82
Curlew	5.35	0.01	0.33	0.08	0.42
Black-headed Gull	2.29	0.01	0.25	0.07	0.33
Common Gull	2.40	0.01	0.24	0.06	0.31
Other birds	6.75	0.01	0.50	0.14	0.65
Mallard	69.47	0.09	2.91	1.74	4.74
Sediment bacteria	625.00	314.50	192.60	67.41	367.59
Meiobenthos	1000.00	43.30	83.40	38.02	143.34

Total subsystem production: About 1170.5 mg C $m^{-2}d^{-1}$ is produced together with microphytobenthos production by the total subsystem of a muddy sand flat. This is close to the average value of the total bight (1265.79 mg C $m^{-2}d^{-1}$). About 50% is contributed by primary production of microphytobenthos. Thus autotrophic and heterotrophic processes are balanced. In total 12.5 t C are produced by muddy sand flats of the Bay. This is 9.7% of the production of the total Sylt-Rømø Bay.

Production to biomass ratio: The P/B-ratio of 0.02 is lower than that of the total Bay (0.036) and it is also lower than that measured for an *Arenicola* sand flat (0.032). This is probably because muddy sand flats have a higher biomass of heterotrophic compartments.

Respiration: About 1095 mg C m^{-2} d^{-1} is lost by respiration processes from the community. 31% of this is due to plant respiration. The major part of respiration is contributed by macrobenthos species (43%) and bacteria (18%), whereas meiobenthos has only a share of 8%. Fish (< 1%) and birds (1%) have very low percentages.

Excretion: Approximately 860.3 mg C $m^{-2}d^{-1}$ is deposited within the sediment by faecal production. About 87% of this detritus is produced by macrofauna, 5% by meiofauna and 3% by bacteria. Fish and birds are insignificant for total faecal production. Because of the low current velocities and the low turbulences in the water column over muddy sand flats, most of the detrital material stays in the sediment.

x. Food web of muddy sands

(1) Trophic analysis

Diversity and biomass of trophic groups: Only a small biomass is formed at the first trophic level. Most of the biomass of a muddy sand flat contributes to the second trophic level, followed by the third and fourth trophic level at 82%, 17% and <1%, respectively. The second trophic level is dominated by the biomass of suspension feeders namely *Mya arenaria*, followed by benthic grazers and detritus feeders. Also bacteria contribute to the detritus users. At the third trophic level bacteria feeders have the largest share whereas predators on invertebrates, such as birds and fish contribute at small percentages.

In total 27 compartments are considered in muddy sand flats. Macrobenthos feed with 12 species at the second trophic level together with meiobenthos and bacteria. In total 14 different primary consumers could be distinguished for muddy sand flats. At the third trophic level diversity is even higher. 22 compartments contribute to this level, mainly macrobenthos (9), fish (5) and birds (8). Top carnivores at trophic level 4 were represented by the same groups but with a lower diversity. In total 12 species belong to this group distributed on macrobenthos, fish and birds with 3, 4 and 5 species, respectively.

Total system throughput: Total system throughput is higher than in other sand flat communities. 5852 mg C $m^{-2}d^{-1}$ pass this community and this TST indicates a similar functional and trophic activity as a sparse seagrass bed, but it is distinctly less active as a dense seagrass bed and a mussel bed.

Average path length: The food web of a muddy sand flat is slightly more complex than that of an *Arenicola* sand flat. However, 3.3 compartments are connected on average and this mostly includes bacteria and sediment POC. Flow diversity in a muddy sand flat is higher compared to all other communities and this indicates a system with many but quite short cycles.

Average residence time: The average residence time is lower than in *Arenicola* sand flats but by far higher than that of sandy shoales and sandy beaches (Table 26). The large biomass of macrobenthic animals reduces the material turnover and increases the average residence time of a system compared to systems driven by bacteria or meiobenthos.

Lindeman spine: 1267 mg C $m^{-2}d^{-1}$ is imported into a muddy sand flat and most of this carbon (75%) is incorporated into plant biomass. A large portion of this biomass (210 mg C $m^{-2}d^{-1}$) enters the detritus pool which is additionally filled up with an external import of 82 mg C $m^{-2}d^{-1}$. 736 mg C $m^{-2}d^{-1}$ is consumed by herbivores and 1050 by detritivores. The efficiency of energy transfer at the second trophic level is with 20.3% highest among unvegetated sand flats. It decreases drastically at the third level and shows again a slight increase at the fourth level of top carnivores. The fifth level is also significant and shows a further increase of energy transfer (Fig. 12).

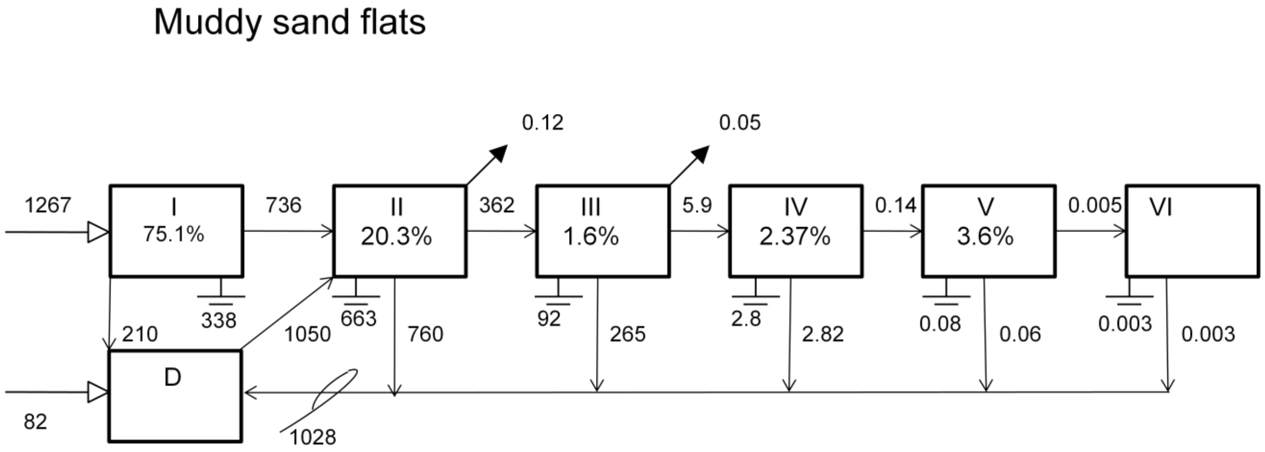


Fig. 12. Lindeman spine of muddy sands in the Sylt-Rømø Bight. The box indicated D refers to the detrital pool, and the Roman numbers in the boxes of the Spine to discrete trophic levels. Percent values in Spine boxes refer to the efficiency of energy transfer between the integer trophic levels. Fluxes are given in mg $Cm^{-2}d^{-1}$.

Mean trophic efficiency: In muddy sands mean trophic efficiency of 7.31% is among the highest of all observed communities and is only surpassed by the trophic efficiency of mussel beds. This is in contrast to *Arenicola* sand flats or sandy shoales and sandy beaches.

In muddy sands as well as in mussel beds the relatively high trophic efficiencies can be explained by the existing short cycles involving plants or detritus and secondary producers and birds which find in muddy sand flats their most important feeding grounds.

(2) Structure and magnitude of cycling

Number of cycles: Muddy sand flats reveal with 342 different cycles the highest number of cycles among all communities in the Sylt-Rømø Bight (Table 26).

Cycle distribution: Most of these cycles include only a limited number of compartments, thus 50% of the material is transferred over cycles with only 2 compartments involved and 47% of the material is cycled over 3 compartments. Cycles of higher order are rare and only 1.9% of the material is cycled over 4 step cycles and 0.08 over 5 step cycles.

Finn Cycling Index: Muddy sands are characterised by a high recycling of carbon. About one third (27.53%) of the material flowing through a muddy sand flat community is recycled which is a high value compared to the other communities of the SRB.

(3) System level properties and system organization

Development capacity: Muddy sands show the highest DC (28506 mg C $m^{-2}d^{-1}$ bits) among the sand flat communities. This shows that muddy sands have a high potential to realize flows and to develop the community. Development capacity of this community is only surpassed by mussel beds and dense seagrass beds.

Redundancy: Redundancy is higher in this community (11904 mg C $m^{-2}d^{-1}$ bits) than that of *Arenicola* flats. 41.8% of the development capacity is due to redundant trophic pathways. This indicates a high stability of this system which is only slightly surpassed by mudflats.

Ascendency: An ascendency of 10216 mg C $m^{-2}d^{-1}$ bits could be analysed for a muddy sand flat. Compared to the high development capacity it indicates that only 35.8% of the potential flows are realized. Muddy sand flats are therefore less well organised than *Arenicola* sand flats. The internal relative ascendency (34.4%) is a function of internal exchanges only and this value decreases when compared to relative ascendency. A decrease of 1.4% shows that muddy sand flats show a slightly lower degree of dependence on exogenous sources than *Arenicola* sandflats.

Average mutual information: AMI of muddy sand flats are in the same range as that for *Arenicola* sand flats and dense seagrass beds. This means that muddy sand flats show a similar level of organisation and specialisation (Table 26).

Flow diversity: Flow diversity is highest in muddy sand flats compared to all other communities in the SRB. The number of interactions is thus high. This is due to the rich endofauna but also due to the rich bird community which has the main feeding ground in muddy sand flats. The flow diversity reflects also the biodiversity of the system because it includes also functional aspects and not only structural parameters such as species number and abundance (Table 26).

Connectance indices: Muddy sand flats range next to dense seagrass beds with respect to overall connectance (2.43) showing a high number of connections between the compartments. External transfers are of even less importance than in *Arenicola* transfers as could be shown by the higher value of intercorpartmental connectance (2.99) compared to overall connectance. The difference between intercompartmental connectance and the food web connectance (2.52) is significanty lower as in the *Arenicola* sand flat and shows that in muddy sand flats the exchange between dead material and living material is of lower importance.

Table 26. Global system attributes derived from network analysis for muddy sand flats subsystem of the Sylt-Rømø Bight. Values reflect results from network models where excess production and sediment POC were not exported from the system. No artificial import was made to balance the compartments.

System Attributes	Muddy-sand Flats
Trophic efficiency (logarithmic mean. %. Sed POC retained)	7.31
Detrivory (detritus pool to TL2. mgCm-^{2}d-1. Sed POC retained)	1050
Detrivory:herbivory ratio (D:)	1.5:1
Number of cycles (Sed POC retained)	342
Finn Cycling Index (%)	27.53
Average Path Lenght (APL=TST-Z/Z)	3.29
Ave Res Time (ART; days)(Sum Biomass/Sum Exports. Resp)	37.36
Total System Throughput (mgCm-^{2}d-1)	5852
Total System Throughput (tonnesCarea-1d-1)	77.54
Development Capacity (mgCm-^{2}d-1bits)	28506
Ascendency (mgCm-^{2}d-1bits)	10216
Relative Ascendancy (A/DC. %)	35.8
Average Mutual Information (A/TST)(normalized A)	1.75
Average Internal Mutual Information (Ai/TST)	1.05
Overheads on imports (mgCm-^{2}d-1bits)	1561
Overheads on exports (mgCm-^{2}d-1bits)	1.5
Dissipative Overheads (mgCm-^{2}d-1bits)	4824
Redundancy (mgCm-^{2}d-1bits)	11904
Relative Redundancy (R/DC. %)	41.8
Normalized Redundancy (R/TST)	2.03
Internal Development Capacity (mgCm-^{2}d-1bits)	18145
Internal Ascendency (mgCm-^{2}d-1bits)	6241
Relative Internal Ascendancy (Ai/DCi. %)	34.4
Internal Redundancy (mgCm-^{2}d-1bits)	11904
Relative Internal Redundancy (Ri/DCi. %)	65.6
Flow Diversity DC (DC/TST. %)(normalized DC)	4.87
Φsum of overheads/TST (+#58)	3.14
Overall connectance	2.429
Intercompartmental connectance	2.986
Foodweb connectance (living compartments only)	2.516
GPP/TST	0.17

xi. Carbon exchange processes in sandy shoals

In total, sandy shoals are sources for carbon. Especially fine organic material is exported from the system as soon as it is produced. The main characteristic is therefore the export of POC which is 269 mg C $m^{-2}h^{-1}$ (Table 27) as long as organic material is available within the sediment. Sandy shoals are sinks for inorganic C and also to a low extent for organisms. Sandy shoals act totally different to other benthic communities in the Wadden Sea that are mainly sinks for particles and organisms but sources for dissolved material. Sandy shoals represent separate but extreme conditions within the intertidal communities. The spatial extent of sandy shoals increase when hydrodynamic forces become stronger. In such a situation sandy shoals are a kind of climax stage within the development of tidal sand flats in a regime of increasing hydrodynamic forces.

Table 27. Carbon budget of sandy shoals based upon annual means.

	pelagic-benthic mgC $m^{-2}h^{-1}$	benthic-pelagic mgC $m^{-2}h^{-1}$	net exchange mgC $m^{-2}h^{-1}$	
Carbon budget for organism exchange	48.50	45.22	-3.27	uptake
Carbon budget for particle exchange	0.52	270.15	269.63	release
Carbon budget for DOC	15.30	7.76	-7.54	uptake
Carbon budget for DIC	40.53	23.82	-16.71	uptake
Σ Total	104.84	346.95	242.11	release

xii. Nitrogen exchange in sandy shoals

About 16.53 mg N $m^{-2}h^{-1}$ is imported to a sandy shoal. This import mainly occurs by postlarval organisms settling down from drifting. Loss of postlarvae into the water column is in the same order of magnitude than import, thus this process does not affect the N budget. There is a net loss of particles (26.8 mg N $m^{-2}h^{-1}$) (Table 28), while dissolved organic N (2.66 mg N $m^{-2}h^{-1}$), organisms (0.5 mg N $m^{-2}h^{-1}$) and dissolved inorganic material (0.76 mg N $m^{-2}h^{-1}$) show a net import. In total, sandy shoals act as N source with 22.88 mg N $m^{-2}h^{-1}$.

Table 28. Nitrogen budget of sandy shoals.

	pelagic-benthic mg N $m^{-2}h^{-1}$	benthic-pelagic mg N $m^{-2}h^{-1}$	net exchange mg N $m^{-2}h^{-1}$	
Nitrogen budget for organism exchange	10.36	9.86	-0.50	uptake
Nitrogen budget for particle exchange	0.05	26.85	26.80	release
Nitrogen budget for DON	3.06	0.40	-2.66	uptake
Nitrogen budget for DIN	3.06	2.30	-0.76	uptake
Σ Total	16.53	39.41	22.88	release

xiii. Phosphorus exchange in sandy shoals

Concerning phosphorus, sandy shoals act as a source (Table 29). As a net result 7.15 mg P $m^{-2}h^{-1}$ is released by the benthic community. 84% of the release is generated by particulate organic P during the process of outwelling of detritus particles from the sediment. 16% is contributed by dissolved inorganic P due to remineralisation by the heterotrophic part of the community, especially bacteria. Dissolved organic P and phosphorus in form of living organisms may be taken up at low rates.

Table. 29. Phosphorus budget for sandy shoals based on annual means.

	pelagic-benthic mg P $m^{-2}h^{-1}$	benthic-pelagic mg P $m^{-2}h^{-1}$	net exchange mg P $m^{-2}h^{-1}$	
Phosphorus budget for organism exchange	0.62	0.58	-0.32	uptake
Phosphorus budget for particle exchange	0.01	6.32	6.31	release
Budget for DOP	0.04	0.03	-0.01	uptake
Budget for DIP	0.25	1.20	1.17	release
Σ Total	0.93	8.13	7.15	release

xiv. Ecological carbon transfer in sandy shoals

Biomass of the dominant compartments: In general the biomass of sandy shoals is low and does not reach the values found in sheltered communities. Macrobenthos dominates the biomass followed by meiobenthos and bacteria. Microphytobenthos attains only small biomass values (Table 30).

Total biomass autotrophs: As in all intertidal sand flats microphytobenthos is the only autotrophic compartment within the community of sandy shoals. The biomass, mainly consisting of diatoms is in the same order of magnitude than that of *Arenicola* sand flats. The biomass has a share of 1% on total biomass.

Total biomass heterotrophs: Heterotrophic biomass attains 9434.3 mg C m^{-2} or 99% of total biomass. Macrobenthos is the dominant part of the heterotrophic biomass with a share of 83%. *A. marina* is the dominant species in this community, where it occurs in few but large animals. *C. edule* is the second most important species with respect to biomass. Both occupy 34% and 20% , respectively. *S. intertidalis, M. balthica* and *L. conchilega* follow with 13%, 8% and 4%, respectively. Meiobenthos has a share of 11% and is therefore more significant in sandy shoals than in other sand flat communities. Bacterial biomass is also quite high with 7% of the total biomass. The only fish fauna are flat fish holding less than 0.01% of the heterotrophic biomass. Birds do not feed on sandy shoals and are therefore absent from the trophic net of the community.

Table 30. Biomass, production (GPP= gross primary production; NPP= net primary production. production= heterotrophic production), respiration, egestion and consumption of dominant compartments in sandy shoals.

Sandy shoals	Biomass mg Cm^{-2}	GPP mg Cm^{-2}d^{-1}	NPP mg Cm^{-2}d^{-1}	Respiration mg Cm^{-2}d^{-1}	
Microphytobenthos	130	991.78	647.63	344.15	
	Biomass mg Cm^{-2}	Production mg Cm^{-2}d^{-1}	Respiration mg Cm^{-2}d^{-1}	Egestion mg Cm^{-2}d^{-1}	Consumption mg Cm^{-2}d^{-1}
Arenicola marina	3224.8	25.04	21.5	109.4	155.94
Scoloplos intertidalis	1230	1.17	8.8	23.3	33.4
Lanice conchilega	340	1.86	3.56	1.56	6.98
Cerastoderma	1856	9.3	2.8	34.1	46.2
small polychaetes	40,6	0.2	0.9	0.3	1.4
Macoma balthica	736,6	6.6	32.6	32.0	71.2
small Crustacea	40.6	0.2	0.7	0.2	1.1
Crangon	9.2	0.1	0.4	0.1	0.6
Nepthys spp.	330.0	3.6	3.5	12.5	19.6
P. microps	0.4	0.004	0.009	0.077	0.090
P. minutus	0.47	0.005	0.01	0.16	0.175
P. platessa	0.03	0.0002	0.0003	0.0009	0.0014
M. merlangus	0.56	0.003	0.008	0.015	0.026
sediment bacteria	625.0	93.6	69.3	24.3	187.2
Meiobenthos	1000.0	21.9	83.4	38.0	143.3

Primary production:

Gross primary production: Primary productivity is in the same order of magnitude than in *Arenicola* sand flats and is exclusively built by microphytobenthos (Table 30).

Net primary production: 647.6 mg C $m^{-2}h^{-1}$ is converted into plant biomass but only 24% is consumed by herbivores. Most of the excess production enters the detritus pool, which is not stored in the sediment but exported from the system. The efficiency of net primary productivity is low with 11.7%.

Consumption: Consumption of the total community (667 mg C $m^{-2}d^{-1}$) of a sandy shoal is lower than in most other communities. Macrobenthos uses 50% of this consumption whereas the other part flows into the microbial food chain of the system. The consumption is mainly based on detrital sources and the attached bacteria (60% of consumption). Benthic grazing contributes only with 28% to total consumption and predation has with 3% the lowest share. Most consumers depend on benthic food sources (87% of consumption) whereas only 13% of the consumption is due to pelagic food sources.

Heterotrophic production: About 164 mg C $m^{-2}d^{-1}$ is produced by the heterotrophic part of a sandy shoal community. In contrast to the more sheltered types of sand flats, production is dominated by bacterial production (57%) followed by macrobenthos (29%) and meiobenthos (13%). The share of fish is below 1%.

Total subsystem production: In total 811 mg C $m^{-2}d^{-1}$ is produced by a sandy shoal. 80% of this production is contributed by microphytobenthos and only 20% by the heterotrophic part of the community.

Production to biomass ratio: Because small organisms dominate the energy flow in a sandy shoal, the production to biomass ratio of 0.08 is higher than in most other intertidal sand flat areas and is much higher than the average value of the Sylt-Rømø Bight.

Respiration: Approximately 572 mg C $m^{-2}d^{-1}$ is lost by respiration processes of the community. Respiration is dominated by microphytobenthos (60%). Bacteria share 12% of the carbon lost by respiration of the system and meiofauna contribute 15%. Macrofauna only shows a percentage of 13% on total community respiration. Fish are insignificant.

Egestion: The detritus pool plays a central role within the carbon cycling of sandy shoals. 276 mg C $m^{-2}d^{-1}$ is produced by the heterotrophic part of the sandy shoal community. Most of this material enters the detrital pool which is used by organisms as food or is exported from the system by wave action. In addition it was assumed that the excess production of plants enters the detritus pool. The excess detrital material produced in the sandy shoal is assumed to leave the system.

xv. Food web of sandy shoals

(1) Trophic analysis

Diversity and biomass of trophic groups: Only a small biomass is developed at the first trophic level. The major part of the total benthic biomass is accumulated within the second trophic level. Macrofauna dominate the second level at 77%, followed by meiofauna at 14%

and bacteria at 9%. Even at trophic level III and IV biomass is dominated by macrofauna, while fish are around 1%. Birds do not contribute to the biomass of sandy shoals.

In total 16 compartments have been included in the food web of sandy shoals. The second trophic level is shared among bacteria, meiofauna and 7 species of macrofauna. The most important species concerning the biomass of the system is *Arenicola marina*, which occurs at sandy shoals at low abundance but with a high individual biomass. Other species show only low biomass values either due to the low abundance or the small size. At the third trophic level 10 macrobenthic species can be found including the deposit feeders that feed also upon bacteria. Among the predators that feed upon macroinvertebrates are here small predatory polychaetes, *Crangon crangon* and *Nephthys* spp. In addition 3 fish species contribute to biomass of the trophic level but only with less than 1%. The 3 predatory invertebrate species also form the main biomass at the fourth trophic level. Fish species are represented by *M. merlangus* at this trophic level.

Total System Throughput: Total system throughput (3739 mg C $m^{-2}d^{-1}$) is low but slightly higher than that of sandy beaches. The reason is the low biomass of biotic components resulting in a very low activity of the community.

Average Path length: Average path length is similar as in *Arenicola* sand flats and sandy beaches. This indicates a low complexity of the food web and shows a large contribution of organisms at a low trophic level such as bacteria, detritus feeders and grazers. For example , Heymans & McLachlan (1996) reported a similar low APL of 2.3% for a sandy beach system in South Africa.

Average residence time: Because of high physical activity such as sediment turnover or wave action, the material entering a sandy shoal system does not remain in the system, but is quickly exported to the water column. Thus every residence time of a carbon atom is only 8.85 days before it leaves the system. There are no storage compartments in sandy shoal that may retard the material flow.

Lindeman spine: About 1068 mg C $m^{-2}d^{-1}$ is consumed by the primary producers of a sandy shoal (Fig. 13). About 68% of this is transferred to plant biomass. Only 21% of this organic matter is consumed by heterotrophic organisms directly and the biomass not consumed (79%) is transferred to the detritus pool from which 406 mg C $m^{-2}d^{-1}$ consumed by secondary producers. The transfer efficiency of secondary producers is 20%. 206 mg C $m^{-2}d^{-1}$ is lost by respiration and 240 mg C $m^{-2}d^{-1}$ by excretion. 112 mg C $m^{-2}d^{-1}$ is available for higher trophic levels whereas higher trophic levels have only low efficiencies of 4.1% at the third and insignificant efficiencies of 0.3% and 0.4% at the fourth and fifth level, respectively.

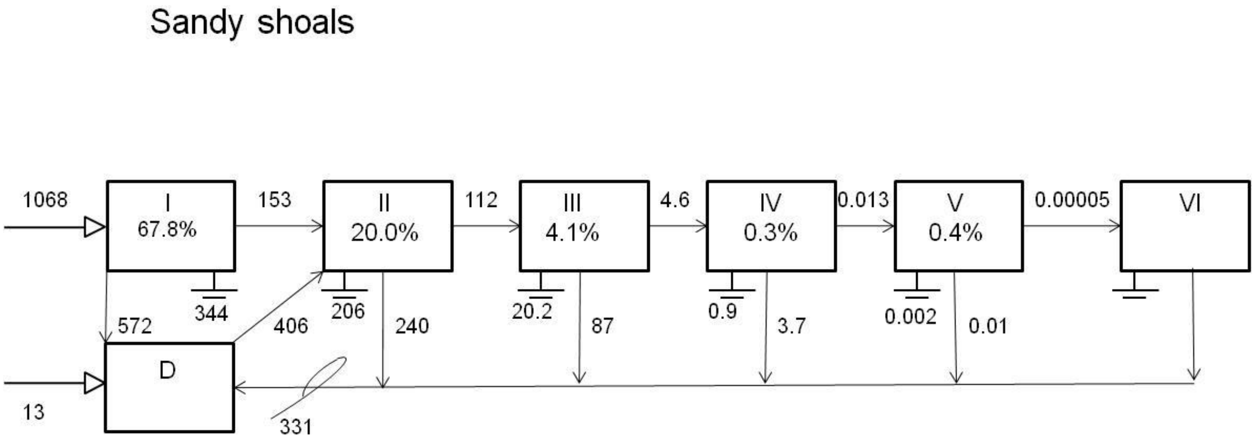


Fig. 13. Lindeman spine of sandy shoalsin the Sylt-Rømø Bight. The box indicated D refers to the detrital pool, and the Roman numbers in the boxes of the Spine to discrete trophic levels. Percent values in Spine boxes refer to the efficiency of energy transfer between the integer trophic levels. Fluxes are given in mg Cm^{-2}d^{-1}.

Mean trophic efficiency: Sandy shoals have the lowest mean trophic efficiency among all communities in the intertidal area. Due to the dominance of short cycles with compartments of a low trophic level a mean trophic efficiency of only 3.3% could be determined.

(2) Structure and magnitude of cycling

Number of cycles: Only 87 cycles were apparent in sandy shoals reflecting low structural complexity and low biodiversity of the system (Table 31).

Cycle distribution: 604 mg C m^{-2}d^{-1} is transported over the different cycles of a sandy shoal community. 60% of this amount is transported over cycles of only 2 compartments. 38% of the material is cycled involving 3 compartments and only 2% of the material passes cycles with 4 elements. Thus material cycling is dominated by the activity of very small cycles.

Finn Cycling Index: About 16.5 % of the material is recycled within the community of the sandy shoal. This is similar to the recycling within sandy beaches but less than the recycling potential of the majority of communities in the Sylt-Rømø Bight. This is in accordance with an FCI of 13% for similar exposed communities in South Africa (Heymans & McLachlan 1996)

(3) System level properties and system organization

Development capacity: The development capacity is 14 043 (mg C m^{-2}d^{-1}bits) and is between an *Arenicola* sand flat and a sandy beach system.

Redundancy: Also redundancy lies between both systems mentioned above. However, regarding relative redundancy, sandy shoals show values of 35% and thus can be regarded as representing average values for tidal flats.

Table 31. Global system attributes derived from network analysis for a sandy shoal subsystem of the Sylt-Rømø Bight. Values reflect results from network models where excess production and sediment POC were not exported from the system. No artificial import was made to balance the compartments.

System Attributes	sandy shoals
Trophic efficiency (logarithmic mean % Sed POC retained)	3.3
Detrivory (detritus pool to TL2, mgCm-^{2}d^{-1}, Sed POC retained)	3.996
Detrivory:herbivory ratio (D:)	2.7:1
Number of cycles (Sed POC retained)	87
Finn Cycling Index (%)	16.5
Average Path Lenght (APL=TST-Z/Z)	2.46
Ave Res Time (ART; days)(Sum Biomass/Sum Exports. Resp)	8.85
Total System Throughput (mgC m^{-2}d^{-1})	3739
Total System Throughput (tonnesC area^{-1}d^{-1})	13.8
Development Capacity (mgC m^{-2}d^{-1}bits)	14043
Ascendency (mgC m^{-2}d-1bits)	6281
Relative Ascendancy (A/DC. %)	44.7
Average Mutual Information (A/TST)(normalized A)	1,68
Average Internal Mutual Information (Ai/TST)	0.69
Overheads on imports (mgC m^{-2}d^{-1}bits)	505
Overheads on exports (mgC m^{-2}d^{-1}bits)	421
Dissipative Overheads (mgC m^{-2}d^{-1}bits)	1911
Redundancy (mgCm-^{2}d-1bits)	4926
Relative Redundancy (R/DC. %)	35.1
Normalized Redundancy (R/TST)	1.32
Internal Development Capacity (mgC m^{-2}d^{-1}bits)	7512
Internal Ascendency (mgC m^{-2}d^{-1}bits)	2586
Relative Internal Ascendancy (Ai/DCi. %)	34.4
Internal Redundancy (mgC m^{-2}d^{-1}bits)	4926
Relative Internal Redundancy (Ri/DCi. %)	65.6
Flow Diversity DC (DC/TST. %)(normalized DC)	3.76
Φsum of overheads/TST (+#58)	2.08
Overall connectance	1.992
Intercompartmental connectance	2.312
Foodweb connectance (living compartments only)	1.8
GPP/TST	0.27

Ascendency: An ascendency of 6281 is estimated for sandy shoals. The relative ascendency is 44.7% and shows a slightly higher level as most other communities except mussel beds indicating a better organisation and a higher maturity of the system. The internal relative ascendency (34.4%) shows a strong decrease compared to the relative ascendency indicating a relatively high degree of dependence on exogenous sources and characterises thus a high intensity of benthic-pelagic coupling.

Average mutual information: Sandy shoals reveal a low AMI of 1.68 (bits) which is lower than in other intertidal communities except sandy beaches. This low value seems to be characteristic for such types of exposed communities.

Flow diversity: Due to the low diversity and the relative low number of interactions between compartments within sandy shoals, this system reveals a flow diversity lower than all other benthic communities except sandy beaches (Table 31). A low flow diversity seems to be a characteristic feature for exposed and thus harsh environments.

Connectance indices: Overall connectance (1.99) was in the lower range of the communities compared. However, it was still higher than mussel beds and sandy beaches. Intercompartimental Connectance (2.3) was slightly higher and shows that internal transfers are still significant but of lower importance than in the other communities. Also the difference between intercompartimental connectance and food web connectance (1.8) shows that detritus feeders play still a large role in the system but that the system depends to a large extent on the exchange between dead and living material.

xvi. Carbon exchange in sandy beaches

Sandy beaches are distinct sources for carbon (Table 32). Effluxes of particles and dissolved organic C are characteristic for this community showing a great similarity to the C flow of sandy shoals. Both communities are sinks for organisms and dissolved C. Sandy beaches can be described as autotrophic because assimilation of CO_2 is higher than respiration. For a part of this system we have to consider an irregular input of macro-detritus which is the base for a high microbial activity and thus may contribute significantly to the C-budget.

Table 32. Carbon Budget for sandy beaches based on annual means.

	pelagic-benthic mgC $m^{-2}h^{-1}$	benthic-pelagic mgC $m^{-2}h^{-1}$	net exchange mgC $m^{-2}h^{-1}$	
Carbon budget for organism exchange	46.13	43.80	-2.33	uptake
Carbon budget for particle exchange	0.41	270.03	269.62	release
Carbon budget for DOC	39.75	14.14	-25.61	uptake
Carbon budget for DIC	37.56	20.98	-16.58	uptake
Σ Total	123.85	348.95	225.10	release

xvii. Nitrogen exchange in sandy beaches

About 25.70 mg N $m^{-2}h^{-1}$ is imported to a sandy beach. This import mainly occurs by postlarval organisms settling down from drifting. Loss of postlarvae into the water column is in the same order of magnitude than import, thus this process does not affect the N budget. There is a net loss of particles (26.83 mg N $m^{-2}h^{-1}$). Dissolved organic N (7.2 mg N $m^{-2}h^{-1}$), living organisms (0.3 mg N $m^{-2}h^{-1}$) and dissolved inorganic material (5.4 mg N $m^{-2}h^{-1}$) show a net import. In total, sandy beaches act as N sources at 13.94 mg N $m^{-2}h^{-1}$ (Table 33).

Table 33. Nitrogen budget for sandy beaches based on annual means.

	pelagic-benthic mg N $m^{-2}h^{-1}$	benthic-pelagic mg N $m^{-2}h^{-1}$	net exchange mg N $m^{-2}h^{-1}$	
Nitrogen budget for organism exchange	9.76	9.43	-0.32	uptake
Nitrogen budget for particle exchange	0.04	26.87	26.83	release
Nitrogen budget for DON	7.95	0.75	-7.20	uptake
Nitrogen budget for DIN	7.95	2.59	-5.36	uptake
Σ Total	25.70	39.64	13.94	release

xviii. Phosphorus exchange in sandy beaches

Sandy beaches act as phosphorus source (Table 34). As a net result 5.99 mg P $m^{-2}h^{-1}$ is released by the benthic community. Most of this release (90%) is generated by particulate organic P during the process of outwelling of detrituts particles from the sediment. 10% is contributed by dissolved inorganic P due to remineralisation by the heterotrophic part of the community, especially bacteria. Dissolved organic P-exchange is more or less balanced between uptake and release. The only import pathway is due to the import of organisms.

Table 34. Phosphorus budget for a sandy beach community.

	pelagic-benthic mg P m^{-2} h^{-1}	benthic-pelagic mg P m^{-2} h^{-1}	net exchange mg P m^{-2} h^{-1}	
Phosphorus budget for organism exchange	1.52	0.54	-0.98	uptake
Phosphorus budget for particle exchange	0.01	6.30	6.29	release
Budget for DOP	0.12	0.11	-0.01	
Budget for DIP	0.52	1.20	0.68	release
Σ Total	2.16	8.15	5.99	release

xix. Ecological carbon transfer in sandy beaches

Biomass of the dominant compartments: Biomass is dominated by the heterotrophic compartments of a sandy beach system. In total the biomass is low compared to other intertidal communities (Table 35). This is due to the low indundation period of 1-2 hours per average tide promoting mainly smaller organisms such as bacteria and meiofauna.

Total biomass autotrophs: Microphytobenthos is the only autotrophic compartment within the community of sandy beaches. The biomass mainly consisting of diatoms are in the same order of magnitude than that of *Arenicola* sand flats and sandy shoals. The biomass has a share of 4% on total biomass.

Total biomass of heterotrophs: Heterotrophic biomass attains 6952.34 mg C m^{-2} or 96% of total biomass. Macrobenthos is the dominant part of the heterotrophic biomass with a share of 74%. *Pygospio elegans* is the dominant species in this community followed by different small polychaete species together they occupy 57% and 42% of the macrobenthic and total biomass, respectively. *Corophium arenarium*, small crustaceans and *N. diversicolor* follow with a share on macrobenthic biomass of 18%, 18% and 3% respectively. Meiobenthos has a share of 14% and is therefore more significant in sandy beaches than in other sand flat communities. Bacterial biomass is also quite high with 9% of the total biomass. The only represents of the fish fauna are gobies and flat fish holding about 0.01% of the heterotrophic biomass.

Primary production:

<u>Gross primary production</u>*:* Primary productivity is in the same order of magnitude than in *Arenicola* sand flats and is exclusively build by microphytobenthos (Table 35).

<u>Net primary production</u>*:* 588.59 mg C $m^{-2}h^{-1}$ is converted into plant biomass but only 27% is consumed by herbivores. Most of the excess production enters the detritus pool, which is not stored in the sediment but exported from the system. The efficiency of net primary productivity is low with 13.9%.

Table 35. Biomass, production (GPP= gross primary production; NPP= net primary production. production= heterotrophic production), respiration, egestion and consumptiuon of dominant compartments in sandy beaches of the Sylt-Rømø Bight.

Sandy beaches	Biomass mgC m^{-2}d^{-1}	GPP mgC m^{-2}d^{-1}	NPP mgC m^{-2}d^{-1}	Respiration mgC m^{-2}d^{-1}	
Microphytobenthos	270.00	901.37	588.59	312.78	
	Biomass mgC m^{-2}d^{-1}	Production mgC m^{-2}d^{-1}	Respiration mgC m^{-2}d^{-1}	Egestion mgC m^{-2}d^{-1}	Consumption mgC m^{-2}d^{-1}
Oligochaeta	75.40	0.20	2.00	1.00	3.20
Nereis diversicolor	170.00	0.50	0.70	5.20	6.40
Pygospio elegans	1520.00	4.20	31.70	11.10	47.00
Corophium arenarium	960.00	2.60	6.30	0.90	9.90
small polychaetes	1519.60	4.20	31.10	12.70	48.00
Macoma balthica	92.80	0.09	4.80	4.03	8.92
small Crustacea	957.00	2.60	16.40	5.20	24.10
Crangon	31.64	0.35	1.20	0.35	1.89
P. microps	0.40	0.00	0.01	0.08	0.09
P. minutus	0.47	0.01	0.01	0.16	0.18
P. platessa	0.03	0.00	0.00	0.00	0.00
Sediment bacteria	625.00	93.60	325.80	114.00	533.40
Meiobenthos	1000.00	21.90	83.40	38.00	143.30

Consumption: Consumption of the total community (826.38 mg C m^{-2}h^{-1}) of a sandy beach is lower than that of most other communities. Macrobenthos uses 18% of this consumption whereas the dominant part (82%) flows into the microbial food chain of the system including meiobenthos (17%). The consumption is mainly based on detrital sources and the attached bacteria (70% of consumption). Benthic grazing contributes only with 19% to total consumption and predation has with 3% the lowest share. Most consumers depend on benthic food sources (92%), whereas only 8% of the consumers use pelagic food sources.

Heterotrophic production: About 130 mg C m^{-2}d^{-1} is produced by the heterotrophic part of a sandy beach community. In contrast to the more sheltered types of sand flats, production is dominated by bacterial production (72%) followed by meiobenthos (17%) and macrobenthos (11%). The share of fish is below 1%.

Total subsystem production: In total 718.84 mg C m^{-2}d^{-1} is produced by a sandy beach. 82% of this production is contributed by microphytobenthos and only 18% by the heterotrophic part of the community.

Production to biomass ratio*:* Because small organisms dominate the energy flow in a sandy beach, the production to biomass ratio of 0.10 is the highest value found in intertidal sand flat areas and is much higher than the average value of the Sylt-Rømø Bight.

Respiration: 816.2 mg C m^{-2}d^{-1} is lost by respiration processes of the community. Respiration is dominated by bacteria (40%). Microphytobenthos share 38% of the C lost by respiration of the system and meiofauna contribute 10%. Macrofauna only shows a percentage of 12% on total community respiration. Fish are insignificant.

Egestion: The detritus pool plays a central role within the carbon cycling of sandy beaches. 192 mg C $m^{-2}d^{-1}$ is produced by the heterotrophic part of the sandy beach community. Most of this material enters the detrital pool which is used by organisms as food or is exported from the system by wave action. In addition it was assumed that the excess production of plants enters the detritus pool. The excess detrital material produced in the sandy beach is assumed to leave the system.

xx. Food web of sandy beaches

(1) Trophic analysis

Diversity and biomass of trophic groups: Biomass in sandy beaches is dominated by the biomass of primary consumers (Table 35). At the second trophic level macrofauna dominates the biomass at 74%, followed by meiobenthos (18%) and bacteria (11%). Among the benthic grazer guild, meiobenthos and macrobenthos show similar percentages, while deposit feeder are distinctly dominated by macrofauna. The predator guild is dominated by the macrofauna such as *Crangon crangon*, *Nereis diversicolor* and small predatory polychaete species that make together 99% of the biomass representing this trophic level. Fish are the only vertebrate predators in the sandy beach system, and they contribute only at about 1% to the third as well as fourth trophic level.

For the present analysis of the sandy beach system 14 compartments have been considered, that are distributed among the bacteria meio- and macrofauna and the fish. At the second trophic level 7 macrobenthic species build up 99% of the biomass. At the third trophic level the 8 species including 7 species that are bacterial feeders have been included. There were no obligate top predator at the fourth trophic level, however this niche was occupied by species such as *Nereis*, small polychaetes and *Crangon* which feed also on lower trophic levels. These 3 species have been considered to feed on trophic level four, together with 3 vertebrate predator species such as *Pomatoschistus microps*, *P. minutus* and *Pleuronectes platessa*.

Total system throughput: Total system throughput (3556 mg C $m^{-2}d^{-1}$) (Table 36) is slightly lower than that of sandy shoals. The reason is the low biomass of biotic components resulting in a very low activity of the community.

Average Path length: Average path length is slightly higher as in *Arenicola* sand flats and sandy shoals. However, this indicates a low complexity of the food web and shows a large contribution of organisms at a low trophic level such as bacteria, detritus feeders and grazers (Table 36).

Average residence time: Because of high physical activity such as sediment turnover or wave action, the material entering a sandy shoal system does not remain in the system, but is quickly exported to the water column. Thus every residence time of a carbon atom is only 7.47 days before it leaves the system. There are no storage compartments in a sandy beach that may retard the material flow.

Lindeman spine: In total 958 mg C $m^{-2}d^{-1}$ is taken up by the primary producers of a sandy beach (Fig. 14). 63% of this material is transferred to plant biomass. Only 14% of this organic matter is consumed by heterotrophic organisms directly and the biomass not consumed

(53%) is transferred to the detritus pool from which 656 mg C m^{-2}d^{-1} is consumed by secondary producers. The transfer efficiency of secondary producers is only 3.9%. From the secondary producer compartment 485 C m^{-2}d^{-1} is lost by respiration and 278 C m^{-2}d^{-1} by excretion. Only 31.3 C m^{-2}d^{-1} is available for higher trophic levels, whereas higher trophic levels have only low efficiencies of 4.2% and 1.7% at the third and fourth trophic level, respectively. Insignificant efficiencies are observed at the fifth and sixth level.

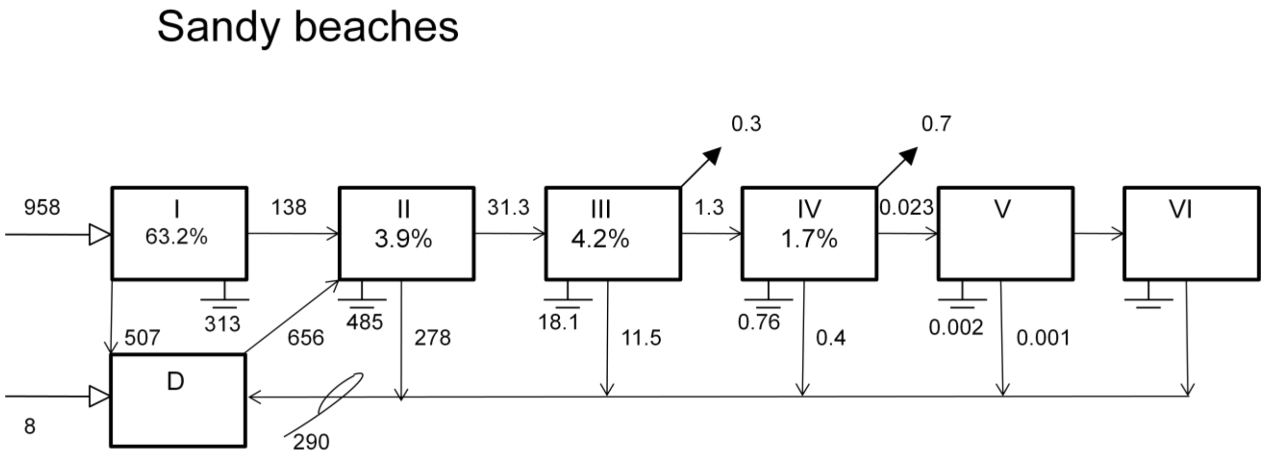


Fig. 14. Lindeman spine of the food web of sandy beaches. The box indicated D refers to the detrital pool, and the Roman numbers in the boxes of the Spine to discrete trophic levels. Percent values in Spine boxes refer to the efficiency of energy transfer between the integer trophic levels. Fluxes are given in mg Cm^{-2}d^{-1}.

Mean trophic efficiency: Sandy beaches have next to muddy sand flats the highest mean trophic efficiency among all communities in the intertidal area. Because two component interactions dominate this food web and predator-prey interactions are closely linked, a mean trophic efficiency of 6.5% could be determined.

(2) Structure and magnitude of cycling

Number of cycles: Only 92 cycles were apparent in sandy beaches, reflecting low structural complexity and low biodiversity of the system (Table 36).

Cycle distribution: 573 mg C m^{-2}d^{-1} is transported over the different cycles of a sandy beach community. 87% of this amount is transported over cycles of only 2 compartments. 12% of the material is cycled involving 3 compartments and only 1% of the material passes cycles with 4 elements. Thus material cycling is dominated by the activity of very small cycles or two component interactions.

Finn Cycling Index: About 16% of the material is recycled within the community of the sandy beach. This is similar to the recycling within sandy shoals, but less than the recycling potential of the majority of communities in the Sylt-Rømø Bight.

(3) System level properties and system organization

Development capacity: The development capacity is 12775 C m^{-2}d^{-1} bits is the lowest among the intertidal communities.

Redundancy: Also redundancy is lowest. Relative redundancy of sandy beaches show values of 30% and thus can be regarded as representing values lowest next to mussel beds. This indicates a quite low stability of the system.

Ascendency: An ascendency of 5633 C $m^{-2}d^{-1}$ bits is estimated for sandy beaches. The relative ascendency is 44.1% and shows a slightly higher level as most other communities except mussel beds indicating a better organisation and a higher maturity of the system. The internal relative ascendency (39.9%) shows a decrease compared to the relative ascendency indicating a relatively high degree of dependence on exogenous sources but characterises still a high intensity of benthic-pelagic coupling.

Average mutual information: Sandy beaches reveal a low AMI of 1.58 bits, which is lowest compared to other intertidal communities. This low value seems to be characteristic for such types of exposed communities.

Flow diversity: Due to the low diversity and the relatively low number of interactions between compartments within sandy beaches, this system reveals a flow diversity lower than all other benthic communities. A low flow diversity seems to be a characteristic feature for exposed and thus harsh environments.

Connectance indices: Overall connectance (1.87) was in the lower range of the communities compared. However, it was still higher than mussel beds. Intercompartimental connectance shows the same value as overall connectance and shows that internal transfers are of less importance compared to external exchanges. The difference between internal connectance (1.87) and food web connectance (2.2) shows that grazing and predation play still a larger role in the system than the dependence on the exchange between dead and living material. Also sandy beaches are quite similar to sandy shoals, this is a distinct difference between both systems.

Table 36. Global system attributes derived from network analysis for a sandy beach subsystem of the Sylt-Rømø Bight. Values reflect results from network models where excess production and sediment POC were not exported from the system. No artificial import was made to balance the compartments.

System Attributes	sandy beaches
Trophic efficiency (logarithmic mean %, Sed POC retained)	6.5
Detrivory (mgC $m^{-2}d^{-1}$)	656
Detrivory:herbivory ratio (D:)	4.7:1
Number of cycles	92
Finn Cycling Index (%)	16.16
Average Path Length (APL=TST-Z/Z)	2.68
Ave Res Time (ART; days)(Sum Biomass/Sum Exports, Resp)	7.47
Total System Throughput (mgC $m^{-2}d^{-1}$)	3556
Total System Throughput (tonnes C $area^{-1}d^{-1}$)	26.03
Development Capacity (mgC $m^{-2}d^{-1}$bits)	12775
Ascendency (mgC $m^{-2}d^{-1}$bits)	5633
Relative Ascendancy (A/DC. %)	44.1
Average Mutual Information (A/TST)(normalized A)	1.58
Average Internal Mutual Information (Ai/TST)	0,73
Overheads on imports (mgC $m^{-2}d^{-1}$bits)	384
Overheads on exports (mgC $m^{-2}d^{-1}$bits)	366
Dissipative Overheads (mgC $m^{-2}d^{-1}$bits)	248
Redundancy (mgC $m^{-2}d^{-1}$bits)	3914
Relative Redundancy (R/DC. %)	30.6
Normalized Redundancy (R/TST)	1.10
Internal Development Capacity (mgC $m^{-2}d^{-1}$bits)	6508
Internal Ascendency (mgC $m^{-2}d^{-1}$bits)	2594
Relative Internal Ascendancy (Ai/DCi. %)	39.9
Internal Redundancy (mgC $m^{-2}d^{-1}$bits)	3914
Relative Internal Redundancy (Ri/DCi. %)	60.1
Flow Diversity DC (DC/TST. %)(normalized DC)	3.59
Φsum of overheads/TST (+#58)	1.38
Overall connectance	1.87
Intercompartmental connectance	1.87
Foodweb connectance (living compartments only)	2.2
GPP/TST	0.25

e. Exchange processes and food web organisation in mud flats

i. Carbon exchange in mud flats

From the 340 mg C $m^{-2}h^{-1}$ entering intertidal mudflats mainly by sedimentation processes of detritus material, 152 mg C $m^{-2}h^{-1}$ leave the system in form of living organisms or remineralisation products. The main part of imported carbon remains in the system and except for dissolved organic C, mudflats are distinct sinks for most organic components and organisms (Table 37).

Table 37. Carbon Budget for a mud flat community based on annual means.

	pelagic-benthic mgC m^{-2} h^{-1}	benthic-pelagic mgC m^{-2} h^{-1}	net exchange mgC m^{-2} h^{-1}	
Carbon budget for organism exchange	112.10	105.72	-6.38	uptake
Carbon budget for particle exchange	167.20	0.00	-166.19	uptake
Carbon budget for DOC	20.51	6.62	-13.89	release
Carbon budget for DIC	40.53	39.50	-1.03	uptake
Σ Total	340.34	151.84	-188.50	uptake

ii. Nitrogen exchange in mud flats

22.25 mg N m^{-2}h^{-1} is the net import to a mud flat. This import mainly occurs by particles (71%) either settling passively or filtered by suspension feeding organisms. Loss of postlarvae into the water column is in the same order of magnitude than import, thus this process does not affect the N budget. However, organisms show a week net import into a mudflat (2%). For dissolved organic N mud flats seem to be an important sink, since 27% of the net N import is due to DON. Regarding most of the living and non living organic materials mud flats act as a sink for nitrogen. For dissolved inorganic N mud flat is a distinct source. There is a net loss of dissolved inorganic material (0.86 mg N m^{-2}h^{-1}) (Table 38).

Table 38. Budget of nitrogen for a mud flat community based on annual means.

	pelagic-benthic mg N m^{-2} h^{-1}	benthic-pelagic mg N m^{-2} h^{-1}	net exchange mg N m^{-2} h^{-1}	
Nitrogen budget for organism exchange	23.87	23.30	-0.57	uptake
Nitropgen budget for particle exchange	16.72	0.00	-16.72	uptake
Nitrogen budget for DON	6.35	0.53	-5.82	uptake
Nitrogen budget for DIN	3.54	4.40	0.86	release
Σ Total	50.48	28.23	-22.25	uptake

iii. Phosphorus exchange in mud flats

Mud flats act as a phosphorus sink. As a net result 2.88 mg P m^{-2}h^{-1} is taken up by the benthic community. This uptake is generated by particulate organic P during the process of sedimentation of detrituts particles. Dissolved organic P is also taken up by microphytobenthos and bacteria. Dissolved inorganic P is released by a mud flat due to remineralisation by the heterotrophic part of the community, especially bacteria (Table 39).

Table 39. Phosphorus budget of a mud flat community based on annual means.

	pelagic-benthic mg P m^{-2} h^{-1}	benthic-pelagic mg P m^{-2} h^{-1}	net exchange mg P m^{-2} h^{-1}	
Phosphorus budget for organism exchange	1.54	1.59	0.05	uptake
Phosphorus budget for particle exchange	3.90	0.00	-3.90	release
Budget for DOP	0.12	0.003	-0.12	uptake
Budget for DIP	0.23	1.32	1.09	release
Σ Total	5.79	2.91	-2.88	uptake

iv. Ecological carbon transfer in mud flats

Total biomass autotrophs: Microphytobenthos is the only autotrophic compartment within the community of mud flats. The biomass mainly consists of benthic diatoms. The biomass has a share of less than 1% on total biomass (Table 40).

Total biomass heterotrophs: Heterotrophic biomass attains 23 256.2 mg C m^{-2} or 99% of total biomass. Macrobenthos is the dominant part of the heterotrophic biomass with a share of 91%. *Hydrobia ulvae* is the dominant species in this community followed by *Macoma balthica* and *Nereis diversicolor*. These invertebrates occupy 34%, 22% and 12% of the total biomass, respectively. *A. marina. C. edule* and Oligochaeta follow with a share on macrobenthic biomass of 10%, 4% and 4%, respectively. Meiobenthos has a share of 2% and is therefore less significant in mud flats than in sand flat communities. Bacterial biomass is also comparatively low with 3% of the total biomass. The fish fauna is represented by gobies, flat fish and whiting holding about 0.01% of the heterotrophic biomass. Birds are very abundant in this community and are dominated by *Tadorna tadorna* (3%). Birds´ biomass is with 4% high compared with sand flat communities.

Primary production:

Gross primary production: Gross primary productivity has a value of 972.6 mg C m^{-2}h^{-1} and is exclusively built by microphytobenthos.

Net primary production: About 635.1 mg C m^{-2}d^{-1} is converted into plant biomass but 66% is consumed by herbivores. Most of the excess production enters the detritus pool which is stored in the sediment or consumed by detritus feeders. The efficiency of net primary productivity is high with 65%.

Consumption: Consumption of the total community (1750.6 mg C m^{-2}h^{-1}) of a mud flat is similar to muddy sands but distinctly higher than other sand flat communities. Macrobenthos uses the dominant part (68%) of this consumption whereas 26% flows into the microbial food chain of the system including meiobenthos (4%). The consumption is mainly based on detrital sources and the attached bacteria (52% of consumption). Grazing contributes with 38% to total consumption and predation has with 10% the lowest share. Most consumers depend on benthic food sources (using 83% of consumption) whereas only 17% of consumption is taken from pelagic food sources.

Heterotrophic production: Approximately 245 mg C m^{-2}d^{-1} is produced by the heterotrophic part of a mud flat community. In contrast to the more exposed sand flats, production is dominated by bacterial production (50%) followed by macrobenthos (45%) and meiobenthos (4%). The share of fish is negligible but birds have a share of 1% in heterotrophic production.

Total subsystem production: In total 880.1 mg C m^{-2}h^{-1} is produced by a mud flat. 72% of this production is contributed by microphytobenthos and only 28% by the heterotrophic part of the community.

Production to biomass ratio: Because small organisms dominate the energy flow in a mud flat, the production to biomass ratio of 0.043 is higher than the average value of the Sylt-Rømø Bight.

Respiration: About 1034 mg C m^{-2}d^{-1} is lost by respiration processes of the community. Respiration is dominated by macrofauna (36%). Microphytobenthos share 33% of the C lost by respiration of the system and bacteria contribute 19%. Meiofauna only shows a percentage of 4% on total community respiration. Fish are insignificant. Birds contribute with 8%.

Egestion: The detritus pool plays a central role within the carbon cycling of mud flats. Faeces are produced in an order of 808.7 mg C $m^{-2}h^{-1}$ by the heterotrophic part of the mud flat community. Most of this material enters the detrital pool which is used by organisms as food. In addition it was assumed that the excess production of plants enters the detritus pool. The excess detrital material produced in the mud flat is assumed to remain within the system.

Table 40. Production (GPP= gross primary production; NPP= net primary production, production = heterotrophic production), respiration, egestion and consumption of dominant compartments in a mud flat community of the Sylt –Rømø Bight.

Mud flats	Biomass mg C m^{-2}	GPP mg C m^{-2} h^{-1}	NPP mg C m^{-2} h^{-1}	Respiration mg C m^{-2} h^{-1}	
Microphytobenthos	120.00	972.60	635.11	337.49	
	Biomass mg C m^{-2}	Production mg C m^{-2} h^{-1}	Respiration mg C m^{-2} h^{-1}	Egestion mg C m^{-2} h^{-1}	Consumption mg C m^{-2} h^{-1}
Hydrobia ulvae	8004.00	24.05	59.75	233.15	317.10
Arenicola marina	2354.80	18.28	15.70	80.00	113.98
Oligochaeta	904.80	2.48	24.15	12.25	39.00
Heteromastus	638.00	3.50	6.66	44.65	54.90
Nereis diversicolor	2710.00	7.78	32.85	83.10	123.73
Pygospio elegans	170.00	0.93	1.75	1.24	3.92
Cerastoderma	928.00	4.67	1.40	17.05	23.12
Mya arenaria	81.20	0.17	0.41	0.30	0.88
Small polychaetes	168.20	0.90	3.90	1.38	6.18
Tharyx killariensis	191.40	1.05	4.16	2.50	7.71
Macoma balthica	5075.00	45.70	224.60	220.80	491.10
Crangon	31.64	0.35	1.20	0.35	1.90
P. microps	0.40	0.00	0.01	0.08	0.09
P. minutus	0.47	0.01	0.01	0.16	0.18
P. platessa	0.03	0.00	0.00	0.00	0.00
P. flesus	0.02	0.00	0.01	0.01	0.02
M. merlangus	0.56	0.00	0.01	0.01	0.03
Shelduck	652.21	1.75	67.32	17.18	86.25
Avocet	31.56	0.35	5.26	1.40	7.01
Golden Plover	3.50	0.01	0.30	0.08	0.39
Knot	2.95	0.01	0.58	0.15	0.74
Dunlin	5.02	0.02	0.64	0.16	0.82
Curlew	5.35	0.01	0.33	0.08	0.42
Black-headed Gull	2.29	0.01	0.25	0.07	0.33
Common Gull	2.40	0.01	0.24	0.06	0.31
Other birds	6.75	0.01	0.50	0.14	0.65
Mallard	69.47	0.09	2.91	1.74	4.74
Pintail	91.17	0.35	7.36	4.21	11.92
Sediment bacteria	625.00	121.53	192.60	67.41	381.54
Meiobenthos	500.00	10.96	41.70	19.01	71.67

v. Food web of mud flats

(1) Trophic analysis

Diversity and biomass of trophic groups: Six trophic levels could be distinguished within the mud flat community but only four trophic levels contribute significantly to the energy transfer. Biomass at the second trophic level is dominated by macrozoobenthos followed by bacteria and meiobenthos. About 12 species of macrozoobenthos could be found at this trophic level. *Hydrobia ulvae* has the highest biomass contributing to the biomass of grazers as well as to the detritus feeders. Also *Arenicola marina, Nereis diversicolor* and small polychaete species belong to different food sources within this trophic level. Obligate detritus feeders such as Oligochaeta, *Heteromastus,* and *Tharyx* also occur in this group. Phytoplankton and suspended detritus was used by *Cerastoderma edule, Mya arenaria* as well as *Pygospio.* Small polychaetes, *Nereis diversicolor* and *Macoma balthica* use pelagic as well as benthic food sources.

At the third trophic level most biomass is due to macrobenthos, particularly those species that feed on bacteria. This group is identical to that feeding on detritus and in total 12 macrobenthos species can be found at the trophic level III. Fish contribute with 4 species to this trophic level, particularly 2 species of gobies and 2 species of flatfish. Because of the high importance of mud flats for the feeding of birds, this group is represented by 9 species at the third trophic level. This group is dominated by the shell duck *Tadorna tadorna* that feeds at a large amount on *H. ulvae*. The Avocette *Recurvirostra avocetta* is feeding upon more or less the same source. Both species are to a high degree dependent on mud flats and were not present in other communities of the Sylt-Rømø Bight.

At the third trophic level birds become the dominant component in biomass with 6 species, however fish are also important (4 species), and the whiting is feeding exclusively at this trophic level. For the macrofauna only omnivores such as *Nereis diversicolor* represent the invertebrate top predator guild with 1 species.

Total System Throughput*:* Total system throughput (5248 mg C $m^{-2}d^{-1}$) (Table 41) is in a medium range but slightly lower than that of muddy sands.

Average Path length: Average path length is the highest (3.13) next to muddy sands. This indicates a high complexity of the food web and shows a large contribution of organisms at higher trophic level such as especially birds.

Average residence time: Residence time of a carbon atom is 22.62 days before it leaves the system. This is lower than in other complex trophic systems like mussel beds, seagrass beds and sheltered sandflats, but distinctly higher than that of exposed sandy systems. ART increases with biomass of the community but decreases with export function and respiration. Macrofauna has a large share in this system but is characterized by small individuals such as *Hydrobia ulvae* that has a low biomass but a high respiration.

Lindeman spine: 1221 mg C $m^{-2}d^{-1}$ is consumed by the primary producers of a mud flat (Fig. 15). 69 % of this material is transferred to plant biomass. 54 % of this organic matter is consumed by heterotrophic organisms directly and the biomass not consumed (18%) is transferred to the detritus pool from which 812 mg C $m^{-2}d^{-1}$ is consumed by secondary producers. The transfer efficiency of secondary producers is 24.5 %. From the secondary producer compartment 448 mg C $m^{-2}d^{-1}$ is lost by respiration and 664 mgC $m^{-2}d^{-1}$ by excretion. 361 mg C $m^{-2}d^{-1}$ is available for higher trophic levels whereas higher trophic levels have efficiencies of 5.6 % at the third but only 0.15 % at the fourth level.

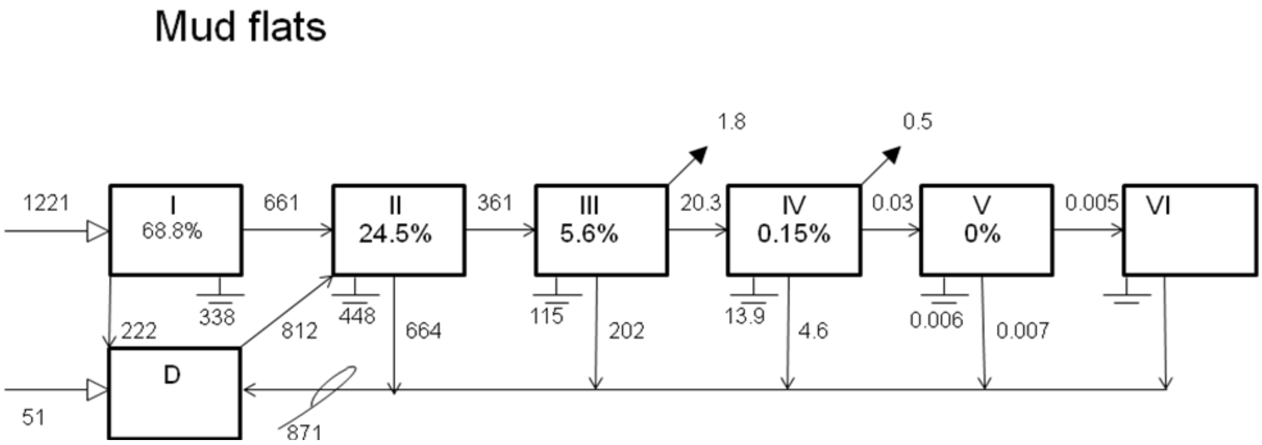


Fig. 15. Lindeman spine of the fod web of an intertidal mud flat. The box indicated D refers to the detrital pool, and the Roman numbers in the boxes of the Spine to discrete trophic levels. Percent values in Spine boxes refer to the efficiency of energy transfer between the integer trophic levels. Fluxes are given in mg $Cm^{-2}d^{-1}$.

Mean trophic efficiency: Mud flats have next to muddy sand flats and sandy beaches the highest mean trophic efficiency among all communities in the intertidal area. Because of the contribution of vertebrate predators, especially birds have a relatively high significance in this food web. A mean trophic efficiency of 6.13% could be determined (Table 41).

(2) Structure and magnitude of cycling

Number of cycles: 158 cycles were apparent in mud flats, reflecting a similar structural complexity and functional diversity of the system as mussel beds and seagrass beds.

Cycle distribution: 1357.87 mg C $m^{-2}d^{-1}$ is transported over the different cycles of a mud flat community. 40 % of this amount is transported over cycles of only 2 compartments, 56 % of the material is cycled involving 3 compartments and 4% of the material passes cycles with 4 elements. Thus material cycling is more evenly distributed over the different cycle sizes compared especially to sand flat communities.

Finn Cycling Index: About 26% of the material is recycled within the community of a mud flat. This is the highest FCI next to the muddy sand flat community and indicates a higher recycling potential than the majority of communities in the Sylt-Rømø Bight.

(3) System level properties and system organization

Development capacity: The development capacity is 24 936 mg C $m^{-2}d^{-1}$ bits and is in a medium range among the intertidal communities (Table 41).

Redundancy: Redundancy is also in a medium range. Relative redundancy of mud flats shows a value of 43% and thus can be regarded as representing the highest value among all intertidal communities. This indicates a relatively high stability of the system.

Ascendency: An ascendency of 8714 mg C m^{-2} d^{-1} bits is estimated for mud flats. The relative ascendency is 34.9% and shows the lowest level of the communities except mussel beds indicating a lower organisation and maturity of the system. The internal relative ascendency (32.3%) shows a decrease of 2.6% compared to the relative ascendency indicating a relatively high degree of dependence on exogenous sources and characterises still a high intensity of benthic-pelagic coupling.

Average mutual information: Mud flats reveal a low AMI of 1.66 bits compared to other intertidal communities. This was mainly found for exposed communities but may show also conditions where mainly small sized organisms characterize the material cycling.

Flow diversity: Due to the relatively high diversity and the high number of interactions between compartments within mud flats, this system reveals a flow diversity higher than most other benthic communities except muddy sand flats (Table 41). A high flow diversity seems to be a characteristic feature for sheltered and diverse environments.

Table 41. Global system attributes derived from network analysis for a mud flat subsystem of the Sylt-Rømø Bight. Values reflect results from network models where excess production and sediment POC were not exported from the system. No artificial import was made to balance the compartments.

System Attributes	mud flats
Trophic efficiency (logarithmic mean %, Sed POC retained)	6.13
Detrivory (detritus pool to TL2. Mg C $m^{-2}d^{-1}$. Sed POC retained)	812.0
Detrivory:herbivory ratio (D:)	1.2:1
Number of cycles (Sed POC retained)	158
Finn Cycling Index (%)	25.89
Average Path Lenght (APL=TST-Z/Z)	3.13
Ave Res Time (ART; days)(Sum Biomass/Sum Exports, Resp)	22.62
Total System Throughput (mg C $m^{-2}d^{-1}$)	5248
Total System Throughput (tonnes C $area^{-1}d^{-1}$)	20.20
Development Capacity (mg C $m^{-2}d^{-1}$bits)	24936
Ascendency (mg C m-^{2}d^{-1}bits)	8714
Relative Ascendancy (A/DC. %)	34.9
Average Mutual Information (A/TST)(normalized A)	1.66
Average Internal Mutual Information (Ai/TST)	0.94
Overheads on imports (mg C $m^{-2}d^{-1}$bits)	1200
Overheads on exports (mg C $m^{-2}d^{-1}$bits)	15
Dissipative Overheads (mg C $m^{-2}d^{-1}$bits)	4277
Redundancy (mg C $m^{-2}d^{-1}$bits)	10730
Relative Redundancy (R/DC. %)	43.0
Normalized Redundancy (R/TST)	2.04
Internal Development Capacity (mg C $m^{-2}d^{-1}$bits)	15843
Internal Ascendency (mg C $m^{-2}d^{-1}$bits)	5113
Relative Internal Ascendency (Ai/DCi. %)	32.3
Internal Redundancy (mg C$m^{-2}d^{-1}$bits)	10730
Relative Internal Redundancy (Ri/DCi. %)	67.7
Flow Diversity DC (DC/TST. %)(normalized DC)	4.75
Φsum of overheads/TST (+#58)	3.20
Overall connectance	2.457
Intercompartmental connectance	3.098
Foodweb connectance (living compartments only)	2.398
GPP/TST	0.19

Connectance indices: Overall connectance (2.46) was the highest value of the communities compared. Intercompartimental connectance shows a higher value as overall connectance and shows that internal transfers are of larger importance compared to external exchanges. The difference between internal connectance (3.10) and food web connectance (2.4) shows that the dependence on the exchange between dead and living material plays still a larger role in the system than grazing and predation.

5. General Discussion

a. Energy flow and material budget of the Sylt-Rømø Bight

From molecules to ecosystems, biological systems show a hierarchical organisation (O'Neill et al. 1986). At the level of the ecosystem the energy flow of the intertidal part of the SRB has been described as a system of high ecological productivity and activity (Asmus & Asmus 1990; 1998 a,b; 2000; 2005). The SRB shows comparable characteristics and functionality with other estuarine and coastal ecosystems (Sprung, Asmus & Asmus 2001; Baird, Asmus & Asmus 2004), but exhibits also unique community properties and rates of productivity.

Primary productivity in the Sylt-Rømø Bight is high and is approximately equal to pelagic and benthic production at the total system level (Asmus et al. 1998 c). Focussing on the intertidal region only, benthic primary production surpasses pelagic primary production. The autochthonous pelagic primary production is not sufficient to meet the energy requirements of the suspension feeders, thus an additional import of North Sea phytoplankton is necessary. This supporting import has been described for the Wadden Sea and similar coastal systems (Baird, Asmus & Asmus 2004; 2007). The magnitude of this import is, however, not precisely quantified even not for other estuaries and coastal systems (Nixon 1980; Ridd et al. 1988; Alongi 1998; Odum 2002; Wolanski 2007). However, to meet the requirements of the suspension feeders an import of at least 140 mg C $m^{-2}d^{-1}$ is required (Baird, Asmus & Asmus 2004; 2007).

In addition to phytoplankton, detritus is produced in the coastal zone of the North Sea and is transported into the Wadden Sea supporting its food web (Straaten & Kuenen 1957; Postma 1967; 1981; Groen 1967; Austen 1997; Austen et al. 1998). To what extent the Wadden Sea food web depends on the imported phytoplankton and detritus is indicated by the dominance of suspension feeders in most benthic assemblages of the system (Asmus & Asmus 2005). Mussel beds reveal a low areal coverage but control the seston input into those assemblages situated further landward (Asmus & Asmus 1990).

As in most other ecosystems, secondary producers are the dominant consumer group in the energy flow of the SRB. Here this group includes a broad range of organisms from bacteria, meiobenthos, zooplankton, macroinvertebrates to herbivorous fish and herbivorous birds. Regarding biomass, most benthic invertebrates are suspension feeders followed by benthic detritus feeders and benthic grazers. Including the detritus feeding consumers among the suspension feeders, the detritus feeder to grazer ratio is 1.44 to 1 (Baird, Asmus & Asmus 2004). The energy transfer between primary and secondary consumers is characterized by a low trophic efficiency (Baird, Asmus & Asmus 2004; 2007). This is determined by a low use of the rich microphytobenthos production by consumers and by an overexploited autochthonous primary production of phytoplankton which requires allochthonous auxiliary import.

Higher trophic levels include macro-invertebrates, fish and birds. There is a remarkable bottle neck between the secondary producers and the higher trophic levels, indicated by a minimum trophic transfer within tertiary producers compared to higher trophic levels. This can be ascribed to the relatively high returns to the detrital pool at this group (Baird, Asmus &

Asmus 2004; 2007). There is only little energy transported within trophic levels higher than level 3.

At community level there is a high variability of energy flow among the different habitats and their floral and faunal assemblages of the Sylt-Rømø Bight (Baird, Asmus & Asmus 2007). Mussel beds show about a ten times higher productivity compared to sandy shoals and sandy beaches. Mussel beds and dense seagrass beds show the highest production, followed by muddy sand flats, sparse seagrass beds, *Arenicola* sand flats and mud flats. The lowest productivity was measured in sandy shoals and sandy beaches (Asmus et al. 1998a; Baird, Asmus & Asmus 2007).

Primary productivity is highest in mussel beds, where macroalgal growth predominates in this process (Fig. 16). In other communities microphytobenthos growing on sediments or on macrophytes especially seagrasses is the main primary producer, whereas phytoplankton is contributing less to primary production due to its limited appearance over the tidal flats during high tides. Hence primary production of microphytobenthos and of phytoplankton do not show large differences in magnitude between the communities. The main differences in primary production depend on macrophytobenthos, which is only present to a significant extent in mussel beds and seagrass beds.

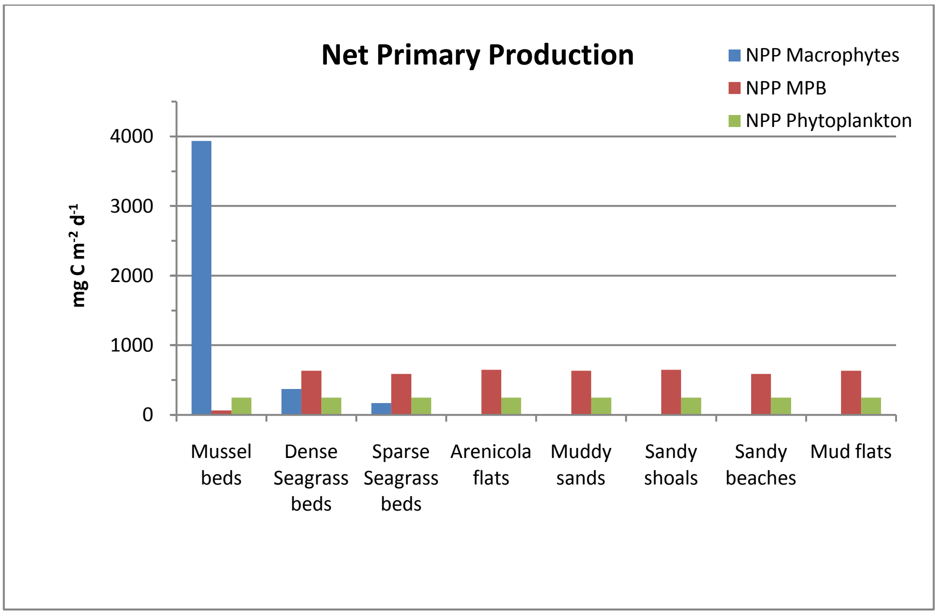


Fig. 16. Net primary production (NPP) of different intertidal benthic communities in mg C $m^{-2}d^{-1}$. Macrophytes (blue), microphytobenthos (MPP) (red) and phytoplankton (green).

Heterotrophic productivity is dominated by macrozoobenthos production followed by bacteria and meiobenthos (Fig. 17). The productivity of fish and birds is an order of magnitude less than those of these groups. Bacterial production is less variable among the different communities as macrobenthic production, which is highest in mussel beds and lowest in sandy beaches. Macrobenthos productivity is responsible for most of the spatial differences in total heterotrophic productivity. Except mussel beds, dense seagrass beds, muddy sands and mudflats reveal a high productivity, whereas *Arenicola* flats, sparse seagrass beds, sandy shoals and sandy beaches only comprise about half of this production. Secondary productivity contributes mainly to heterotrophic production (Fig. 18). It is highest in mussel beds and is minimal in sandy beaches.

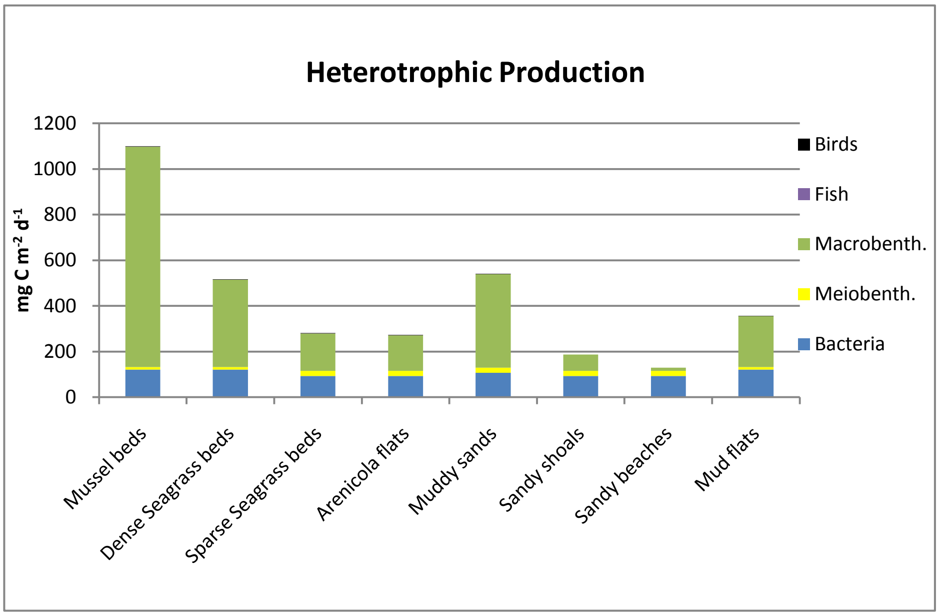


Fig. 17. The contribution of different groups of organisms (from bacteria to birds) to heterotrophic production in the Sylt- Rømø Bight in mg C m^{-2} d^{-1}.

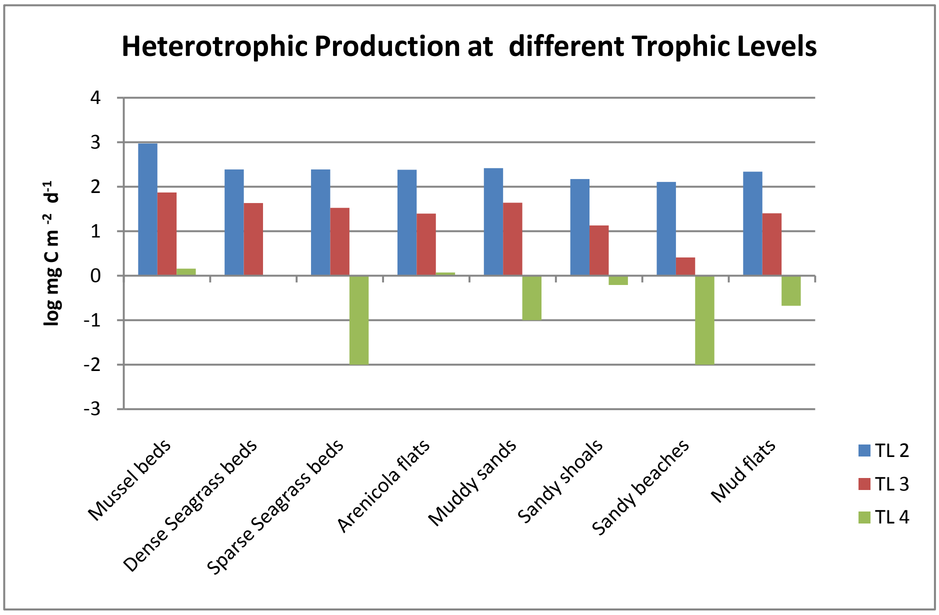


Fig. 18. The contribution of different trophic levels (TL) to heterotrophic production at a logarithmic scale in mg C m^{-2} d^{-1}.

Secondary production is dominated by macrofauna in mussel beds, sparse seagrass beds, *Arenicola* sand flats, muddy sands, whereas in dense seagrass beds, mud flats, sandy shoals and sandy beaches bacteria is the dominant component (Fig. 19). Meiobenthos is of minor importance in all habitats but is higher in biomass in sandy shoals and sandy beaches, where the oxygenated layer of the sediment is deep compared to the other communities. In both types of seagrass beds birds also contribute to secondary production, but in an order of magnitude less compared to the other compartments.

Productivity at higher trophic levels is due primarily to macrozoobenthos, fish and birds. At the third trophic level macrobenthos is the dominant component. In mussel beds and mud flats birds have larger shares compared to the other communities (Fig. 19).

At the fourth trophic level fish dominate the production in mussel beds, and on sparse seagrass beds where birds have a large predatory impact through feeding on predatory crustaceans (i.e. *Crangon*). Birds show higher production in muddy sands and mudflats, whereas the production of predatory invertebrates predominate quaternary production in these communities as well as in *Arenicola* flats, dense seagrass beds, sandy shoals and sandy beaches (Fig. 19).

The contribution of different consumer groups at the different trophic levels gives a lot of information on the functioning of these systems.

The composition of sizes may also determine the pattern of energy flow (Sprung & Asmus 1995). Energy equivalence assumes equal contribution of large and small species to production and energy flow in communities. In intertidal communities of the Sylt-Rømø Bight macrobenthic biomass and production displayed two distinct peaks. One peak at small body sizes was caused by benthic grazers or browsers. The other peak at larger sizes was caused by animals which potentially extract their food from the water column. In systems where detritus feeders dominate the community this bimodality was vaguely reflected (Sprung & Asmus 1995). However, except for mussel beds the communities' size spectra imply a dominance of small individuals in biomass and production. This has been interpreted as a consequence of permanent disturbances (Sprung & Asmus 1995)

The proportion of net primary production that is passed along each of the possible pathways depend on transfer efficiencies in the way energy is taken up, used and passed from one compartment to the next. Three categories of transfer efficiencies are required to predict the pattern of energy flow. These are consumption efficiency, assimilation efficiency and production efficiency.

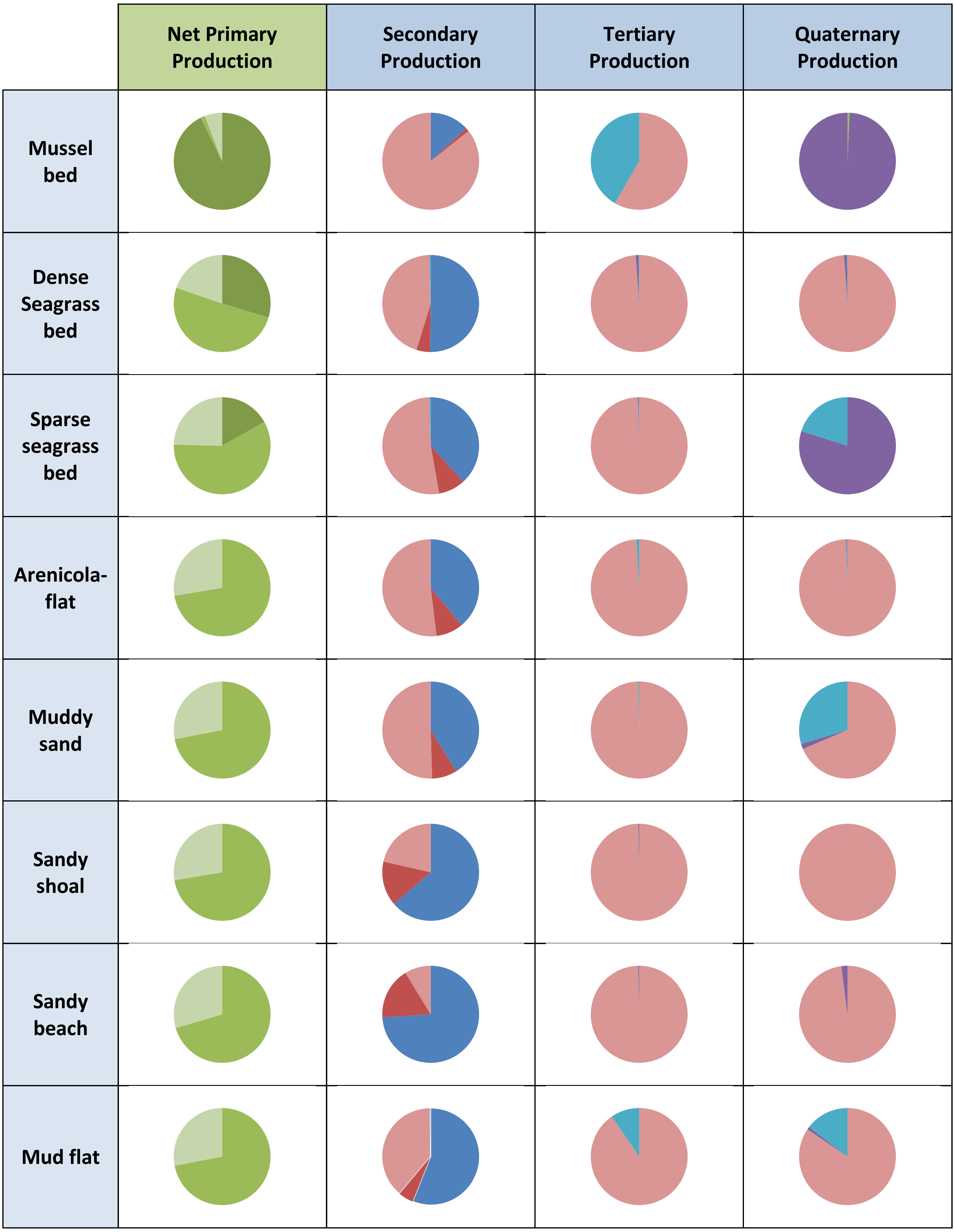


Fig. 19. Percentage of net primary, secondary, tertiary and quaternary production in 8 benthic communities of the Sylt-Rømø Bight, contributed by different organism groups: ■ macrophytes, ■ microphytobenthos, ■ phytoplankton, ■ bacteria, ■ meiobenthos, ■ macrobenthos, ■ fish and ■ birds.

i. Consumption efficiency

Consumption efficiency is the percentage of total productivity available at one trophic level that is actually consumed by trophic compartments at one higher level. Various reported values for the consumption efficiencies at the second trophic level are less than 5% for forests, around 25% in grasslands and more than 50% in phytoplankton–dominated communities (see also Cebrian 1999). In the intertidal communities of the Sylt-Rømø Bight, consumption efficiencies at the second trophic level range from 42% in sandy shoals to 92% in muddy sand flats (Fig. 20). Mussel beds show values higher than 100% because the autochthonous primary production and detritus production is too low to support secondary production. Secondary production is only possible by an auxiliary import of phytoplankton from the deeper parts of the Wadden Sea or the North Sea. This additional import of phytoplankton and detritus from outside is made possible by tidal transport. The consumption efficiency shows that primary food resources in the Wadden Sea are used by the heterotrophic community to a high degree. The high consumption efficiency in mussel beds indicates food limitation, and also in those communities where suspension feeders contribute most to biomass, consumption efficiency is high.

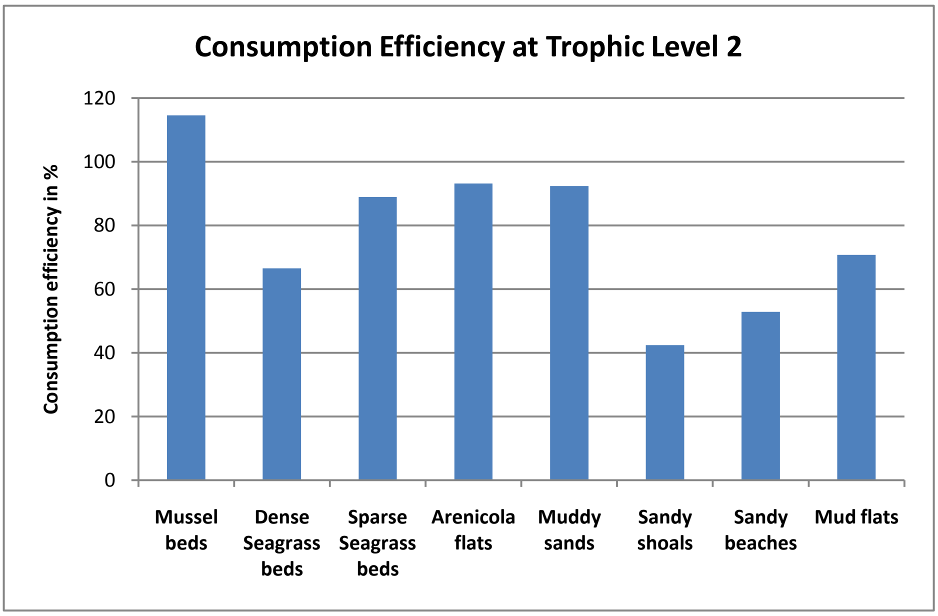


Fig. 20. Consumption efficiency at trophic level 2 in 8 benthic communities of the Sylt-Rømø Bight.

Much less is known about the consumption efficiencies of carnivores feeding on their prey and most estimates are speculative. For the benthic communities in the Sylt-Rømø Bight consumption efficiencies at the trophic level 3 showed high values of more than 100% for most of the investigated communities (Fig. 21). Only sandy beaches, sandy shoals and *Arenicola* flats show values below 100%. Consumption at trophic level 3 includes also feeding on bacteria. Thus I divided the secondary production into bacterial production and non bacterial production and estimated the consumption efficiency separately.

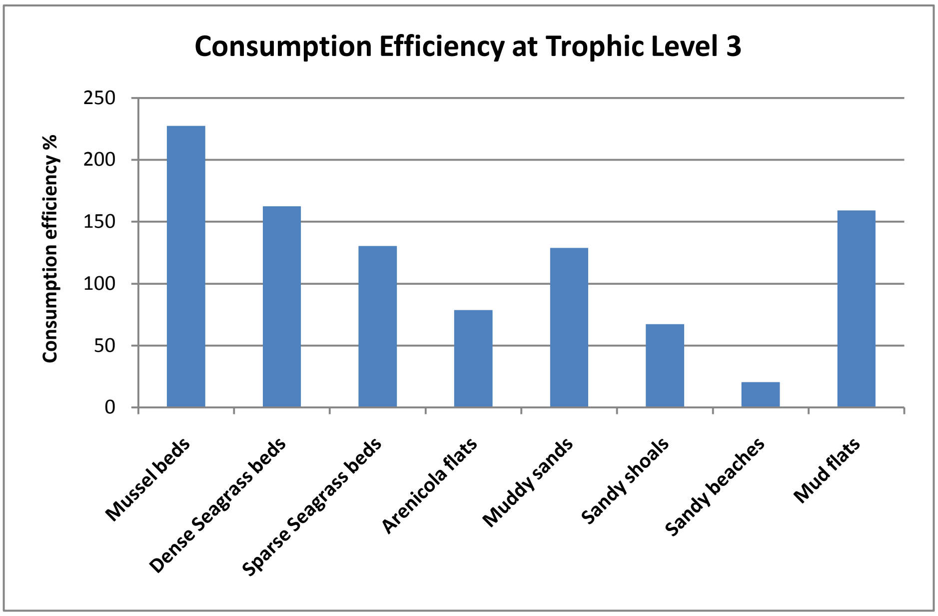


Fig. 21. Consumption efficiency at trophic level 3 of eight benthic communities in the Sylt-Rømø Bight.

The consumption efficiency of bacterivores has very high values indicating that this food source seems to be overexploited by their consumers, with the exception of sandy shoals and sandy beaches (Fig. 22a). In seagrass beds and muddy sand flats consumption of bacteria is three times higher than their production. In mussel beds, *Arenicola* flats and mud flats consumption efficiency of bacterivores ranges from 150% to 200%. This suggests that for most communities autochthonous bacteria production is not high enough to support the consumer guild of bacterivores. Bacteria production is not easy to measure and these measurements are subject to some bias, so that an underestimation is possible. Also, the estimation of bacterial contribution to the diet of many deposit feeders may include errors. However, it is obvious that even in those communities a deficit of bacteria as food is observed where the carbon import from outside is high. This may indicate that in addition to autochthonous bacterial production in the sediment, an import of bacteria, probably attached to organic detritus, probably contributes to the food requirements of bacterivorous macrofauna (Fig. 22b).

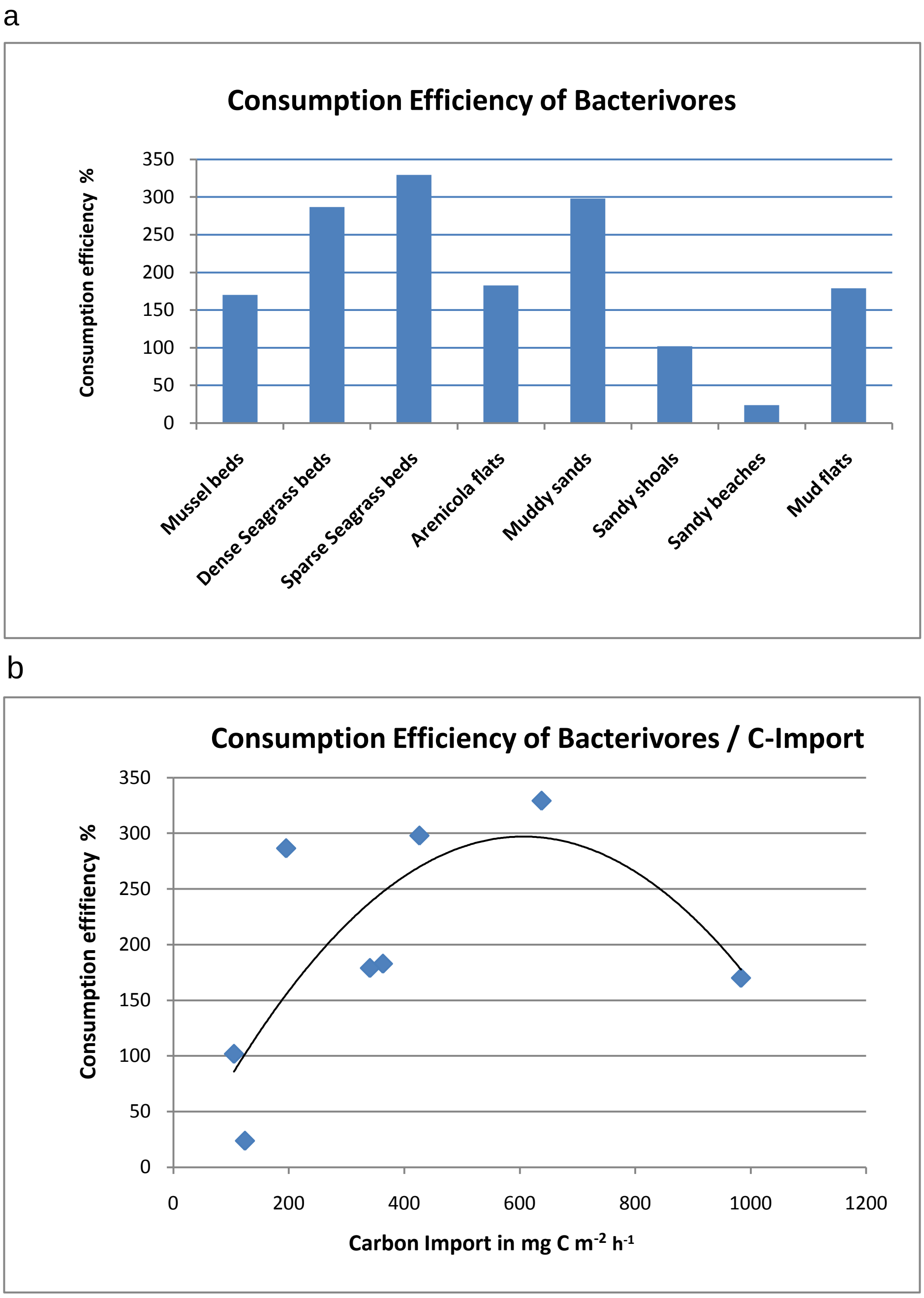


Fig. 22a. Consumption efficiency of bacterivorous macrofauna at trophic level 3 in eight communities of the Sylt-Rømø Bight. b. Consumption efficiency of bacterivorous macrofauna scaled versus carbon import into the different communities of the Sylt-Rømø Bight (Spearman rank coeff, log transformed of values without mussel beds: 0,82¸α=0,025).

Predation on non bacterial secondary producers can be estimated as the difference between total consumption at trophic level 3 and consumption of bacterivores.

Consumption efficiency of predators in mussel beds and mudflats show values higher than 100% (Fig. 23), indicating an overexploitation of the resources in both communities. In these communities we observe a high predation by birds on invertebrates. In mussel beds, Eider ducks (*Somateria mollissima*) consume more than the total production of *Mytilus edulis* each year, and other birds such as oystercatchers and herring gulls also contribute to this predation pressure. In mudflats there is a strong predation of shell ducks (*Tadorna tadorna*) on mud snails (*Hydrobia ulvae*). The strong predation pressure of birds on these communities may be a local effect in the Sylt-Rømø Bight, where mud flats and mussel beds are relatively small in relation to the total intertidal area of the bight. This may lead to a concentration effect of birds relying on these particular communities, and thus to an overexploitation of food resources that may influence also the standing stock of the particular prey populations.

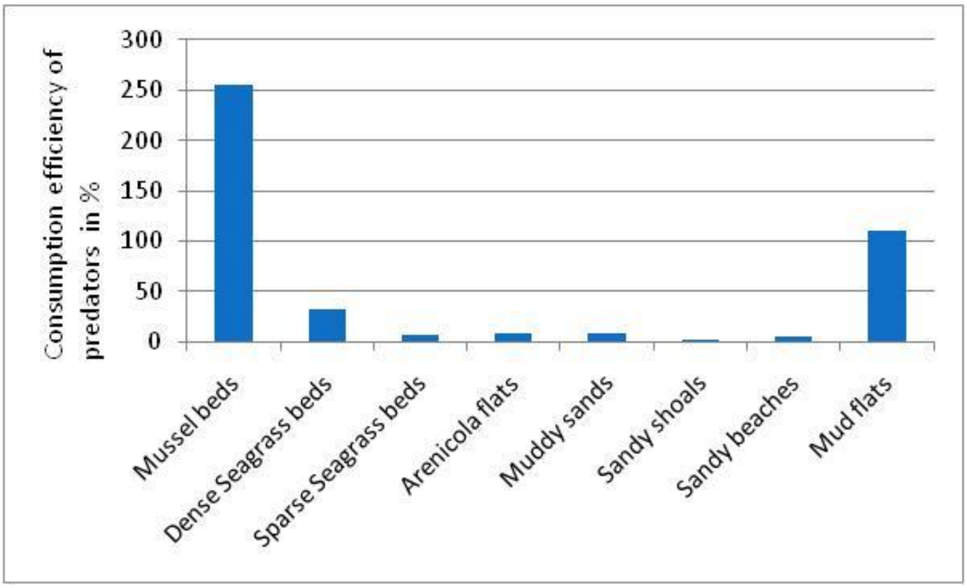


Fig. 23:. Consumption efficiency of predators at trophic level 3 in eight benthic communities of the Sylt-Rømø Bight.

At trophic level 4 consumption efficiencies range from 0.33% in mussel beds to 26.51% in *Arenicola* sand flats (Fig. 24). In mussel beds consumption at this level is dominated by fish such as the sea-scorpion *Myoxocephalus scorpius* and the cod *Gadus morrhua* feeding on shrimps. In sparse seagrass beds predation of small gobiids on small predatory polychaetes constitute a major energy pathway. In *Arenicola* sand flats, dense seagrass beds and sandy shoals, consumption is dominated by the large predatory polychaete *Nephthys* spec. feeding on smaller predatory polychaetes. The main trophic flow at this level in muddy sands is the feeding of mallards on *Nephthys.* In mud flats and in sandy beaches the main trophic flow is formed by *Nereis* feeding on smaller predatory polychaetes.

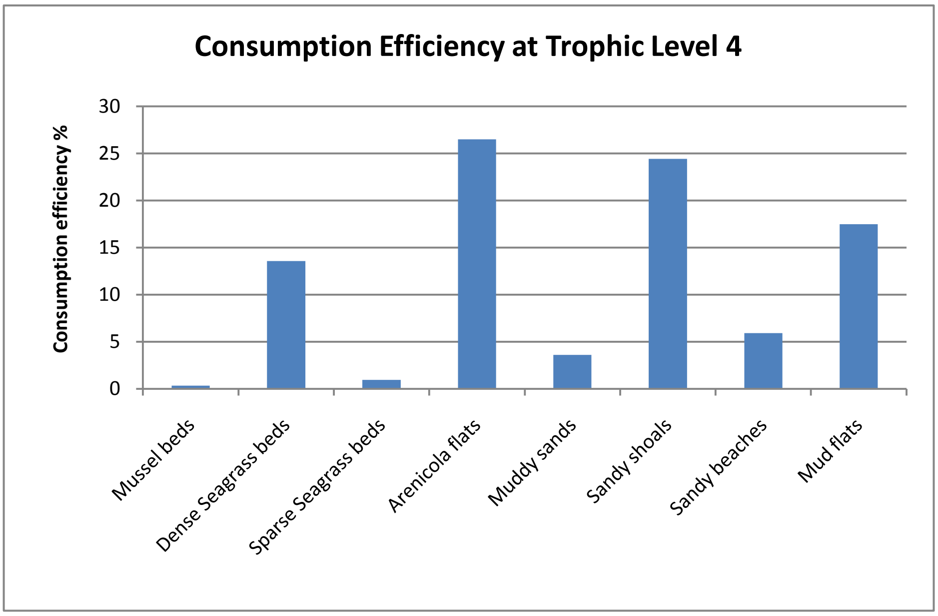


Fig. 24. Consumption efficiency at trophic level 4 of eight benthic communities in the Sylt-Rømø Bay.

The consumption efficiency of top carnivores is highest among invertebrates, low when the main trophic interaction is the feeding of birds on invertebrates, and less when fish feed on invertebrates. This trend in the consumption efficiency is more an effect of mass relations because of decreasing predator density from invertebrates to fish in relation to the production of their prey than on individual conversion rates of food.

Seals, piscivorous fish and birds contribute also to the consumption at level 4. However, they are not included in the food web of this study because they feed on a much wider spatial scale and it is therefore not appropriate to relate their consumption to the level of the communities investigated here.

ii. Assimilation efficiency

Assimilation efficiency is the percentage of the food energy taken into the guts of consumers in a trophic compartment that is assimilated across the gut wall and becomes available for incorporation by anabolism. Assimilation efficiency is defined as $AE=A_n/I_n*100$, where A_n is the food energy or material that is assimilated across the gut wall at a certain trophic level, and I_n is the percentage of productivity that is actually consumed at one trophic level .

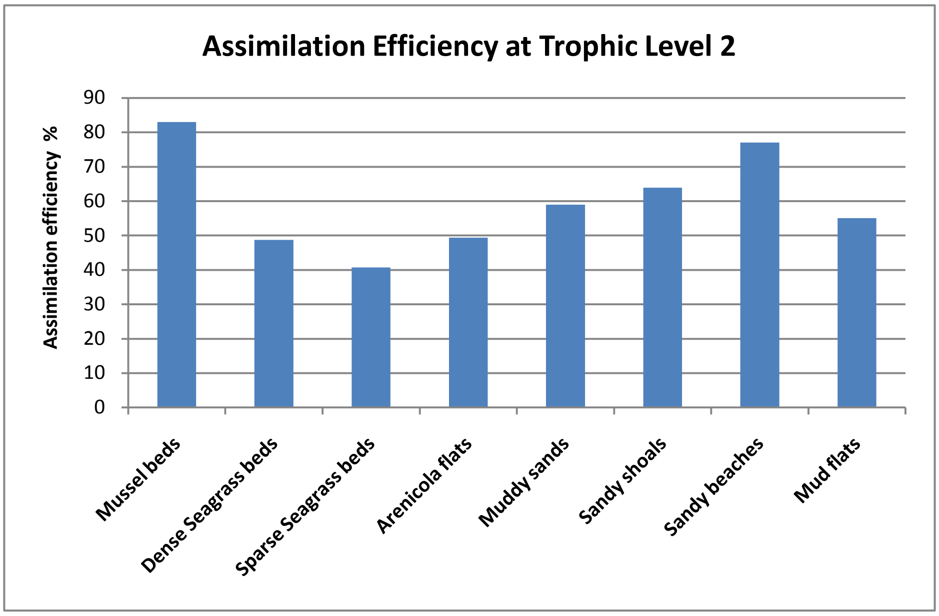


Fig. 25. Assimilation efficiency at trophic level 2 of eight intertidal communities of the Sylt-Rømø Bight.

At the trophic level 2 the assimilation efficiency is highest in mussel beds and lowest in seagrass beds (Fig. 25). In general the assimilation efficiency is low for herbivores, detritivores and microbivores, because animals are poorly equipped to deal with dead organic matter and living vegetation. The assimilation efficiency of secondary producers is thus surprisingly high in the investigated communities ranging from 83% in mussel beds to 41% in sparse seagrass beds. This can be explained that the assimilation efficiency of bacteria, which is assumed to range from 80 to 100%, is also taken into account at trophic level 2. Thus the high assimilation efficiencies correspond to the high bacterial consumption in relation to total consumption (Fig. 26).

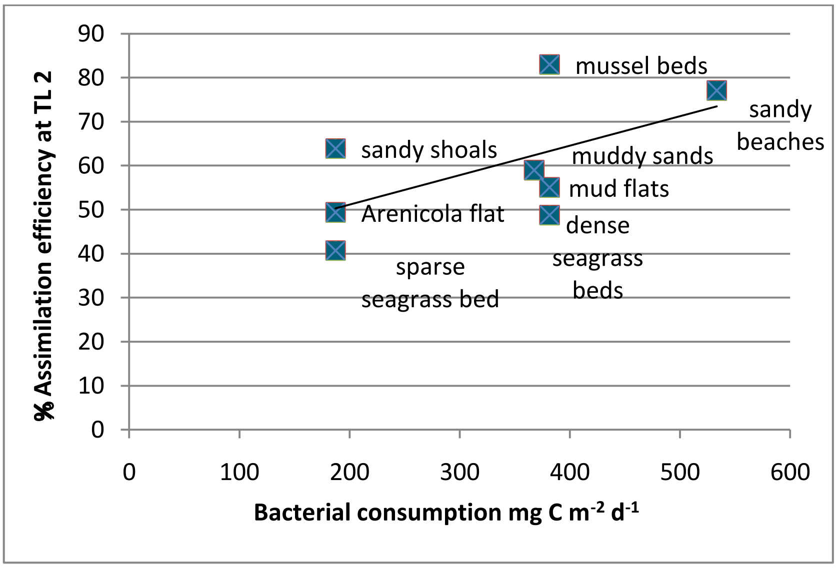


Fig. 26. Assimilation efficiencies versus bacterial consumption of eight intertidal communities of the Sylt-Rømø Bight (tendency, n.s.).

The assimilation efficiency ranges between 28% in sparse seagrass beds and 78% in mussel beds for predators at trophic level 3. Also, assimilation efficiencies for individual predators are around 80% at this level in intertidal mussel beds and sandy beaches whereas this efficiency is comparatively low at other communities where it fluctuates between 28 and 51% (Fig. 27).

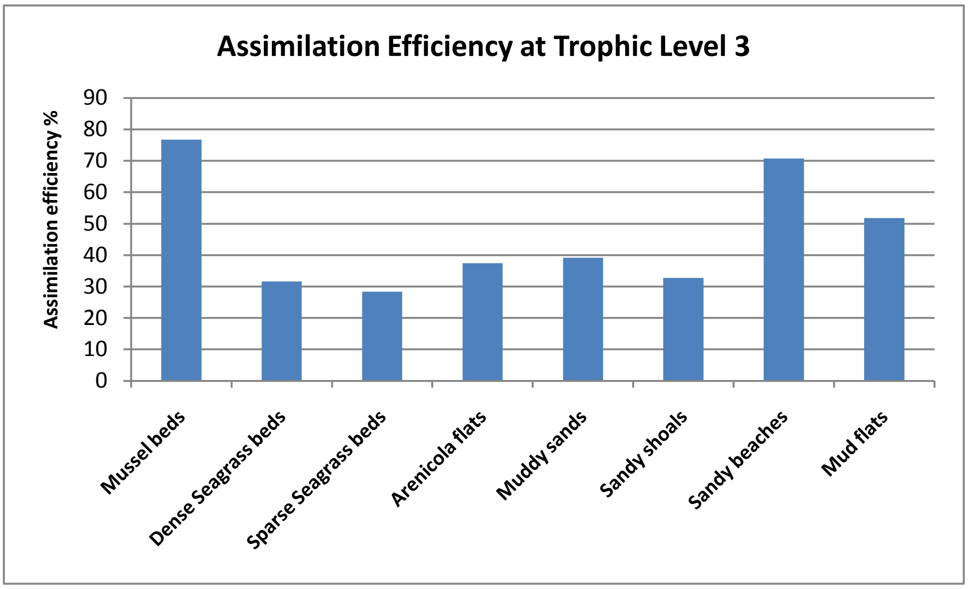


Fig. 27. Assimilation efficiencies at trophic level 3 of eight intertidal communities of the Sylt-Rømø Bight.

The assimilation efficiency at the trophic level 3 is negatively correlated with increasing consumption of bacterivores (Fig. 28). Comparable to herbivores, bacterivores have low assimilation efficiencies of about 20 – 50%, whereas carnivores show higher efficiencies of up to 80%. Mussel beds and sandy beaches show high assimilation efficiencies at this trophic level through the dominance of carnivore predators and a small share of bacterivores.

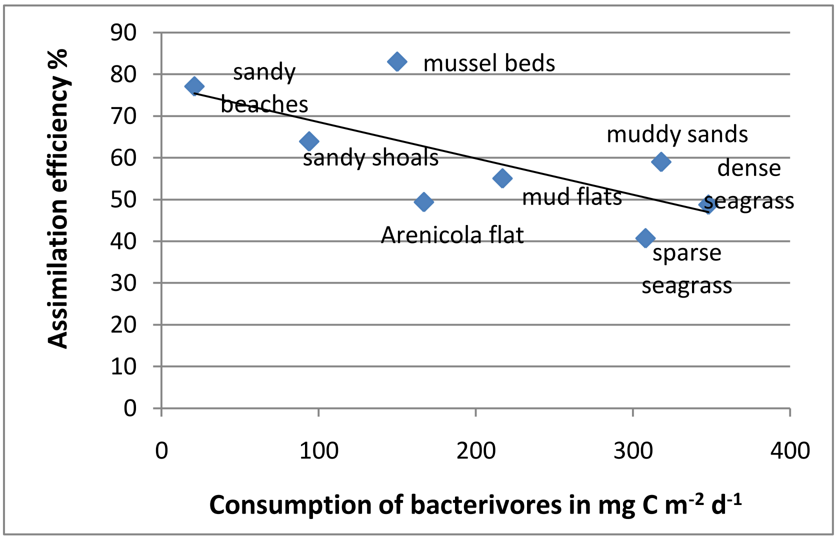


Fig. 28. Negative correlation between assimilation efficiency at the trophic level 3 of eight intertidal communities and consumption of bacterivores in a community (Spearman rank corr. coeff.: r =-0.71, α<0.025).

In general individual assimilation efficiencies at trophic level 4 are in the same order of magnitude as at trophic level 3 (Fig. 29). At the community level the species composition changed but in some communities there is a shift in dominance from invertebrate predators to vertebrate predators. At trophic level 4 half of the communities reveal higher assimilation values than 40%, such as mussel beds, sparse seagrass beds, muddy sands and mudflats (Fig. 29). With the exception of mud flats, these communities are dominated by vertebrate predators, such as fish in mussel beds and sparse seagrass beds and birds in muddy sand flats. Low assimilation efficiencies at this level may be a consequence of the dominance of invertebrate predators that have probably lower assimilation efficiencies, while some of them feed only partly at this trophic level, as for example *Nereis diversicolor*.

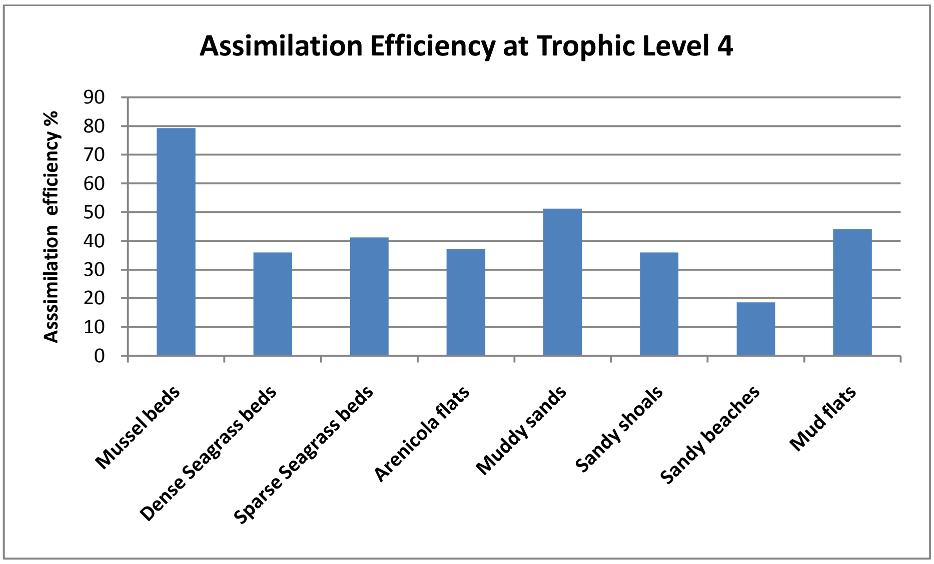


Fig. 29. Assimilation efficiency at the trophic level 4 of eight intertidal communities of the Sylt- Rømø Bight.

iii. Production efficiency

The production efficiency (PE) is the percentage of assimilated energy that is incorporated into new biomass. The remainder of energy is spent into metabolic processes and is subsequently lost as respiration heat. Energy rich secretory or excretory products which have taken part in the metabolic processes may be viewed as part of production.

Production efficiencies vary mainly according to the taxonomic class of organisms concerned. Invertebrates in the Sylt-Rømø Bight in general have high efficiencies (30 – 40% to as high as 80%), losing relatively little energy in respiratory heat and converting more assimilated energy to production. Among the vertebrates, ectotherms have intermediate values for production efficiency (around 30%) whilst endotherms, with their high energy expenditure associated with maintaining a constant body temperature, convert only 2-3% of assimilated energy into production. Small bodied endotherms have the lowest efficiency. On the other hand microorganisms, including bacteria, protozoa and meiofauna tend to have high production efficiencies.

At the community level the production efficiency reflects the potential of a community for biomass production. Thus it is increasing with the heterotrophic P/B –level of the community and decreases with community respiration. In Fig. 30a the production efficiency is illustrated for the second trophic level. The correlation with heterotrophic P/B – level is only weak at trophic level 2 (Fig. 30b), while the correlation with community respiration is high (Fig. 30c).

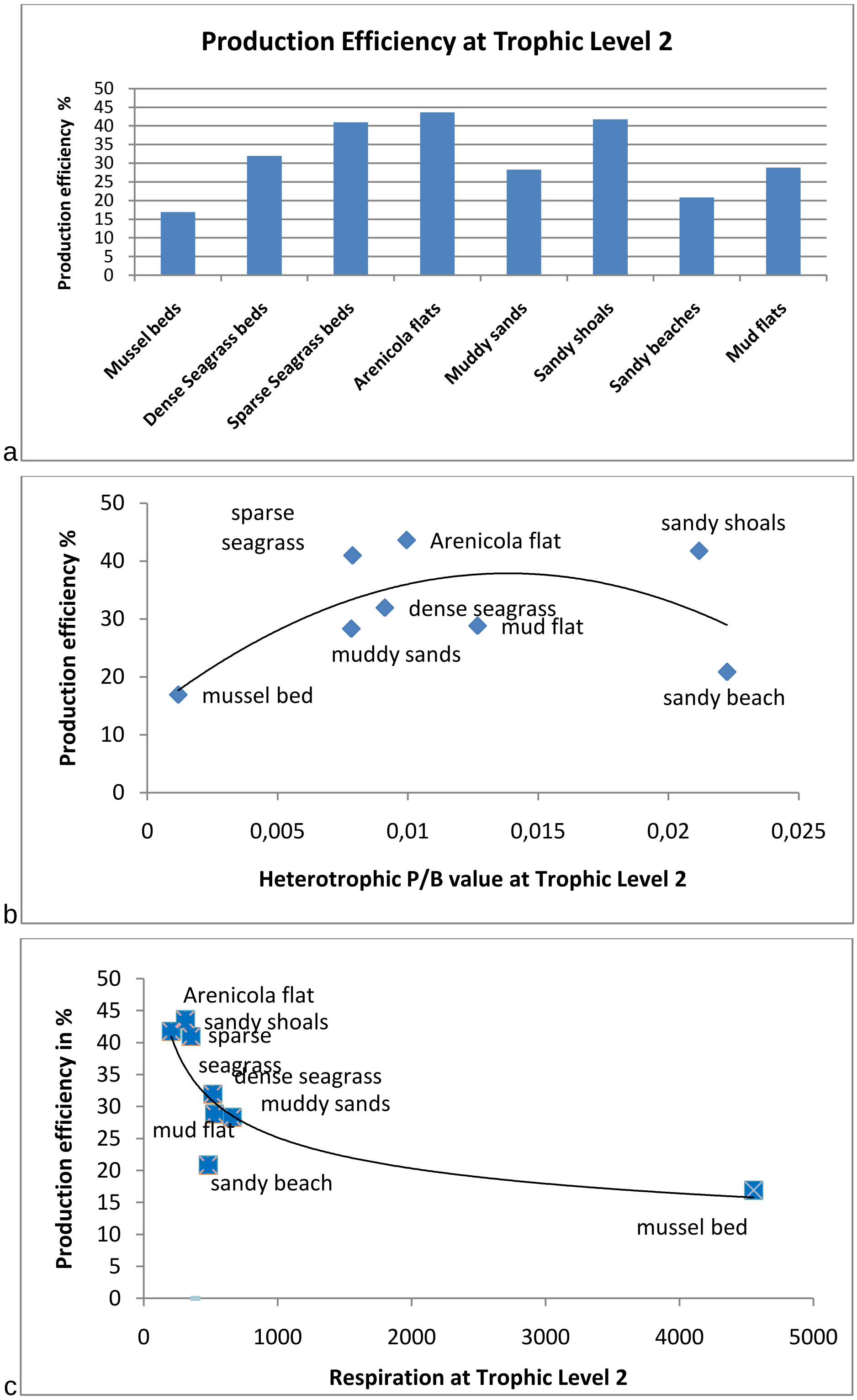
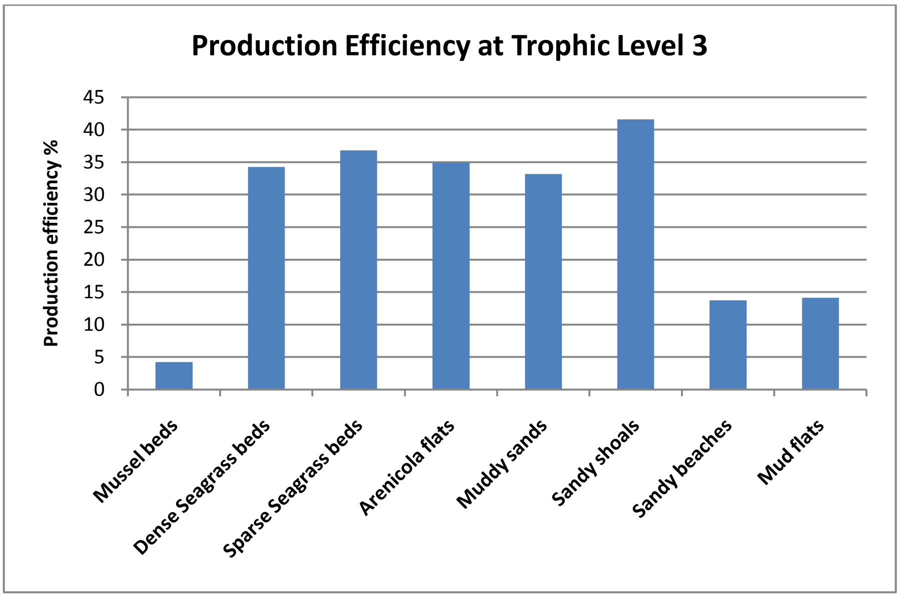


Fig. 30. a. Production efficiency of primary consumers in eight intertidal benthic communities of the Sylt-Rømø Bight. b. Correlation of production efficiency at trophic level 2 of eight intertidal benthic communities of the Sylt-Rømø Bight with b. heterotrophic P/B-value (n.s.) and c. respiration (at the same level) (Spearman rank corr. coeff.: -0.83, α<0.01.)

The production efficiency seems to be strongly influenced by the species composition of a community, because at trophic level 2 individual PE´s show a high variability from less than 10 to 80% due to the particular species in the community.

At higher trophic levels the variability of production efficiency within taxonomic groups is lower, but distinctly different between them (Fig. 31a, b). At level 3 and 4 the highest production efficiencies are found when macrobenthic species dominate the trophic level, whereas production efficiencies are small when birds form the dominating group or have a large share in production.

a



b

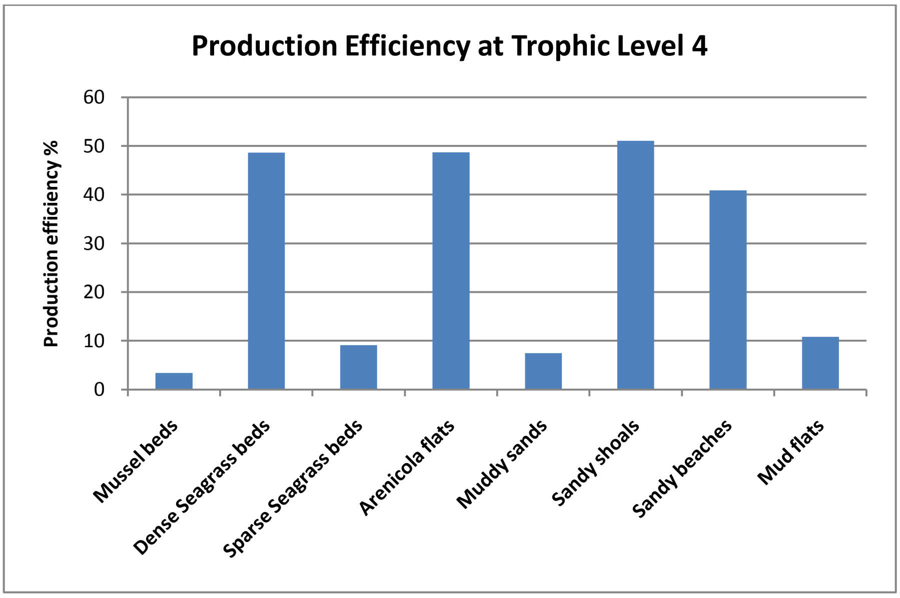


Fig. 31a. Production efficiency of eight intertidal benthic communities in the Sylt-Rømø Bight for the third trophic level. b. Production efficiency for the fourth trophic level.

iv. Trophic efficiency

The overall trophic transfer efficiency (TTE) indicates how much of the production at a certain trophic level ends up in the production of the next trophic level. In the years after Lindeman's paper (1942) it has been assumed that trophic efficiencies average at around 10%. A compilation of trophic efficiencies of different freshwater and marine systems revealed a range of 2 to 24% although the mean was 10.13% ± 0.49 (Pauly & Christensen 1995). In the investigated communities of the Sylt-Rømø Bight the arithmetic mean of trophic transfer efficiencies (integrated over trophic levels 2-4) derived from Network analysis is 8.13% ± 3.21 (Fig. 32).

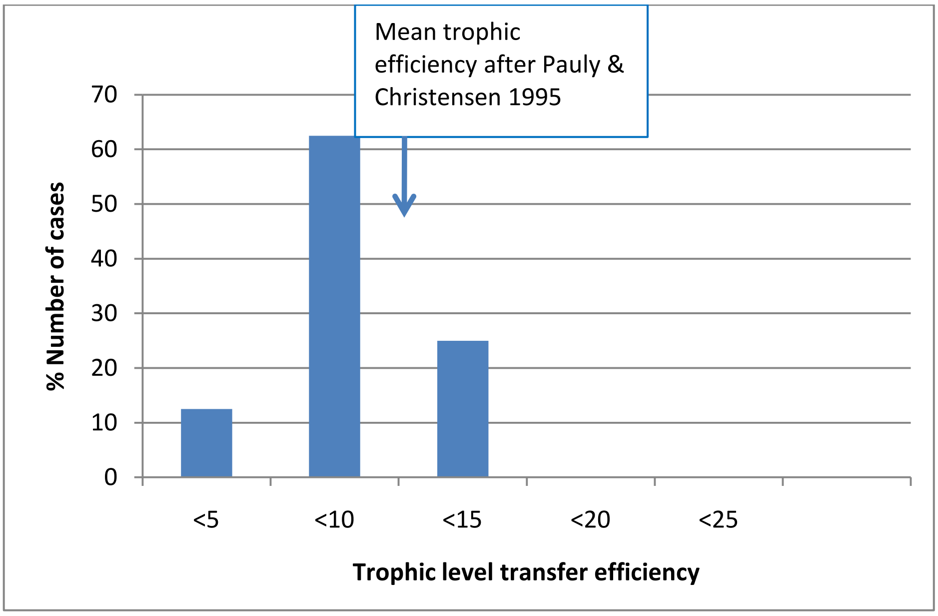


Fig. 32. Frequency distribution of trophic level transfer efficiencies of 8 intertidal benthic communities of the Sylt-Rømø Bight. The mean is 8.13% ± 3.21 (n= 8), which is less than 10.13% ± 0.49 that was estimated by Pauly & Christensen (1995) for 42 different freshwater and marine systems.

Highest trophic transfer efficiencies are found between trophic level 1, the primary producers and trophic level 2, the herbivores, detritivores and bacteria (Fig. 33). Mussel beds incorporate up to 30% of available primary production into the trophic level of secondary producers. This is an unusual high value, although autochthonous primary production in this community is dominated by the production of *Fucus vesiculosus* which is hardly used by the secondary producers of this community. However, this value considers already an auxiliary phytoplankton and detritus input which is computed on the basis of the requirement of the suspension feeders.

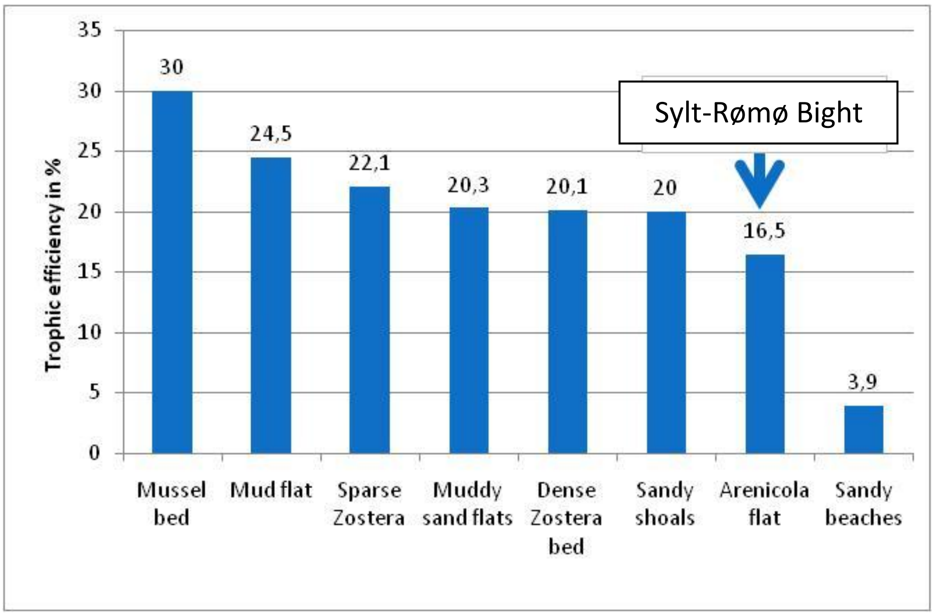


Fig. 33. Trophic transfer efficiencies between primary and secondary producers of eight intertidal benthic communities in the Sylt-Rømø Bight. Trophic transfer efficiency of the total bight ecosystem is indicated by a blue arrow.

Trophic transfer efficiencies (TTE) of most other communities are high and indicate the tight coupling between phytoplankton production and production by suspension feeders as well as detritus decomposition by bacteria. In the *Arenicola* sand flats the TTE is 16.5% which corresponds with that of the total bight system, derived from network analysis and underlines the dominance of this extended community to the total system. In sandy beaches the TTE is very low due to low consumer biomass and activity in relation to primary production.

Between the secondary producers and the tertiary producers (i.e. between trophic levels 2 and 3) the TTE decreases rapidly compared with that between levels 1 and 2 (Fig. 34). This is due to the high detritus production within this level, which reflects the low assimilation efficiency of the bacterivores that predominate at this trophic level. Highest transfer efficiencies were calculated for the mud flats, sandy beaches, sandy shoals and mussel beds, where the predation of invertebrate predators is high. Here the assimilation efficiency and production efficiency are also higher and thus the increase in trophic transfers. In muddy sand flats, the *Arenicola* flats, and both types of seagrass beds the TTE is very low, mainly because of the high abundance of bacterivores with a low assimilation efficiency, and thus low production compared to consumption. The trophic transfer efficiency for the total bight is 1.6% which is higher than that of the *Arenicola* flat at 0.9% and the seagrass beds at 0.7 and 0.6, respectively.

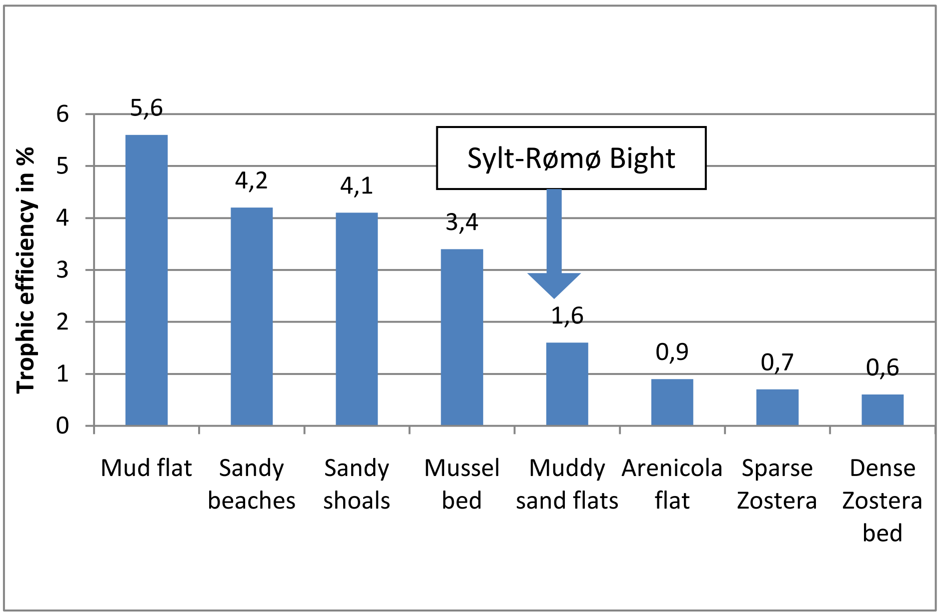


Fig. 34. Trophic transfer efficiency of tertiary producers estimated by network analysis of eight intertidal benthic communities of the Sylt–Rømø Bight. Trophic transfer efficiency of the total bight ecosystem is indicated by a blue arrow.

Trophic transfer efficiencies of trophic level four are higher by a factor 2-3 compared with tertiary producers for mussel beds but also for dense seagrass beds and muddy sands. This can be mainly explained by the higher assimilation and production efficiency of the top carnivores determining this trophic level compared to the mixed assemblage of bacterivores and carnivores at trophic level 3. In some communities this level is dominated by vertebrate predators such as cod and sea-scorpions in mussel beds, which have a high assimilation and a medium production efficiency, but have a low consumption due to their low biomass at community level (Fig. 35). In sparse seagrass beds as well as *Arenicola* sand flats the TTE in tertiary and quaternary producers is quite similar. In sandy beaches, sandy shoals and mud flats, TTE is lower than in level 3.

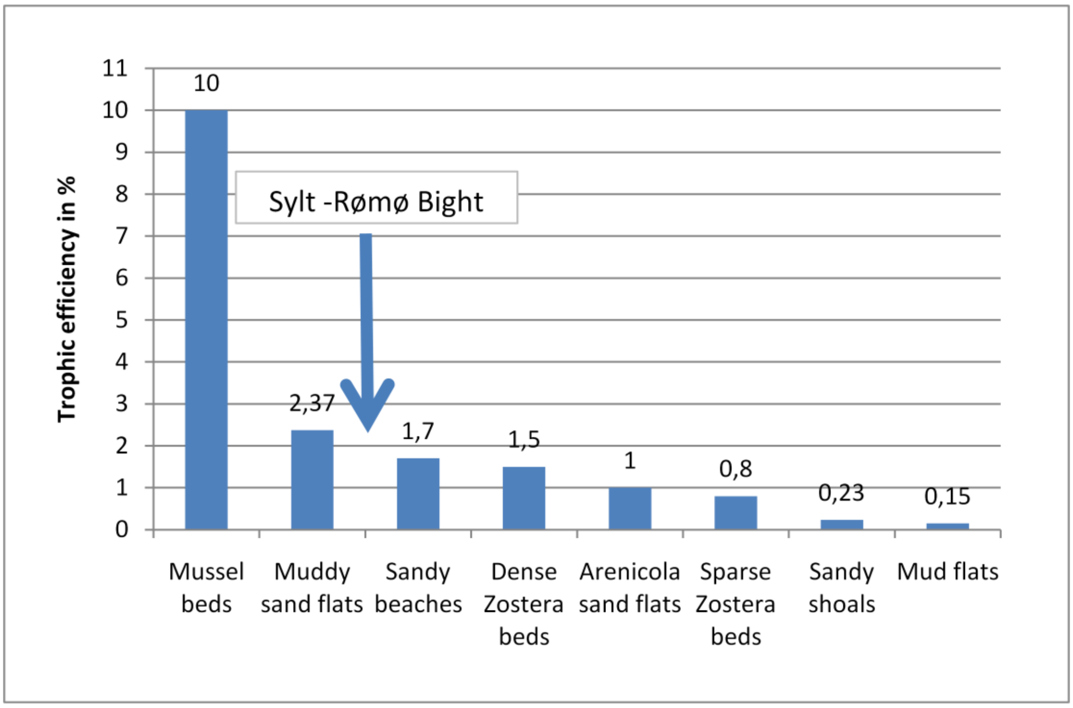


Fig. 35. Trophic transfer efficiency of quaternary producers estimated by network analysis of eight intertidal benthic communities of the Sylt–Rømø Bight. Trophic transfer efficiency of the total bight ecosystem is indicated by a blue arrow.

There are also large differences in the energy flow on a per meter square basis. The energy flow of the total bight is the sum of the contributions of the different communities. If the areal extent of the constituent habitats and communities are considered (Baird, Asmus & Asmus 2007) the percent production of, for example the *Arenicola* sand flats, is only 7.5% on a per meter square basis, but their contribution to the production of the total bight is 83.6%. Mussel beds, on the other hand, produce 41.5% on a per meter square basis but their contribution to the total production of the bay is only 1.8%.

b. Exchange processes - sink and source function

In the Wadden Sea, communities contribute differently to pelagic-benthic as well as to benthic-pelagic exchange due to physical factors such as currents or biological factors such as population density of plants and animals and their species specific potential for exchange. In some of the investigated communities, such as mussel beds, dense seagrass beds, *Arenicola* sand flats, muddy sands and mud flats, the import of carbon exceeds its export (Fig. 36). These communities together represent about 88% of the intertidal area of the SRB. Mussel beds show the highest net import of carbon followed by dense seagrass beds, *Arenicola* sand flats, muddy sands, as well as mud flats reveal a similar range.

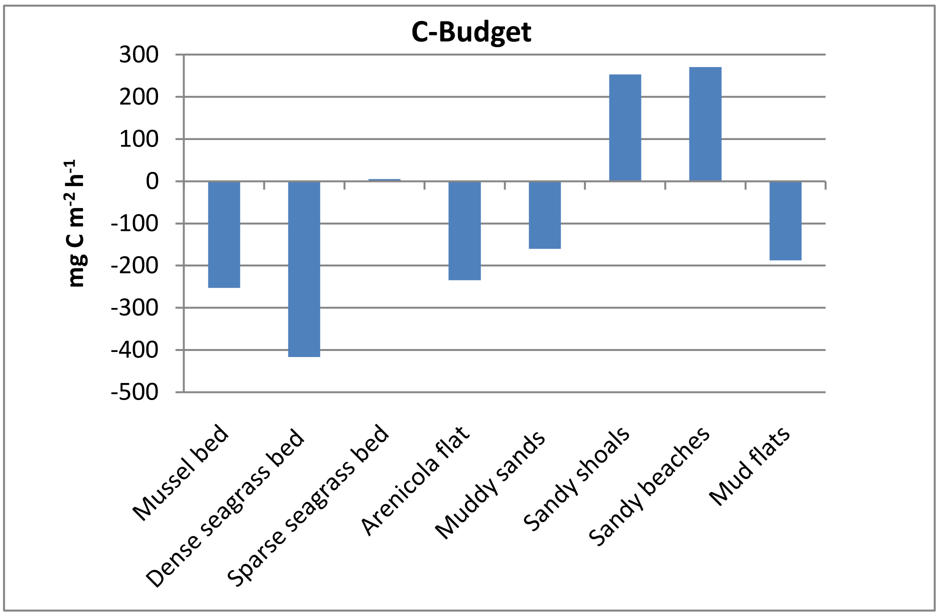


Fig. 36. Carbon budget for 8 intertidal communities of the Sylt-Rømø Bight in mg carbon per meter square per hour. Positive values represent net carbon exports, negative values net imports into the community.

In the *Arenicola* sand flats, muddy sands and mud flats, most of the carbon import is due to abiotic sedimentation of particles from the water column (Fig. 37a) with 70%, 59% and 49%, respectively, of the total particle uptake from the water column on these three communities. In dense seagrass beds and mussel beds the passive sedimentation is about 42% and 31%, respectively and thus the major part of the carbon uptake in these communities is due to biological processes, such as filtration of particles.

Resuspension and erosion of particles is the dominant abiotic process in exposed communities such as sandy shoals, sandy beaches and sparse seagrass beds (Fig. 37b).

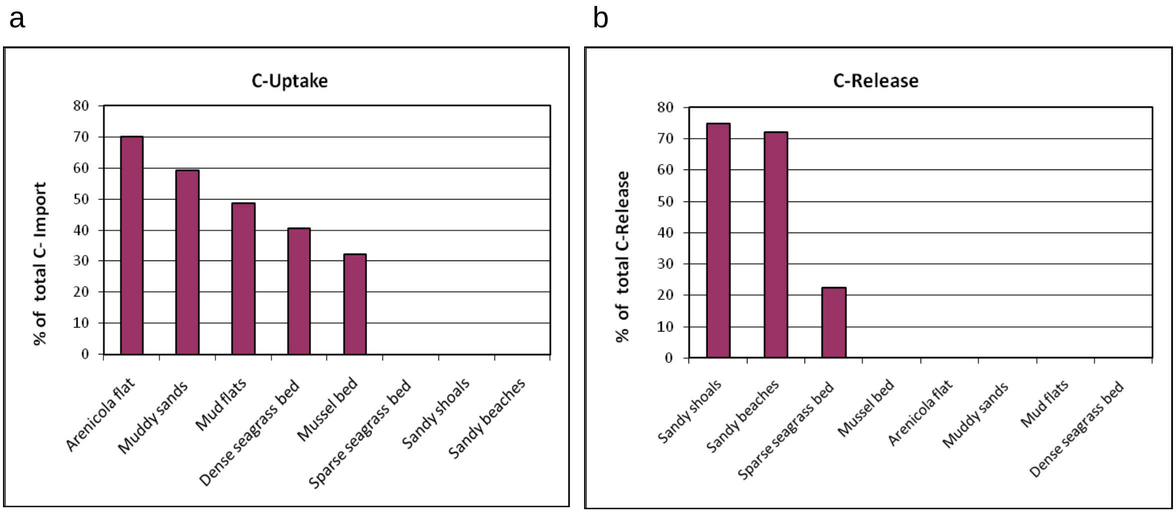


Fig. 37a. Carbon uptake due to sedimentation of particles and b. carbon release due to resuspension and erosion of particulate carbon in 8 intertidal communities in the Sylt-Rømø Bight.

Uptake of suspended detritus, bacteria, phytoplankton and zooplankton can be roughly subsumed to characterize the filtration potential of the community. Mussel beds have the highest filtration potential on a meter square basis, followed by dense seagrass beds. All other communities show a lower filtration potential by an order of magnitude. Mussel beds are characterised by a large biomass of the suspension feeding bivalve, *Mytilus edulis,* dominating this community with filtration rates of about 240 mg C m^{-2} h^{-1} (Fig. 38a). In seagrass beds filtration by the bivalve *C. edule* attains 170 mg C $m^{-2}h^{-1}$. Although mussel beds surpass the filtration potential of most other communities on a per meter square basis, they have only an impact of 2% on the filtration potential of the total SRB due to their relatively low areal cover of 0.36 km^2 (Fig. 38b). Because dense seagrass beds have an areal cover of 10.77 km^2 and a high filtration potential on a per meter square basis, they attain 45% filtration potential of the total Bight. The *Arenicola* sand flats have a relatively low filtration potential on a per meter square basis but they have the largest areal coverage of 67% and thus they contribute at 44% to the filtration potential of the total bight compared to other much smaller habitat communities whose collective filtration potential range between 0.3 to 5% (Fig. 38b).

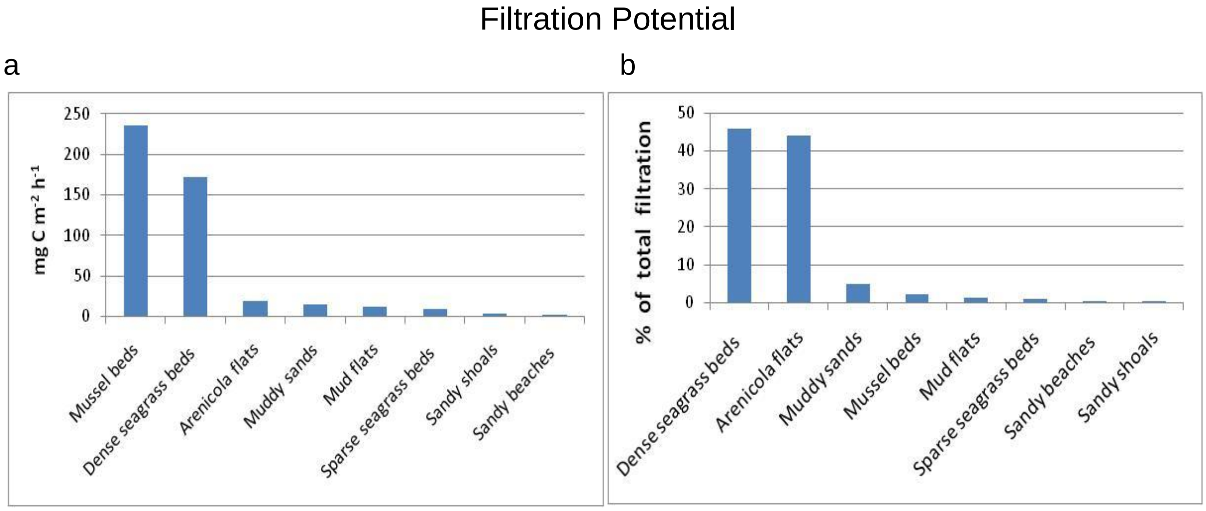


Fig. 38a. Filtration potential (sum of uptake of detritus+phytoplankton+bacteria+zooplankton by organisms) of 8 intertidal benthic communities of the Sylt-Rømø Bight on a per square meter basis. b. Community contribution to the total filtration potential of the Sylt-Rømø Bight.

We may therefore ask whether the intertidal part of the Wadden Sea acts as a biological filter or as a sedimentation area. The answer is that the intertidal region of the Sylt- Rømø Bight as portrayed in this thesis acts as a sedimentation area, because 87% of the carbon input is due to sedimentation processes and only 13% is contributed by biological filtering. This may have been reversed in the past when up to 70% of the intertidal flats have been covered by seagrass beds. The future situation may be also altered because of the introduction and establishment of alien filter feeders, such as *Crassostrea gigas* and *Crepidula fornicata.* These species may have increased the filtration potential and have definitely increased the areal cover of communities dominated previously by other suspension feeding organisms.

On the other hand the carbon input is dominated by the abiotic settling of detritus particles which is entirely dependent on the physical forces such as currents and waves. 87% of the carbon input is thus sensitive to changing weather conditions, whereas the biological filtration is more stable, in that suspension feeding can also take place when water movements do not allow the settling of particles.

Sparse seagrass beds, sandy shoals and sandy beaches show an increasing tendency for carbon loss (Fig. 37 b). In sandy shoals and sandy beaches most of this release of carbon is due to abiotic processes induced by the high hydrodynamics over these communities. In sparse seagrass beds biological release processes such as export of organisms by drift and respiration processes prevail with 77% of the total carbon release.

Within a benthic community settlement of postlarval stages of macrobenthos after metamorphosis are rarely considered as a contribution to mass balance of a benthic system, but are mainly seen to contribute to population dynamics of single species (Troost et al. 2009). Therefore results of the biomass of settling stages are hardly published. In these few studies (Beukema 1974; Starr et al. 1990; Beukema et al. 1998, 2001; Schürmann 1998; Bos et al. 2006) the biomass of estimated spat fall for North Sea bivalves, gastropods and polychaetes is about of 40% of the parental on a yearly average. This is a very rough benchmark that I have chosen for computing settling processes for the communities of the Sylt-Rømø Bight (Fig. 39). Although this can be considered as a maximum value, on an hourly rate this yearly average is very small ranging from 0.1 mg C m^{-2} h^{-1} in sandy shoals to 1.7 mg C m^{-2} h^{-1} in mussel beds. It seems to be negligible compared to other processes such as filtration or carbon fixation by photosynthesis. However, these processes occur only during a limited time period of several days to weeks and during this time settlement processes can dominate other processes.

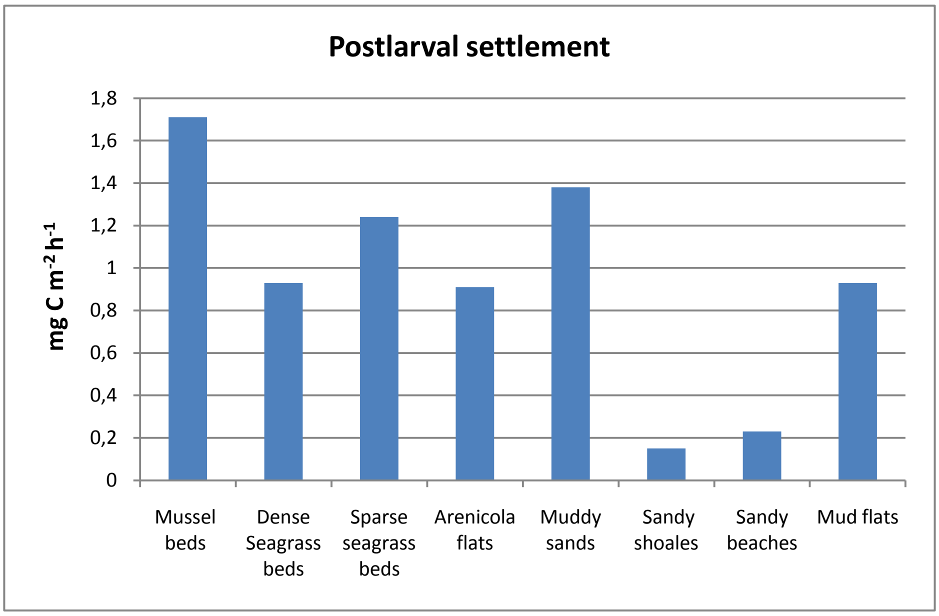


Fig. 39. Postlarval settlement of macrobenthic animals in eight communities of the Sylt-Rømø Bight.

After settlement a substantial part of postlarval macrobenthos can again leave the sediment and is drifting within the water column. It has been estimated that biomass of drifting animals is conspicuous (Armonies 1992; 1998). However, it has not yet been quantified as a rate in terms of biomass per m^{-2} and day^{-1}, it could be shown that drifting is more an active process, intended by the juvenile animals to change the place of settlement at low water currents by means of special floating mechanisms such as slime rafts. Because drifting is in the same order of magnitude than settling after drifting at a suitable place there should be a balanced budget for drifting and settling per community and it is therefore assumed that these processes do not influence the material budget in the course of a year. However, exchange of biomass between water and sediment can reach significant values during short term events. We assume in this study that drifting is more or less balanced at the scale of the community and year, although it can lead within the community to large redistribution of biomasses. Using drifting values after Armonies (1998) we made an assessment of rates which is shown in Fig. 40.

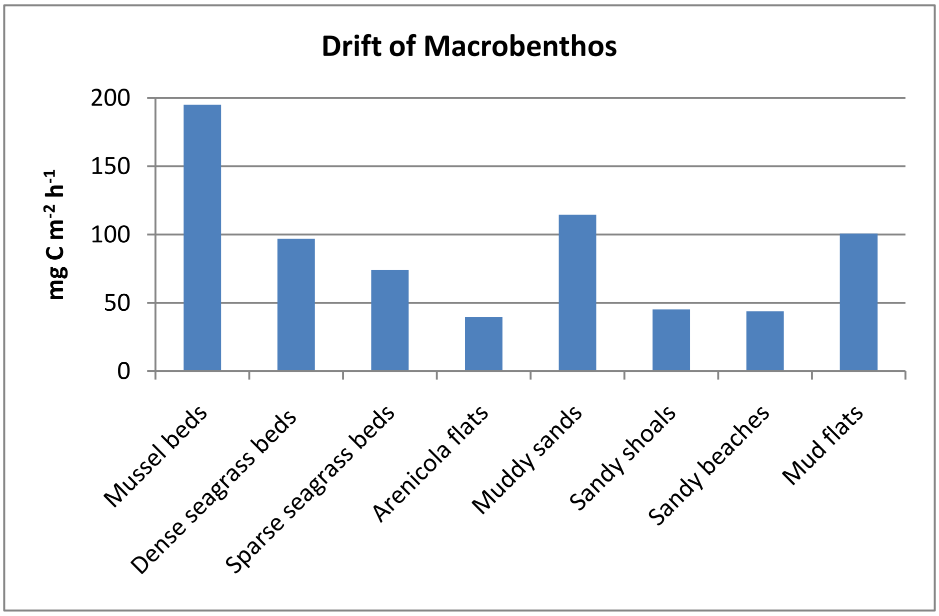


Fig. 40. Drift of macrobenthic animals from the sediment into the water column for eight benthic communities calculated after values from Armonies (1992; 1998). The settlement after drifting is assumed to be in the same order of magnitude.

Sandy bottoms animals (e.g. *Arenicola* flats, sandy shoals and sandy beaches) show a lower tendency of drifting compared to organisms occurring in muddy areas (Armonies 1992; 1998). The drifting process seems to be negatively correlated with the water movement, which is higher above sandy substrates compared to muddy bottoms. This is underlined by the fact that drifting is an active process, and during higher currents and turbulence animals “wait “ in the sediment until the water movements are lower and the drifting process can be initiated. Drifting seems to be also the response of intertidal settled macrobenthos on unfavourable feeding or other environmental conditions at the place of first settlement.

There are large variations in carbon fixation of the different communities due to macrophyte coverage (Fig. 41). Mussel beds and seagrass beds show the highest carbon fixation rate whereas sand and mud bottoms show only slight variations between 40 and 50 mg C $m^{-2}h^{-1}$. In mussel beds macrophytes are the dominant component, however macroalgal cover varies due to location of the mussel bed, especially exposed beds show less or no algal coverage. For the present study algal coverage was estimated to be 50% of the total mussel bed area.

In seagrass beds the leaf surface of seagrass plants provides additional space for microphytobenthos. In tropical seagrass beds the available space for microphytobenthos has been estimated to reach 20 times the value of that of unvegetated bottoms in tropical areas but about 6% in temperate areas (Couchman 1987; Hily & Bouteille 1999). Although this value will be lower in the *Zostera noltii* bed of the Wadden Sea, there is still a high spatial availability compared to pure sand and mud bottoms. Although the macrophytobenthic biomass in sparse seagrass beds is only half of that in dense seagrass beds, CO_2 fixation seems to be only slightly lowered. Sparse seagrass beds have only half the grazer biomass that control microphytobenthic biomass because of higher current velocity that flushes the small sized grazers (Schanz et al. 2002). This cascading effect allows a higher biomass and production of epiphytes in sparse seagrass beds that compensates nearly for the loss of macrophytes.

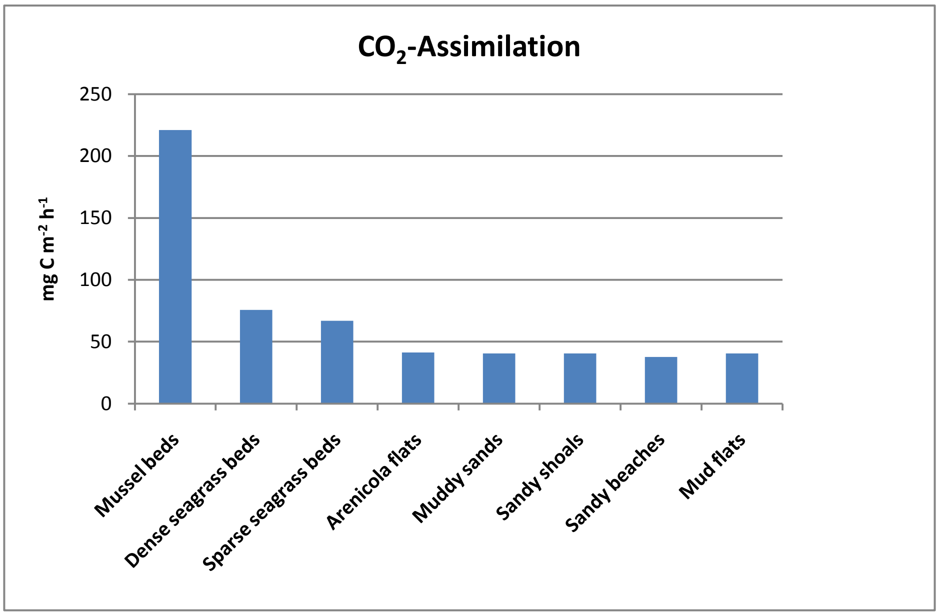


Fig. 41. CO_2-assimilation by benthic primary producers in eight different benthic communities of the Sylt-Rømø Bight.

Although mussel beds show the highest CO_2 fixation rate among the communities of the Sylt-Rømø Bight, the DIC budget shows a distinct net release of CO_2 by the high respiration of the faunal and bacterial assemblages (Fig. 42). In muddy sands there is also a net release. In most other communities the benthic primary production surpasses respiration and these communities act as distinct sinks for DIC within the course of a year. Especially seagrass beds have a high net carbon uptake. These communities act as carbon sinks and oxygen donors. Most of the carbon assimilated by plants is entering the detritus chain of the community where it is partly recycled and reassimilated during the whole vegetation period. These active carbon fixation and subsequent intra-community recycling that occur within the vegetation period surpass the low carbon fixation rates in winter, when no above surface biomass of macrophytes is present and the compensating respiration processes are also low. In addition the carbon fixation of microphytobenthos starts already in February and ends late in autumn whereas seagrass and also its epiphytes show a less long period from April to September.

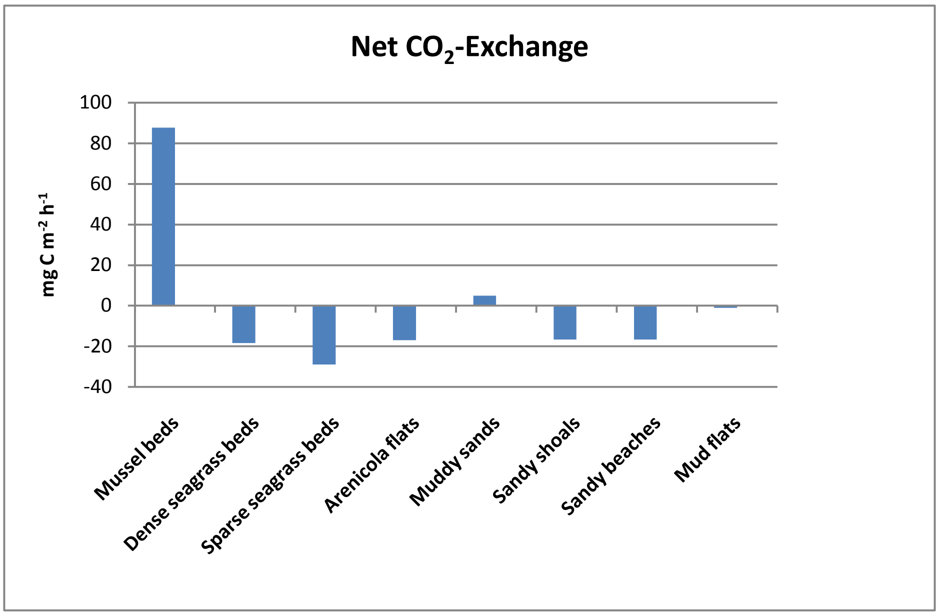


Fig. 42. Net CO_2-exchange in eight different benthic communities of the Sylt-Rømø Bight. Negative values indicate a net uptake of CO_2, positive values a net release.

c. Trophic structure of the food web

The trophic structure of a community has been characterised by the Lindeman Spine which is a concatenated form of the entire food web showing discret trophic levels and the connecting consumption flows. The Lindeman Spines for all communities of the Sylt–Rømø Bight are shown in chapter 4 (Figs. 8-15). While in mussel beds, *Arenicola* flats and sparse seagrass beds the main flow of energy and material is via the grazing food web, the other five communities canalize the main amount of material from the detritus pool to bacteria and detritus feeders to higher trophic levels. In the grazing based food webs suspension feeders have a higher share compared to grazers using microphytobenthos or macrophytes as a food source. The division into grazing food chain and detritus food chain is sometimes artificial, because particularly marine species use both food sources while in terrestrial systems there is a larger specification into both groups. With respect to mussel beds two of the secondary producer compartments use only living plants and five only detritus material while four species use both food sources. Suspension feeders consume phytoplankton as well as suspended particulate detritus, although with the focus on phytoplankton. There occur some selective mechanisms in mussels to discriminate detritus in favour of phytoplankton (Zemlys et al. 2003; Zemlys & Daunys 2005). On the predator level the detritus and grazing food chain is mixed up, because predators use both organism groups. However, a rough quantitative difference can be drawn to show which of both main food chains is more important in supporting the community (Fig. 43). In case of mussel beds the major part of carbon flow is transferred via the grazing food chain to higher trophic level, while detritus feeders support most of the diversity of the system including fish and crabs that play a minor part in carbon flow. The main part of primary production in this community is due to macrophytes such as *Fucus vesiculosus*, which is consumed only to a minor extent and its yearly produced biomass is disrupted by storms in autumn and winter, so that most of this material is exported. The basis of the food web is the primary production of phytoplankton. The consumption by grazing is higher than the autochthonous net primary production and the community is thus largely dependent on auxiliary phytoplankton import. The detritus pool is fuelled mainly by faeces of the secondary producers and this material originates from phytoplankton that is not produced within the community and thus enriches the community with additional organic material. The different branches of energy flow are unevenly distributed in the mussel bed community, dominated by the food chain starting from phytoplankton to mussels to eider ducks. Because of the large biomass of grazing macrobenthos respiration of grazer surpasses that of bacteria and detritus feeders by far.

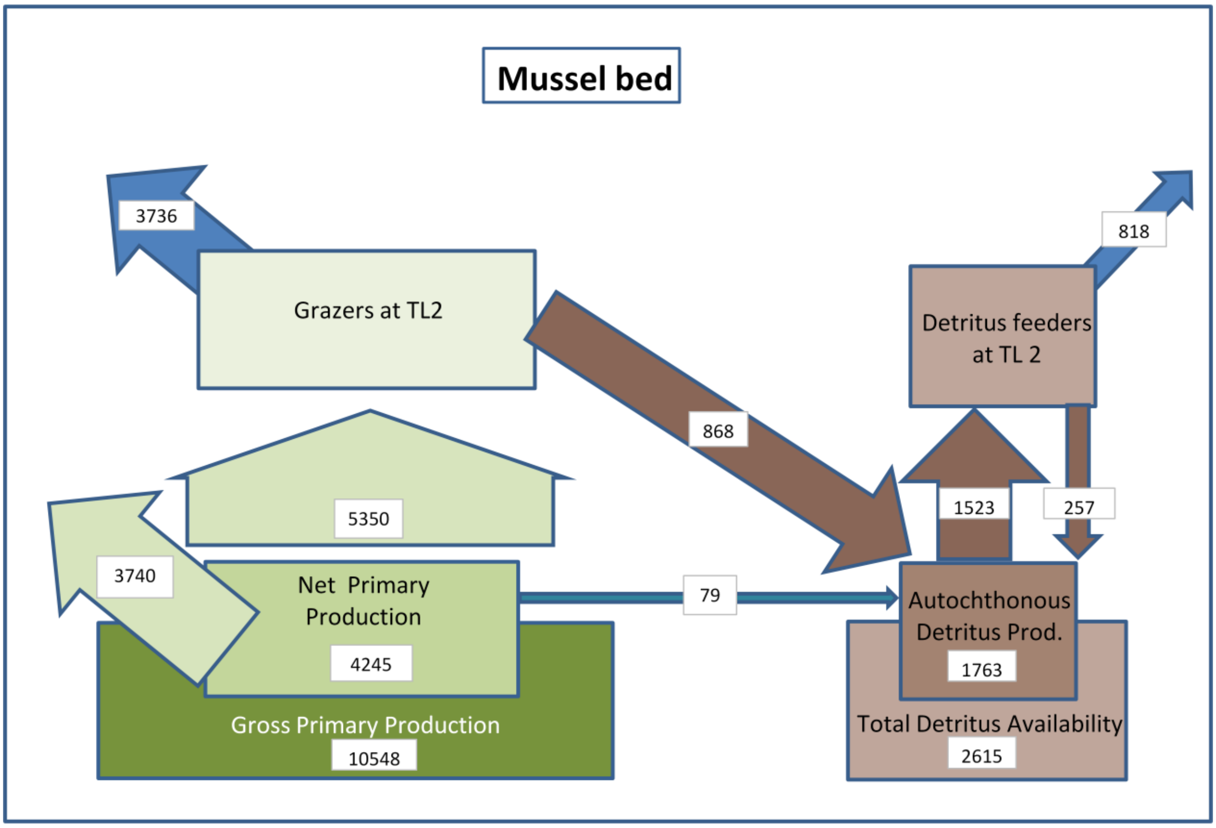


Fig. 43. Schematic concept of a mussel bed system showing the carbon flow between trophic level 1 and 2 divided into grazing and detritus food chain. Fluxes are in mg C $m^{-2}d^{-1}$.

In *Arenicola* sand flats (Fig. 44) primary production is much lower and consists mainly of microphytobenthic and phytoplankton production. Nearly one third of the autochthonous net production is channelled into the grazing food chain, while phytoplankton is the main food source for the community. Whereas microphytobenthos and phytoplankton contribute to production in a ratio of 2.56:1, it is consumed at a ratio of 1:1.86. The remaining plant material dies and enters the detritus pool. Phytodetritus is a higher source of autochthonous detritus production in sand flats compared to mussel beds. In *Arenicola* flats phytodetritus and faecal material enter the detritus pool in similar amounts. Only about one half of the autochthonous detritus production is consumed, but the detritus availability is higher due to the continuous import of detritus from outside. Therefore a continuous enrichment of organic material in an *Arenicola* sand flat would occur, if bioturbation by lugworms would not be controlling sediment organic matter.

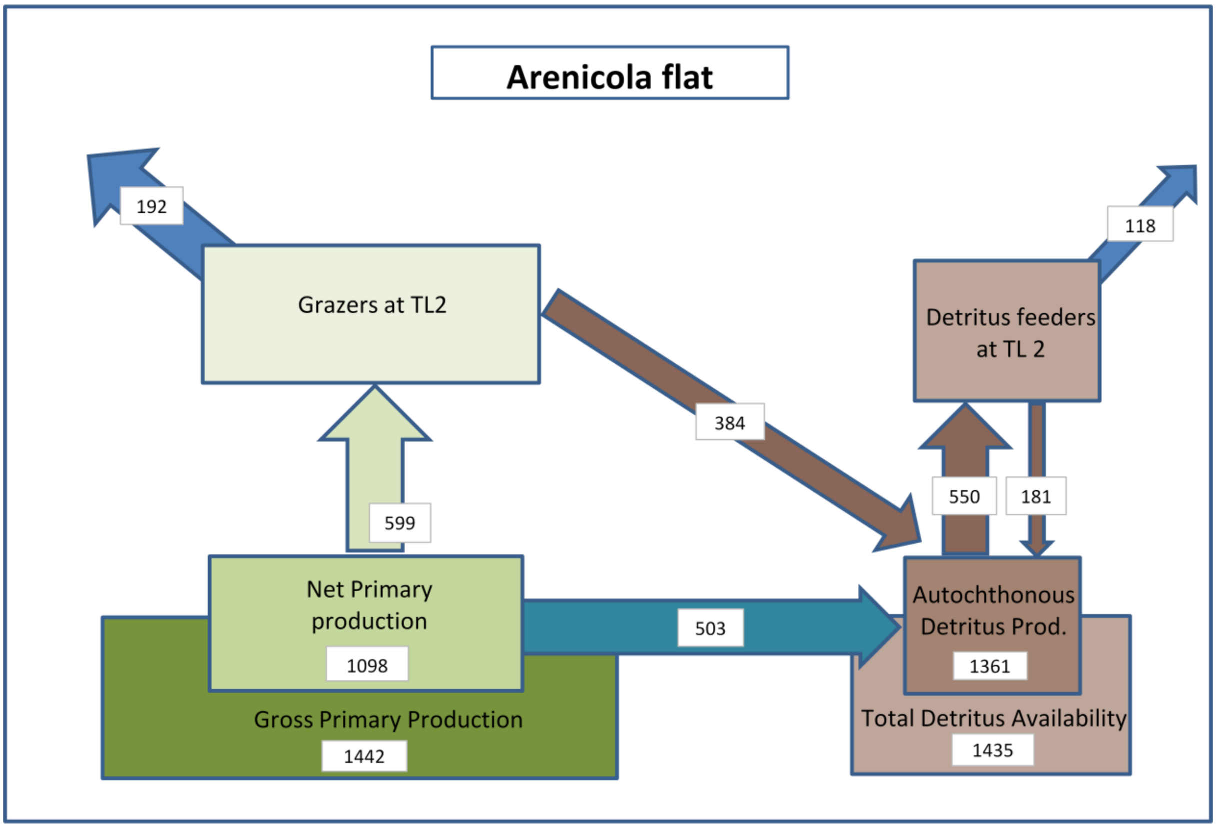


Fig. 44. Schematic concept of an *Arenicola* flat showing the carbon flow between trophic level 1 and 2 divided into grazing and detritus food chain. Fluxes are in mg C $m^{-2}d^{-1}$.

A totally different type of food web is that of a dense seagrass bed (Fig. 45). In seagrass beds macrophytes characterise the community and thus macrophytes, microphytobenthos and phytoplankton contribute to primary production in relation of 1.5: 2.5 :1. As in mussel beds macrophytes (in this case *Zostera noltii*) are only partly eaten by herbivores. Brent geese and wigeons are specialised seagrass grazers, but these birds are arctic and boreal migrants and are only present in autumn when they feed upon the total biomass that is still available at that time. Consumption of plant material is focussed on benthic components with a ratio of macrophytes to microphytobenthos to phytoplankton of 1 : 9.17 : 6.63. In contrast to mussel beds and *Arenicola* sand flats that are mostly dependent on phytoplankton, a seagrass bed community is based on benthic primary production. The rich autochthonous net primary production is only used by consumers with about 30%, most of the remaining material therefore enters sooner or later the detritus pool. The largest autochthonous detritus source is faeces production of the associated fauna. In addition to the autochthonous detritus production of about 1798 mg C m^{-2} d^{-1} seagrass plants act as sedimentation traps and thus accumulate allochthonous detritus material with 6216 mg C $m^{-2}d^{-1}$. This is a rich basis for bacteria and detritus feeders that form the main branch of energy flow in this community. Consumption of detritus components is nearly double as high as in sand flats, but only two third of the value found in mussel beds. The main branch of energy flow in seagrass beds is channelled along the detritus food chain.

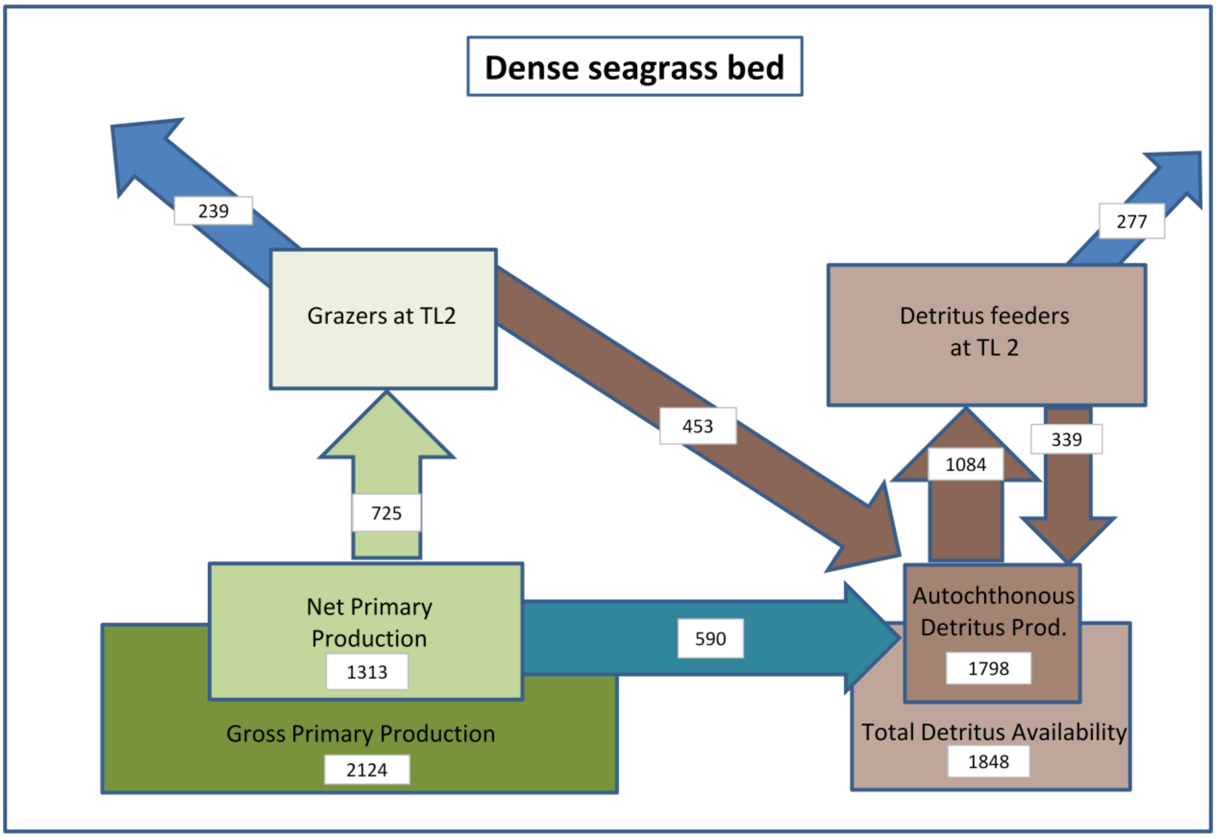


Fig. 45. Schematic concept of a dense seagrass bed showing the carbon flow between trophic level 1 and 2 divided into grazing and detritus food chain. Fluxes are in mg C $m^{-2}d^{-1}$.

Most of the communities in the SRB are based on the detritus food chain, especially when the primary consumers are dominated by deposit feeders. This can be observed in dense seagrass beds, mud flats, muddy sand flats, sandy shoals and sandy beaches. In most of these communities (with a share of grazing in total consumption of less than 50%) suspension feeders consume less than 400 mg C $m^{-2}d^{-1}$ (Fig. 46).

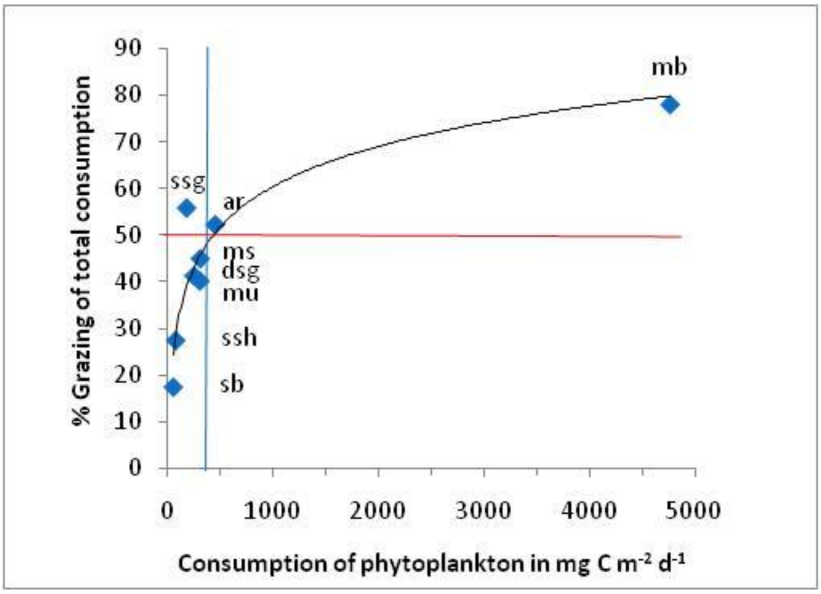


Fig. 46. Percentage of grazing on total consumption in relation to phytoplankton consumption in mg C m^{-2} d^{-1} in eight intertidal communities including mussel beds (α = 0.025, r =0.77). Red line separates grazer dominated (above) from detritus feeder dominated communities (below). Blue line marks the consumption of phytoplankton of 400 mg C $m^{-2}d^{-1}$. mb: mussel bed, ssg: sparse seagrass bed, ar: *Arenicola* flat, ms: muddy sand, dsg: dense seagrass bed, mu: mud flat, ssh: sandy shoal, sb: sandy beach

The magnitude of internal cycling within the food web seems to depend on the pelagic-benthic and benthic-pelagic exchange. If we correlate the net carbon exchange of a community, i.e. the difference between the pelagic-benthic and benthic-pelagic exchange, with its Total System Throughput (TST), as a measure of internal cycling, a negative correlation indicates the higher the source function of a community the lower is the TST (Fig. 47 a). It means also that communities having a high allochthonous material input are able to show a high internal material turnover. However, if a high percentage of productivity of the system is spent in material export as in mussel beds by high *Fucus* production and bird predation, this would not fit into this relation between internal cycling end material exchange (Fig. 47 b).

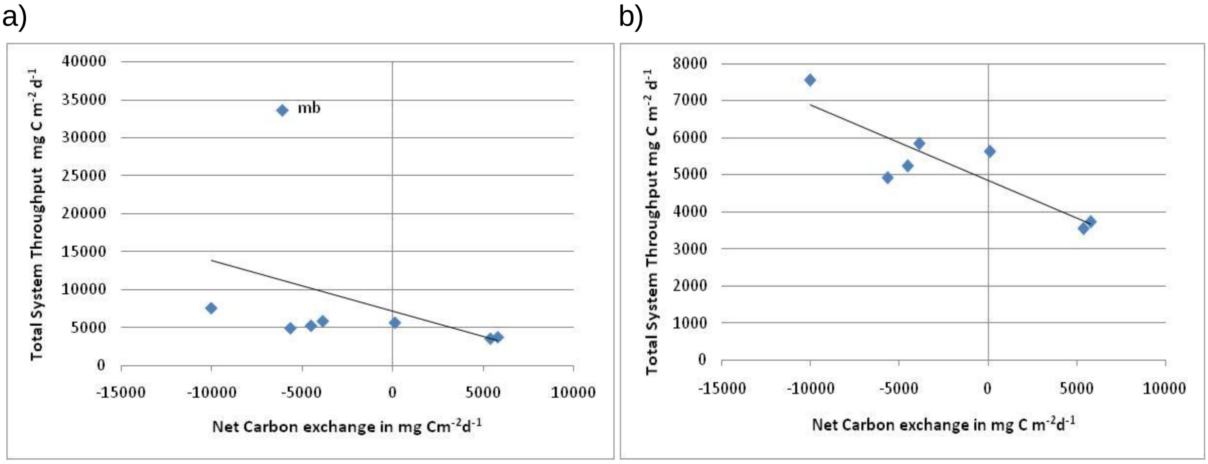

a)
b)

Fig. 47. Relation between material exchange (net carbon exchange in mg C $m^{-2}d^{-1}$) and the Total System Throughput (mg C $m^{-2}d^{-1}$). a) with mussel beds (mb)(r=0,86; α=0,025), (b) without mussel beds (r= -0,90; α=0,001) .

An even better indicator for internal material turnover may be the Finn Cycling Index showing the direct recycling of material as a percentage of the Total System Throughput. A comparison with the net exchange of a community shows a negative correlation, with the exception of mussel beds having a low Finn Cycling Index inspite of a high allochthonous material import (Fig. 48).

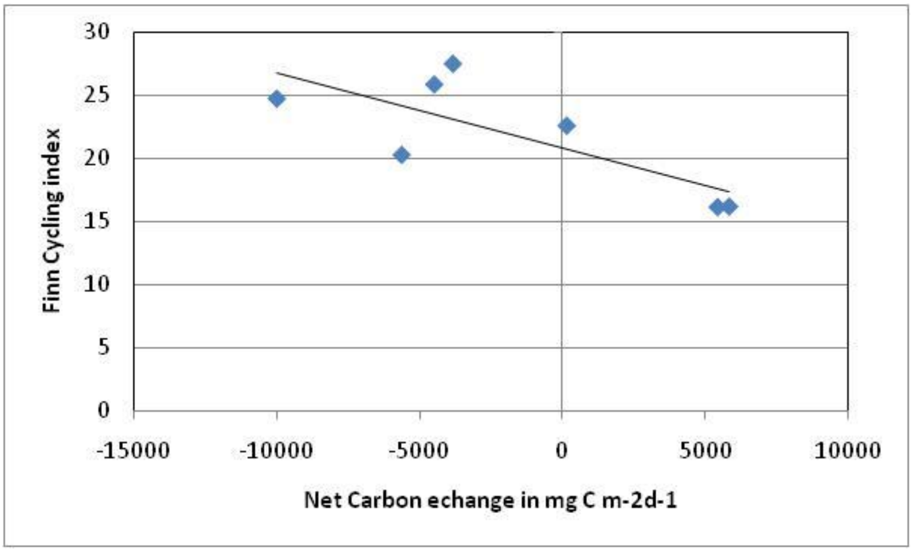


Fig. 48. Correlation between Finn Cycling Index as a measure of internal recycling and the net carbon exchange of a community, mussel beds excluded (Spearman rank corr. coeff.: r = 0.71; α = 0.025).

The comparison of the magnitude of internal cycling and the exchange of material with the ambient environment shows for those communities such as sparse seagrass beds revealing a higher internal cycling than net export of carbon, values larger than 1. For those communities that are characterised by a higher internal cycling than a net import this value is lower than -1. This is estimated for mussel beds, muddy sands and mudflats. All other communities show values between -1 and 1, indicating a low internal cycling compared with the exchange with their surrounding (Fig. 49).

The latter communities are mainly the different types of sand flats and the dense seagrass bed. In the dense seagrass bed the internal material cycling is high but due to the function of a dense leaf canopy as a sediment trap, there is a high detritus import into this community that surpasses the internal productivity and cycling processes within the food web.

Among the sand flat communities sandy shoals and sandy beaches show only a low internal material cycling but a continuous material loss to the environment that surpasses the internal material flow. In contrast to that are *Arenicola* flats characterized by an import of carbon that is slightly higher than the material flow within the community.

Those communities which show a TST/Exchange ratio lower than +1 and higher than 0, act as material through flow systems, with only poor storage capacities and very low average residence times of only 8.85 and 7.47 days for sandy shoals and sandy beaches, respectively. Dense seagrass beds and *Arenicola* flats are close to -1, showing that internal cycling and import of carbon with the surrounding is in a similar order of magnitude by a slightly larger allochthonus import than internal cycling. These communities are not really through flow systems having a higher storage capacity with relatively high average residence times of 48.06 and 46.54 for *Arenicola* flats and dense seagrass beds, respectively.

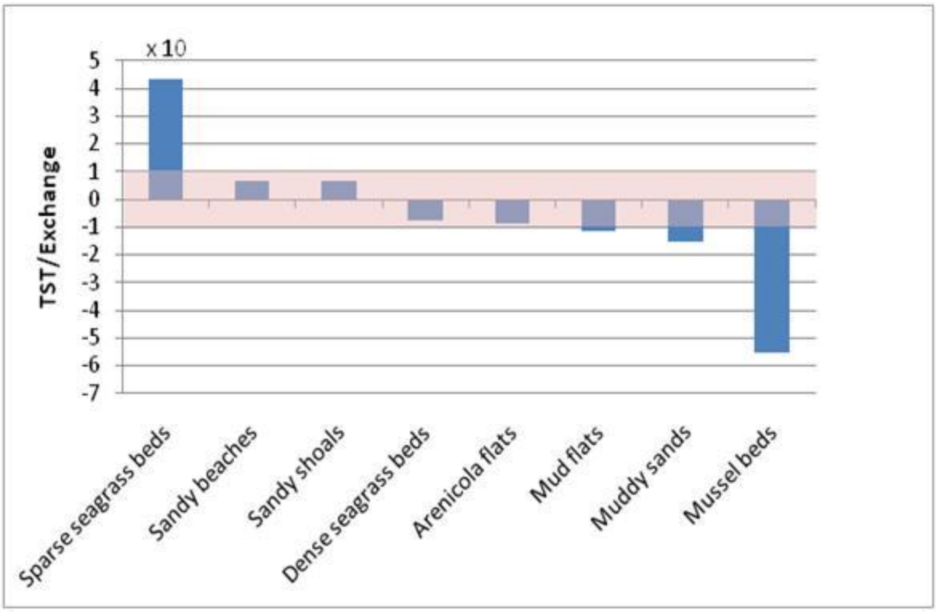


Fig. 49. Ratio between Total System Throughput and Net Exchange of eight intertidal communities of the Sylt-Rømø Bight. Pink area includes ratios >-1 and < +1. Communities within this range have higher net import (-) or net export (+) of material compared to the internal cycling. These are mainly the sand flat communities and the dense seagrass bed. For other communities internal material cycling is higher than the allochthonous net input (mussel beds, muddy sands) or net output (sparse seagrass beds).

d. Material cycles

Material exchange and material cycles differ distinctly between the communities of the Sylt-Rømø Bight. As already discussed in the chapter 5b on sinks and sources, the exchange of carbon varies both in magnitude and in the distribution pattern into different carbon forms, such as particulate, dissolved and living matter. Considering the different elements of the organic material such as carbon, nitrogen and phosphorus there are also differences in flow characteristics and the prevalent form of material transport within one community.

In the mussel bed the uptake of carbon and nitrogen is similarly distributed among the different forms, while phosphorus flux is based on a larger import of the particle fraction into the system (Fig. 50). Import of living organisms is more important for the carbon and nitrogen import than for the phosphorus import into a mussel bed. Dissolved inorganic components are of higher importance for the carbon and nitrogen import than for the phosphorus import. Mussel beds are sinks for organic matter but they release dissolved inorganic matter and living organisms as result of their high potential of remineralisation and production. The efficiency of conversion from imported to exported material is 74%, 65% and 57% for carbon, nitrogen and phosphorus, respectively. Phosphorus export is the highest of the dissolved components, whereas nitrogen export is dominated by living organisms. For carbon export also living organisms play a large role, but also the export of carbon via DIC (i.e.CO_2)

occupies a high portion. The relatively low share of exported dissolved inorganic nitrogen compared to carbon and phosphorus is an indication of nitrogen limitation of the plant components within a mussel bed, which require more nitrogen compared to phosphorus.

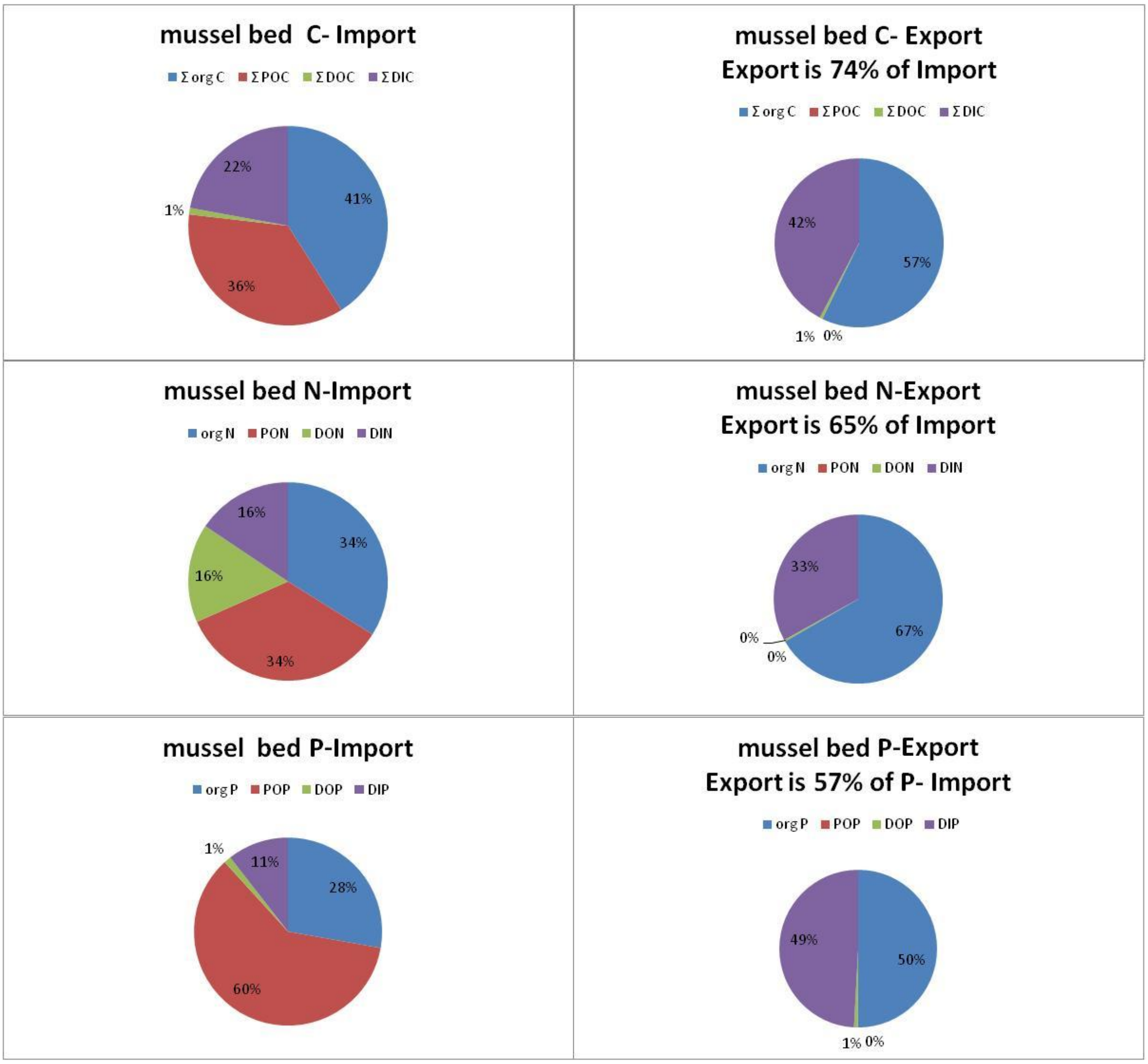


Fig. 50. Distribution pattern during import (left) and export (right) of different forms of carbon, nitrogen and phosphorus in an intertidal mussel bed of the Sylt-Rømø Bight. Org C,N,P = C,N,P bound in organisms; POC,N,P = particulate matter, DOC= dissolved organic matter; DIC = dissolved inorganic matter.

In dense seagrass beds carbon import is distributed equally over particulate matter and matter bound in living organisms (Fig. 51). This is caused by the dense carpet of seagrass leaves that act as a particle trap and a collector for small postlarval benthos and drifting benthos settling in large amounts in the shelter of the leaves where these organisms are protected from stronger tidal currents and waves. On the other hand the dense population of *Cerastoderma edule* in dense seagrass beds filters a large amount of phytoplankton from the water column into the seagrass bed and thus induces a large input of carbon via living organisms. Dissolved inorganic carbon is imported only by 12%. Although this is a relatively low percentage the absolute value is quite high and reflects the high primary productivity of this community due to the *Zostera* plants, their epiphytes and the microphytobenthos between the plants at the bottom of the community. In contrast to carbon, nitrogen is mainly imported by living organisms (i.e. org N) into the system, showing the high importance of settling processes of juvenile organisms into the system in addition to phytoplankton uptake by the suspension feeders within the seagrass bed. The low particle contribution to the nitrogen import may be caused by the low nitrogen content of detritus particles settling between the plants. Phosphorus is mainly imported by particles while dissolved inorganic matter plays a minor role for P import compared to carbon and nitrogen and uptake of dissolved inorganic phosphorus contributes only with 6% to budget. From all communities within the Sylt-Rømø Bight dense seagrass beds show the highest efficiency of material import in relation to export. Only 35% of the imported carbon into a dense seagrass bed is subsequently exported, while nitrogen and phosphorus show higher export ratios of 44% and

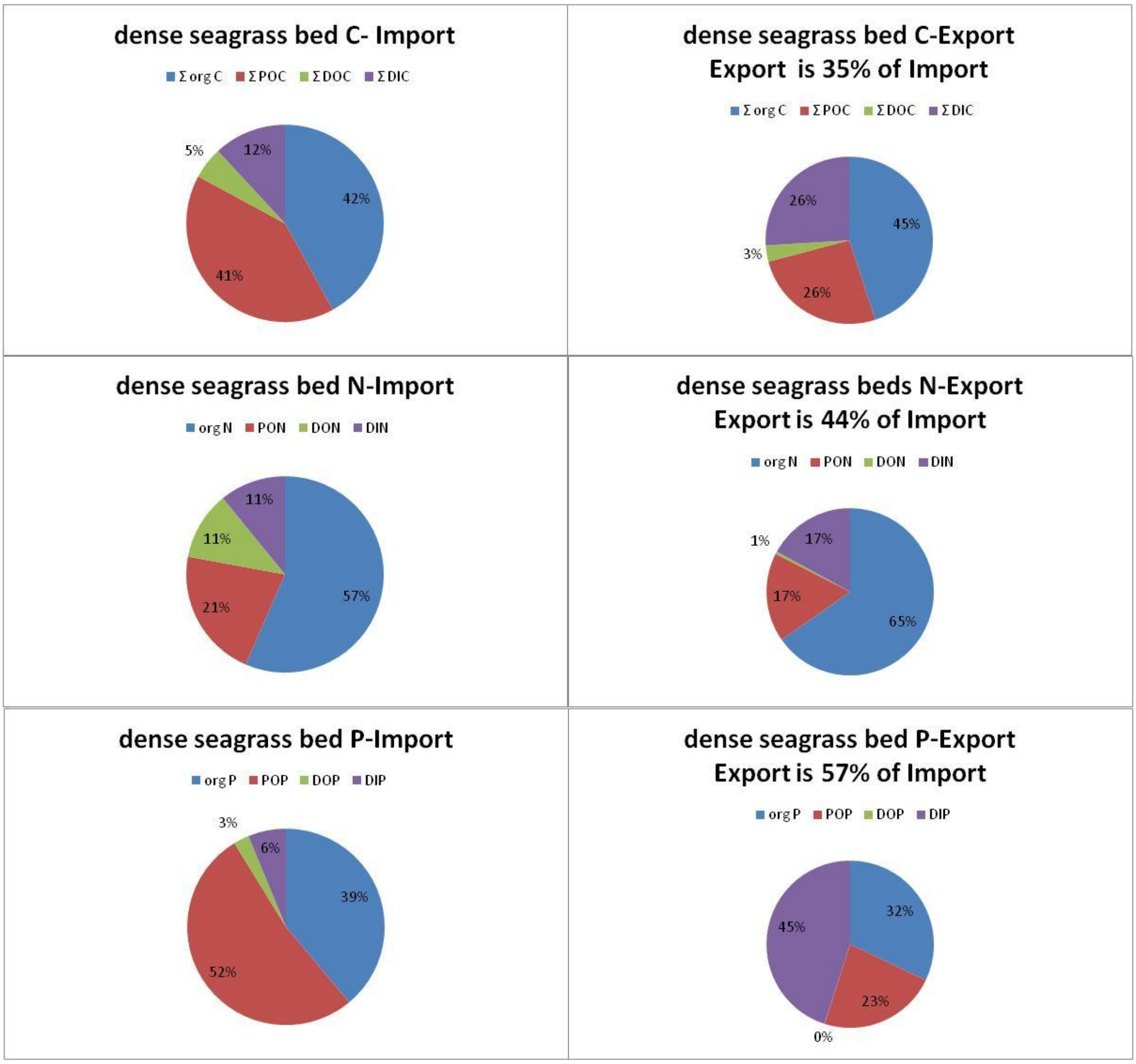


Fig. 51. Distribution pattern during import (left) and export (right) of different forms of carbon, nitrogen and phosphorus in a dense seagrass bed of the Sylt-Rømø Bight. Org C,N,P = C,N,P bound in organisms; POC,N,P = particulate matter, DOC,N,P= dissolved organic matter; DIC;N,P = dissolved inorganic matter.

57% respectively. This may reflect the strong dependence of seagrass beds on the CO_2 import, which may be supported by a high recycling and re-using of CO_2 produced by autochthonous respiration processes. Nitrogen export shows a similar distribution into facies than import underlining the role of a seagrassbed as a sedimentation trap for nitrogen, where the same material is resuspended in a similar contribution but a lower amount.

Phosphorus export indicates a distinct remineralisation pattern, where dissolved inorganic phosphorus has a higher share than particles and living organisms. However, also there are qualitative differences in the shares of elemental constituents between import and export, all phosphorus but also nitrogen and carbon compounds are distinctly taken up by the seagrass bed.

In a sparse seagrass bed only half of the macrophytic biomass of a dense seagrass bed is present. This reduction already suffices to change the character of the system from a

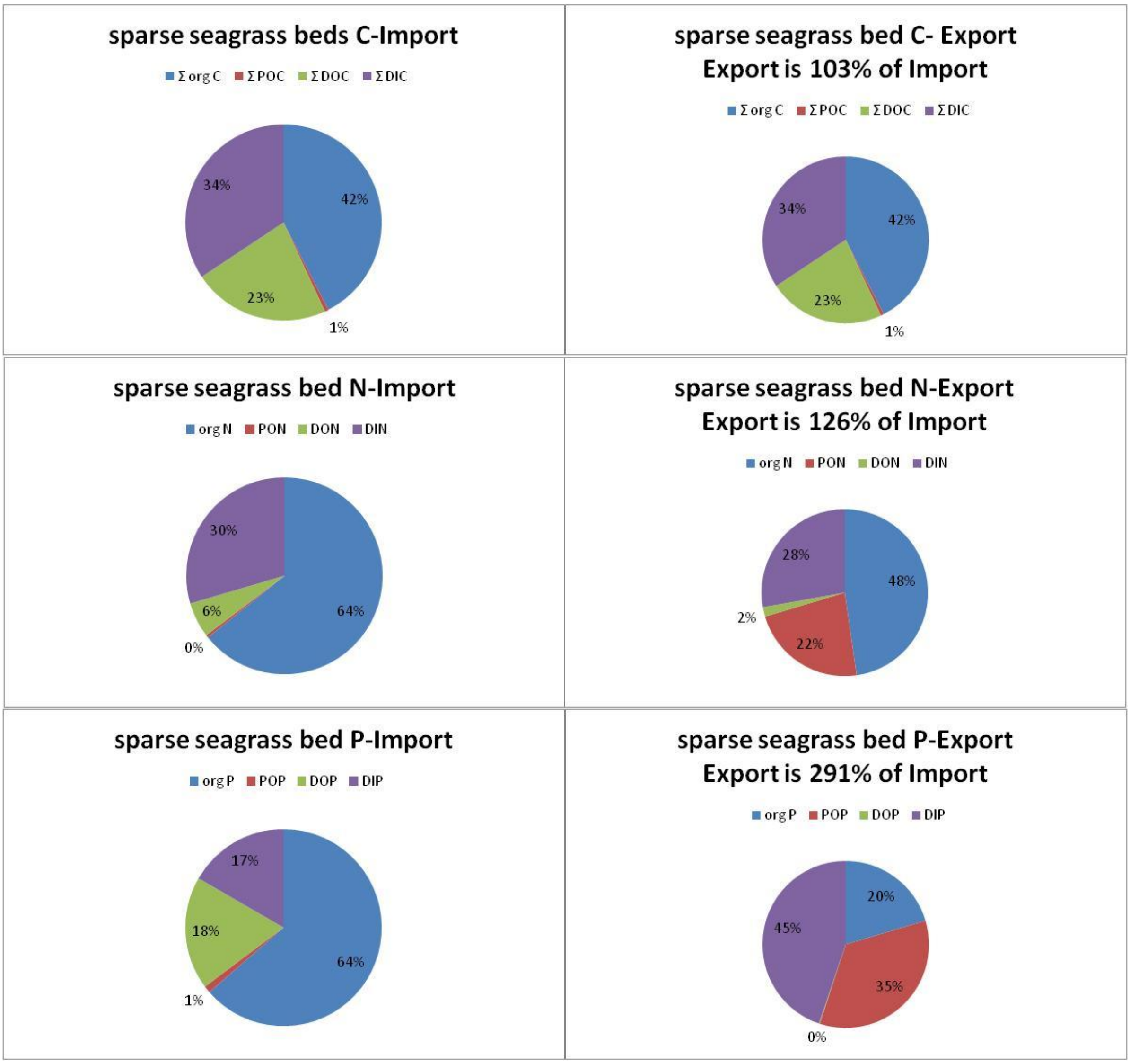


Fig. 52. Distribution pattern during import (left) and export (right) of different forms of carbon, nitrogen and phosphorus in a sparse seagrass bed of the Sylt-Rømø Bight. Org C,N,P = C,N,P bound in organisms; POC,N,P = particulate matter, DOC,N,P= dissolved organic matter; DIC;N,P = dissolved inorganic matter.

material sink to a material source. Carbon is imported by organisms and dissolved inorganic carbon and to a significant extent also by dissolved organic carbon (Fig. 52). Import of living organisms dominates the nitrogen and phosphorous import. However, nitrogen and to a lesser extent phosphorus is also imported by the uptake of the dissolved inorganic form (Fig. 52). Especially dissolved organic phosphorus contributes distinctly to phorsphorus import. Particles are formed within the community and are released by means of the relatively high water currents in this community. In general the export exceeds the imports by 3% and 26% for carbon and nitrogen, respectively. In contrast to that phosphorus export was about threefold the import.

The high export of particles indicates a decrease of the organic material pool in the sediment of a seagrass bed over time that may lead to a change of the community to a sandy area if currents and turbulences persist to be high. Loss of particulate carbon dominates carbon export, while nitrogen export is dominated by organismic drift and phosphorus by release of inorganic phosphorus from the sediment.

In an *Arenicola* sand flat particles dominate the import of carbon, nitrogen and phosphorus (Fig. 53). Settling organisms play only a larger role for phosphorus uptake, while dissolved components are generally less important. Export of material accounts for 35%, 30% and 78% of import for carbon, nitrogen and phosphorus respectively (Fig. 52). *Arenicola* sand flats are sinks for all three elements. However the imported particles are not retained and remineralised totally and thus contribute also to the export of material. This is a consequence of bioturbation by the lugworm, which is reworking the sediment releasing it at the sediment surface, where it is exposed to tidal currents flushing out the small organic particles.

Especially for carbon and phosphorus, particle release contributes largely to the export of matter. Although living organisms occupy a larger percentage particularly for the carbon and nitrogen export, their absolute amount is lower compared to the import. Dissolved material is proportionally higher in export than in import, but only for nitrogen and phosphorus there could be observed a net release. Especially phopsphorus seems to show a large remineralisation and recycling potential, because it is imported mainly by particles and exported by dissolved phosphorus and recycled particles probably after bioturbation. Both processes delay the accumulation of organic material within the sediment in the *Arenicola* sand flat.

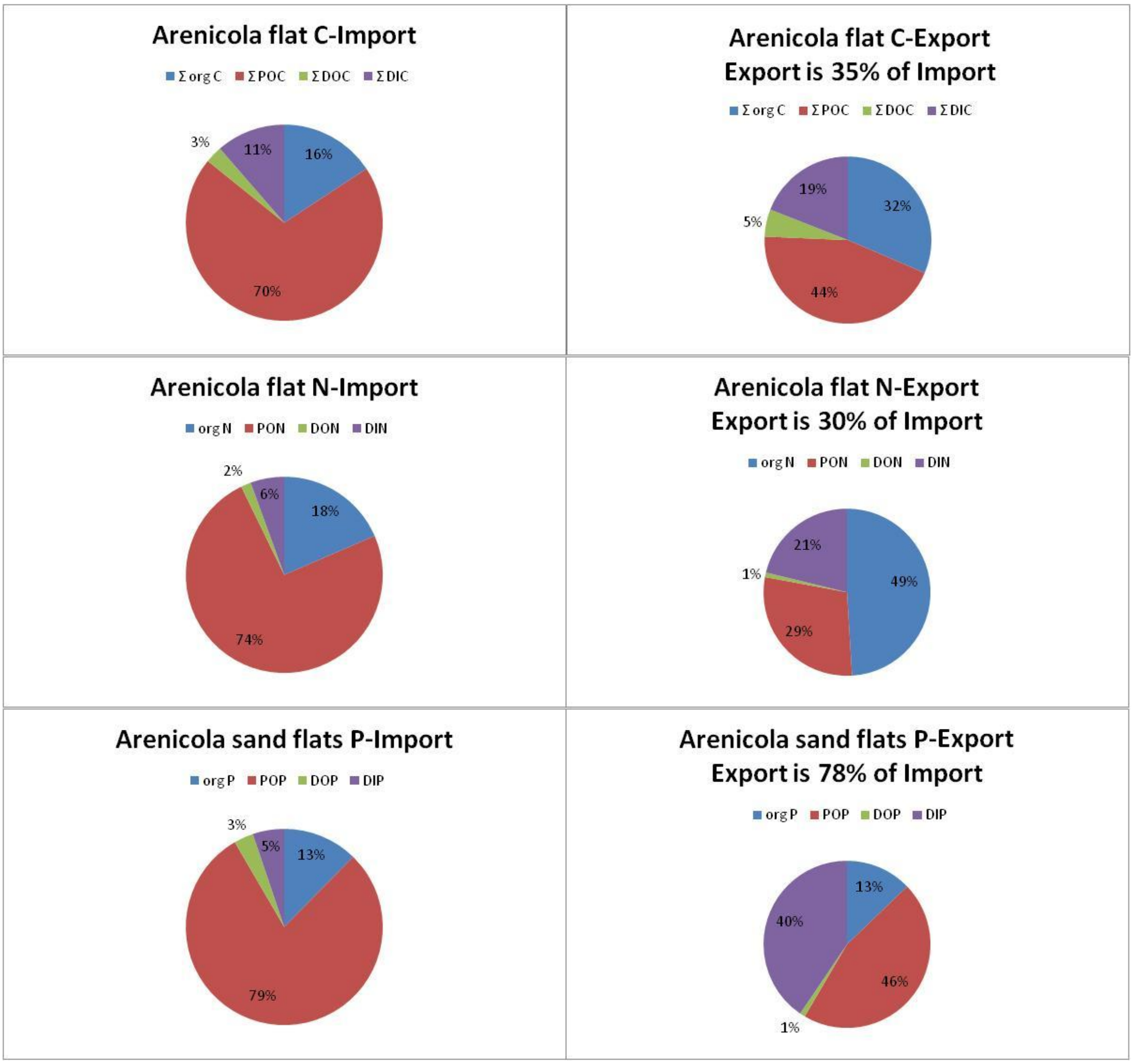


Fig. 53. Distribution pattern during import (left) and export (right) of different forms of carbon, nitrogen and phosphorus in an *Arenicola*- sand flat of the Sylt- Rømø Bight. Org C,N,P = C,N,P bound in organisms; POC,N,P = particulate matter, DOC,N,P= dissolved organic matter; DIC;N,P = dissolved inorganic matter.

Muddy sands show similar import pattern of carbon, nitrogen and phosphorus compared to *Arenicola* flats, however the percentage of settling organisms is higher, particularly in the carbon and nitrogen budget (Fig. 54). In contrast to *Arenicola* sand flats there is a minor release of particles especially for carbon and nitrogen, while the export of these elements is dominated by drifting living organisms. Although there is a huge accumulation of dead organic material in this community, the release of living mass is also large and determines the comparably greater release of carbon and nitrogen compared to the *Arenicola* flat. For phosphorus particle release plays a larger role in muddy sands, but the process behind is still unknown. It seems that bioturbation plays a smaller role in muddy sands compared to *Arenicola* sand flats and this explains the higher accumulation of organic matter.

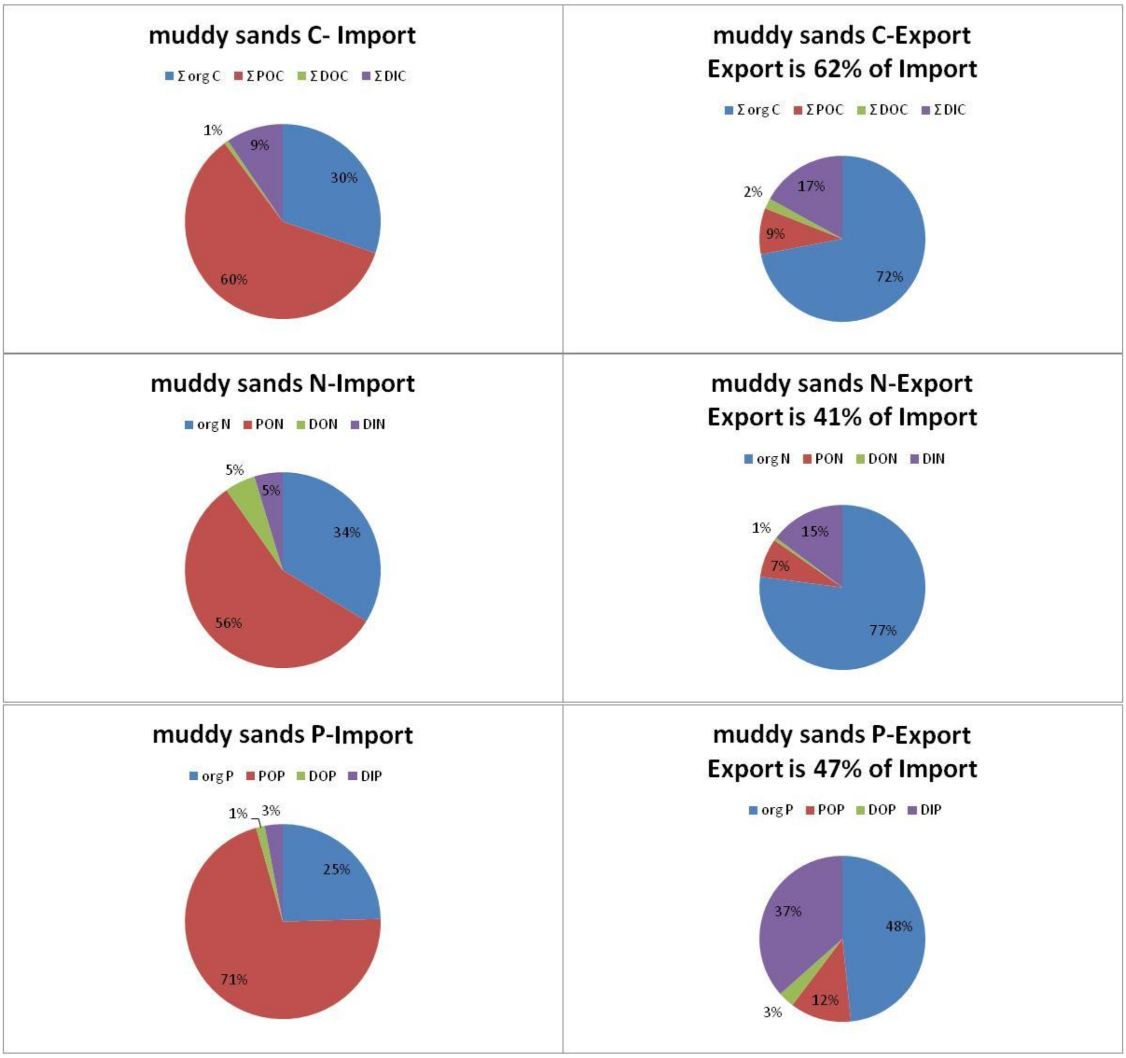


Fig. 54. Distribution pattern during import (left) and export (right) of different forms of carbon, nitrogen and phosphorus in muddy sands of the Sylt-Rømø Bight. Org C,N,P = C,N,P bound in organisms; POC,N,P = particulate matter, DOC,N,P= dissolved organic matter; DIC;N,P = dissolved inorganic matter.

Sandy shoals are sand flats that are situated at places where currents and turbulence exert a dominating influence. There is only a small import of material and most of the material which is produced within this community is exported (Fig. 55). As a result these communities reveal only clean sandy sediments with only low or no organic enrichment. Particle import does not occur in this community and the input of carbon, nitrogen and phosphorus is restricted to the uptake of dissolved inorganic facies due to microphytobenthos that are firmely attached to sand grains and the active settling of animals which can bury themselves into the moving sands to be sheltered from currents and turbulence.

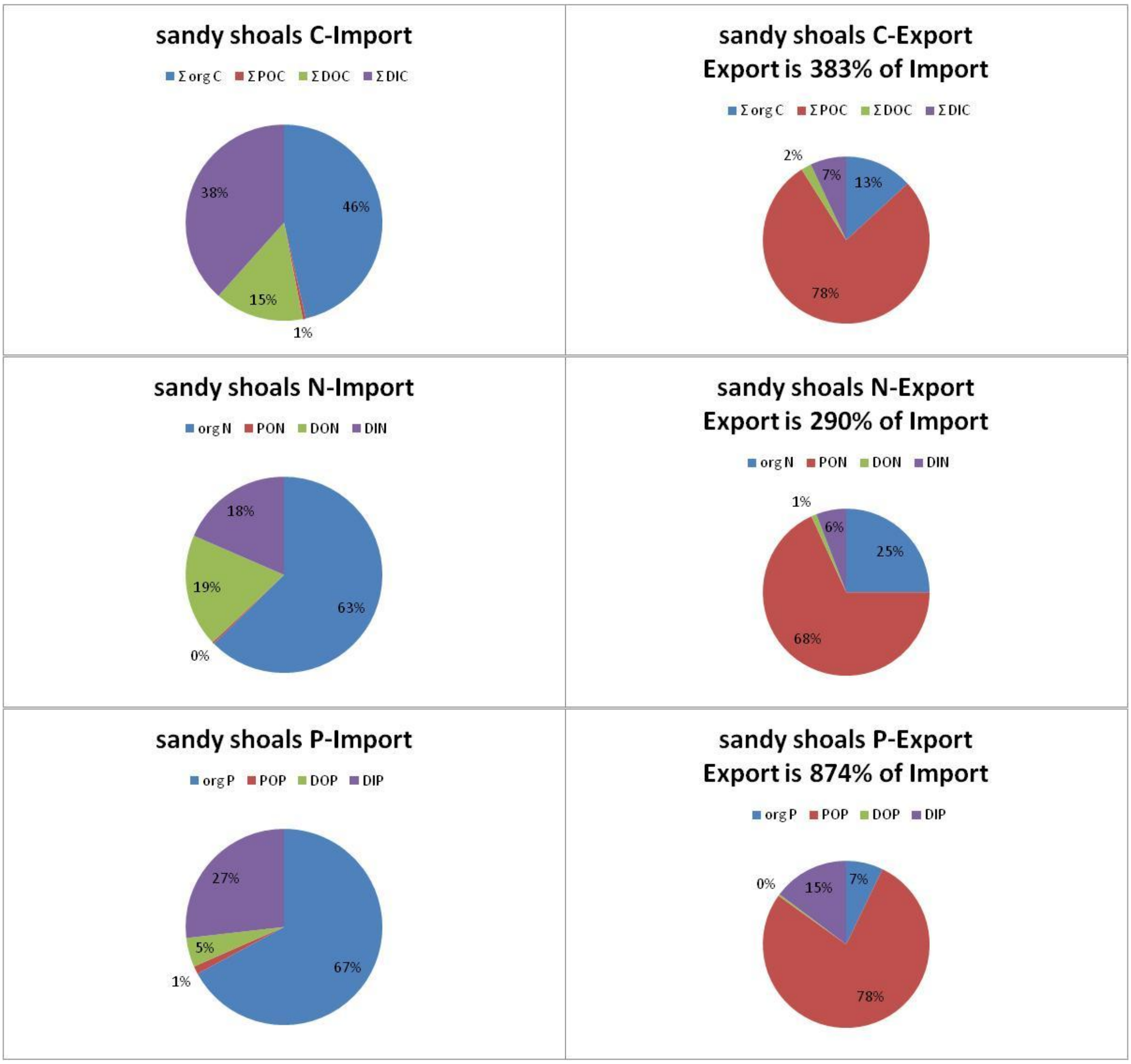


Fig. 55. Distribution pattern during import (left) and export (right) of different forms of carbon, nitrogen and phosphorus in sandy shoals of the Sylt-Rømø Bight. Org C,N,P = C,N,P bound in organisms; POC,N,P = particulate matter, DOC,N,P= dissolved organic matter; DIC;N,P = dissolved inorganic matter.

Whatever is produced as particle in this community is exported to the water column. The share of particles on the total carbon, nitrogen and phosphorus export is high. The export surpassses the import by a factor of 3.8, 2.9 and 8.7 for carbon, nitrogen and phosphorus respectively which is mainly due to organic matter from the sediment pool. In the investigated communities this sediment pool was still relatively high, but in more exposed sites of this type of sediments this pool is already depleted and thus a lower particle export can be expected.

Sandy beaches have a similar exchange pattern than sandy shoals, however they are situated at the high tide line and show longer emersion periods, during which these communities are decoupled from benthic-pelagic exchange for longer periods.

Mud flats are characterised by a high import of particles from the water column, followed by organism import and import of dissolved inorganic matter (Fig. 56). 48%, 61% and 50% of this import is again exported for carbon, nitrogen and phosphorus. The export is also dominated by the organismic release but dissolved inorganic material is released especially as phosphorus.

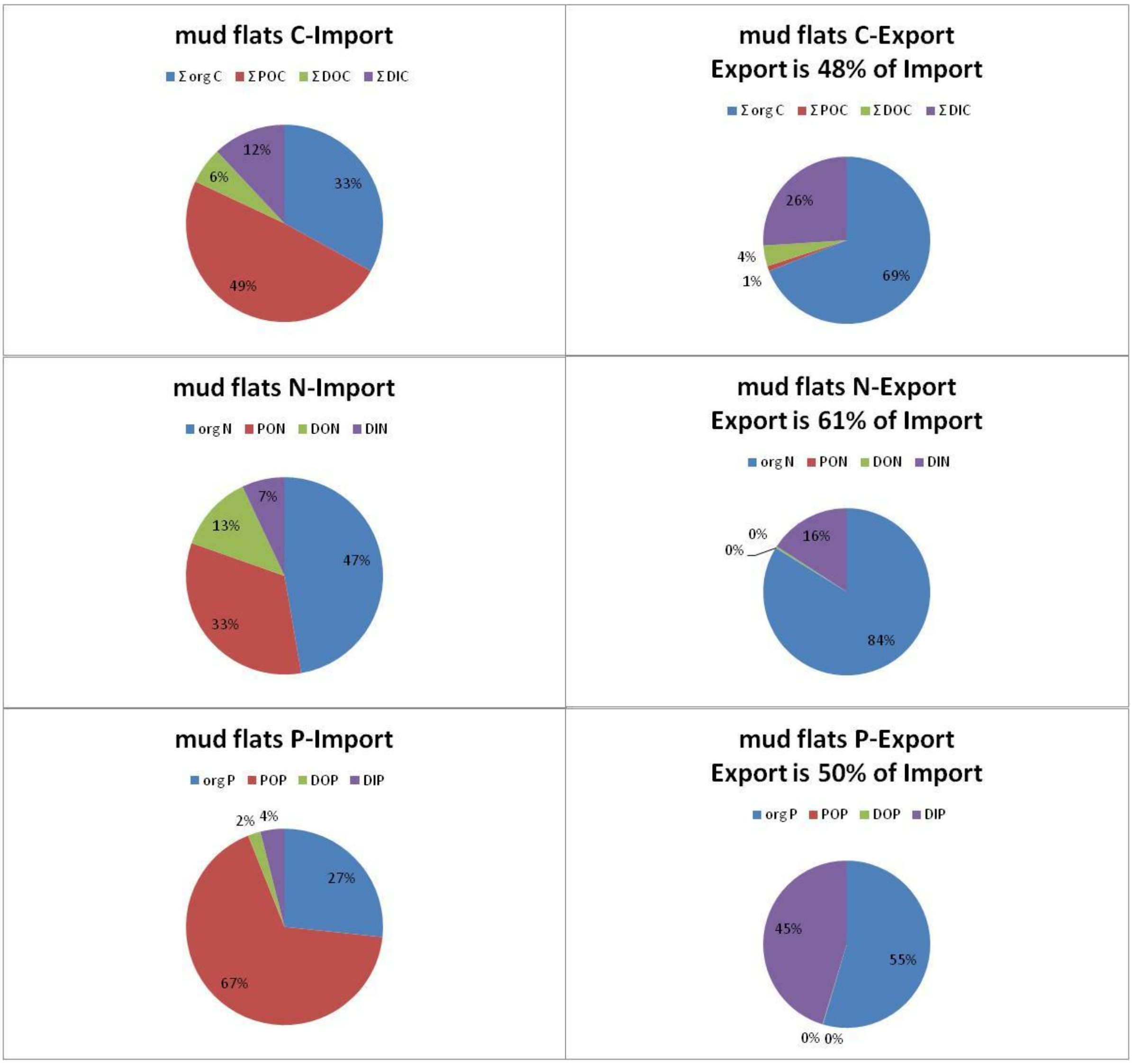


Fig. 56. Distribution pattern during import (left) and export (right) of different forms of carbon, nitrogen and phosphorus in mud flats of the Sylt-Rømø Bight. Org C,N,P = C,N,P bound in organisms; POC,N,P = particulate matter, DOC,N,P= dissolved organic matter; DIC;N,P = dissolved inorganic matter.

e. Material exchange and cycling in the Sylt-Rømø Bight

If I estimate the material exchange of the total tidal flat area of the Sylt-Rømø Bight as the sum of the exchange rates of the different communities considering their areal extent, then the total tidal flat acts as a sink for all carbon facies (Fig. 57). The tidal flats act also as a sink for nitrogen, although DIN shows a very small net release which is less than 1% of the total net uptake. Phosphorus POP- uptake (2.26 mg P m^{-2} h^{-1}) and DIP-release (1.85 mg P m^{-2} h^{-1}) are in a similar order of magnitude but also for this element the tidal flats have the character of a sink. The dominating sink character, in terms of C and N, of the tidal flats suggests a persistent enrichment of organic material within the sediment. However, a long term increase in sediment organic matter is not observed in the investigated area. We therefore assume that a balance of organic matter within the sediment may be controlled by irregular processes such as storm surges and frequent events of sediment erosion, that forms the morphology of the intertidal area but also may control the quantitative element composition of the sediment.

Long term studies and geological surveys of the area suggests a decrease of mudflats in favour of sand flats within the last hundred years (Austen 1997). This suggests that future investigations of elemental budgets should be done on a temporal scale that include storm events which has rarely been done in the past.

Elemental budget for the total tidal flat area of the Sylt-Rømø Bight

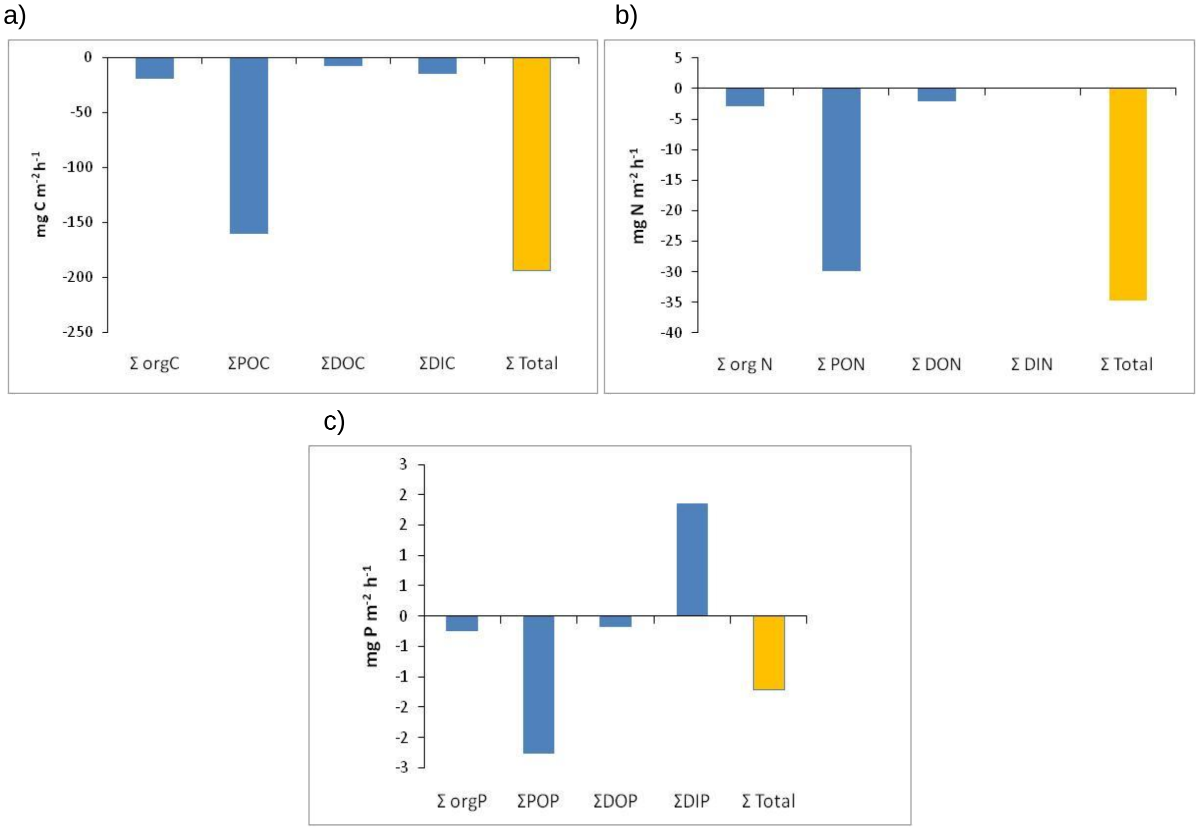


Fig. 57. Budget of different facies (organismic, particulate dissolved organic and dissolved inorganic material) of a) carbon, b) nitrogen and c) phosphorus of the total tidal flat area in the Sylt-Rømø Bight. Org C,N,P = C,N,P bound in organisms; POC,N,P = particulate matter, DOC,N,P= dissolved organic matter; DIC;N,P = dissolved inorganic matter.

The cycling of energy and material is an inherent and universal process in all natural ecosystems (Odum 1969) that contribute to their autonomous behaviour (Ulanowicz 1986). Cycling occurs through a number of cycles of different path lengths and their distribution as a function of cycle length (Ulanowicz 1983). We have identified a total of 1197 cycles for the intertidal area of the SRB through which 1162 mg C $m^{-2}d^{-1}$ of the TST is recycled on a daily basis. 170 cycles, or 14.2% of all cycles are grouped into 10 nexi each containing 17 cycles but sharing a different weak arc in each of the nexi. The greatest proportion of cycles (i.e. >50%) are clustered in nexi containing 19 cycles or more. A large nexus generally contains longer pathways involving a number of compartments and species occupying higher trophic positions (i.e. more than 3). In contrast a nexus containing fewer cycles invariably involves benthic compartments, particularly sediment bacteria, meiobenthos and sediment POC. The paucity of nexi with few cycles and the greater frequency occurrence of large-cycle nexi indicate the presence of a rather complex cycling structure in the bight.

The numbers of cycles per community varies from 87 in sandy shoals to 342 in the muddy sand flat subsystem. In most systems, with the exception of the mussel beds, more than 95% of the cycled material takes place via cycles containing 2 and 3 compartments involving mostly microbial compartments or species that prey on them, with small amounts cycled through loops involving 4 or more compartments (Fig. 58).

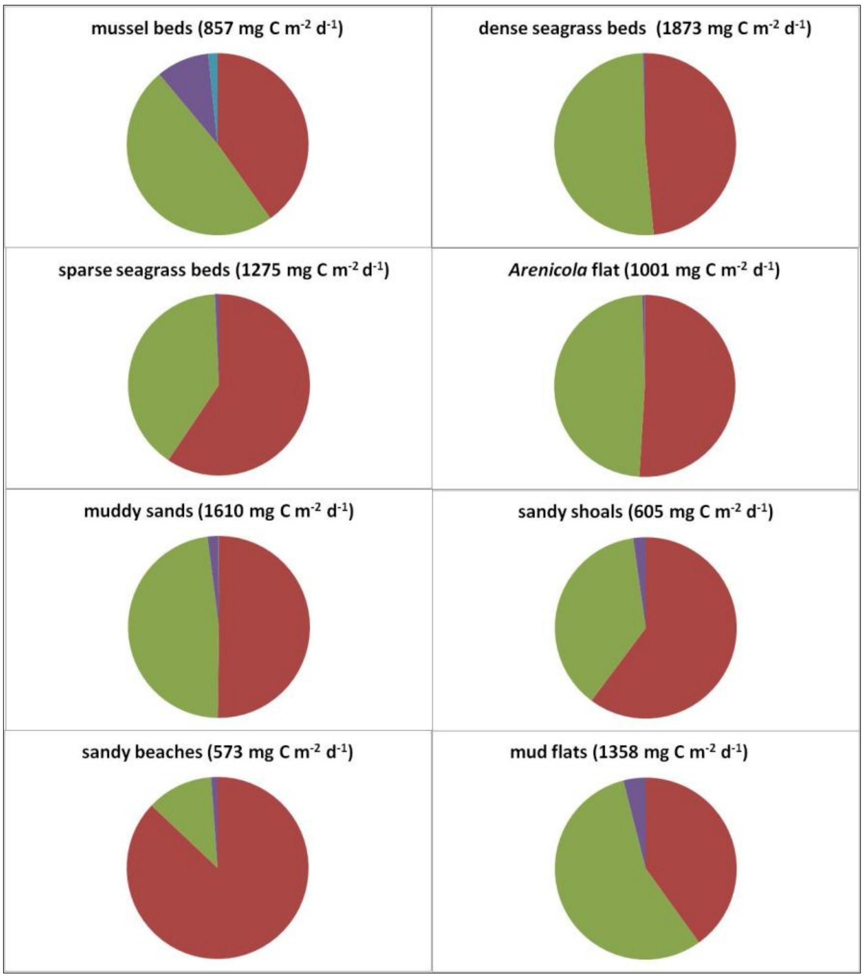


Fig. 58. Cycle distribution of the 8 dominant benthic communities of the Sylt-Rømø Bight showing the amount of carbon cycling through loops of various path lengths expressed as a fraction (%) of the total amount cycled in each community in mg C m^{-2} d^{-1}(value in brackets) Brown sectors represent cycles with 2, green: with 3, purple: with 4, dark blue: with 5, orange: with 6 and light blue: with 7 compartments.

Short pathways are also indicative of fast rates of cycling (Baird & Ulanowicz 1993) as opposed to systems where cycling occurs over longer pathways (Baird et al. 1991). In the mussel beds, however, about 11% of cycling takes place over longer pathways involving 4-6 compartments because of heavy predation of top predators on prey at lower trophic positions. Sediment bacteria and sediment POC are virtually always involved in these longer cycles and in which invertebrates and vertebrate species compartments frequently participate. The involvement of fish and invertebrates is clearly through their egesta, retained in the sediment as sediment POC which is subsequently used by invertebrates and which are in turn subjected to vertebrate predation.

In subsystems exposed to higher currents and wave action, such as sparse seagrass beds, sandy shoals and sandy beaches I observe a higher percentage of small cycles involving 2 compartments, compared to sheltered communities such as mud flats, dense seagrass beds and muddy sands, where 2 compartment cycles transport half or less than half the total amount of cycled material. This indicates both a quick cycling and a larger importance of a self-contained microbial loop in exposed communities.

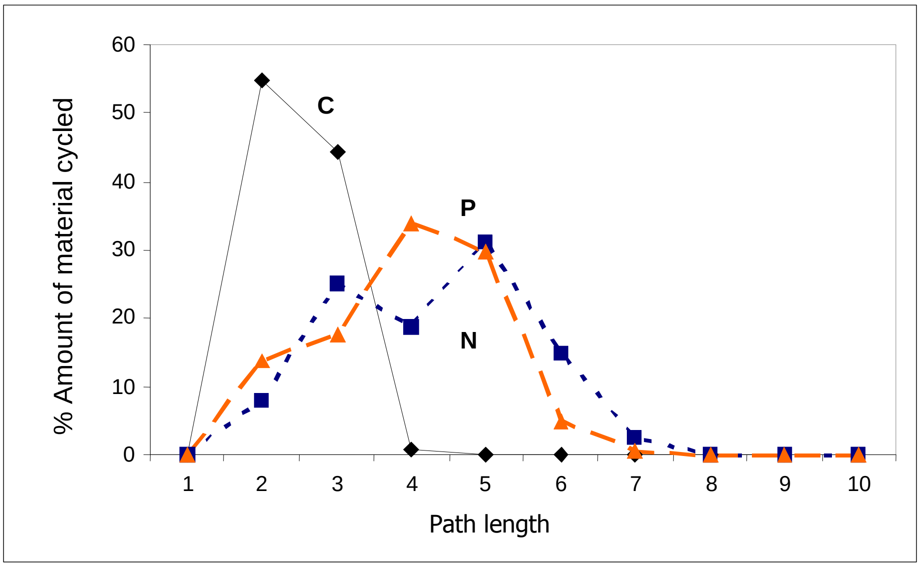


Fig. 59. Percentage of total carbon, nitrogen and phosphorus activity of total tidal flat area of the Sylt-Rømø Bight, involved in recycling over cycles with different path lengths. Black line = carbon, stippled blue line = nitrogen, orange line = phosphorus.

Of further interest is how the amounts of the elements C, N, P recycled are distributed amongst the path length by which these elements are cycled (Fig. 59). About 99% of C is cycled over short path lengths involving 2–3 model compartments, and although path lengths of up to 9 were identified, the amount involved over longer ones is miniscule. Nitrogen shows a clear bimodal distribution showing one peak of activity over cycles of three transfers, followed by a drop at path length 4, and a strong second peak at loops of 5. A possible explanation for the bimodality is bacterial activity during the nitrification–denitrification processes which involve shorter path lengths (as with carbon), while N is transferred over longer loops involving organisms at higher trophic levels. About 52% of N is cycled over path lengths of between 2 and 4, and about 48% over longer loops. P on the other hand shows a peak of recycling at path lengths 3, 4 and 5, over which about 81% of P is recycled. Both N and P appear to be cycled over longer path lengths than C (Fig. 59). This may also underline the importance of higher trophic levels such as invertebrates, fish and birds for element cycles such as nitrogen and phosphorus, whereas in carbon cycling clearly short cycles and with this the microbial components are dominant.

These patterns of recycling are reflected in the APL (or average path length), which quantifies the average number of transfers a unit of an element will undergo from the time it enters the food web until it leaves the system, and the ART (or average residence time) of an element in the system; both indices reflect on the trophic function of an ecosystem (Kay et al. 1989). The APLs calculated were 2.8 for C, 3.7 for N, and 9.8 for P (see Table 4). The APL is a measure of the retention of energy or an element within a system, and the APL values calculated for C, N and P illustrate that P flows through many more compartments before it leaves the ecosystem than either C or N. The ART calculated for P was also much longer (201 days) than the 26 and 29 days derived for C and N, respectively. P is thus retained for a longer time in the system, and participates in longer cycles than N or C (see Table 4). Furthermore, the FCIs also show that 80.8% of P is recycled, to a far greater extent than C (17.2%) and N (43.3%). The cycling structures of both N and P are complex, and although the residence time of N appears to be the shortest, more than 40% of the systems´ N throughput is recycled. Little C is recycled, whilst it is transferred over short cycles with much of the C energy dissipated through respiration of the biota.

f. System characteristics

Various system level indices were derived from network analysis (see Tables 6; 11; 16; 21; 26; 31; 36; 41 in chapter 4). The comparison of whole system indices reveals interesting similarities and differences between the 8 intertidal benthic subsystems in the bight. Greater cycling was assumed to be indicative of system maturity. Here the FCI of the mussel beds (2.53%) is low compared with the relative ascendency of 49.8%, whereas this relationship (between the FCI and the A/C ratios) is much smaller for the other intertidal subsystems.

There also appears to be in general an inverse relationship between the FCI and the relative ascendancy (A/C) (cf. Baird et al. 1991) and the larger this relationship is, the less organized and more stressed a system could be. The inverse relationship between the FCI and relative ascendency is evident for all systems, but appears to be the highest in the mussel beds and the lowest in the muddy sand flats.

High APL and flow diversity values have been associated with high degrees of interactions and diversity in terms of flows within the system, and these can also be viewed in conjunction with the connectance indices and the normalized ascendency ratio (or the AMI). The highest values for all of these were derived for the mussel beds, *Arenicola* flats, dense and sparse *Zostera noltii* beds, and mud and muddy sand flats. Values of these indices fluctuate within narrow ranges, which are consistently higher than the values of the same indices computed for the pelagic, sandy shoals and sandy beach subsystems. From these observations it would appear that the benthic subsystems can roughly be grouped into 2 groups. The first group consists of the mussel bed, *Arenicola* flats, dense and sparse *Z. noltii* beds, and mud and muddy sand flats, all of which show high degrees of interactions, evenness of flows and low degrees of variability in interactions and flows when compared with the second group of sandy shoals and sandy beaches. The magnitude of redundancy is often referenced to the susceptibility of a system to perturbations and, thus, its stability (e.g. Rutledge et al. 1976). High redundancy signifies that the system is maintaining a high number of parallel trophic pathways by which energy or material passes between any 2 arbitrary components in the system (Ulanowicz 2004). Should a perturbation occur, the system then has the capacity to use the remaining pathways to function the way it does. The relative and normalized redundancy indices (R/DC and R/TST, respectively) are lower in the mussel beds indicating fewer parallel pathways exist here than in any of the other benthic subsystems. The mussel beds are indeed heavily exploited by a number of bird species including the eider duck, oystercatcher *Haematopus ostralegus*, 3 gull species and an assortment of other bird predators feeding essentially on *Mytilus edulis*. A perturbation that would cause a dramatic decrease in the productivity of prey species on the mussel beds will inevitably affect the bird populations adversely in one way or another. In view of the existence of strong links between many predators and few prey species (i.e. few alternative or parallel pathways) this system can be considered to posses less stability when faced with external perturbations. The redundancy indices for the other subsystems are relatively high, reflecting multiple parallel pathways and, thus, more resistance to external perturbations.

g. Role of biodiversity for material and energy flow

The relation between biodiversity and ecosystem function is currently an important focus in ecological research. With an increase in the number of species within a system the number of interactions increases and this could influence also the amount and order of magnitude of material exchange between the system and the ambient environment. One frequently used experimental method to investigate the relationship between ecosystem functioning and biodiversity is to create model systems reducing the natural complexity (for review see Bulling et al. 2006). The authors see these set ups as valuable tools for ecosystem understanding and recommend to consider the spatial scaling, multiple trophic levels, variation and environmental stochasticity and to select representative combinations of species critically. Because such model systems have limitations especially in spatial scale and complexity, a combination with mathematical models could help to find an integrated view to understand the mechanisms for the relation of biodiversity and ecosystem function at least for parts of the ecosystem. Model systems need to be viewed as parts of a holistic approach explaining the biodiversity and ecosystem functioning, but they are tools with strengths and weaknesses.

I would recommend the Ecological Network Analysis of ecosystems as a suitable tool to get more insight into the relationship between biodiversity and ecosystem function. However this needs models with a high resolution down to species level. If we compare the biodiversity of the different communities in the Sylt-Rømø Bight with indices derived from ENA, we see some relations of biodiversity and ecosystem function. Finn Cycling Index and the different connectivity indices were significantly correlated with the diversity of the system (expressed as Shannon Wiener Index or as flow diversity) (Asmus unpubl.) (Figs. 60 and 61). Hence Finn Cycling Index is positively correlated with flow diversity, recycling of material and with this the cycling within a community is increasing with increasing biodiversity and thus the dependence on exchange with the environment is lowered. Since more members in a food web of a community are interacting (indicated by higher internal and food web connectivity), the resources may be used more efficiently without larger losses (indicated by Finn Cycling Index).

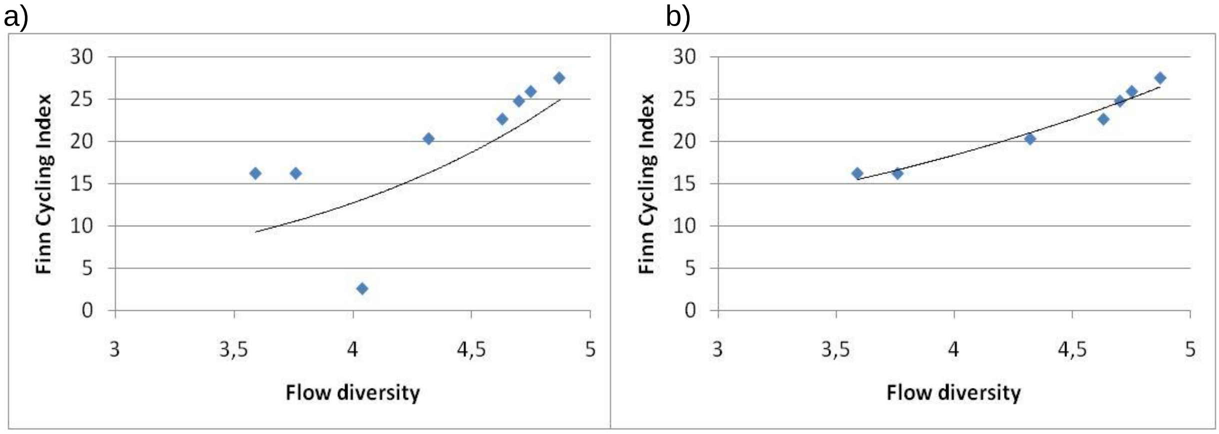


Fig. 60. Finn Cycling Index as measure for the recycling potential plotted versus flow diversity as measure for diversity of 8 (7) intertidal communities of the Sylt-Rømø Bight. a) with mussel beds and (Spearmann rank corr. coeff: r = 0.92; α = 0.005) b) without mussel beds (Spearmann rank corr. coeff: r = 0.97; α = 0.001).

The connectivity indices (Fig. 61) show a better correlation with species diversity as a measure for the structural diversity as compared with flow diversity which can be interpreted as functional diversity. Food web connectance was only significantly correlated with species diversity. Food web connectance only refers to the living compartments of a system. Especially in systems that are extremely influenced by external forces connectance is relatively high compared to the low flow diversity. Biomass of living compartments is low in those systems but more evenly distributed between the compartments, and this eveness increases the connectivity index, but on the other hand the number of compartments is lower in these systems and thus flow diversity decreases. If I exclude sandy shoals and sandy beaches from the analysis the food web connectance of the other communities shows a significant correlation (Spearman rank coeff.: 0.94; α = 0.005)

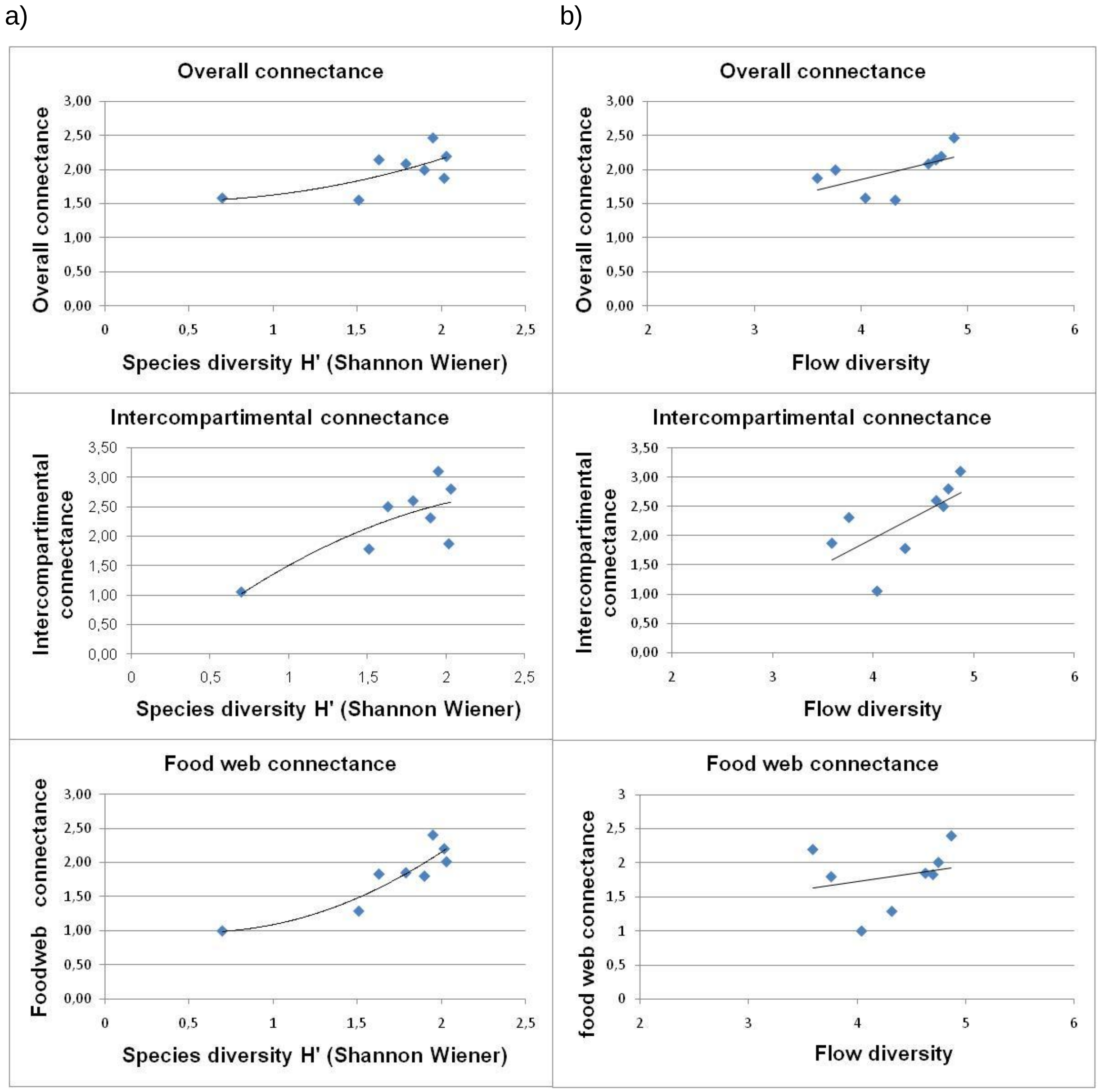


Fig. 61. Connectivity indices as measures for the strength of connections between species or compartments within communities a. plotted versus species diversity (H’) (Spearman rank corr. coeff overall: 0.59; α = 0.05; intercom.: 0.64; α = 0.05; food web: 0.83; α = 0.01), b. plotted versus flow diversity (as a measure for functional diversity) (Spearman rank corr. coeff. overall: = 0.79; α = 0.01; intercom.:0.79; α = 0.01; food web: not significant).

If I plot the net carbon import into a community as well as the net carbon export from a community with the recycling potential indicated as Finn Cycling Index (Fig. 62), a bell shape curve is resulting, showing a maximum at a carbon import of about 50 mg C m^{-2} h^{-1}. Mussel beds show a high particle import but an exceptionally low Finn Cycling Index, because recycling in this community is low and the material flux is unidirectionally aligned to production of macroalgae which is mainly exported from the system during storms and to high bird predation directing the carbon into bird biomass which is also exported mainly due to migration of most birds to places outside the Wadden Sea in spring and summer.

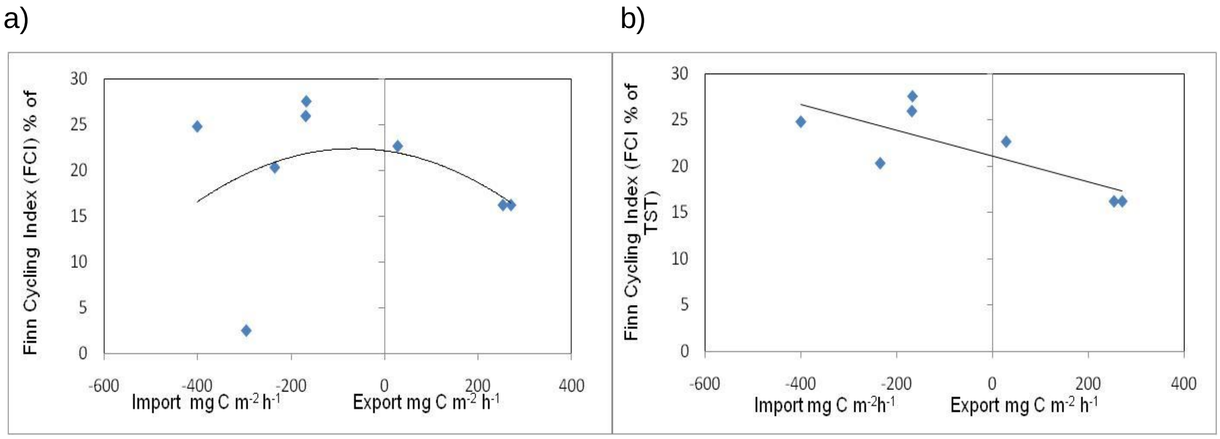


Fig. 62. Finn Cycling Index FCI scaled over net carbon import (negative fluxes) and net carbon export (positive fluxes) of the intertidal community of the Sylt-Rømø Bight. a. including mussel beds, b. excluding mussel beds (both not significant).

Excluding this special case of mussel beds the communities show a negative linear trend of recycling potential with the export of communities. This suggests that with decreasing recycling of carbon within a community the export or loss of material is increasing. Because biodiversity and the recycling potential are positively correlated, we may conclude from these results that the more diverse a community is and the more niches and members occupying these niches (in terms of species) it provides, the less is the material loss from this community. However this is only a tendency and should be confirmed by a larger set of habitats and networks.

There are some hints that the higher the diversity of a system the more efficient is the use of the material and the energy within the community, but this is only possible if the connection and interrelation between the different members of a community is stronger in diverse communities compared to less diverse communities. One hint is the positive correlation between the different connectance indices and the flow diversity (Fig. 61). The intercompartimental connectance only focusses on the strength of linkage between compartments of a system without considering the linkage to export and import functions. Intercompartimental connectance increases with increasing flow diversity, but the shape of the curve has a hyperbolic form suggesting a lower decrease towards lower flow diversities. The food web connectance only regards the living compartments, and the correlation between food web connectance and flow diversity suggests a more u-shaped curve showing an increase towards lower as well as higher diversities. This could be explained by the existence of two effects. One is that the strength of connections between compartments is increasing when only few food sources and few consumers are present, because a consumer is under constraint to use the only available food source. The other is that if more food sources have to be distributed among more consumers all parties will exert a strong influence on each other by tending to avoid using the same food sources and to occupy different niches. This implies a better “co-operation” between members of a community. This co-operation is probably improved in mature systems where the members of a community have the chance for co-evolution. Food web connectance may be also higher if the community is structured by certain key species, that are playing a crucial role for many members of a community.

The overall connectance includes all flows also the external ones. The difference between the overall connectance and the intercompartimental connectance reflects the dependence of a community from external food sources. The lower the difference is the more depends the community on external sources. In the tidal flat communities of the Sylt-Rømø Bight a gradient of dependence occurs from mussel beds and sandy beaches with a high dependence on external food sources to dense and sparse seagrass beds, mud flats and muddy sands where internal cycling is more important (Fig. 63).

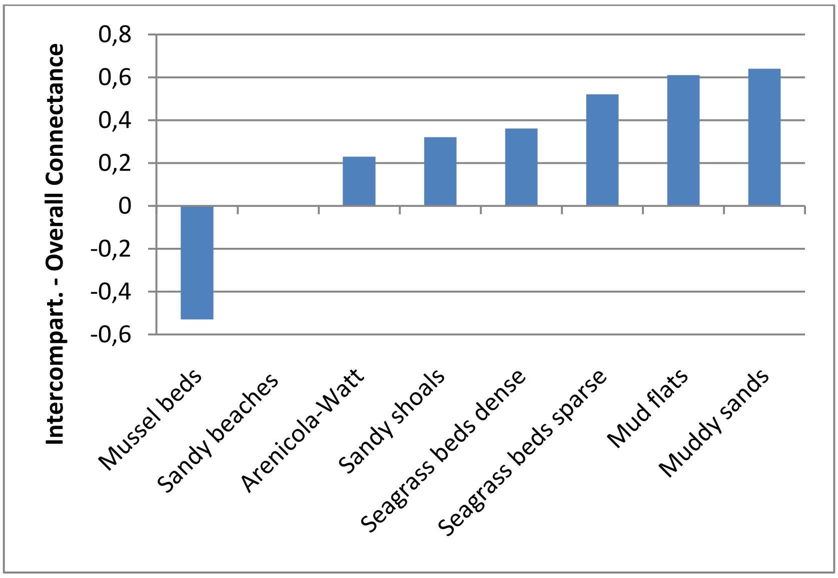


Fig. 63. Difference between intercompartimental and overall connectance index scaled over the different intertidal communities of the Sylt-Rømø Bight. High difference indicates a relatively low dependence of the community on external food sources.

Mussel beds are the community most rich in species, but the fluxes connecting the different species are unevenly distributed because of the high aggregation of mussels which dominate the biomass in this community by 90%. This is resulting in a low Shannon Wiener index (0,7) and also in a relatively low flow diversity (4.04). Although mussel beds show a high species richness but a strong dominance of few species, only few cycles are developed that have a parallel function and thus redundancy is low in this community.

A high reduncancy would indicate the existence of parrallel and probably competing cycles within a community, it would also indicate the share of food resource among different cycles.

Higher redundancy could therefore indicate a better use of food resources and thus a decrease of material that leaves the community without use.

Scaling relative redundancy to the import and export of the community shows an increase of redundancy in most communities with increasing import (Fig. 64). Because of the low redundancy in mussel beds and the high import of carbon into this community, the relation between relative redundancy and the carbon import is bell shaped.

Considering the export function of communities there is a clear decreasing trend of relative redundancy with increasing export of carbon from the community, supporting the hypothesis that more parallel cycles in a community improve the use and processing of the food sources and deminish the export of unused food.

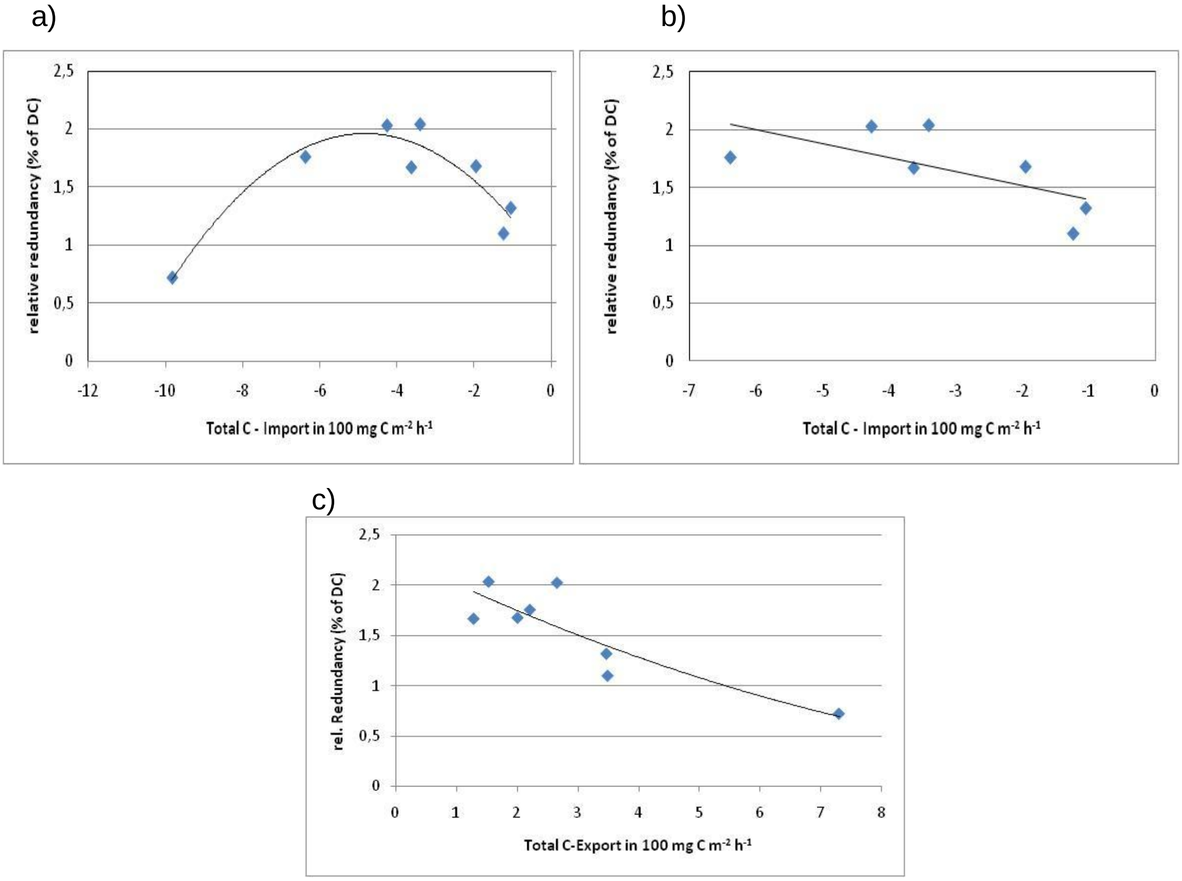


Fig. 64. Relationship between relative redundancy (in % of TST) and total import and export of carbon into and from a community a. import of carbon including mussel beds (Spearman rank corr. coeff: n.s.) b. import of carbon without mussel beds (Spearman rank corr. coeff.: R = 0.68; α = 0.05), c. export of carbon (Spearman rank corr. coeff.: r = 0.67; α = 0.05).

Until now only few systems are investigated in such a detail that comparisons like in this study are possible. There is an urgent need to make similar estimations and analyses with more different ecosystems showing a wider range of diversity.

6. Summary

Functioning of intertidal ecosystems of the Wadden Sea - Material exchange of the Sylt-Rømø Bight and its relation to habitat and species diversity

The Wadden Sea can be considered as a functionally diverse ecosystem. In the present thesis, various global system indices based on information theory describe the developmental and organizational state of the ecosystem. The wide range illustrates different states of organization in the various communities of the Sylt- Rømø Bight.

Energy flow studies of the Wadden Sea were up to now restricted to pure sand and mud flats, and have not been combined with studies on material exchange processes. I could show that energy flow varies considerably among the different habitats and that there is varying trophic efficiency due to habitat type. This results in low trophic efficiency when considering the total intertidal area of a tidal basin, and is primarily caused by low use of microphytobenthos and an overexploitation of autochthonous planktonic primary production in the dominant sand flat communities.

Material fluxes of 8 different habitats were measured using large *in situ* flumes (a special type of large scale field enclosure). Investigations on community metabolism and community production were performed and the results were synthesized by Ecological Network Analysis (ENA). The innovative potential of this work arises out of the combination of material flux studies, carried out with the novel *in situ* flume technology, and the ENA analysing the elemental flow and the food web from a holistic point of view.

I consider the sink and source functions on a community basis. This approach allows estimation of the filtration potential of a community and can distinguish it from passive sedimentation. This demonstrates that, presently, sedimentation in the intertidal part of the Sylt-Rømø Bight is the more relevant process compared to the function as a biological filter.

Material exchange and material cycles differ distinctly between the communities of the Sylt-Rømø Bight. The exchange of carbon varies both in magnitude and in the distribution pattern into different carbon forms, such as particulate, dissolved and living matter. Considering the different elements of the organic material such as carbon, nitrogen and phosphorus, there are also differences in flow characteristics and the prevalent form of material transport within one community. The present work shows that communities with a high allochthonous material input show a high internal material turnover.

In communities exposed to higher currents and wave action such as sparse seagrass beds, sandy shoals and sandy beaches, I observe a higher percentage of “small” material cycles

involving 2 compartments, compared to sheltered communities such as mud flats, dense seagrass beds and muddy sands, where 2 compartment cycles transport half or less than half the total amount of cycled material. This indicates both a quick cycling and a larger importance of a self-contained microbial loop in exposed communities.

In view of the existence of strong links between many predators and few prey species (i.e. few alternative or parallel pathways), especially the natural mussel bed system can be considered to possess less stability when faced with external perturbations (indicated by a low redundancy value). Redundancy indices for other communities are relatively high, reflecting multiple parallel pathways and thus, more resistance to external perturbations.

A further new insight from this analysis is how the amounts of the recycled elements carbon, nitrogen and phosphorus are distributed amongst the path length by which these elements are cycled. This new result was estimated for the total Sylt-Rømø Bight but will be of general importance for ecosystems: About 99% of carbon (C) is cycled over short path lengths involving 2–3 model compartments, and although path lengths of up to 9 were identified, the amount of carbon transported over longer ones is miniscule. Nitrogen (N) shows a clear bimodal distribution. Phosphorus (P) on the other hand shows a peak of recycling at path lengths 3 to 5, over which about 81% of P is recycled. Both N and P appear to be cycled over longer path lengths than C. This may also underline the importance of higher trophic levels such as invertebrates, fish and birds for element cycles such as nitrogen and phosphorus, whereas in carbon cycling, clearly short cycles are important, and microbial components are dominant.

Because the present network analysis is made with a high resolution down to species level, it can also be used to highlight the relationship between biodiversity and ecosystem functioning based on trophic system. I therefore found new quantitative evidence for the hypothesis of whether higher diversity is coupled with higher internal use of resources and with a more efficient cooperation within the system. This was tested by using simple correlations between certain system level indices and the diversity considered for the particular community. Since more members in a food web of a community are interacting (indicated by higher internal and food web connectivity), the resources may be used more efficiently without larger losses (indicated by Finn Cycling Index). Because biodiversity and the recycling potential are positively correlated, we conclude from these results a new theory that the more diverse a community is and the more niches and members occupying these niches (in terms of species) it provides, the less the material loss is from this community.

Considering the export function of communities, there is a clear decreasing trend of relative redundancy with increasing export of carbon from the community, supporting the hypothesis that more parallel cycles in a community improve the use and processing of the food sources and diminish the export of unused food.

The Sylt-Rømø Bight is thus one of the first marine intertidal systems where the food web structure has been described including the habitat constituents. We now understand better the spatial differences of functional resource use and resource partitioning in a tidal basin, and we know that the characteristics of the food web of the communities differ widely with respect to their dependence on benthic or pelagic sources.

It is also the first time in a marine intertidal system that exchange processes have been related with food web structure, and that global system indices derived from network analysis were used for understanding the relation between diversity and functioning of benthic systems.

7. Perspectives and implications for the future

The Wadden Sea is generally viewed as a subsidiary system that depends to a large extent on import processes that occur by tidal movements of North Sea coastal water into the system, as well as by riverine input from the land. The community based consideration in this synopsis emphasizes the importance of internal cycling for the system, and shows that internal cycling as well as the exchange between the community and its surrounding are mutually balanced. The behaviour of the ecosystem as a whole can thus be interpreted as the net result of the balance of internal cycling and exchange for the sum of the communities. This behaviour is expected to change with changes of the constitutional components of the system.

One goal of the present thesis is to relate the function of a food web described by ecological network analysis to exchange processes between intertidal communities and their ambient environment. It shows that increasing complexity and functional diversity result in an increase of the potential for material recycling and connectivity between elements, and an intensification of material exchange.

Investigating ecosystem function by analysing its community constituents is hardly practiced, particularly for the Wadden Sea. This allows evaluation of the relative importance of community functions for the total system, and assessment of the significance of communities for the energy flow. The community aspect is often poorly represented in energy flow studies. Including community aspects shows the influence of habitat structure and habitat diversity on ecosystem functioning.

The present study shows that network analysis is a suitable tool for elucidating the relationship of trophic ecosystem function as well as exchange processes to both habitat and species diversity. The model presented in this synopsis corresponds to a snapshot of the system which is representative of a time frame of the mid nineties of the last century. Thus it represents a quantitative picture of a part of the Wadden Sea before the major system alterations that are occurring presently, e.g. the invasion of neophytes and neozoics, but also sea level rise, temperature increase and a possible reduction of nutrient input due to better waste water management.

The above mentioned alterations could be accounted for by including these new parameters and changes into the model. The consequences for the total system, stability characteristics and the susceptibility to perturbations can be assessed and theories on the future of the Wadden Sea could be developed.

The model is also open to dramatic historic changes. The reduction of seagrass beds in the Wadden Sea since the thirties of the last century and the loss of subtidal benthic communities such as oyster beds and *Sabellaria* reefs could be estimated quantitatively by modifying the model with data for the altered extent of communities and their energy and material flow of components.

The relation of food web dynamics to exchange processes form a link between the system and the material import, thereby considering the system response by feed back mechanisms. This allows an action-oriented consideration of the impacts of human activities such as eutrophication or pollution on the food web.

Data on food web structure and function are converted by network analysis into a standardized form, such as the Lindeman spine, facilitating the comparison between food webs and ecosystems with different ecological backgrounds. Consideration of the community level allows the selection of comparable scales within systems of different sizes, and helps to exclude scaling artifacts when comparing different systems and scenarios.

Network analysis should obtain a wider application within ecological research, because it helps to strengthen theories and hypotheses of complex ecosystem functions that could be subsequently tested by experimental work. It also helps to synthesize ecological data gained from long term studies or monitoring programmes, and facilitates putting them into an ecosystem theoretical context. In this way it may also support the development of management strategies for the use of environmental resources by considering goods and services of an ecosystem as the result of its functioning.
In my eyes this study contributes a step toward explaining the complexity and multifunctional behaviour of a natural system.

8. Acknowledgements

With more than thanks I am indebted to my wife Ragnhild, who always encouraged and promoted me to start and never to dismiss this thesis. Although this thesis took long, she never lost confidence in me and held the belief that this work will once be finished.

Many of the thanks are due to Dan Baird who visited the Wadden Sea Station through many years and introduced me into the network analysis. Thus he gave me new ideas to see my own data in a new light and this gave the impetus to synthesise many years of field experimental work and formulate it in a context of system theory. I am especially grateful for his valuable and critical comments to this work and for the corrections of the English language.

My thanks are due to Sigrid Schiel who gave many helpful and valuable comments and corrections in a late stage of the text. She convinced me to go ahead with this work even after long time periods when other activities have had priority.

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10. Zusammenfassung

Funktion von eulitoralen Ökosystemen im Wattenmeer – Stoffaustausch in der Sylt-Rømø Bucht und ihr Bezug zur Habitat- und Artendiversität.

Das Wattenmeer kann als ein funktionell diverses Ökosystem angesehen werden. In der vorliegenden Habilitationsschrift beschreiben verschiedene allgemeine System-Indizes, die auf der Informationstheorie beruhen, den Entwicklungs- und Organisationszustand des Ökosystems. Der Organisationsstatus der einzelnen Lebensgemeinschaften der Sylt-Rømø Bucht unterscheidet sich dabei über einen weiten Bereich.

Untersuchungen zum Energiefluss des Wattenmeeres waren bisher auf reine Sand- und Schlickwatten beschränkt, und wurden nicht im Zusammenhang mit Stoffaustauschraten behandelt. In der vorliegenden Arbeit konnte ich zeigen, dass sich der Energiefluss stark innerhalb der verschiedenen Lebensgemeinschaften unterscheidet ebenso wie die Effizienz des trophischen Transfers. Dies ergibt eine geringe trophische Effizienz des gesamten Wattengebietes der Sylt-Rømø Bucht bedingt durch die Dominanz durch Sandwatten mit ihrer geringen Nutzung des Mikrophytobenthos und einer Übernutzung der autochthonen pelagischen Primärproduktion.

Stoff-Flüsse von 8 verschiedenen Lebensgemeinschaften wurden in großen *in-situ* Flumes (einer Einschluss-Methode auf großer Skala) gemessen. Untersuchungen zum Gemeinschaftsstoffwechsel und zur Gemeinschaftsproduktion wurden durchgeführt und die Ergebnisse wurden mit Hilfe der Ökologischen Network –Analyse synthetisiert. Das innovative Potential der vorliegenden Arbeit besteht in der Kombination von Stoff-Fluss-Untersuchungen mit Hilfe der neuen Flume Technik mit der Ökologischen Network Analyse (ENA), die den Stoff-Fluss der Elemente und das Nahrungsnetz nach einem holistischen Ansatz analysiert.

In der vorliegenden Synthese betrachte ich die Quellen- und Senken-Funktion auf der Basis der Lebensgemeinschaften und dies erlaubt mir die Berechnung des Filtrationspotentials jeder Gemeinschaft getrennt von der Berechnung des Stoffeintrages durch passive Sedimentation vorzunehmen. Gegenwärtig überwiegt im Gezeitengebiet der Sylt-Rømø Bucht die Sedimentation im Vergleich zur Funktion als biologischer Filter.

Stoffaustausch und Stoffkreisläufe unterscheiden sich deutlich zwischen den Lebensgemeinschaften der Sylt-Rømø Bucht. Der Austausch von Kohlenstoff unterscheidet sich sowohl in der Menge als auch in seiner Verteilung auf partikuläre, gelöste und lebende Zustandsformen. Bei Betrachtung der verschiedenen Elemente des organischen Materials wie Kohlenstoff, Stickstoff und Phosphor ergeben sich deutliche Unterschiede im Charakter der Stoffflüsse und der vorherrschenden Form des Materialaustausches innerhalb einer

Gemeinschaft. Die vorliegende Arbeit zeigt, dass Lebensgemeinschaften mit einem hohen natürlichen, allochthonen Stoffeintrag einen hohen internen Umsatz vollbringen.

In Lebensgemeinschaften, die hoher Strömung und Wellenenergie ausgesetzt sind, wie schüttere Seegraswiesen, Sandbänke und Sandstrände, beobachte ich einen höheren Prozentsatz an kleinen Stoffkreisläufen mit nur 2 Gliedern als in geschützten Lebensgemeinschaften, wie in Schlickwatten, dichten Seegraswiesen, und Mischwatten, in denen Kreisläufe mit 2 Gliedern nur die Hälfte oder weniger als die Hälfte an Material, das durch das gesamte Nahrungsnetz geschleust wird, transportieren. Dies zeigt sowohl einen schnellen Umsatz als auch eine höhere Bedeutung eines sich selbst erhaltenden „Microbial loop“ in solchen exponierten Lebensgemeinschaften an.

Infolge intensiver Kopplung vieler Räuber mit nur wenigen Beutearten (d.h. wenige alternative oder parallele Nahrungsbeziehungen) besitzt insbesondere das System einer natürlichen Muschelbank weniger Stabilität bei äußeren Störungen (charakterisiert durch einen geringen Redundancy Index). Diese Redundancy –Indizes sind aber für die anderen Lebensgemeinschaften relativ hoch und spiegeln dort viele parallele Nahrungsbeziehungen und daher eine größere Resistenz gegenüber äußeren Störungen wieder.

Eine weitere neue Einsicht dieser Analyse belegt, wie die Mengen der recycelten Elemente Kohlenstoff, Stickstoff und Phosphor auf einzelne Nahrungsketten unterschiedlicher Länge verteilt sind. Dies wurde für die gesamte Sylt-Rømø Bucht berechnet, ist aber eine neue Erkenntnis von genereller Bedeutung für Ökosysteme. 99% des Kohlenstoffs (C) wird über Kreisläufe mit nur 2-3 beteiligten Elementen geschleust. Obwohl für dieses System Nahrungsketten mit einer Länge bis zu 9 Elementen identifiziert werden konnten, war der Transport von C über längere Ketten nur minimal. Stickstoff (N) zeigte dagegen eine deutlich bi-modale Verteilung. Phosphor (P) zeigte ein Maximum der recycelten Menge in Nahrungsketten mit 3-5 Gliedern über die 81% des Phosphors transportiert wurden. Sowohl Stickstoff als auch Phosphor scheinen daher über längere Nahrungsketten transportiert zu werden als Kohlenstoff. Das könnte die Bedeutung höherer trophischer Niveaus wie Wirbellose, Fische und Vögel für den Stickstoff- und Phosphorkreislauf betonen, während im Kohlenstoffkreislauf deutlich kurze Nahrungsketten und damit mikrobielle Komponenten dominieren.

Da die vorliegende Networkanalyse mit hoher Auflösung bis zum Artniveau vorgenommen wurde, können wir damit auf der Basis trophischer Systeme die Beziehungen zwischen Biodiversität und Ökosystemfunktion beleuchten. Es konnte durch einfache Korrelationen zwischen bestimmten System- und Diversitäts-Indizes ein neuer quantitativer Nachweis für die Hypothese erbracht werden, nach der eine hohe Diversität einer Gemeinschaft mit einem hohen internen Verbrauch an Resourcen und einer engeren Zusammenarbeit innerhalb des Systems gekoppelt ist. Da mehr Mitglieder in einem Nahrungsnetz einer Gemeinschaft interagieren (dargestellt durch eine höhere „internal“ und „food web connectivity“), können die Resourcen effizienter ohne größere Verluste (dargestellt durch einen hohen Finn cycling Index) genutzt werden. Da Biodiversität und Recycling-Potential positiv korreliert sind, leiten wir daraus die neue Aussage ab, dass je diverser eine Lebensgemeinschaft ist und je mehr Nischen und Mitglieder oder Arten, die solche Nischen besetzen, es in ihr gibt, umso geringer wird der Materialverlust für diese Gemeinschaft sein.

Bei Betrachtung der Exportfunktion der Gemeinschaften wird ein deutlich abnehmender Trend der relativen Redundanz mit einem Anstieg des Kohlenstoffexportes aus einer Gemeinschaft sichtbar. Dies stützt die Hyopothese, dass mehr parallele Kreisläufe in einer Lebensgemeinschaft die Nutzung und die Verwertung der Nahrungsquellen verbessern und den Export von ungenutzter Nahrung verringern.

Die Sylt-Rømø Bucht ist daher eines der ersten marinen Gezeitengebiete, in dem die Nahrungsnetzstruktur unter Berücksichtigung der Zusammensetzung der Lebensräume und Gemeinschaften untersucht wurde. Nach diesem Ansatz verstehen wir die räumlichen Unterschiede in der Nutzung und der Verteilung der Nahrungsresourcen in einem Tidebecken besser und erkennen, daß sich der Charakter der Nahrungsnetze der Gemeinschaften besonders im Hinblick auf ihre Abhängigkeit von benthischen und pelagischen Nahrungsquellen stark unterscheidet.

Erstmalig für ein marines Gezeitensystem wurden die Austauschprozesse mit der Struktur und Funktion des Nahrungsnetzes in Beziehung gesetzt. Es wurden allgemeine System-Indizes aus der Networkanalysis verwendet, um das Verhältnis zwischen Biodiversität und Funktion benthischer Gemeinschaften zu verstehen.

11. Appendix

Tab. 1. Pelagic- benthic exchange of carbon for an intertidal mussel bed of the Sylt- Rømø Bay in mgC m^{-2} h^{-1} (yearly average), values were derived from the network model which does not give variance indications (SD or SE). Org C =living organic carbon, POC= particulate organic carbon, DOC =dissolved organic carbon, DIC = dissolved inorganic carbon.

Recipient → Donor ↓	**Bacteria**	**Fucus vesiculosus**	**Mikrophytobenth.**	**Mytilus edulis**	**Semi-Balanus balanoides**	**Balanus crenatus**	**Macoma balthica**	**Littorina littorea**	**Capitella capitata**	**Oligochaeta**	**Small Crustacea**	**Gammarus**	**Jaera albifrons**	**Malaco-ceros fuligi-nosus**	**Carcinus maenas**	**Sedim.**	**Org C**	**Partial flux**	**Type of flux**
$C_{Detritus}$	0	0	0	32.48			0.28	0	0	0	0	0	0	0	0	316.41	0	349.18	**POC-uptake**
$C_{Bacteria}$	0	0	0	2.32			0	0	0	0	0	0	0	0	0	0	2.32	2.32	**Org C-uptake**
$C_{Phyto-plankton}$	0	0	0	194.76	0.746	0.57	0.87	0	0	0	0	0	0	0	0	0	196.94	196.94	**Org C-uptake**
$C_{Zoopl\ food}$	0	0	0	2.47	0.746	0.57	0	0	0	0	0	0	0	0	0	0	3.79	3.79	**Org C-uptake**
$C_{Zoopl\ settlement}$	0	0	0	1.39			0.01	0.21	0.02	0	0.01	0	0	5.9E-06	0.07	0	1.71	1.71	**Org C-uptake**
C_{Drift}				57.49	0	0	88.71	0	0	0.69	0.01	34.73	0	0	13.36	0.00	194.99	194.99	**Org C-uptake**
C_{Fish}	0	0	0	0			0	0	0	0	0	0	0	0	0	0	0.00	0	**POC-uptake**
$C_{div\ birds}$	0	0	0	0			0	0	0	0	0	0	0	0	0	0	0.00	0	**POC-uptake**
C_{DOC}	10.22	0	3.1	0			0	0	0	0	0	0	0	0	0	0	0.00	13.32	**DOC-uptake**
C_{DIC}	0	216.82	4.11	0			0	0	0	0	0	0	0	0	0	0	0.00	220.93	**DIC-uptake**
	0	0	0	0			0	0	0	0	0	0	0	0	0	0	0.00	0	**Inorg. Sed.**
Flux per species	10.22	216.82	7.21	290.91	1.49	1.15	89.86	0.21	0.02	0.69	0.02	34.73	0	5.9E-06	13.43	316.41	399.75	983.18	

Tab. 1a. Sum of pelagic- benthic fluxes

Σ Org C	399.75
Σ POC	349.18
Σ DOC	13.32
Σ DIC	220.93
Σ Total	983.18

Tab.2. Benthic-pelagic exchange of carbon for an intertidal mussel bed of the Sylt- Rømø Bay in mgC m^{-2} h^{-1} (yearly average), values were derived from the network model which does not give variance indications (SD or SE). Org C =living organic carbon, POC= particulate organic carbon, DOC= dissolved organic carbon, DIC = dissolved inorganic carbon.

Recipient Donor	C_{Detritus}	C_{Bacteria}	$C_{\text{Phytopl.}}$	$C_{\text{Zoopl.}}$	$C_{\text{settlement}}$	$C_{\text{Macrophytes}}$	$C_{\text{Macro-Zoob.}}$	C_{DOC}	C_{DIC}	C_{Nekton}	C_{birds}	Flux per species
Bacteria	0	0	0	0	0	0	0	0	8.03	0	0	8,03
Fucus	0	0	0	0	0	163.90	0	3.28	56.06	0	0	223.24
Mikro-Phytob.os	0	0	0	0	0	0	0	0.67	1.43	0	0	2.10
Meiobenthos	0	0	0	0	0	0	0	0	1.74	0	0	1.74
Mytilus edulis	0	0	0	0	13.91	0	57.49	0	172.17	0	35.57	279.13
Semibalanus balanoides	0	0	0	0	0.18	0	0	0	1.00	0	0.0000	1.19
Balanus crenatus	0	0	0	0	0.14	0	0	0	0.77	0	0.0000	0.91
Macoma balthica	0	0	0	0	0.01	0	88.71	0	1.02	0.00001	3.81	93.54
Littorina littorea	0	0	0	0	0.35	0	0	0	58.29	0	0.32	58.96
Capitella capitata	0	0	0	0	0.03	0	0	0	1.81	0.0002	0.00	1.85
ΣOligochaet	0	0	0	0	0.00	0	0.69	0	0.74	0.0002	0.00	1.43
Kl Crustacea	0	0	0	0	0.02	0	0.02	0	2.31	0.002	0.0004	2.35
Gammarus spec.	0	0	0	0	0	0	34.73	0	0.93	5.8E-09	0	35.65
Jaera	0	0	0	0	0	0	0	0	0	0	0	0
Malacoceros	0	0	0	0	0.03	0	0	0	0.06	0.001	0.000	0.08
Carcinus maenas	0	0	0	0	0.12	0	13.36	0	2.31	0.009	3.973	19.77
SedPOC	0	0	0	0	0	0	0	0	0	0	0	0
Partial flux	0	0	0	0	14.80	163.90	194.99	3.95	308.65	0.01	43.67	
Type of flux	**POC**	**org C**	**org C**	**org C**	**org C**	**org C**	**org C**	**DOC**	**DIC**	**org C**	**org C**	729.97
								ΣDOC	**ΣDIC**	**ΣPOC**	**Σ Org C**	**TOTAL**
								3,95	308.65	0.00	417.37	

Tab. 3. Pelagic-benthic exchange of nitrogen for an intertidal mussel bed of the Sylt- Rømø Bay in mg N $m^{-2}h^{-1}$ (yearly average), values were derived from the network model which does not give variance indications (SD or SE). Org N =living organic nitrogen, PON= particulate organic nitrogen, DON =dissolved organic nitrogen, DIN = dissolved inorganic nitrogen.

Recipient Donor	**Bacteria**	**Fucus vesiculosus**	**Mikrophyto-benth.**	**Mytilus edulis**	**Semibalanus balanoides**	**Balanus crenatus**	**Macoma balthica**	**Littorina littorea**	**Capitella capitata**	**Oligochaeta spp.**	**small Crustacea**	**Gammarus spp.**	**Jaera albifrons**	**Malacoceros fuliginosus**	**Carcinus maenas**	**Sedim.**	**Org N**	**Partial flux**	**Type of flux**
N_{Detritus}	0	0	0	3.25	0	0	0.03	0	0	0	0	0	0	0	0	71.39	0	74.67	**PON**
N_{Bacteria}	0	0	0	0.45	0	0	0	0	0	0	0	0	0	0	0	0	0.45	0.45	**orgN**
$N_{\text{Phytopl.}}$	0	0	0	29.38	0.11	0.09	0.13	0	0	0	0	0	0	0	0	0	29.70	29.70	**orgN**
$N_{\text{Zoopl.}}$	0	0	0	0.56	0.17	0.13	0	0	0	0	0	0	0	0	0	0	0.86	0.86	**orgN**
$N_{\text{settlement}}$	0	0	0	0.32	0	0	0.00	0.05	0.00	0	0.00	0	0	1.3E-06	0.02	0	0.39	0.39	**orgN**
N_{Drift}	0	0	0	12.23	0	0	18.87	0.00	0.00	0.21	0.002	7.72	0.00	0.0E+00	2.97	0	42.00	42.00	**orgN**
N_{Fish}	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**orgN**
$N_{\text{div. birds}}$	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**orgN**
N_{DON}	1.02	33.18	0.62	0	0	0	0	0	0	0	0	0	0	0	0	0	0	34.82	**DON**
N_{DIN}	0	33.18	0.62	0	0	0	0	0	0	0	0	0	0	0	0	0	0	33.80	**DIN**
N_{sediment}	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**PON**
Flux per species	1.02	66.36	1.24	46.19	0.28	0.22	19.03	0.05	0.00	0.21	0.01	7.72	0.00	0.00	2.98	71.39	76.69	216.70	

Tab. 3a. Sum of pelagic-benthic

Σ Org N	73,41
Σ PON	74,67
Σ DON	34,82
Σ DIN	33,80
Σ Total	216,70

Tab.4. Benthic-pelagic exchange of nitrogen for an intertidal mussel bed of the Sylt- Rømø Bay in mgN m^{-2} h^{-1} (yearly average), values were derived from the network model which does not give variance indications (SD or SE). Org N =living organic nitrogen, PON= particulate organic nitrogen, DON= dissolved organic nitrogen, DIN = dissolved inorganic nitrogen.

Donor	**$N_{\text{Detr.}}$**	**$N_{\text{Bakterien}}$**	**$N_{\text{Phytoplankton}}$**	**$N_{\text{Zooplankton}}$**	**$N_{\text{settlement}}$**	**$N_{\text{Macrophytes}}$**	**$N_{\text{Macrozoob.}}$**	**N_{DON}**	**N_{DIN}**	**N_{Nekton}**	**N_{birds}**	**Flux per species**
Bakterien	0	0	0	0	0	0	0	0	1.17	0	0	1.17
Fucus	0	0	0	0	0	24.72	0	0.08	0	0	0	24.80
Mikrophytobenthos		0	0	0	0	0	0	0	0	0	0	0.00
Meiobenthos	0	0	0	0	0	0	0	0	0.37	0	0	0.37
Mytilus edulis		0	0	0	0	0	0	0.02	0	0	0	0.02
Semibalanus balanoides	0	0	0	0	3.17	0	12.23	0	22.99	0	7.57	45.96
Balanus crenatus	0	0	0	0	0.04	0	0	0	0.19	0	0	0.23
Macoma balthica	0	0	0	0	0.03	0	0	0	0.15	0	0	0.18
Littorina littorea	0	0	0	0	0	0	18.87	0	0.15	0.000001	0.81	19.84
Capitella capitata	0	0	0	0	0.08	0	0	0	0.94	0	0.07	1.09
ΣOligochaet	0	0	0	0	0.01	0	0	0	0.52	0.0001	0	0.53
small Crustacea	0	0	0	0	0	0	0.21	0	0.12	0.0001	0	0.33
Gammarus spec.	0	0	0	0	0	0	0.002	0	0.10	0.0005	0.0001	0.11
Jaera	0	0	0	0	0	0	7.72	0	0.15	1.3E-09	0	7.87
Malacoceros	0	0	0	0	0	0	0	0	0.10	0	0	0.1
Carcinus maenas	0	0	0	0	0.01	0	0	0	0.06	0.0004	0	0.067
SedPOC	0	0	0	0	0.03	0	2.97	0	0.76	0.002	0.883	4.64
Flume correction	0	0	0	0	0	0	0	0	11.58	0	0	11.58
Teil-flux	0.00	0	0	0	3.37	24.72	42.00	0.09	39.35	0.003	9.33	118.88
Type of flux	**PON**	**Org N**	**Org N**	**Org N**	**Org N**	**Org N**	**Org N**	**DON**	**DIN**	**Org N**	**Org N**	
								ΣDON	ΣDIN	ΣPON	Σ Org N	TOTAL
								0.09	39.35	0.00	79.43	

Tab. 5. Pelagic-benthic exchange of phosphorus for an intertidal mussel bed of the Sylt- Rømø Bay in mgP m^{-2} h^{-1} (yearly average), values were derived from the network model which does not give variance indications (SD or SE). Org P =living organic phosphorus, POP= particulate organic phosphorus, DOP =dissolved organic phosphorus, DIP = dissolved inorganic phosphorus.

Donor	**Bacteria**	**Fucus vesicu-losus**	**Mikro-phytob.**	**Mytilus edulis**	**Semiba-lanus balano-ides**	**Balanus crenatus**	**Macoma balthica**	**Littorina littorea**	**Capitella capitata**	**Oligo-chaeta**	**Small Crusta-cea**	**Gam-marus spp.**	**Jaera**	**Malaco ceros fuligin osus**	**Carcinus maenas**	**Sedim.**	**Org C**	**Teil-flux**	**Type of flux**
P_{Detritus}	0	0	0	0.76			0.01	0	0	0	0	0	0	0	0	11.16	0	11.92	**POP**
P_{Bact}	0	0	0	0.14			0	0	0	0	0	0	0	0	0	0	0.14	0.14	**Org P**
$P_{\text{Phytopl.}}$	0	0	0	1.84	0.01	0.01	0.01	0	0	0	0	0	0	0	0	0	1.86	1.86	**Org P**
$P_{\text{Zoopl.}}$	0	0	0	0.06	0.02	0.01	0	0	0	0	0	0	0	0	0	0	0.09	0.09	**Org P**
$P_{\text{settl.}}$	0	0	0	0.03			0	0.01	0	0	0	0	0	0	0	0	0.04	0.04	**Org P**
P_{Drift}				0.66	0	0	1.02	0	0	0.02	0	1.19	0	0	0.46	0	3.35	3.35	**Org P**
P_{Fish}	0	0	0	0			0	0	0	0	0	0	0	0	0	0	0	0	**POP**
$P_{\text{div.birds}}$	0	0	0	0			0	0	0	0	0	0	0	0	0	0	0	0	**POP**
P_{DOP}	0.24	0.48	0.01	0			0	0	0	0	0	0	0	0	0	0	0	0.73	**DOP**
P_{DIP}	0	2.05	0.04	0			0	0	0	0	0	0	0	0	0	0	0	2.08	**DIP**
Flux per species	0.24	2.53	0.05	3.48	0.02	0.02	1.03	0.01	0	0.02	0	1.19	0	0	0.46	11.16	5.47	20.21	

Tab. 5a. Sum of pelagic-benthic fluxes

Σ OrgP	5.48
Σ POP	11.92
Σ DOP	0.73
Σ DIP	2.08
Total	20.21

Tab.6. Benthic-pelagic exchange of phosphorus for an intertidal mussel bed of the Sylt- Rømø Bay in mgP m^{-2} h^{-1} (yearly average), values were derived from the network model which does not give variance indications (SD or SE). Org P =living organic phosphorus, POP= particulate organic phosphorus, DOP= dissolved organic phosphorus, DIP = dissolved inorganic phosphorus.

Donor	$P_{Detritus}$	$P_{Bacteria}$	$P_{Phytoplankton}$	$P_{Zooplankton}$	$P_{Zooplankton}$	$P_{Makro-phyten}$	$P_{Makro-Zoobenthos}$	**DOP**	**DIP**	P_{Nekton}	P_{birds}	**Flux per species**
Bacteria	0	0	0	0	0	0			3.42			3.42
Fucus					0	1.55	0	0.08	0			1.62
Microphytobenthos	0	0	0	0	0	0	0	0.02	0	0		1.43
Meiobenthos	0								0.06			0.06
Mytilus edulis	0.00	0	0	0	0.28	0	0.66	0	1.97	0	0.41	3.32
Semibalanus balanoides	0	0	0	0	0.0037	0	0	0	0.01	0	0	0.01
Balanus crenatus	0	0	0	0	0.0028	0	0	0	0.01	0	0	0.01
Macoma balthica	0.00	0	0	0	0.0002	0	1.02	0	0.02	0.0000001	0.04	1.04
Littorina littorea	0.00	0	0	0	0.0071	0	0	0	0	0	0.01	0.01
Capitella capitata	0.00	0	0	0	0.0007	0	0	0	0.13	0.00001	0	
Oligochaeta	0.00	0	0	0	0.0000	0	0.02	0	0.03	0.00001	0	0.05
Small Crustacea	0.00	0	0	0	0.0004	0	0.00	0	0.02	0.00007	0.00001	0.02
Gammarus spec.	0.00	0	0	0	0.0000	0	1.19	0	0.01	2.0E-10	0	1.20
Jaera	0.00				0.0000		0	0				
Malacoceros	0.00	0	0	0	0.0006	0	0	0	0.002	0.00005	0	0.00
Carcinus maenas	0.00	0	0	0	0.0023	0	0.46	0	0	0.0003	0.136	24.33
SedPOC	0	0	0	0	0.00	0	0	0	0	0	0	
Partial flux	0.00	0	0	0	0.30	1.55	3.35	0.09	5.68	0.0005	0.60	11.56
Type of flux	POP	org P	org P	org P	org P	org P	org P	DOP	DIP	org P		
								ΣDOP	ΣDIP	ΣPOP	Σ Org P	**TOTAL**
								0.09	5.68	0	5.79	**11.56**

Tab. 7. Pelagic- benthic exchange of carbon for an intertidal dense seagrass bed of the Sylt- Rømø Bay in mgC m^{-2} h^{-1} (yearly average), values were derived from the network model which does not give variance indications (SD or SE). Org C =living organic carbon, POC= particulate organic carbon, DOC =dissolved organic carbon, DIC = dissolved inorganic carbon.

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Recipient Donor	Bacteria Art n	Macro-phytes	Micro-phyto-benthos	Hydr. ulvae	Aren. marina	Oligo-chaeta spp.	Hetero-mastus filiformis	Cerastod. edule	Mya arenaria	small polychaetes	Tharyx kilari-ensis	M. bal-thica	Phyllodo-cidae	small Crusta-ceans	C. cran-gon	P. mi-crops	Neph. spp.	Sed.POC	partial flux	type of flux
$C_{Detritus}$	0	0	0	0	0	0	0	1.13	0.05	0.01	0	0.90	0	0	0	0	0	259.00	261.09	POC
$C_{Bacteria}$	0	0	0	0	0	0	0	0.08	0.003	0	0	0	0	0	0	0	0	0	0.08	Org C
$C_{Phytoplankton}$	0	0	0	0	0	0	0	163.70	0.30	0.07	0	5.54	0	0	0	0	0	0	169.60	Org C
$C_{Zooplankton}$	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Org C
$C_{settlement}$	0	0	0	0.33	0	0	0.004	0.35	0.04	0.01	0.010	0.150	0.004	0.010	0.001	0.001	0.025	0	0.93	Org C
C_{Drift}	0	0	0	4.27	5.98	0	0	0.21	0.02	0	0.010	85.33	0.145	0.020	0	0	0	0	96.89	Org C
C Fishes	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Org C
$C_{diving\ birds}$	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Org C
C_{DOC}	2.81	0	30.56	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	33.39	DOC
C_{DIC}	0	35.26	40.53	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	75.79	DIC
Flux per species	2.81	35.26	71.09	0.33	5.98	0	0.004	165.26	0.38	0.09	0.010	6.59	0.004	0.01	0.001	0.001	0.03	259.00	637.75	

Tab. 7a.
Sum of pelagic- benthic fluxes

Σ Org C	267.51
Σ POC	261.08
Σ DOC	33.36
Σ DIC	75.79
Total	637.75

Tab.8. Benthic-pelagic exchange of carbon for an intertidal dense seagrass bed of the Sylt- Rømø Bay in mgC m^{-2} h^{-1} (yearly average), values were derived from the network model which does not give variance indications (SD or SE). Org C =living organic carbon, POC= particulate organic carbon, DOC= dissolved organic carbon, DIC = dissolved inorganic carbon.

Donor	**C_{Detritus}**	**C_{Bacteria}**	**$C_{\text{Phytopl.}}$**	**$C_{\text{Zooplankton}}$**	**$C_{\text{settlement}}$**	**$C_{\text{Macrophytes}}$**	**$C_{\text{Macro-Zoobenthos}}$**	**DOC**	**DIC**	**C_{Nekton}**	**C_{birds}**	**flux per species**
Bacteria	2.81	0	0	0	0	0	0		8.03	0		10.83
Macrophytes	13.64	0	0	0	0	0	0	0.32	19.75	0	1.88	35.58
Microphytobenthos	0	0	0	0	0	0	0	6.62	14.07	0		20.68
Meiobenthos	1.01	0	0	0	0	0	0	0	1.740	0		2.75
Hydrobia ulvae	8.71	0	0	0	0.13	0	4.27	0	1.87	0	0.03	15.01
Littorina littorea	0	0	0	0	0	0	0	0	0	0		
Arenicola marina	17.80	0	0	0	0	0	5.98	0	3.50	0	0.02	27.30
Oligochaeta spp.	0	0	0	0	0	0	0.69	0	0.18	0.001	0.004	0.88
Heteromastus filiformis	0.25	0	0	0	0.002	0	0	0	0.04	0.001	0	0.30
Cerastoderma edule	5.88	0	0	0	0.14	0	0.21	0	0.75	0	0.06	7.02
Mya arenaria	0.08	0	0	0	0.01	0	0.02	0	0.16	0	0.003	0.27
small polychaetes	0.08	0	0	0	0.004	0	0.22	0	0.20	0.03	0.001	0.53
Tharyx kilariensis	0	0	0	0	0	0	0.01	0	0	0		0.01
Macoma balthica	5.97	0	0	0	0.06	0	85.33	0	6.56	0	0.01	97.93
Phyllodoce sp.	0.02	0	0	0	0	0	0.15	0	0.12	0	0.001	0.28
small crustaceans	0.05	0	0	0	0.004	0	0.02	0	0.15	0.002	0.01	0.24
Crangon crangon	0.02	0	0	0	0.001	0	0	0	0.05	0	0	0.07
Nephthys spp.	0.88	0	0	0	0.01	0	0	0	0.24	0.01	0.003	1.14
Pomatoschistus microps	0.11	0	0	0	0	0	0	0	0.01	0	0	0.12
SedPOC	0	0	0	0	0	0	0	0	0	0		
partial flux	57.29	0	0	0	0.37	0	96.885	6.932	57.40	0.045	2.02	**220.93**
Type of flux	**POC**	**org C**	**org C**	**org C**	**org C**	**org C**	**org C**	**DOC**	**DIC**	**org C**	**org C**	

ΣDOC	**ΣDIC**	**ΣPOC**	**Σ Org C**	**TOTAL**
6.93	57.39	57.29	99.31	**220.93**

Tab.9. Pelagic-benthic exchange of nitrogen for an intertidal dense seagrass bed of the Sylt- Rømø Bay in mgN m^{-2} h^{-1} (yearly average), values were derived from the network model which does not give variance indications (SD or SE). Org N =living organic nitrogen, PON= particulate organic nitrogen, DON =dissolved organic nitrogen, DIN = dissolved inorganic nitrogen.

Donor	Bacteria	Macro-phytes	Micro-phyto-benthos	H. ulvae	A. mari-na	Oligochaeta spp.	Hetero-mastus filiformis	C. edule	Mya arenaria	small polych.	Tharyx kilari-ensis	M. balthi-ca	Phyllo-docidae	small Crusta-ceans	C. cran-gon	P. microps	Neph-thys spp.	Sed. POC	partial flux	type of flux
$N_{Detritus}$	0	0	0	0	0		0	0,11	0	0	0	0,09	0	0	0	0	0	17,53	17,74	PN
$N_{Bakterien}$	0	0	0	0	0	0	0	0,02	0	0	0	0	0	0	0	0	0	0	0,02	Org N
$N_{Phytoplankton}$	0	0	0	0	0	0	0	24,69	0,04	0,01	0	0,84	0	0	0	0	0	0	25,58	Org N
$N_{Zooplankton}$	0	0	0	0	0	0	0				0		0	0	0	0	0	0	0,00	OrgN
$N_{settlement}$		0	0	0,07	0	0	0	0,08	0,01	0	0	0,03	0	0	0	0	0,01	0	0,21	Org N
N_{Drift}	0	0	0	0,91	1,79	0,21	0	0,04	0	0,07	0	18,16	0,04	0	0	0	0	0	21,22	Org N
N_{Fishes}	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0,00	Org N
N Tauchvögel	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0,00	Org N
N_{DON}	0,28	2,94	6,11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	9,33	DON
N_{DIN}		2,94	6,11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	9,05	DIN
Flux per species	0,28	5,88	12,22	0,98	1,79	0,21	0	24,94	0,06	0,08	0,01	19,12	0,04	0,01	0,00	0,00	0,01	17,53	83,15	

Tab. 5a. Sum of pelagic-benthic fluxes

Σ Org N	47,03
Σ PON	17,74
Σ DON	9,33
Σ DIN	9,05
Total	83,15

Tab.10. Benthic-pelagic exchange of nitrogen for an intertidal dense seagrass bed of the Sylt- Rømø Bay in mgN m^{-2} h^{-1} (yearly average), values were derived from the network model which does not give variance indications (SD or SE). Org N =living organic nitrogen, PON= particulate organic nitrogen, DON= dissolved organic nitrogen, DIN = dissolved inorganic nitrogen.

Recipient Donor	**$N_{Detritus}$**	**$N_{Bacteria}$**	**N Phytoplankton**	**N Zooplankton**	**$N_{settlement}$**	**N Macrophytes**	**$N_{Macro-Zoobenthos}$**	**DON**	**DIN**	**N_{Nekton}**	**N_{birds}**	**flux per species**
Bacteria	0.28	0	0	0	0	0	0	0	1.17	0		1.46
Macrophytes	1.36	0	0	0	0	0	0	0.01	0	0	0.28	1.65
Microphytobenthos	0	0	0	0	0	0	0	0.16	0	0		0.16
Meiobenthos	0.07	0	0	0	0	0	0		0.37	0		0.44
Hydrobia ulvae	0.87	0	0	0	0.03	0	0.91	0	0.30	0	0.01	2.12
Arenicola marina	1.78	0	0	0	0	0	1.79	0	1.57	0	0.01	5.14
Oligochaeta spp.	0.00	0	0	0	0	0	0.21	0	0.03	0	0.001	0.24
Heteromastus filiformis	0.03	0	0	0	0	0	0	0	1.09	0	0	1.12
Cerastoderma edule	0.59	0	0	0	0.03	0	0.04	0	0.35	0	0.01	1.03
Mya arenaria	0.01	0	0	0	0.003	0	0.003	0	0.01	0	0.001	0.03
small polychaetes	0.01	0	0	0	0.001	0	0.07	0	0.03	0.008	0	0.11
Tharyx kilariensis	0	0	0	0	0	0	0.003	0	0.01	0	0	0.01
Macoma balthica	0.60	0	0	0	0.01	0	18.16	0	0.48	0	0.002	19.25
Phyllodoce	0.001	0	0	0	0	0	0.04	0	0.01	0	0	0.06
small crustaceans	0.01	0	0	00	0.001	0	0.004	0	0.02	0	0.002	0.03
Crangon crangon	0.001	0	0	0	0	0	0	0	0.03	0	0	0.03
Nephthys spp.	0.09	0	0	0	0.002	0	0	0	0.16	0.004	0.001	0.26
Pomatoschistus microps	0.01	0	0	0	0.	0	0	0	0	0	0	0.01
SedPOC	0	0	0	0	0	0	0	0	0	0	0	0
partial flux	5.698	0	0.000	0.000	0.083	0.000	21.22	0.165	5.63	0.01	0.32	33.13
type of flux	**PON**	**org N**	**org N**	**org N**	**org N**	**org N**	**org N**	**DON**	**DIN**	**org C**	**org C**	

PON	**org N**	**DON**	**DIN**	**Total**
5.70	21.63	0.17	5.63	33.13

Tab. 11. Pelagic-benthic exchange of phosphorus for an intertidal dense seagrass bed of the Sylt- Rømø Bay in mgP m^{-2} h^{-1} (yearly average), values were derived from the network model which does not give variance indications (SD or SE). Org P =living organic phosphorus, POP= particulate organic phosphorus, DOP = dissolved organic phosphorus, DIP = dissolved inorganic phosphorus.

Recipient Donor	**Bacteria**	**Macrophytes**	**Microphytobenth**	**H. ulvae**	**A. marina**	**Oligochaeta spp.**	**H. filiformis**	**C. edule**	**M. arenaria**	**small polychaetes**	**Tharyx kilariensis**	**M. balthica**	**Phyllodocidae**	**small Crustaceans**	**C. crangon**	**P. microps**	**Nepht. spp.**	**Sed. POC**	**partial flux**	**type of flux**
P_{Detritus}	0	0	0	0	0	0	0	0.03	0.001	0.0003	0	0.021	0	00	0	0	0	3.98	4.03	POP
P_{Bacteria}	0	0	0	0	0	0	0	0.01	0.0002	0.000	0	0	0	0	0	0	0	0	0.005	Org P
$P_{\text{Phytopl.}}$	0	0	0	0	0	0	0	1.54	0.003	0.001	0	0.052	0	0	0	0	0	0	1.60	Org P
$P_{\text{Zooplankt.}}$	0	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0	0	Org P
$P_{\text{settlement}}$	0	0		0.007	0	0	0.0001	0.01	0.001	0.0002	0.0002	0.003	0.0001	0.0002	0.00003	0.00001	0.001	0	0.02	Org P
P_{Drift}	0	0	0	0.15	0.20	0.02	0	0.002	0.0002	0.008	0.0003	0.981	0.005	0.001	0	0	0	0	1.37	Org P
P_{Fishes}	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Org P
$P_{\text{div.birds}}$	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Org P
DOP	0.07	0.04	0.09	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.20	DOP
DIP	0	0.10	0.38	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.48	DIP
Flux pro Art	0.07	0.14	0.47	0.15	0.20	0.024	0.000	1.59	0.005	0.009	0.001	1.057	0.005	0.001	0.000	0.000	0.001	3.98	7.70	

Tab. 11a. Sum of pelagic-benthic fluxes

Σ Org P	2.99
Σ POP	4.03
Σ DOP	0.20
Σ DIP	0.48
Total	7.70

Tab.12. Benthic-pelagic exchange of phosphorus for an intertidal dense seagrass bed of the Sylt- Rømø Bay in mgP m^{-2} h^{-1} (yearly average), values were derived from the network model which does not give variance indications (SD or SE). Org P =living organic phosphorus, POP= particulate organic phosphorus, DOP= dissolved organic phosphorus, DIP = dissolved inorganic phosphorus.

Recipient **Donor**	**$P_{Detritus}$**	**$P_{Bacteria}$**	**$P_{Phytopl.}$**	**$P_{Zooplankton}$**	**$P_{settlement}$**	**$P_{Macrophytes}$**	**$P_{Macro-Zoobenthos}$**	**DOP**	**DIP**	**P_{Nekton}**	**P_{birds}**	**flux per species**
Bacteria	0.07	0	0	0	0	0	0	0	1.21	0	**0**	1.28
Macrophytes	0.04	0	0	0	0	0	0	0.0001	0	0	0.02	0.06
Microphytobenthos	0	0	0	0	0	0	0	0.0023	0	0	0	0.002
Hydrobia ulvae	0.26	0	0	0	0.003	0	0.146	0	0.03	0.000004	0.001	0.44
Arenicola marina	0	0	0	0	0	0	0	0	0	0	0	0
Oligochaeta spp.	0.42	0	0	0	0	0	0.20	0	0.28	0.000014	0.001	0.90
Heteromastus filiformis	0.000	0	0	0	0	0	0.02	0	0.01	0.000046	0	0.03
Cerastoderma edule	0.01	0	0	0	0.00003	0	0.000	0	0.30	0.000046	0	0.31
Mya arenaria	0.09	0	0	0	0.003	0	0.002	0	0.000	0	0.001	0.09
small polychaetes	0.001	0	0	0	0.0003	0	0.0002	0	0.000	0	0	0.002
Tharyx kilariensis	0.002	0	0	0	0.0001	0	0.008	0	0.000	0.000309	0	0.01
Macoma balthica		0	0	0	0	0	0.0003	0	0.01		0	0.01
Phyllodoce	0.09	0	0	0	0.001	0	0.98	0	0.04	0.000002	0	1.11
small crustaceans	0.0003	0	0	0	0	0	0.005	0	0.	0.000000	0	0.005
Crangon crangon	0.0001	0	0	0	0.0001	0	0.001	0	0	0.000060	0	0.001
Nephthys spp.	0.00004	0	0	0	0.00001	0	0.000	0	0.01	0.000000	0	0.01
Pomatoschistus microps	0.02	0	0	0	0.0002	0	0.000	0	0	0.000432	0	0.02
SedPOC	0.01	0	0	0	0.00001	0	0.000	0	0.07	0.000006	0	0.08
partial flux	1.00	0	0	0	0.007	0	1.37	0.002	1.96	0.001	0.021	**4.37**
type of flux	POP	org P	org P	org P	org P	org P	org P	DOP	DIP	org P	org P	Total

Σ Org P	ΣPOP	ΣDOP	Σ DIP	Total
1,40	1,00	0,002	1,96	4,37

Tab.13. Pelagic- benthic exchange of carbon for an intertidal sparse seagrass bed of the Sylt- Rømø Bay in mgC m^{-2} h^{-1} (yearly average), values were derived from the network model which does not give variance indications (SD or SE). Org C =living organic carbon, POC= particulate organic carbon, DOC =dissolved organic carbon, DIC = dissolved inorganic carbon.

Recipient Donor	**Bacteria**	**Macrophytes**	**Mikrophytobenth.**	***H. ulvae***	***Littorina littorea***	***A. marina***	***S. armiger***	***Capitella capitata***	**Oligochaeta spp.**	***C.edule***	***M. arenaria***	***M. balthica***	***Phyllodoce***	***Carcinus maenas***	***Crangon crangon***	***P.microps***	**Sed. POC**	**partial flux**	**type of flux**
C_{Detritus}	0	0	0	0	0	0	0	0	0	0.84	0.06	0.34	0	0	0	0	0.00	1.24	POC
C_{Bacteria}	0	0	0	0	0	0	0	0	0	0.06	0.004	0	0	0	0	0		0.06	org C
$C_{\text{Phytoplank.}}$	0	0	0	0	0	0	0	0	0	5.12	0.36	2.07	0	0	0	0		7.55	org C
$C_{\text{Zooplankton}}$	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		0.00	org C
$C_{\text{settlement*}}$	0	0	0	0.80	0.02	0.00	0.02	0.01	0.00	0.27	0.04	0.05	0.00	0.02	0.001	0.00004		1.24	org C
C_{Drift}	0	0	0	9.26	0	2.72	0.52	0	0.3	0.255	0.035	42.13	0.09	18.62	0	0		73.93	org C
C_{Fishes}	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		0.00	org C
$C_{\text{diving birds}}$	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		0.00	org C
DOC	15.90	0	28.30	0	0	0	0	0	0	0	0	0	0	0	0	0		44.20	DOC
DIC		29.41	37.56	0	0	0	0	0	0	0	0	0	0	0	0	0		66.97	DIC
Flux per species	15.90	29.41	65.86	10.06	0.02	2.72	0.54	0.01	0.30	6.55	0.50	44.59	0.09	18.64	0.00	0.00	0.00	195.19	

Tab. 13a. Sum of pelagic-benthic fluxes

Σ org C	**82,79**
Σ POC	**1,24**
Σ DOC	**44,20**
Σ DIC	**66,97**
Total	**195,20**

Tab.14. Benthic-pelagic exchange of carbon for an intertidal sparse seagrass bed of the Sylt- Rømø Bay in mgC m^{-2} h^{-1} (yearly average), values were derived from the network model which does not give variance indications (SD or SE). Org C =living organic carbon, POC= particulate organic carbon, DOC= dissolved organic carbon, DIC = dissolved inorganic carbon.

Donor	C_{Detritus}	C_{Bacteria}	$C_{\text{Phytoplankton}}$	$C_{\text{Zooplankton}}$	$C_{\text{settlement}}$	$C_{\text{Makrophyten}}$	$C_{\text{Makro-Zoobenthos}}$	C_{DOC}	C_{DIC}	C_{Nekton}	C_{birds}	**Flux per species**
Bacteria	0	0	0	0	0	0	0	0	2.89	0	0	2.89
Macrophytes	5.17	0	0	0	0	0	0	0.14	8.98	0	1.74	16.03
Microphytobenthos	0	0	0.00	0	0	0	0	6.1	13.0	0	0	19.16
Meiobenthos	2.02	0	0	0	0	0	0	0	3.5	0	0	5.50
Hydrobia ulvae	21.21	0	0	0	0.32	0	9.3	0	3.03	0.0002	0.05	33.90
Littorina littorea	0.24	0	0	0	0.01	0	0	0	0.05	0.0008	0.00	0.30
Arenicola marina	0	0	0	0	0	0	2.72	0	2.54	0.0008	0.02	5.28
Scoloplos armiger	0	0	0	0	0	0	0	0	0.17	0.0075	0.003	0.18
Capitella capitata	0	0	0	0	0.005	0	0	0	0.25	0.0138	0.003	0.27
Oligochaeta spp.	0	0	0	0	0	0	0.3	0	0.29	0.0138	0.00	0.60
Cerastoderma edule	4.45	0	0	0	0.11	0	0.255	0	0.38	0.00003	0.06	5.24
Mya arenaria	0.10	0	0	0	0.02	0	0.035	0	0.20	0.00	0.003	0.35
Macoma balthica	2.25	0	0	0	0	0	42.13	0	2.53	0.0003	0.01	46.92
Phyllodoce	0.01	0	0	0	0.001	0	0.09	0	0.10	0.000	0.007	0.21
Carcinus maenas	0.26	0	0	0	0.01	0	18.62	0	0.05	0.001	0.003	18.94
Crangon crangon	0.02	0	0	0	0.0006	0	0	0	0.05	0	0	0.07
Pomatoschistus microps	0.11	0	0	0	0	0	0	0	0.01	0.00004	0	0.12
SedPOC	44.64	0	0	0	0	0	0	0	0	0	0	44.64
Partial flux	80.48	0.00	0.00	0.00	0.46	0	73.44	6.27	38.01	0.04	1.89	200.60
Type of flux	POC	org C	org C	org C	org C	org C	org C	DOC	DIC	org C	org C	**TOTAL**

ΣDOC	ΣDIC	ΣPOC	Σ Org C	TOTAL
6.27	38.01	80.48	75.84	200.60

Tab.15. Pelagic-benthic exchange of nitrogen for an intertidal sparse seagrass bed of the Sylt- Rømø Bay in mgN m^{-2} h^{-1} (yearly average), values were derived from the network model which does not give variance indications (SD or SE). Org N =living organic nitrogen, PON= particulate organic nitrogen, DON =dissolved organic nitrogen, DIN = dissolved inorganic nitrogen.

Donor	**Bacteria**	***Macro-phytes***	**Mikrophyto-benthos**	***Hydrobia ulvae***	***Littorina littorea***	***Arenicola marina***	***Scoloplos armiger***	***Capitella capitata***	**Oligochaeta spp.**	***Cerastoderma edule***	***Mya arenaria***	***Macoma balthica***	***Phyllodoce***	***Carcinus maenas***	***Crangon crangon***	***Pomatoschistus microps***	**Sediment POC**	**partial flux**	**type of flux**
N_{Detritus}	0	0	0	0	0	0	0	0	0	0.08	0.01	0.03	0	0	0	0	0	0.12	PON
N_{Bacteria}	0	0	0	0	0	0	0	0	0	0.01	0.001	0	0	0	0	0	0	0.01	org N
$N_{\text{Phytopl.}}$	0	0	0	0	0	0	0	0	0	0.77	0.05	0.31	0	0	0	0	0	1.14	org N
$N_{\text{Zoopl.}}$	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.00001	0	<0.001	org N
$N_{\text{settlement*}}$	0	0	0	0.18	0.005	0	0.01	0	0	0.06	0.01	0.01	0	0	0	0	0	0.28	org N
N_{Drift}	0	0	0	1.97	0	0.81	0.16	0	0.09	0.05	0.01	8.96	0.03	4.14	0	0	0	16.22	org N
N_{Fishes}	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	PON
$N_{\text{diving birds}}$	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	PON
DON	1.59	2.45	5.66	0	0	0	0	0	0	0	0	0	0	0	0	0	0	9.70	DON
DIN	0	2.45	5.66	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8.12	DIN
Flux per species	1.59	4.90	11.32	2.15	0.006	0.81	0.16	0	0.09	0.98	0.08	9.32	0.03	4.14	0	0.00001	0	35.59	

Tab. 15a. Sum of pelagic-benthic fluxes

Σ orgN	**17.65**
Σ PON	**0.12**
Σ DON	**1.59**
Σ DIN	**8.12**
Total	**27.48**

Tab.16. Benthic-pelagic exchange of nitrogen for an intertidal sparse seagrass bed of the Sylt- Rømø Bay in mgN m^{-2} h^{-1} (yearly average), values were derived from the network model which does not give variance indications (SD or SE). Org N =living organic nitrogen, PON= particulate organic nitrogen, DON= dissolved organic nitrogen, DIN = dissolved inorganic nitrogen.

Donor	**$N_{Detritus}$**	**$N_{Bacteria}$**	**$N_{Phytoplankton}$**	**$N_{Zooplankton}$**	**$N_{settlement}$**	**$N_{Makrophytes}$**	**$N_{Makro-Zoobenthos}$**	**DON**	**DIN**	**N_{Nekton}**	**N_{birds}**	**Flux per species**
Bakterien	0	0	0	0	0	0	0	0,00	5,99	0	0	5,99
Seegras	0.52	0	0	0	0	0	0	0,003	0,00	0	0,15	0,67
Mikrophytobenthos	0	0	0.00	0	0	0	0	0,613	0,0	0	0	0,61
Hydrobia ulvae	2.93	0	0	0	*0.07*	0	1,98	0	0,51	0,0000	0,01	5,49
Littorina littorea	0.03	0	0	0	0.00	0	0,00	0	1,32	0,0002	0,00	1,35
Arenicola marina	0.00	0	0	0	0.00	0	0,81	0	1,14	0,0003	0,01	1,96
Scoloplos armiger	0.00	0	0	0	0.00	0	0,16	0	0,06	0,002238806	0,001	0,22
Capitella capitata	0.00	0	0	0	0.001	0	0	0	0,08	0,0041	0,001	0,09
Oligochaeta spp.	0.00	0	0	0		0	0,09	0	0,05	0,0041	0,0	0,14
Cerastoderma edule	0.44	0	0	0	0.02	0	0,05	0	0,10	0,00001	0,01	0,63
Mya arenaria	0.01	0	0	0	0.00	0	0,01	0	0,04	0,00	0,001	0,07
Macoma balthica	0.30	0	0	0	0.00	0	8,96	0	0,26	0,0001	0,002	9,53
Phyllodoce	0.00	0	0	0	0.000	0	0,02	0	0,02	0,000	0,002	0,04
Carcinus maenas	0.06	0	0	0	0.00	0	4,14	0	0	0,0002	0,0007	4,20
Crangon crangon	0.00	0	0	0	0.0001	0	0,00	0	0,043	0	0	0,05
Pomatoschistus microps	0.02	0	0	0	0.00	0	0,00	0	0,01	0,00001	0	0,03
SedPOC	3.53	0	0	0	0	0	0	0		0	0	3,53
partial flux	7.85	0	0.00	0.00	0.11	0,00	16,22	0,62	9,63	0,01	0,18	34,61
type of flux	PON	org N	org N	org N	org N	org N	org N	DON	DIN	org N	org N	

ΣDON	ΣDIN	ΣPON	Σ Org N	**TOTAL**
0.62	9.63	7.85	16.52	**34.61**

Tab. 17. Pelagic-benthic exchange of phosphorus for an intertidal sparse seagrass bed of the Sylt- Rømø Bay in mgP m^{-2} h^{-1} (yearly average), values were derived from the network model which does not give variance indications (SD or SE). Org P =living organic phosphorus, POP= particulate organic phosphorus, DOP =dissolved organic phosphorus, DIP = dissolved inorganic phosphorus.

Donor	**Bacteria**	***Macro-phytes***	**Mikro-phyto-benthos**	***H. ulvae***	***Litto-rina littorea***	***A. marina***	***Scol. armiger***	**Oligo-chaeta spp.**	***C. edule***	***Mya aren-aria***	***M. balthica***	***Phyllo-doce spp.***	***C. maenas***	***C. crangon***	***P. microps***	**Sed.POP**	**partial flux**	**type of flux**
P $_{\text{Detritus}}$	0	0	0	0	0	0	0	0	0.02	0	0.01	0	0	0	0	0	0.03	POP
P $_{\text{Bacteria}}$	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.00	org P
P $_{\text{Phytopl.}}$	0	0	0	0	0	0	0	0	0.05	0	0.02	0	0	0	0	0	0.07	org P
P $_{\text{Zooplankton}}$	0	0	0	0	0	0	0	0	0	0.002	0	0	0	0	0	0	0.00	org P
P $_{\text{settlement*}}$	0	0	0	0.02	0	0	0.00	0	0.01	0.002	0	0.005	0.02	0.001	0.001	0	0.04	org P
P $_{\text{Drift}}$	0	0	0	0.32	0	0.09	0.02	0.01	0	0.002	0.48	0.005	0.64	0	0	0	1.56	org P
P $_{\text{Fishes}}$	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.00	org P
P $_{\text{diving birds}}$	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.00	org P
DOP	0.37	0.04	0.08	0	0	0	0	0	0	0	0	0	0	0	0	0	0.49	DOP
DIP		0.08	0.35	0	0	0	0	0	0	0	0	0	0	0	0	0	0.44	DIP
Flux per species	0.37	0.12	0.44	0.33	0	0.09	0.02	0.01	0.08	0.01	0.51	0.01	0.65	0.001	0.001	0	2.63	

Tab. 17a. Sum of pelagic-benthic fluxes

Σ org P	1.68
Σ POP	0.03
Σ DOP	0.49
Σ DIP	0.44
Total	2.64

Tab.18. Benthic-pelagic exchange of phosphorus for an intertidal sparse seagrass bed of the Sylt- Rømø Bay in mgP m^{-2} h^{-1} (yearly average), values were derived from the network model which does not give variance indications (SD or SE). Org P =living organic phosphorus, POP= particulate organic phosphorus, DOP= dissolved organic phosphorus, DIP = dissolved inorganic phosphorus.

Donor	**P** $_{\text{Detritus}}$	**P** $_{\text{Bacteria}}$	**P** $_{\text{Phytoplankton}}$	**P** $_{\text{Zooplankton}}$	**P** $_{\text{settlement}}$	**P** $_{\text{Makro-phytes}}$	**P** $_{\text{Makro- Zoobenthos}}$	**P** $_{\text{DOP}}$	**P** $_{\text{DIP}}$	**P** $_{\text{Nekton}}$	**P** $_{\text{birds}}$	**Flux pro Art**
Bacteria		0.00	0	0	0	0	0	0.00	2.89	0	0	2.89
Seagrass	0.01	0	0	0	0	0	0	0.00	0.00	0	0.01	0.02
Mikrophytobenthos		0	0	0	0	0	0	0.01	0.00	0	0	0.01
Hydrobia ulvae	0.72	0	0	0	0.01	0	0.32	0	0.08	0.00	0.00	1.13
Littorina littorea	0.01	0	0	0	0	0	0.00	0	0.08	0.00	0.00	0.09
Arenicola marina	0.00	0	0	0	0	0	0.09	0	0.26	0.00	0.00	0.35
Scoloplos armiger	0.00	0	0	0	0	0	0	0	0.01	0.00	0.00	0.01
Capitella capitata	0.00	0	0	0	0	0	0	0	0.02	0.00	0.00	0.02
Oligochaeta spp.	0.00	0	0	0	0	0	0.01	0	0.02	0.00	0.00	0.03
Cerastoderma edule	0.07	0	0	0	0	0	0.00	0	0.00	0.00	0.00	0.07
Mya arenaria	0.00	0	0	0	0	0	0.00	0	0.00	0.00	0.00	0.00
Macoma balthica	0.03	0	0	0	0	0	0.48	0	0.01	0.00	0.00	0.53
Phyllodoce	0.00	0	0	0	0	0	0.00	0	0.00	0.00	0.00	0.00
Carcinus maenas	0.01	0	0	0	0	0	0.64	0	0.00	0.00	0.00	0.64
Crangon crangon	0.00	0	0	0	0	0	0.00	0	0.01	0	0	0.01
Pomatoschistus microps	0.01	0	0	0	0	0	0.00	0	0.07	0.00	0	0.08
SedPOC	1.81	0	0	0	0	0	0	0	0	0	0	1.81
Teil-flux	2.67	0.00	0	0.00	0.01	0.00	1.55	0.01	3.45	0.00	0.01	7.70
Art flux	**POP**	**org P**	**org P**	**org P**	**org P**	**org P**	**org P**	**DOP**	**DIP**	**org P**	**org P**	
								ΣDOP	ΣDIP	ΣPOP	Σ Org P	Total
								0.01	3.45	2.67	1.57	7.70

Tab.19. Pelagic- benthic exchange of carbon for an *Arenicola* sand flat of the Sylt- Rømø Bay in mgC m^{-2} h^{-1} (yearly average), values were derived from the network model which does not give variance indications (SD or SE). Org C =living organic carbon, POC= particulate organic carbon, DOC =dissolved organic carbon, DIC = dissolved inorganic carbon.

Recipient Donor	**Bacteria**	**Micro-phyto-benthos**	***H. ulvae***	***Littorina littorea***	***Arenicola marina***	***Scoloplos armiger***	***Capitella capitata***	***Lanice conchilega***	***Pygospio elegans***	***C. edule***	***Mya arenaria***	**small polychaetes**	***Macoma balthica***	***P. microps***	***Nephthys spp.***	**Sed. POC**	**partial flux**	**type of flux**
C_{Detritus}	0	0	0	0	0	0	0	0,009	0,01	2,26	0,05	0,003	0,41	0	0	251,41	254,16	POC
C_{Bacteria}	0	0	0	0	0	0	0	0,0007	0,0007	0,16	0,004	0	0	0	0	0	0,17	Org C
$C_{\text{Phytoplankton}}$	0	0	0	0	0	0	0	0,06	0,06	13,75	0,33	0,02	2,52	0	0	0	16,73	Org C
$C_{\text{Zooplankton}}$	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0,00	Org C
$C_{\text{settlement}}$	0	0	0,002	0	0	0	0,001	0,004	0,003	0,71	0,04	0,003	0,12	0,00008	0	0	0,88	Org C
C_{Drift}	0	0	9,29	0	2,72	0,52	0		0,060	15,66	1,09	0,030	10,08	0	0,03	0	39,45	Org C
C_{Fishes}	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0,00	Org C
$C_{\text{diving birds}}$	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0,00	Org C
DOC	10,22	17,20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	27,42	DOC
DIC		41,33	0	0	0	0	0	0	0	0	0	0	0	0	0	0	41,33	DIC
Flux per species	10,22	58,53	9,29	0,00	2,72	0,52	0,00	0,07	0,13	32,54	1,52	0,05	13,13	0,00	0,03	251,41	380,13	

Tab. 19a. Sum of pelagic-benthic fluxes

Σ Org C	**57,22**
Σ POC	**254,16**
Σ DOC	**27,42**
Σ DIC	**41,33**
Total	**380,13**

Tab.20. Benthic-pelagic exchange of carbon for an *Arenicola* sand flat of the Sylt- Rømø Bay in mgC m^{-2} h^{-1} (yearly average), values were derived from the network model which does not give variance indications (SD or SE). Org C =living organic carbon, POC= particulate organic carbon, DOC= dissolved organic carbon, DIC = dissolved inorganic carbon.

Donor	$C_{Detritus}$	$C_{Bacteria}$	$C_{Phytoplankton}$	$C_{Zooplankton}$	$C_{settlement}$	$C_{Macro-Zoobenthos}$	DOC	DIC	C_{Nekton}	C_{birds}	**Flux pro Art**
Bakterien	0	0	0	0	0	0	0	2,89	0	0	2,89
Meiofauna	2,02	0	0	0	0	0	0	3,48	0	0	5,50
Mikrophytobenthos	22,27	0	0	0	0	0	6,75	14,3	0	0	43,35
Hydrobia ulvae	0,05	0	0	0	*0,001*	9,29	0	0,01	0	0,004	9,36
Littorina littorea		0	0	0	0	0,00	0	0	0	0	0
Arenicola marina	9,10	0	0	0	0	2,72	0	1,49	0,00002	0,05	13,36
Scoloplos armiger	1,17	0	0	0	0	0,52	0	0,44	0,007	0,013	2,15
Capitella capitata	0,04	0	0	0	0,0003	0	0	0,02	0	0	0,06
Lanice conchilega	0,02	0	0	0	0,001	0	0	0,03	0,0018	0,01	0,07
Pygospio elegans	0,02	0	0	0	0,001	0,06	0	0,04	0,0025	0,0017	0,12
Cerastoderma edule	14,89	0	0	0	0,28	15,66	0	0,98	0,00003	0,30	32,11
Mya arenaria	0,20	0	0	0	0,02	1,09	0	0,18	0	0,003	1,49
kl. Polychaeten	0,02	0	0	0	0,001	0,00	0	0,004	0,004	0,004	0,03
Macoma balthica	5,60	0	0	0	0,05	10,08	0	0,22	0,00001	0,04	15,99
Crangon crangon	0,01	0	0	0	0	0	0	0	0	0	0
Nephthys spp.	1,26	0	0	0	0,01	0,00	0	0,28	0	0,04	1,58
Pomatoschistus microps	0	0	0	0	0	0	0	0	0	0	0
SedPOC	0,00	0	0	0	0	0	0	0	0	0	0
Partial flux	56,68	0	0	0	0,365	39,41	6,75	24,40	0,01	0,46	128,06
Type of flux	POC	org C	org C	org C	org C	org C	DOC	DIC	org C	org C	
							ΣDOC 6,75	ΣDIC 24,40	ΣPOC 56,68	Σ Org C 40,25	Total 128,06

Tab.21. Pelagic-benthic exchange of nitrogen for an intertidal *Arenicola* sand flat of the Sylt- Rømø Bay in mgN m^{-2} h^{-1} (yearly average), values were derived from the network model which does not give variance indications (SD or SE). Org N =living organic nitrogen, PON= particulate organic nitrogen, DON =dissolved organic nitrogen, DIN = dissolved inorganic nitrogen.

Recipient Donor	**Bacteria**	**Micro-phyto-benthos**	***H. ulvae***	***L. littorea***	***A. marina***	***S. armiger***	***C. capita-ta***	***Lanice conchile-ga***	***P. elegans***	***C. edule***	***M. arenaria***	**small polychaet-es**	***Macoma balthica***	***Pomatoschistus microps***	***Nephthys spp.***	**Sed. POC**	**partial flux**	**type of flux**
$N_{Detritus}$	0	0	0	0	0	0	0	0.001	0.00	0.23	0.01	0.000	0.04	0	0	45.53	45.80	PN
$N_{Bacteria}$	0	0	0	0	0	0	0	0.0001	0.0001	0.03	0.001	0	0	0	0	0	0.03	Org N
$N_{Phytoplankton}$	0	0	0	0	0	0	0	0.01	0.01	2.07	0.05	0.00	0.38	0	0	0	2.52	Org N
$N_{Zooplankton}$	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.00	Org N
$N_{settlement}$	0	0	0.0004	0	0	0	0.0002	0.001	0.001	0.16	0.01	0.001	0.03	0.00002	0.01	0	0.21	Org N
N_{Drift}	0	0	1.977	0	0.81	0.16	0	0	0.018	3.33	0.23	0.009	2.14	0	0		8.68	Org N
N_{Fishes}	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.00	Org N
$N_{diving\ birds}$	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.00	Org N
DON	1.02	3.44	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4.46	DON
DIN	0	3.44	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3.44	DIN
Flux per species	1.02	6.88	1.98	0.00	0.81	0.16	0.00	0.01	0.03	5.83	0.30	0.01	2.59	0.00	0.01	45.53	65.15	

Tab. 21a. Sum of pelagic-benthic fluxes

Σ Org N	**11.44**
Σ PON	**45.80**
Σ DON	**4.46**
Σ DIN	**3.44**
Total	**65.14**

Tab.22. Benthic-pelagic exchange of nitrogen for an *Arenicola* sand flat of the Sylt- Rømø Bay in mgN m^{-2} h^{-1} (yearly average), values were derived from the network model which does not give variance indications (SD or SE). Org N =living organic nitrogen, PON= particulate organic nitrogen, DON= dissolved organic nitrogen, DIN = dissolved inorganic nitrogen.

Donor	N_{Detr}	$N_{Bakterien}$	$N_{Phytoplankton}$	$N_{Zooplankton}$	$N_{settlement}$	$N_{Makro\text{-}phyten}$	$N_{Makro\text{-}Zoobenthos}$	**DON**	**DIN**	N_{Nekton}	N_{birds}	**Flux per species**
Bacteria	0	0	0	0	0	0	0	0	1.44	0	0	1.44
Meiofauna	0.13	0	0	0	0	0	0	0	0.74	0	0	0.88
Microphytobenthos	2.23	0	0	0	0	0	0	0.16	0	0	0	2.39
Hydrobia ulvae	0.01	0	0	0	*0*	0	1.98	0	0.0027	0	0.001	1.99
Littorina littorea	0	0	0	0	0	0	0	0	0	0	0	
Arenicola marina	0	0	0	0	0	0	0.81	0	0.90	0.0000050	0.01	1.72
Scoloplos armiger	0	0	0	0	0	0	0.16	0	0.20	0.002	0.004	0.36
Capitella capitata	0	0	0	0	0.0001	0	0	0	0.01	0	0	0.01
Lanice conchilega	0	0	0	0	0	0	0	0	0.01	0.0005	0	0.01
Pygospio elegans	0	0	0	0	0	0	0.02	0	0.01	0.0007	0.0005	0.03
Cerastoderma edule	1.98	0	0	0	0.06	0	3.33	0	0.28	0.00001	0.06	5.73
Mya arenaria	0.03	0	0	0	0	0	0.23	0	0.03	0	0.001	0.29
kl. Polychaeten	0.00	0	0	0	0	0	0	0	0.008	0.001	0.001	0.01
Macoma balthica	0.75	0	0	0	0.01	0	2.14	0	0.12	0.0000018	0.01	3.03
Crangon crangon	0	0	0	0	0	0	0	0	0	0	0	0.0014
Nephthys spp.	0.08	0	0	0	0	0	0	0	0.08	0	0.01	0.18
Pomatoschistus microps	0	0	0	0	0	0	0	0	0	0	0	0.00
SedPOC	0	0	0	0	0	0	0	0	0	0	0	0.00
Teil-flux	5.22	0	0	0	0.083	0.00	8.67	0.16	3.83	0.0045	0.10684	18.07
Art flux	PN	org N	org N	org N	org N	org N	org N	DON	DIN	org N	org N	
								ΣDON	ΣDIN	ΣPN	Σ Org N	**TOTAL**
								0.16	3.83	5.22	8.86	**18.07**

Tab. 23. Pelagic-benthic exchange of phosphorus for an *Arenicola* sand flat of the Sylt- Rømø Bay in mgP m^{-2} h^{-1} (yearly average), values were derived from the network model which does not give variance indications (SD or SE). Org P =living organic phosphorus, POP= particulate organic phosphorus, DOP =dissolved organic phosphorus, DIP = dissolved inorganic phosphorus.

Donor	Bacteria	Microphyto-benthos	*Hydrobia ulvae*	*Littorina littorea*	*Arenicola marina*	*Scoloplos armiger*	*Capitella capitata*	*Lanice conchilega*	*Pygospio elegans*	*Cerastoderma edule*	*Mya arenaria*	small polychaetes	*Macoma balthica*	*Pomatoschistus microps*	*Nephthys spp.*	Sed. POC	partial flux	type of flux
P Detritus	0	0	0	0	0	0	0	0	0	0.05	0.00	0	0.01	0	0	5.86	5.93	POP
P Bacteria	0	0	0	0	0	0	0	0	0	0.01	0.000	0	0	0	0		0.0099	OrgP
P Phytoplankton	0	0	0	0	0	0	0	0	0	0.13	0.00	0	0.02	0	0	0	0.16	Org P
P Zooplankton	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Org P
P Zooplankton settlement	0	0	0	0	0	0	0	0	0	0.01	0	0	0	0	0	0	0.02	Org P
P Drift	0	0	0.317	0.00	0.09	0.02	0	0	0.002	0.18	0.01	0.001	0.12	0	0	0	0.74	Org P
P Fishes	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Org P
P diving birds	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Org P
DOP	0.24	0.05	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.29	DOP
DIP	0	0.39	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.39	DIP
Flux per species	0.24	0.44	0.32	0.00	0.09	0.02	0.00	0	0.002	0.39	0.02	0.001	0.15	0		5.86	7.53	

Tab. 23a. Sum of pelagic-benthic fluxes

Σ Org P	**0.92**
Σ POP	**5.93**
Σ DOP	**0.24**
Σ DIP	**0.39**
Total	**7.48**

Tab.24. Benthic-pelagic exchange of phosphorus for an *Arenicola* sand flat of the Sylt- Rømø Bay in mgP m^{-2} h^{-1} (yearly average), values were derived from the network model which does not give variance indications (SD or SE). Org P =living organic phosphorus, POP= particulate organic phosphorus, DOP= dissolved organic phosphorus, DIP = dissolved inorganic phosphorus.

Recipient Donor	P_{Detr}	$P_{\text{Bakterien}}$	$P_{\text{Phytoplankton}}$	$P_{\text{settlement}}$	$P_{\text{settlemment}}$	$P_{\text{Makro-phyten}}$	$P_{\text{Makro-Zoobenthos}}$	P_{DOP}	P_{DIP}	P_{Nekton}	P_{birds}	**Flux per species**
Bacteria	0	0	0	0	0	0	0	0	0,95	0	0	0,95
Meiofauna	0,05	0	0	0	0	0	0	0	0,12	0	0	0,17
Microphytobenthos	0,52	0	0	0	0	0	0	0,06	0	0	0	0,52
Hydrobia ulvae	0	0	0	0	*0*	0	0,32	0	0,0002	0	0,00014	0,32
Littorina littorea	0	0	0	0	0	0	0,00	0		0	0	0
Arenicola marina	0,21	0	0	0	0	0	0,09	0	0,10	0,0000006	0,0015	0,41
Scoloplos armiger	0,03	0	0	0	0	0	0,02	0	0,02	0	0,0004	0,06
Capitella capitata	0	0	0	0	0	0	0	0	0,0009	0	0	0,00
Lanice conchilega	0	0	0	0	0	0	0,00	0	0,0013	0,0001	0,00034	0,00
Pygospio elegans	0	0	0	0	0	0	0,00	0	0,0017	0,0001	0,0001	0,00
Cerastoderma edule	0,202	0	0	0	0,01	0	0,18	0	0,13	0,00000034	0,0035	0,53
Mya arenaria	0	0	0	0	0	0	0,01	0	0,003	0	0,000034	0,02
kl. Polychaeten	0,01	0	0	0	0	0	0,00	0	0,005	0,00012	0,00014	0,02
Macoma balthica	1,61	0	0	0	0	0	0,12	0	1,02	0,00000010	0,00043	2,75
Crangon crangon	0,00006	0	0	0	0	0	0	0	0,0015468	0	0	0
Nephthys spp.	0,04	0	0	0	0	0	0,00	0	0,02	0	0,0013	0,06
P. microps	0	0	0	0	0	0	0	0	0	0	0	0
SedPOC	0	0	0	0	0	0	0	0	0	0	0	0,00
Partial flux	2,67	0,00	0,00	0,00	0,007	0,00	0,74	0,00	2,37	0,0005	0,01	5,80
Species flux	POP	org P	org P	org P	org P	org P	org P	DOP	DIP	org P	org P	
								ΣDOP	ΣDIP	ΣPOP	Σ Org P	**TOTAL**
								0,06	2,37	2,67	0,75	**5,85**

Tab. 25. Pelagic- benthic exchange of carbon for muddy sands of the Sylt- Rømø Bay in mgC m^{-2} h^{-1} (yearly average), values were derived from the network model which does not give variance indications (SD or SE). Org C =living organic carbon, POC= particulate organic carbon, DOC =dissolved organic carbon, DIC = dissolved inorganic carbon.

Donor	***Bacteria***	***Micro-phyto-bent.***	***H. ulvae***	***A. marina***	**Oligochaeta spp.**	**Heteromastus filiformis**	**Oligochaeta**	***N. diversi-color***	***C. volutator***	***Mya arenaria***	**small poly-chaetes**	***Macoma balthica***	**small Crust.**	***C. maenas***	***Crangon crangon***	**Sed. POC**	**partial flux**	**type of flux**
$C_{Detritus}$	0	0	0	0	0	0	0	0,2075	0	0,91	0,02	1,14	0	0	0	251,69	253,97	POC
$C_{Bacteria}$	0	0	0	0	0	0	0	0	0	0,06	0	0	0	0	0	0	0,06	org C
$C_{Phytopl.}$	0	0	0	0	0	0	0	0,21	0	5,51	0,13	7,02	0	0	0	0	12,87	org C
$C_{Zoopl.}$	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	org C
$C_{settle.}$	0	0	0,21	0	0	0,02	0	0,05	0,12	0,66	0,02	0,19	0,12	0,003	0,001	0	1,38	org C
C_{Drift}	0	0	4,89	5,98	0	0	0,69	0,71	0	0,02	0,08	88,71	0,02	13,36	0	0	114,45	
C_{Fishes}	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0,01	0,011	POC
$C_{diving\ birds}$	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0,03	0,025	POC
DOC	2,81	19,15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	21,96	DOC
DIC	0	40,53	0	0	0	0	0	0	0	0	0	0	0	0	0	0	40,53	DIC
Flux per species	2,81	59,68	5,10	5,98	0,00	0,02	0,69	1,17	0,12	7,15	0,25	97,05	0,14	13,36	0,00	251,73	**445,25**	

Tab. 25a. Sum of pelagic-benthic fluxes

org C	**128,76**
POC	**254,01**
DOC	**21,96**
DIC	**40,53**
Total	**445,26**

Tab.26. Benthic-pelagic exchange of carbon for muddy sands of the Sylt- Rømø Bay in mgC m^{-2} h^{-1} (yearly average), values were derived from the network model which does not give variance indications (SD or SE). Org C =living organic carbon, POC= particulate organic carbon, DOC= dissolved organic carbon, DIC = dissolved inorganic carbon.

Donor	**C_{Detritus}**	**C_{Bacteria}**	**$C_{\text{Phytoplankton}}$**	**$C_{\text{Zooplankton}}$**	**$C_{\text{settlement}}$**	**$C_{\text{Makro-Zoobenthos}}$**	**DOC**	**DIC**	**C_{Nekton}**	**C_{birds}**	**Flux pro Art**
Bacteria	0,00	0,00						8,03			8,03
Mikrophytobenthos	0,00		0,00				6,62	14,1			20,68
Meiobenthos	2,02							3,5			5,50
Hydrobia ulvae	5,38				0,083	4,9		1,41	0,0145	0,041	11,81
Arenicola marina	2,38					6,0		2,37	0,01141	0,031	10,78
Oligochaeta spp.	0,18					0		0,34	0,0109		0,53
Heteromastus	1,39				0,009	0		0,21	0,0167	0,0003	2,83
Nereis diversicolor	1,38				0,020	0,71		0,55	0,0389	0,139	2,81
Corophium volutator	0,52				0,048			2,14	0,0937	0,012	5,64
Mya arenaria	2,30				0,263	0,015		3,05		0,008	75,57
kl. Polychaeten	0,10				0,007	75		0,379	0,01	0,063	103,60
Macoma balthica	7,30				0,074	88,705		7,47	0,007	0,046	2,63
kl. Crustaceen	0,59				0,048	0,02		1,87	0,09417	0,010	13,43
Carcinus maenas	0,04				0,001	13,36		0,02	0,01300	0,001	0,08
Crangon crangon	0,01				0,000	0		0,05	0,01297	0,0002	0,00
Pomatoschistus microps	0,00321					0		0,0004	0,001		0,01
P.minutus	0,00667							0,0004	0,00026		0,00
P.platessa	0,00004							0,00001			0,00
P.flesus	0,00042							0,00042			0,00
M.merlangus	0,00063							0,00033			0,00
SedPOC	0,0										
Partial flux	**23,59**	**0,00**	**0,00**	**0,00**	**0,55**	**188,68**	**6,62**	**45,41**	**0,33**	**0,35**	**265,53**
	POC	**org C**	**org C**	**org C**	**org C**	**org C**	**DOC**	**DIC**	**org C**	**org C**	**Total**

Tab.27. Pelagic-benthic exchange of nitrogen for muddy sands of the Sylt- Rømø Bay in mgN m^{-2} h^{-1} (yearly average), values were derived from the network model which does not give variance indications (SD or SE). Org N =living organic nitrogen, PON= particulate organic nitrogen, DON =dissolved organic nitrogen, DIN = dissolved inorganic nitrogen.

Donor	**Bacteria**	***Microphyto-benthos***	***Hydrobia ulvae***	***Arenicola marina***	**Oligochaeta spp.**	**Heteromastus filiformis**	**Oligochaeta**	***Nereis diversicolor***	***Corophium volutator***	***Mya arenaria***	**small polychaetes**	***Macoma balthica***	**small Crustaceans**	***Carcinus maenas***	***Crangon crangon***	**Sed. POC**	**Partial flux**	**type of flux**
N $_{Detritus}$	0	0	0	0	0	0	0	0,02075	0,00	0,09	0,002	0,114	0,000	0,00	0	45,57	45,80	PON
N $_{Bacteria}$	0	0	0	0	0	0	0	0	0,0000	0,01	0,000	0,000	0,000	0,00	0	0	0,01	org N
N $_{Phytoplankton}$	0	0	0	0	0	0	0	0,031		0,8312	0,019	1,059	0,000	0,00	0	0	1,94	org N
N $_{Zooplankton}$	0	0	0	0	0	0	0	0	0,0000	0,00	0,000	0,000	0,000	0,00	0	0,00	0,00	org N
N $_{settlement}$	0	0	0,047	0,00	0,00	0,005	0,000	0,01	0,0273	0,15	0,004	0,042	0,027	0,001	0,000	0,00	0,31	org N
N $_{Drift}$	0	0	1,040	1,79	0,00	0,000	0,206	0,21	0,0000	0,0032	0,022	18,873	0,004	2,97	0,000	0,00	25,12	org N
N $_{Fishes}$	0	0	0	0	0	0		0	0	0	0	0	0	0,00	0	0,001	0,001	PON
N $_{diving\ birds}$	0	0	0	0	0	0		0	0	0	0	0	0	0,00	0	0,048	0,048	PON
DON	0,28	3,83	0	0	0	0		0	0	0	0	0	0	0,00	0	0	4,11	DON
DIN	0	3,83	0	0	0	0		0	0	0	0	0	0	0,00	0	0	3,83	DIN
Flux per species	0,28	7,66	1,09	1,79	0,00	0,00	0,21	0,28	0,03	1,09	0,05	20,09	0,03	2,97	0,00	45,62	**81,17**	

Tab. 27a. Sum of pelagic-benthic fluxes

org N	**27,38**
PON	**45,85**
DON	**4,11**
DIN	**3,83**
Σ Total	**81,17**

Tab.28. Benthic-pelagic exchange of nitrogen for muddy sands of the Sylt- Rømø Bay in mgN m^{-2} h^{-1} (yearly average), values were derived from the network model which does not give variance indications (SD or SE). Org N =living organic nitrogen, PON= particulate organic nitrogen, DON= dissolved organic nitrogen, DIN = dissolved inorganic nitrogen.

Donor	**N_{Detr}**	**$N_{Bakterien}$**	**$N_{Phytoplankton}$**	**$N_{Zooplankton}$**	**$N_{settlement}$**	**$N_{Makro-Zoobenthos}$**	**DON**	**DIN**	**N_{Nekton}**	**N_{birds}**	**Flux per species**
Bakterien	0,00	0,00						1,24			1,24
Mikrophytobenthos	0,00		0,00				0,19	0,0			0,19
Hydrobia ulvae	0,74				0,019	1,04		0,30	0,0031	0,009	2,12
Arenicola marina	0,16					1,79		1,44	0,00341	0,009	3,39
ΣOligochaet	0,01					0,00		0,08	0,0033		0,09
Heteromastus	0,09				0,002	0,00		0,18	0,0050	0,0001	0,28
Nereis diversicolor	0,09				0,005	0,21		0,21	0,0116	0,042	0,57
Corophium volutator	0,05				0,011			0,36	0,0208	0,003	0,45
Mya arenaria	0,31				0,060	0,00		0,48		0,002	0,85
kl. Polychaeten	0,01				0,002	0,22		0,052	0,004	0,019	0,31
Macoma balthica	0,97				0,017	18,87		0,18	0,001	0,010	20,05
kl. Crustaceen	0,06				0,011	0,00		0,33	0,02093	0,002	0,43
Carcinus maenas	0,00				0,000	2,97		0,0012	0,00289	0,0002	2,98
Crangon crangon	0,00				0,000	0,00		0,01	0,00288	0,00004	0,01
Pomatoschistus microps	0,00029					0,00		0,0008	0,0005		0,00
P.minutus	0,00060							0,0018	0,00009		0,00
P.platessa	0,00000							0,00425			0,00
P.flesus	0,00004							0,00195			0,00
M.merlangus	0,00006							0,00016			0,00
SedPOC	0,0										0,00
Partial flux	**2,50**	**0,00**	**0,00**	**0,00**	**0,13**	**25,11**	**0,19**	**4,87**	**0,08**	**0,09**	**32,97**
	PON	**org N**	**org N**	**org N**	**org N**	**org N**	**DON**	**DIN**	**org N**	**org N**	

Tab. 29. Pelagic-benthic exchange of phosphorus muddy sands of the Sylt- Rømø Bay in mgP m^{-2} h^{-1} (yearly average), values were derived from the network model which does not give variance indications (SD or SE). Org P =living organic phosphorus, POP= particulate organic phosphorus, DOP =dissolved organic phosphorus, DIP = dissolved inorganic phosphorus.

Donor	**Bacteria**	***Microphyto-benthos***	***Hydrobia ulvae***	***Arenicola marina***	**Oligochaeta spp.**	**Heteromastus filiformis**	**Oligochaeta**	***Nereis diversicolor***	***Corophium volutator***	***Mya arenaria***	**small polychaetes**	***Macoma balthica***	**small Crustaceans**	***Carcinus maenas***	***Crangon crangon***	**Sediment POP**	**partial flux**	**type of flux**
$P_{Detritus}$	0	0	0	0	0	0	0	0,00484021	0,00	0,02	0,001	0,027	0,000	0,00	0	5,87	5,92	POP
$P_{Bakterien}$	0	0	0	0	0	0	0	0	0,0000	0,00	0,000	0,000	0,000	0,00	0	0	0,004	org P
$P_{Phytoplankton}$	0	0	0	0	0	0	0	0,00195755		0,0520	0,001	0,066	0,000	0,00	0	0	0,12	org P
$P_{Zooplankton}$	0	0	0	0	0	0	0	0	0,0000	0,00	0,000	0,000	0,000	0,00	0	0,00	0,00	org P
$P_{settlement}$	0	0	0,004	0,00	0,00	0,000	0,000	0,00	0,0024	0,01	0,000	0,004	0,002	0,000	0,000	0,00	0,03	org P
P_{Drift}	0	0	0,167	0,20	0,00	0,000	0,024	0,02	0,0000	0,0002	0,003	1,020	0,001	0,46	0,000	0,00	1,90	org P
P_{Fishes}	0	0	0	0	0	0		0	0	0	0	0	0	0,00	0	0,00003	0,00003	POP
$P_{diving\ birds}$	0	0	0	0	0	0		0	0	0	0	0	0	0,00	0	0,006	0,006	POP
DOP	0,07	0,06	0	0	0	0		0	0	0	0	0	0	0,00	0	0	0,12	DOP
DIP	0	0,25	0	0	0	0		0	0	0	0	0	0	0,00	0	0	0,25	DIP
																	0,00	
Fluxper species	0,07	0,30	0,17	0,20	0,00	0,00	0,02	0,03	0,00	0,09	0,00	1,12	0,00	0,46	0,00	5,88	**8,35**	

Tab. 29a. Sum of pelagic-benthic fluxes

org P	**2,05**
POP	**5,93**
DOP	**0,12**
DIP	**0,25**
Total	**8,35**

Tab.30. Benthic-pelagic exchange of phosphorus for muddy sands of the Sylt- Rømø Bay in mgP m^{-2} h^{-1} (yearly average), values were derived from the network model which does not give variance indications (SD or SE). Org P =living organic phosphorus, POP= particulate organic phosphorus, DOP= dissolved organic phosphorus, DIP = dissolved inorganic phosphorus.

Donor	P_{Detritus}	$P_{\text{Bakterien}}$	$P_{\text{Phytoplankton}}$	$P_{\text{Zooplankton}}$	$P_{\text{settlement}}$	$P_{\text{Makro-Zoobenthos}}$	P_{DOP}	P_{DIP}	P_{Nekton}	P_{birds}	**Flux pro Art**
Bacteria	0,00	0,00						0,95			0,95
Mikrophytobenthos	0,00		0,00				0,12	0,00			0,12
Hydrobia ulvae	0,16				0,00	0,17		0,02	0,00	0,00	0,36
Arenicola marina	0,07					0,20		0,16	0,00	0,00	0,44
Oligochaeta spp.	0,01					0,00		0,01	0,00		0,01
Heteromastus	0,04				0,00	0,00		0,02	0,00	0,00	0,06
Nereis diversicolor	0,04				0,00	0,02		0,02	0,00	0,00	0,09
Corophium volutator	0,00				0,00			0,06	0,00	0,00	0,06
Mya arenaria	0,03				0,01	0,00		0,06		0,00	0,09
small Polychaetes	0,00				0,00	0,00		0,00	0,00	0,00	0,01
Macoma balthica	0,11				0,00	1,02		0,08	0,00	0,00	1,21
small Crustaceans	0,00				0,00	0,00		0,05	0,00	0,00	0,06
Carcinus maenas	0,00				0,00	0,46		0,00	0,00	0,00	0,46
Crangon crangon	0,00				0,00	0,00		0,00	0,00	0,00	0,00
Pomatoschistus microps	0,00					0,00		0,00	0,00		0,00
P.minutus	0,00							0,00	0,00		0,00
P.platessa	0,00							0,00			0,00
P.flesus	0,00							0,00			0,00
M.merlangus	0,00							0,00			0,00
SedPOC	0,00										0,00
partial flux	**0,47**	**0,00**	**0,00**	**0,00**	**0,01**	**1,87**	**0,12**	**1,44**	**0,01**	**0,01**	**3,94**
	POP	**org P**	**org P**	**org P**	**org P**	**org P**	**DOP**	**DIP**	**org P**	**org P**	**Total**

Tab. 31. Pelagic- benthic exchange of carbon for sandy shoals of the Sylt- Rømø Bay in mgC m^{-2} h^{-1} (yearly average), values were derived from the network model which does not give variance indications (SD or SE). Org C =living organic carbon, POC= particulate organic carbon, DOC =dissolved organic carbon, DIC = dissolved inorganic carbon.

Donor	**Bacteria**	**Microphyto-benthos**	***Arenicola marina***	***Scoloplos armiger***	***Lanice conchilega***	***Cerastoderma edule***	**small Polychaetes**	***Macoma balthica***	**small Crustaceans**	***Crangon crangon***	***Nephthys spp.***	**Sediment POC**	**partial flux**	**type of flux**
C_{Detritus}	0	0			0,041	0,27	0,002	0,21	0	0	0	0,00	0,52	POC
C_{Bacteria}	0	0			0,0029	0,02	0	0	0	0	0	0	0,02	Org C
$C_{\text{Phytoplankton}}$	0	0			0,25	1,64	0,01	1,28	0	0	0	0	3,17	Org C
$C_{\text{Zooplankton}}$	0	0			0	0	0	0	0	0	0	0,00	0,00	Org C
$C_{\text{settlement}}$			0		0,01552511	0,08474886	0,00185	0,03360731	0,001853881		0,01506849	0,00	0,15	Org C
C_{Drift}	0	0	2,72		0,000	0,26	0,030	42,13	0,02	0,000	0,00	0,00	45,15	Org C
C_{Fishes}	0	0			0	0	0	0	0	0	0	0,00	0,00	Org C
$C_{\text{diving birds}}$	0	0			0	0,00	0	0	0	0	0	0,00	0,00	Org C
DOC	0,00	15,3			0	0,00	0	0	0	0	0	0	15,30	DOC
DIC	0	40,53			0	0,00	0	0	0	0	0	0	40,53	DIC
Flux per species	0,00	55,83	2,72	0,00	0,31	2,26	0,05	43,65	0,02	0,00	0,00	0,00	104,84	

Tab. 31a. Sum of pelagic-benthic fluxes

Σ Org C	**48,50**
Σ POC	**0,52**
Σ DOC	**15,30**
Σ DIC	**40,53**
	104,84

Tab.32. Benthic-pelagic exchange of carbon for sandy shoals of the Sylt- Rømø Bay in mgC m^{-2} h^{-1} (yearly average), values were derived from the network model which does not give variance indications (SD or SE). Org C =living organic carbon, POC= particulate organic carbon, DOC= dissolved organic carbon, DIC = dissolved inorganic carbon.

Donor	**C_{Detritus}**	**C_{Bacteria}**	**$C_{\text{Phytoplankton}}$**	**$C_{\text{Zooplankton}}$**	**$C_{\text{settlement}}$**	**$C_{\text{Makro-Zoobenthos}}$**	**DOC**	**DIC**	**C_{Nekton}**	**C_{birds}**	**Flux pro Art**
Bacteria	**0,00**	**0,00**					1,0125	**2,89**	0		3,90
Microphytobenthos	**0,00**		**0,00**				6,75	**14,3**	0	0	21,09
Meiobenthos	**2,02**							**3,5**			5,50
Arenicola marina	**4,56**				**0,00**	2,7		**0,90**	0,00002	0,00	8,17
Scoloplos intertidalis	**0,97**				**0,00**			**0,37**	0,007	0,000	1,34
Lanice conchilega	**0,07**				**0,006**	0		**0,15**	0,0014	0,00	0,22
Cerastoderma edule	**1,42**				**0,03**	0,26		**0,12**	0,00003	0,00	1,83
small Polychaetes	**0,01**				**0,001**	0,03		**0,04**	0,001	0,000	0,08
Macoma balthica	**1,33**				**0,01**	42,13		**1,36**	0,00001	0,00	44,84
small Crustaceans	**0,01**				**0,001**	0,02		**0,03**	0,001	0,000	0,06
Crangon crangon	**0,00**				**0,0002**	0		**0,02**	0,001	0,000	0,02
Nephthys spp.	**0,52**				**0,01**	0		**0,15**	0,000001	0,00	0,67
SedPOC	**259,24**				**0**						259,24
partial flux	**270,15**	**0,00**	**0,00**	**0,00**	**0,061**	**45,16**	**7,76**	**23,82**	**0,00003**	**0,00**	**346,97**
type of flux	POC	org C	org C	org C	org C	org C	DOC	DIC	org C	org C	
								ΣDOC 7,76	ΣDIC 23,82	ΣPOC 270,15	Σ Org C 45,22

Tab.33. Pelagic-benthic exchange of nitrogen for sandy shoals of the Sylt- Rømø Bay in mgN m^{-2} h^{-1} (yearly average), values were derived from the network model which does not give variance indications (SD or SE). Org N =living organic nitrogen, PON= particulate organic nitrogen, DON =dissolved organic nitrogen, DIN = dissolved inorganic nitrogen.

Donor	**Bacteria**	**Microphyto-benthos**	***Arenicola marina***	***Scoloplos armiger***	***Lanice conchilega***	***Cerastoderma edule***	**small Polychaetes**	***Macoma balthica***	**small Crustaceans**	***Crangon crangon***	***Nephthys spp.***	**Sediment POC**	**partial flux**	**type of flux**
$N_{Detritus}$	0	0			0,004	0,03	0,000	0,02	0	0	0	0,00	0,05	PON
$N_{Bacteria}$	0	0			0,0006	0,0038	0,00011	0	0	0	0	0	0,004	Org N
$N_{Phytoplankton}$	0	0			0,04	0,25	0,00	0,19	0	0	0	0	0,48	Org N
$N_{Zooplankton}$	0	0			0	0	0	0	0	0	0	0,00	0,00	Org N
$N_{settlement}$			0		0,00353647	0,01930498	0,000422296	0,00765542	0,0004223		0,00343246	0,00	0,03	Org N
N_{Drift}	0	0	0,8119403		0,000	0,05	0,009	8,96	0,00	0,000	0,00	0,00	9,84	Org N
N_{Fishes}	0	0			0	0	0	0	0	0	0	0,0014	0,0014	Org N
$N_{diving\ birds}$	0	0			0	0,00	0	0	0	0	0	0,00	0,00	Org N
DON	0,00	3,06			0	0,00	0	0	0	0	0	0	3,06	DON
DIN	0	3,06			0	0,00	0	0	0	0	0	0	3,06	DIN
Flux per species	0,00	6,12	0,81	0,00	0,05	0,35	0,01	9,18	0,00	0,00	0,00	0,00	16,53	

Tab. 33a. Sum of pelagic-benthic fluxes

Σ Org N	**10,36**
Σ PON	**0,05**
Σ DON	**3,06**
Σ DIN	**3,06**
Total	**16,53**

Tab.34. Benthic-pelagic exchange of nitrogen for sandy shoals of the Sylt- Rømø Bay in mgN m^{-2} h^{-1} (yearly average), values were derived from the network model which does not give variance indications (SD or SE). Org N =living organic nitrogen, PON= particulate organic nitrogen, DON= dissolved organic nitrogen, DIN = dissolved inorganic nitrogen.

Donor	**$N_{Detritus}$**	**$N_{Bacteria}$**	**$N_{Phytoplankton}$**	**$N_{Zooplankton}$**	**$N_{settlement}$**	**$N_{Makro-Zoobenthos}$**	**DON**	**DIN**	**N_{Nekton}**	**N_{birds}**	**Flux pro Art**
Bacteria	0,00	0,00					0,10	1,24	0,00		1,34
Microphytobenthos	0,00		0,00				0,30	0,00	0,00	0	0,30
Meiobenthos	0,13							0,74			0,87
Arenicola marina	0,30				0,00	0,81		0,17	0,00	0,00	1,28
Scoloplos intertidalis	0,06				0,00			0,03	0,00	0,000	0,10
Lanice conchilega	0,00				0,00	0,00		0,03	0,00	0,00	0,04
Cerastoderma edule	0,19				0,01	0,06		0,01	0,00	0,00	0,26
small Polychaetes	0,00				0,00	0,01		0,03	0,00	0,000	0,04
Macoma balthica	0,18				0,00	8,96		0,01	0,00	0,00	9,15
small Crustaceans	0,00				0,00	0,00		0,00	0,00	0,000	0,01
Crangon crangon	0,00				0,00	0,00		0,04	0,00	0,000	0,04
Nephthys spp.	0,05				0,00	0,00		0,00	0,00	0,00	0,05
SedPOC	25,92				0,00						25,92
partial flux	26,85	0,00	0,00	0,00	0,01	9,84	0,40	2,30	0,00	0,00	39,40
type of flux	PON	org N	org N	org N	org N	org N	DON	DIN	org N	org N	**Total**
											39,41
								ΣDON	**ΣDIN**	**Σ org N**	**ΣPON**
								0,40	**2,30**	**9,86**	**26,85**

Tab. 35. Pelagic-benthic exchange of phosphorus sandy shoals of the Sylt- Rømø Bay in mgP m^{-2} h^{-1} (yearly average), values were derived from the network model which does not give variance indications (SD or SE). Org P =living organic phosphorus, POP= particulate organic phosphorus, DOP =dissolved organic phosphorus, DIP = dissolved inorganic phosphorus.

Donor	**Bacteria**	**Microphyto-benthos**	***Arenicola marina***	***Scoloplos armiger***	***Lanice conchilega***	***Cerastoderma edule***	**small Polychaetes**	***Macoma balthica***	**small Crustaceans**	***Crangon crangon***	***Nephthys spp.***	**Sediment POC**	**partial flux**	**type of flux**
P_{Detritus}	0,00	0,00	0,00		0,00	0,01	0,00	0,00	0,00	0,00	0,00	0,00	0,01	POP
P_{Bacteria}	0,00	0,00	0,00		0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	Org P
$P_{\text{Phytoplankton}}$	0,00	0,00	0,00		0,00	0,02	0,00	0,01	0,00	0,00	0,00	0,00	0,03	Org P
$P_{\text{Zooplankton}}$	0,00	0,00	0,00		0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	Org P
$P_{\text{settlement}}$			0,00		0,00	0,00	0,00	0,00	0,00		0,00	0,00	0,00	Org P
P_{Drift}	0,00	0,00	0,10		0,00	0,00	0,00	0,48	0,00	0,00	0,00	0,00	0,59	Org P
P_{Fishes}	0,00	0,00	0,00		0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	Org P
$P_{\text{diving birds}}$	0,00	0,00	0,00		0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	Org P
DOP	0,00	0,04	0,00		0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,04	DOP
DIP	0,00	0,25	0,00		0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,25	DIP
Flux pro Art	0,00	0,29	0,10	0,00	0,00	0,03	0,00	0,50	0,00	0,00	0,00	0,00	0,93	

Tab. 35a. Sum of pelagic-benthic fluxes

Σ Org P	**0,62**
Σ POP	**0,01**
Σ DOP	**0,04**
Σ DIP	**0,25**
Total	**0,93**

Tab.36. Benthic-pelagic exchange of phosphorus for sandy shoals of the Sylt- Rømø Bay in mgP m^{-2} h^{-1} (yearly average), values were derived from the network model which does not give variance indications (SD or SE). Org P =living organic phosphorus, POP= particulate organic phosphorus, DOP= dissolved organic phosphorus, DIP = dissolved inorganic phosphorus.

Donor	**P_{Detr}**	**$P_{\text{Bakterien}}$**	**$P_{\text{Phytoplankton}}$**	**$P_{\text{Zooplankton ohne Ansiedlung}}$**	**$P_{\text{Zooplankton mit Ansiedlung}}$**	**$P_{\text{Makrophyten}}$**	**$P_{\text{Makro-Zoobenthos}}$**	**P_{DOP}**	**P_{DIP}**	**P_{Nekton}**	**P_{birds}**	**Flux per species**
Bakterien	0,00	0,00						0,02	0,95	0,00		0,98
Mikrophytobenthos	0,00		0,00					0,00	0,00	0,00	0,00	0,00
Meiobenthos	0,05								0,12			0,17
Arenicola marina	0,14				0,00		0,09		0,06	0,00	0,00	0,29
Scoloplos intertidalis	0,03				0,00				0,01	0,00	0,00	0,04
Lanice conchilega	0,00				0,00		0,00		0,01	0,00	0,00	0,01
Cerastoderma edule	0,02				0,00		0,00		0,02	0,00	0,00	0,04
small Polychaetes	0,00				0,00		0,00		0,00	0,00	0,00	0,00
Macoma balthica	0,02				0,00		0,48		0,02	0,00	0,00	0,52
small Crustaceans	0,00				0,00		0,00		0,00	0,00	0,00	0,00
Crangon crangon	0,00				0,00		0,00		0,00	0,00	0,00	0,00
Nephthys spp.	0,02				0,00		0,00		0,01	0,00	0,00	0,03
SedPOC	6,05				0,00							6,05
Teil-flux	6,32	0,00	0,00	0,00	0,00	0,00	0,58	0,03	1,20	0,00	0,00	8,14
Art flux	POP	org P	org P	org P	org P	org P	org P	DOP	DIP	org P	org P	
									ΣDOP 0,03	ΣDIP 1,20	ΣPOP 6,32	Σ Org P 0,58

Tab. 37. Pelagic- benthic exchange of carbon for sandy beaches of the Sylt- Rømø Bay in mgC m^{-2} h^{-1} (yearly average), values were derived from the network model which does not give variance indications (SD or SE). Org C =living organic carbon, POC= particulate organic carbon, DOC =dissolved organic carbon, DIC = dissolved inorganic carbon.

Donor	**Bacteria**	**Mikrophyto-benthos**	**Oligochaeta spp.**	***Nereis diversicolor***	***Pygospio elegans***	***Corophium arenarium***	**small Polychaetes**	***Macoma balthica***	**small Crustaceans**	***Crangon crangon***	**Sediment POC**	**partial flux**	**type of flux**
$C_{Detritus}$	0	0	0	0,027	0,274	0,000	0,080	0,03	0	0	0,00	0,41	POC
$C_{Bacteria}$	0	0	0	0	0,0000	0,0000	0	0	0	0	0	0,00	Org C
$C_{Phytoplankton}$	0	0	0	0,027	1,66	0,00	0,42	0,16	0	0	0	2,27	Org C
$C_{Zooplankton}$	0	0	0	0	0	0	0	0	0	0	0,00	0,00	Org C
$C_{settlement}$	0	0	0,00	0,00010	0,069	0,044	0,069	0,00	0,04	0,000	0,00	0,23	Org C
C_{Drift}	0	0	0,30	1,08	0,055	0,000	0,030	42,15	0,02	0,000	0,00	43,63	
C_{Fishes}	0	0	0	0	0	0	0	0	0	0	0,00	0,00	Org C
$C_{diving\ birds}$	0	0	0	0	0	0	0	0	0	0	0,00	0,00	Org C
DOC	0,00	39,75	0	0	0	0	0	0	0	0	0	39,75	DOC
DIC	0	37,56	0	0	0	0	0	0	0	0	0	37,56	DIC
Flux per species	0,00	77,31	0,30	1,13	2,06	0,04	0,60	42,34	0,06	0,00	0,00	123,85	

Tab. 37a. Sum of pelagic-benthic fluxes

Σ Org C	**46,13**
Σ POC	**0,41**
Σ DOC	**39,75**
Σ DIC	**37,56**
	123,85

Tab.38. Benthic-pelagic exchange of carbon for sandy beaches of the Sylt- Rømø Bay in mgC m^{-2} h^{-1} (yearly average), values were derived from the network model which does not give variance indications (SD or SE). Org C =living organic carbon, POC= particulate organic carbon, DOC= dissolved organic carbon, DIC = dissolved inorganic carbon.

Donor	**C_{Detritus}**	**C_{Bacteria}**	**$C_{\text{Phytoplankton}}$**	**$C_{\text{Zooplankton}}$**	**$C_{\text{Zooplankton mit settlement}}$**	**$C_{\text{Makro-Zoobenthos}}$**	**DOC**	**DIC**	**C_{Nekton}**	**C_{birds}**	**Flux per species**
Bakterien	0,00	0,00	0	0			4,75	13,58			18,33
Mikrophytobenthos	0,00		0	0			9,39				9,39
Meiobenthos	2,02							3,48			5,50
Oligochaeta	0,00		0	0	0,00	0,3		0,08	0,00369		0,39
Nereis diversicolor	0,22		0	0	0,003	1,065		0,03	0,016		1,33
Pygospio elegans	0,46		0	0	0,028	0,055		1,32	0,0129		1,88
Corophium arenarium	0,04		0	0	0,02	0		0,26	0,00671		0,32
kl. Polychaeten	0,53		0	0	0,028	0,03		1,30	0,018		1,90
Macoma balthica	0,17		0	0	0,002	42,15		0,20	0,00017		42,52
kl. Crustaceen	0,22		0	0	0,017	0,015		0,68	0,028		0,96
Crangon crangon	0,01		0	0	0,0006	0		0,05	0,003		0,07
SedPOC	266,36		0	0	0	0		0			266,36
partial flux	270,03	0,00	0,00	0,00	0,10	43,62	14,14	20,98	0,09	0,00	348,94
type of flux	POC	org C	org C	org C	org C	org C	DOC	DIC	org C	org C	
								ΣDOC	ΣDIC	ΣPOC	Σ Org C
								14,14	20,98	270,03	43,80

Tab.39. Pelagic-benthic exchange of nitrogen for sandy beaches of the Sylt- Rømø Bay in mgN m^{-2} h^{-1} (yearly average), values were derived from the network model which does not give variance indications (SD or SE). Org N =living organic nitrogen, PON= particulate organic nitrogen, DON =dissolved organic nitrogen, DIN = dissolved inorganic nitrogen.

Donor	**Bacteria**	**Mikrophyto-benthos**	**Oligochaeta spp.**	***Nereis diversicolor***	***Pygospio elegans***	***Corophium arenarium***	**small Polychaetes**	***Macoma balthica***	**small Crustaceans**	***Crangon crangon***	**Sediment POC**	**partial flux**	**type of flux**
N_{Detritus}	0	0	0	0,003	0,027	0,000	0,008	0,00	0	0	0,00	0,04	PON
N_{Bacteria}	0	0	0	0	0,0000	0,0000	0	0	0	0	0	0,00	Org N
$N_{\text{Phytoplankton}}$	0	0	0	0,004	0,25	0,00	0,06	0,02	0	0	0	0,34	Org N
$N_{\text{Zooplankton}}$	0	0	0	0	0	0	0	0	0	0	0,00	0,00	Org N
$N_{\text{settlement}}$	0	0	0,00	0,00000	0,001	0,001	0,001	0,00	0,00	0,000	0,00	0,005	Org N
N_{Drift}	0	0	0,09	0,32	0,016	0,000	0,009	8,97	0,00	0,000	0,00	9,41	Org N
N_{Fishes}	0	0	0	0	0	0	0	0	0	0	0,00	0,00	Org N
$N_{\text{Tauchvögel}}$	0	0	0	0	0	0	0	0	0	0	0,00	0,00	Org N
DON	0,00	7,95	0	0	0	0	0	0	0	0	0	7,95	DON
DIN	0	7,95	0	0	0	0	0	0	0	0	0	7,95	DIN
Flux pro Art	0,00	15,90	0,09	0,33	0,30	0,00	0,08	8,99	0,00	0,00	0,00	25,70	

Tab. 39a. Sum of pelagic-benthic fluxes

Σ Org N	**9,76**
Σ PON	**0,04**
Σ DON	**7,95**
Σ DIN	**7,95**
Total	**25,70**

Tab.40. Benthic-pelagic exchange of nitrogen for sandy beaches of the Sylt- Rømø Bay in mgN m^{-2} h^{-1} (yearly average), values were derived from the network model which does not give variance indications (SD or SE). Org N =living organic nitrogen, PON= particulate organic nitrogen, DON= dissolved organic nitrogen, DIN = dissolved inorganic nitrogen.

Donor	**$N_{Detritus}$**	**$N_{Bakterien}$**	**$N_{Phytoplankton}$**	**$N_{Zooplankton}$**	**$N_{settlement}$**	**$N_{Makro-Zoobenthos}$**	**DON**	**DIN**	**C_{Nekton}**	**C_{birds}**	**Flux pro Art**
Bacteria	0,00	0,00	0	0			0,475	1,24			
Mikrophytobenthos	0,00		0	0			0,28	0,00			
Meiobenthos	0,11							0,74			
Oligochaeta spp.	0,00		0	0	0,00	0,1		0,02	0,00110	0,00	
Nereis diversicolor	0,01		0	0	0,000	0,31791045		0,03	0,005	0,000	
Pygospio elegans	0,03		0	0	0,001	0,01641791		0,24	0,0038	0,00	
Corophium arenarium	0,00		0	0	0,00	0		0,04	0,00149	0,00	
small Polychaetes	0,04		0	0	0,001	0,00895522		0,20	0,005	0,000	
Macoma balthica	0,02		0	0	0,000	8,96808511		0,02	0,00004	0,00	
small Crustaceans	0,02		0	0	0,000	0,00447761		0,04	0,008	0,000	
Crangon crangon	0,00		0	0	0,0000	0		0,01	0,001	0,000	
SedPOC	26,64		0	0	0	0		0			
patrtial flux	26,87	0,00	0,00	0,00	0,002	9,41	0,75	2,59	0,03	0,00	0,00
type of flux	PON	org N	org N	org N	org N	org N	DON	DIN	org N	orgN	
								ΣDON	ΣDIN	ΣPON	Σ Org C
								0,75	2,59	26,87	9,43

Tab. 41. Pelagic-benthic exchange of phosphorus sandy beaches of the Sylt- Rømø Bay in mgP m^{-2} h^{-1} (yearly average), values were derived from the network model which does not give variance indications (SD or SE). Org P =living organic phosphorus, POP= particulate organic phosphorus, DOP =dissolved organic phosphorus, DIP = dissolved inorganic phosphorus.

Donor	**Bacteria**	**Mikrophyto-benthos**	**Oligochaeta spp.**	***Nereis diversicolor***	***Pygospio elegans***	***Corophium arenarium***	**small Polychaetes**	***Macoma balthica***	**small Crustaceans**	***Crangon crangon***	**Sediment POC**	**partial flux**	**type of flux**
$P_{Detritus}$	0	0	0	0,001	0,006	0,000	0,002	0,00	0	0	0,00	0,01	PON
$P_{Bacteria}$	0	0	0	0	0,0000	0,0000	0	0	0	0	0	0,00	Org N
$P_{Phytoplankton}$	0	0	0	0,000	0,02	0,00	0,00	0,00	0	0	0	0,02	Org N
$P_{Zooplankton}$	0	0	0	0	0	0	0	0	0	0	0,00	0,00	Org N
$P_{settlement}$	0	0	0,00	0,00000	0,001	0,001	0,001	0,00	0,00	0,000	0,00	0,005	Org N
P_{Drift}	0	0	0,01	0,04	0,002	0,000	0,001	1,44	0,00	0,000	0,00	1,49	Org N
P_{Fishes}	0	0	0	0	0	0	0	0	0	0	0,00	0,00	Org N
$P_{diving\ birds}$	0	0	0	0	0	0	0	0	0	0	0,00	0,00	Org N
DOP	0,00	0,12	0	0	0	0	0	0	0	0	0	0,12	DOP
DIP	0	0,52	0	0	0	0	0	0	0	0	0	0,52	DIP
Flux pro Art	0,00	0,63	0,01	0,04	0,03	0,00	0,01	1,44	0,00	0,00	0,00	2,16	

Tab. 41a. Sum of pelagic-benthic fluxes

Σ Org P	**1,52**
Σ POP	**0,01**
Σ DOP	**0,12**
Σ DIP	**0,52**
Total	**2,16**

Tab.42. Benthic-pelagic exchange of phosphorus for sandy beaches of the Sylt- Rømø Bay in mgP m^{-2} h^{-1} (yearly average), values were derived from the network model which does not give variance indications (SD or SE). Org P =living organic phosphorus, POP= particulate organic phosphorus, DOP= dissolved organic phosphorus, DIP = dissolved inorganic phosphorus.

Donor	P_{Detritus}	P_{Bacteria}	$P_{\text{Phytoplankton}}$	$P_{\text{Zooplankton}}$	$P_{\text{settlement}}$	$P_{\text{Makro-Zoobenthos}}$	DOP	DIP	P_{Nekton}	P_{birds}	Flux pro Art
Bacteria	0,00	0,00	0	0			0,11080009	0,95			
Mikrophytobenthos	0,00		0	0			0,004				
Meiobenthos	0,05							0,12			
Oligochaeta	0,00		0	0	0,00	0,0		0,00	0,00013		
Nereis diversicolor	0,01		0	0	0,000	0,03634812		0,00	0,001		
Pygospio elegans	0,01		0	0	0,001	0,00187713		0,04	0,0004		
Corophium arenarium	0,00001		0	0	0,00	0		0,01	0,00023		
small Polychaetes	0,02		0	0	0,001	0,00102389		0,02	0,001		
Macoma balthica	0,002		0	0	0,000	0,48448276		0,00	0,000002		
small Crustaceans	0,001		0	0	0,000	0,00051195		0,06	0,001		
Crangon crangon	0,00004		0	0	0,0000	0		0,00	0,000		
SedPOC	6,21		0	0	0	0		0			
partial flux	6,30	0,00	0,00	0,00	0,002	0,53	0,11	1,20	0,003	0,00	0,00
type of flux	POP	org P	org P	org P	org P	org P	DOP	DIN	org P	org P	
								ΣDOP	ΣDIP	ΣPOP	Σ Org P
								0,11	1,20	6,30	0,54

Tab. 43. Pelagic- benthic exchange of carbon for mud flats of the Sylt- Rømø Bay in mgC m^{-2} h^{-1} (yearly average), values were derived from the network model which does not give variance indications (SD or SE). Org C =living organic carbon, POC= particulate organic carbon, DOC =dissolved organic carbon, DIC = dissolved inorganic carbon.

Donor	**Bacteria**	**Mikroph.-benth.**	***Hydrobia ulvae***	***Arenicola marina***	**Oligochaeta spp.**	***Heteromastus filiformis***	***Nereis diversicolor***	***Pygospio elegans***	***Cerastoderma edule***	***Mya arenaria***	**small polychaetes**	***Tharyx kilariensis***	***Macoma balthica***	***Crangon crangon***	**Sediment POC**	**partial flux**	**type of flux**
$C_{Detritus}$	0	0	0	0	0	0	0,52	0,02	0,13	0,01	0,010	0,00	1,43	0	165,08	167,20	POC
$C_{Bacteria}$	0	0	0	0	0	0	0	0,0016	0,01	0,00	0,000	0,00	0,00	0	0	0,01	orgC
$C_{Phytoplankton}$	0	0	0	0	0	0	0,52	0,1381	0,82	0,03	0,054	0,00	8,80	0	0	10,36	orgC
$C_{Zooplankton}$	0	0	0	0	0	0	0	0,0000	0,00	0,00	0,000	0,00	0,00	0	0,00	0,00	orgC
$C_{settlement}$	0	0	0,365	0,11	0,00	0,029	0,12	0,0078	0,04	0,004	0,008	0,01	0,23	0,004	0,00	0,93	orgC
C_{Drift}	0	0	4,390	5,98	0,69	0,000	0,71	0,0200	0,21	0,015	0,075	0,01	88,71			100,80	
C_{Fishes}	0	0	0	0	0	0	0	0	0	0	0	0,00	0,00	0	0,00	0,00	org C
$C_{diving\ birds}$	0	0	0	0	0	0	0	0	0	0	0	0,00	0,00	0	0,00	0,00	org C
DOC	2,81	17,7	0	0	0	0	0	0	0	0	0	0,00	0,00	0	0	20,51	DOC
DIC	0	40,53	0	0	0	0	0	0	0	0	0	0,00	0,00	0	0	40,53	DIC
Flux per species	2,81	58,23	4,76	6,09	0,69	0,03	1,86	0,19	1,21	0,06	0,15	0,02	99,17	0,00	165,08	340,33	

Tab. 43a. Sum of pelagic-benthic fluxes

Σ orgC	**112,10**
ΣPOC	**167,20**
ΣDOC	**20,51**
ΣDIC	**40,53**
Σ Total	**340,34**

Tab.44. Benthic-pelagic exchange of carbon for mud flats of the Sylt- Rømø Bay in mgC m^{-2} h^{-1} (yearly average), values were derived from the network model which does not give variance indications (SD or SE). Org C =living organic carbon, POC= particulate organic carbon, DOC= dissolved organic carbon, DIC = dissolved inorganic carbon.

Donor	C_{Detritus}	C_{Bacteria}	$C_{\text{Phytoplankton}}$	$C_{\text{Zooplankton}}$	$C_{\text{settlement}}$	$C_{\text{Makro-Zoobenthos}}$	DOC	DIC	C_{Nekton}	C_{birds}	Flux per species
Bacteria	0,00	0,00						8,03			8,03
Microphytobenthos	0,00		0,00				6,62	14,1			20,68
Meiobenthos	0,00							1,74			2,75
Hydrobia ulvae	0,00				0,146	4,4		2,49	0,0008	3,485	10,51
Arenicola marina	0,00				0,04	6,0		0,65	0,00250	0,100	6,78
Oligochaeta spp	0,00					0,69		1,01	0,0054	0,034	1,74
Heteromastus	0,00				0,017	0		0,28	0,0001	0,025	0,32
Nereis diversicolor	0,00				0,05	0,71		1,37	0,0017	0,412	2,54
Pygospio elegans	0,00				0,003	0,02		0,05	0,0008	0,023	0,09
Cerastoderma edule	0,00				0,02	0,205		0,06	0,00042	0,227	0,51
Mya arenaria	0,00				0,001	0,015		0,02	0,00	0,009	0,04
small Polychaeten	0,00				0,003	0,075		0,163	0,001	0,030	0,27
Tharyx kilariensis	0,00				0,003	0,01		0,17	0,00	0,005	0,19
Macoma balthica	0,00				0,09	88,705		9,36	0,00125	0,171	98,33
Crangon crangon	0,00				0,0000	0		0,05	0,004	0,006	0,06
P. microps	0,00				0,0000	0		0,0004	0,00008		0,00
P.minutus	0,00				0,0000			0,0004	0,00000		0,00
P.platessa	0,00				0,0000			0,00001	0,00000		0,00
P.flesus	0,00				0,0000			0,00042	0,00000		0,00
M.merlangus	0,00				0,0000			0,00033	0,00000		0,00
SedPOC	0,00										0,00
partial flux	0,00	0,00	0,00	0,00	0,38	100,80	6,62	39,50	0,02	4,53	151,84
type of flux	POC	org C	org C	org C	org C	org C	DOC	DIC	org C	org C	

Tab.45. Pelagic-benthic exchange of nitrogen for mud flats of the Sylt- Rømø Bay in mgN m^{-2} h^{-1} (yearly average), values were derived from the network model which does not give variance indications (SD or SE). Org N =living organic nitrogen, PON= particulate organic nitrogen, DON =dissolved organic nitrogen, DIN = dissolved inorganic nitrogen.

donor	**Bacteria**	**Mikrophyto-benthos**	***Hydrobia ulvae***	***Arenicola marina***	**Oligochaeta spp.**	***Heteromastus filiformis***	***Nereis diversicolor***	***Pygospio elegans***	***Cerastoderma edule***	***Mya arenaria***	**small polychaetes**	***Tharyx kilariensis***	***Macoma balthica***	***Crangon crangon***	**Sediment POC**	**partial flux**	**type of flux**
N_{Detritus}	0	0	0	0	0	0	0,05154167	0,00	0,01	0,00	0,001	0,00	0,14	0	16,51	16,72	PON
N_{Bacteria}	0	0	0	0	0	0	0	0,0003	0,00	0,00	0,000	0,00	0,00	0	0	0,00	orgN
$N_{\text{Phytoplankton}}$	0	0	0	0	0	0	0,07774007	0,0208	0,12	0,00	0,008	0,00	1,33	0	0	1,56	orgN
$N_{\text{Zooplankton}}$	0	0	0	0	0	0	0	0,0000	0,00	0,00	0,000	0,00	0,00	0	0,00	0,00	orgN
$N_{\text{settlement}}$	0	0	0,083	0,02	0,00	0,007	0,03	0,0018	0,01	0,001	0,002	0,00	0,05	0,001	0,00	0,21	orgN
N_{Drift}	0	0	0,934	1,79	0,21	0,000	0,21	0,0060	0,04	0,003	0,022	0,00	18,87			22,09	
N_{Fishes}	0	0	0	0	0	0	0	0	0	0	0	0,00	0,00	0	0,00	0,00	org N
$N_{\text{Tauchvögel}}$	0	0	0	0	0	0	0	0	0	0	0	0,00	0,00	0	0,00	0,00	orgN
DON	2,81	3,54	0	0	0	0	0	0	0	0	0	0,00	0,00	0	0	6,35	DON
DIN	0	3,54	0	0	0	0	0	0	0	0	0	0,00	0,00	0	0	3,54	DIN
Flux per species	2,81	7,08	1,02	1,81	0,21	0,01	0,37	0,03	0,19	0,01	0,03	0,00	20,40	0,00	16,51	50,47	

Tab. 45a. Sum of pelagic-benthic fluxes

Σ orgN	**23,87**
ΣPON	**16,72**
ΣDON	**6,35**
ΣDIN	**3,54**
Σ Total	**50,48**

Tab.46. Benthic-pelagic exchange of nitrogen for mud flats of the Sylt- Rømø Bay in mgN m^{-2} h^{-1} (yearly average), values were derived from the network model which does not give variance indications (SD or SE). Org N =living organic nitrogen, PON= particulate organic nitrogen, DON= dissolved organic nitrogen, DIN = dissolved inorganic nitrogen.

Donor	$N_{Detritus}$	$N_{Bacteria}$	$N_{Phytoplankton}$	$N_{Zooplankton}$	$N_{settelement}$	$N_{Makro-Zoobenthos}$	DON	DIN	N_{Nekton}	N_{birds}	Flux per species
Bacteria	0.00	0.00						1.24			1.24
Microphytobenthos	0.00		0.00				0.53	0.54			1,07
Meiobenthos								0.4			0,37
Hydrobia ulvae	0.00				0.033	0.9		0.54	0.0002	0.742	2,25
Arenicola marina	0.00				0.01	1.8		0.40	0.00075	0.030	2,22
Oligochaeta spp	0.00					0.20597015		0.22	0.0016	0.010	0,44
Heteromastus	0.00				0.004	0		0.23827708	0.0000	0.007	0,25
Nereis diversicolor	0.00				0.01	0.2119403		0.52	0.0005	0.123	0,87
Pygospio elegans	0.00				0.001	0.00597015		0.02	0.0002	0.007	0.04
Cerastoderma edule	0.00				0.00	0.04361702		0.02	0.00009	0.048	0.11
Mya arenaria	0.00				0.000	0.00319149		0.00	0.00	0.002	0.01
small Polychaeten	0.00				0.001	0.02238806		0.02	0.000	0.009	0.05
Tharyx kilariensis	0.00				0.001	0.00298507		0.02	0.00	0.002	0.03
Macoma balthica	0.00				0.02	18.8734043		0.225	0.00027	0.036	19.16
Crangon crangon	0.00				0.0000	0		0.01	0.001	0.001	0.01
Pomatoschistus microps	0.00				0.0000	0		0.0008	0.00008		0,0008
P.minutus	0.00				0.0000			0.0018	0.00000		0,0018
P.platessa	0.00				0.0000			0.00425	0.00000		0,00425
P.flesus	0.00				0.0000			0.00195	0.00000		0,00195
M.merlangus	0.00				0.0000			0.00016	0.00000		0,00016
SedPOC	0.00										0
partial flux	0.00	0.00	0.00	0.00	0.09	22.09	0.5	4.40	0.00497	1.02	28,23
type of flux	PON	org N	org N	org N	org N	org N	DON	DIN	org C	org C	Total

Tab. 47. Pelagic-benthic exchange of phosphorus for mud flats of the Sylt- Rømø Bay in mgP m^{-2} h^{-1} (yearly average). values were derived from the network model which does not give variance indications (SD or SE). Org P =living organic phosphorus. POP= particulate organic phosphorus. DOP =dissolved organic phosphorus. DIP = dissolved inorganic phosphorus.

	Bacteria	**Mikrophyto-benthos**	***Hydrobia ulvae***	***Arenicola marina***	**Oligochaeta spp.**	***Heteromastus filiformis***	***Nereis diversicolor***	***Pygospio elegans***	***Cerastoderma edule***	***Mya arenaria***	**small polychaetes**	***Tharyx kilariensis***	***Macoma balthica***	***Crangon crangon***	**Sediment POC**	**partial flux**	**type of flux**
P_{Detritus}	0	0	0	0	0	0	0.01202278	0.00	0.00	0.00	0.000	0.00	0.033	0	3.85	3.90	POP
P_{Bacteria}	0	0	0	0	0	0	0	0.0001	0.00	0.00	0.000	0.00	0.00	0	0	0.00	orgP
$P_{\text{Phytoplankton}}$	0	0	0	0	0	0	0.00486242	0.0013	0.01	0.00	0.001	0.00	0.08	0	0	0.10	orgP
$P_{\text{Zooplankton}}$	0	0	0	0	0	0	0	0.0000	0.00	0.00	0.000	0.00	0.00	0	0.00	0.00	orgP
$P_{\text{settlement}}$	0	0	0.007	0.00	0.00	0.001	0.00	0.0002	0.00	0.000	0.000	0.00	0.00	0.000	0.00	0.02	orgP
P_{Drift}	0	0	0.150	0.20	0.02	0.000	0.02	0.0007	0.00	0.000	0.003	0.00	1.02			1.43	org P
P_{Fishes}	0	0	0	0	0	0	0	0	0	0	0	0.00	0.00	0	0.00	0.00	orgP
$P_{\text{Tauchvögel}}$	0	0	0	0	0	0	0	0	0	0	0	0.00	0.00	0	0.00	0.00	org C
DOP	0.07	0.05130435	0	0	0	0	0	0	0	0	0	0.00	0.00	0	0	0.12	DOP
DIP	0	0.23	0	0	0	0	0	0	0	0	0	0.00	0.00	0	0	0.23	DIP
Flux pro Art	0.07	0.28	0.16	0.21	0.02	0.00	0.04	0.00	0.01	0.00	0.00	0.00	1.14	0.00	3.85	5.79	

Tab. 47a. Sum of pelagic-benthic fluxes

Σ orgC	**1.54**
ΣPOP	**3.90**
ΣDOP	**0.12**
ΣDIP	**0.23**
Σ Total	**5.79**

Tab.48. Benthic-pelagic exchange of phosphorus for mud flats of the Sylt- Rømø Bay in mgP m^{-2} h^{-1} (yearly average). values were derived from the network model which does not give variance indications (SD or SE). Org P =living organic phosphorus. POP= particulate organic phosphorus. DOP= dissolved organic phosphorus. DIP = dissolved inorganic phosphorus.

Donor	P_{Detritus}	P_{Bacteria}	$P_{\text{Phytoplankton}}$	$P_{\text{Zooplankton}}$	$P_{\text{settlement}}$	$P_{\text{Makro-Zoobenthos}}$	**DOP**	**DIP**	C_{Nekton}	C_{birds}	**Flux per species**
Bacteria	0.00	0.00						0.95			0.95
Microphytobenthos	0.00		0.00				0.003	0.0			0.003
Meiobenthos								0.06			0.06
Hydrobia ulvae	0.00				0.003	0.1		0.04	0.0000	0.119	0.32
Arenicola marina	0.00				0.00	0.2		0.04	0.00009	0.003	0.25
Oligochaeta spp	0.00					0.02354949		0.02	0.0002	0.001	0.04
Heteromastus	0.00				0.000	0		0.03	0.0000	0.001	0.03
Nereis diversicolor	0.00				0.00	0.02423208		0.05	0.0001	0.014	0.09
Pygospio elegans	0.00				0.000	0.00068259		0.00	0.0000	0.001	0.01
Cerastoderma edule	0.00				0.00	0.00235632		0.01	0.00000	0.003	0.01
Mya arenaria	0.00				0.000	0.00017241		0.00	0.00	0.000	<0.01
small Polychaeten	0.00				0.000	0.00255973		0.00	0.000	0.001	0.01
Tharyx kilariensis	0.00				0.000	0.01		0.006	0.00	0.000	0.02
Macoma balthica	0.00				0.00	1.0195977		0.11	0.00001	0.002	1.13
Crangon crangon	0.00				0.0000	0		0.00	0.0001	0.000	<0.01
Pomatoschistus microps	0.00				0.0000	0		8.9066E-05	0.000005		<0.01
P.minutus	0.00				0.0000			0.0002	0.00000		<0.01
P.platessa	0.00				0.0000			0.0000	0.00000		<0.01
P.flesus	0.00				0.0000			0.00001	0.00000		<0.01
M.merlangus	0.00				0.0000			0.00003	0.00000		<0.01
SedPOC	0.00										0
partial flux	0.00	0.00	0.00	0.00	0.01	1.44	0.00	1.32	0.001	0.15	2.91
type of flux	POP	org P	org P	org P	org P	org P	DOP	DIP	org P	org P	