

## **Trophic networks and carbon flows in South Eastern Baltic costal ecosystems**

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### **Abstract**

Carbon flows in five South Eastern Baltic coastal ecosystems (Puck Bay, Curonian Lagoon, Open Baltic Coast, exposed Gulf of Riga coast and Pärnu Bay) were compared based on a common 12 compartment ECOPATH model structure. Primary producers were represented by phytoplankton and perennial and annual macrophytes. Zooplankton was divided into meso- and macrozooplankton (mysids) and benthic subsystem comprised suspension- and deposit feeders. Fish were aggregated into three groups on the basis of diet composition (planktivores, benthivores, and piscivores) and fisheries were included into all models. Top predators were represented by one functional group of birds.

The studied systems ranged from the hypertrophic Curonian Lagoon to the mesotrophic exposed Gulf of Riga coast. Three locations out of the five had dense macrophyte beds (75.5 g C m<sup>-2</sup>) leading to high total primary production. However, we found that macrophytes were almost not consumed by grazers, but rather channeled into the detritus food chain. Mesozooplankton biomass was similar in all analyzed systems (0.22 g C m<sup>-2</sup>). The ecotrophic efficiency of phytoplankton was negatively related to phytoplankton primary production. Biomass structure of macrozoobenthos communities varied widely. In systems with high bird populations (Puck Bay, Curonian Lagoon and Pärnu Bay), their share in fish consumption was comparable to fish catches. Fishing pressure was the highest at the open Baltic coast and the lowest in the Curonian Lagoon. To mimic potential changes in external forcing, we tested the sensitivity of system to fishing pressure and bird abundance. Responses depended on the trophic structure of the ecosystems

Key words: Baltic, costal ecosystems, ECOPATH, carbon flows, ecosystem-based management

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## **Introduction**

Recently, the concept of ecosystem-based management has drawn closer attention to the functioning of marine ecosystems. Ecosystem-based management, as adopted in the joint HELCOM/OSPAR Bergen declaration (2002) is “...the comprehensive integrated management of human activities based upon the best available scientific knowledge about the ecosystem and its dynamics in order to identify and take action on influences which are critical to the health of the marine ecosystem, thereby achieving sustainable use of ecosystem goods and services and maintenance of ecosystem integrity”. Understanding trophic interactions is a crucial part of our knowledge on the dynamics of marine ecosystems. Moreover, “taking actions on influences which are critical to the health of marine ecosystems” requires recognizing and prioritizing human impacts to which the system responds most sensitive. Finally, monitoring the results of management actions has to be based on meaningful indicators which are related to the “sustainable use of ecosystem goods and services”.

This study has been initiated by the Baltic Sea Regional Project (BSRP), a Global Environment Facility (GEF) funded project to strengthen ecosystem-based management in the Baltic Sea. We compare the trophic networks in five South-Eastern Baltic coastal ecosystems, namely Puck Bay in the Gulf of Gdansk, the Curonian Lagoon, the Lithuanian Baltic Proper coast (termed Open Baltic Coast), an exposed area on the Eastern shore of the Gulf of Riga (Exposed Gulf of Riga coast) and Pärnu Bay, a shallow bay north of the Exposed Gulf of Riga coast site. Trophic network modeling using ECOPATH software (Christensen et al., 2004) was tested as a tool to identify external impacts and internal relationships critical to their functioning and to quantify and analyze their trophic state and development stage. The network indices and modelled carbon flows in the ecosystems were used to estimate energy transfer efficiency through the trophic groups. Comparative network analysis allowed quantification of the importance of direct and indirect interactions in the investigated coastal ecosystems and showed the impact of human disturbances.

Previous work on modeling Baltic Sea food webs, carbon flows and trophic networks (Harvey et al. 2003, Sandberg et al., 2000, Jarre-Teichmann, 1995) focused on pelagic ecosystems of deep-water areas of the open Baltic Sea. Witek (1995) calculated carbon flows and the utilization of primary production in the Gdansk basin, but the study area comprised only the Gdansk Deep without the shallow coastal waters. Therefore this analysis also helps to close a gap in our knowledge of the functioning of Baltic coastal ecosystems in general.

## Materials and methods

### ECOPATH

Trophic networks of the five coastal ecosystems were constructed using ECOPATH with ECOSIM (EwE) software (Christensen et al., 2004, Christensen and Pauly, 1992). EwE is a tool to analyze matter and energy flows within steady state (ECOPATH) or dynamic (ECOSIM) mass balance models. Originally proposed by Polovina (1984), the ECOPATH steady-state model has been combined with routines for network analysis based on the approach developed by Ulanowicz (1986).

ECOPATH's basic equation represents a mass balance for each trophic group  $i$  in a system of  $n$  trophic groups,

$$B_i \frac{P_i}{B_i} EE_i - \sum_{j=1}^n B_j \frac{Q_j}{B_j} DC_{ji} - EX_i = 0 \quad [\text{Equation 1}]$$

where:  $B_i$  is the biomass of group  $i$ ;  $P_i$  is its total production;  $DC_{ji}$  - the proportion of trophic group  $j$  in the diet of group  $i$  - is a diet matrix coefficient that describes the trophic relationship between groups;  $Q_i$  is the total food consumption of group  $i$ ; the production/biomass ratio  $P_i/B_i$  and the consumption/biomass ratio  $Q_i/B_i$  are metabolic rates that express the productivity and consumption per unit of biomass, respectively.  $EE_i$  is the Ecotrophic efficiency, which is the fraction of production of group  $i$  that is utilized

- i.e. consumed exported of harvested - within the system.  $EX_i$  is the export of  $i$  to other ecosystems such as e.g. net migration.

### **Trophic level decomposition and flows between trophic levels**

Trophic level of consumer groups is calculated as the weighted average of the trophic levels of their prey, using the consumption of each prey item as weighting factor (Christensen et al., 2004). Inversely, flows between model groups can be fractionated according to the trophic level they originate from (Ulanowicz, 1995, Christensen et al., 2004) to construct a linearized foodchain, referred to as a Lindeman spine. Transfer efficiencies between trophic levels can be calculated and the method allows comparing “spines” from different ecosystems and model structures.

### **Mixed Trophic Impact**

The Mixed Trophic Impact (MTI) routine (Majkowski, 1982 in Blanshard et al., 2002) in EwE was used to evaluate critical trophic interactions between groups in the ecosystems. Leontief (1951) originally developed this method to assess direct and indirect interactions in the economy of the USA. A Routine similar to Leontief (1951) has been introduced to study direct and indirect effects of ecological groups on each other by Hannon (1973), Hannon and Joiros (1989) and Ulanowicz and Puccia (1990), and has now been incorporated into ECOPATH (Christensen and Pauly, 1992).

### **Ecosystem Properties**

We have also included a set of commonly used indexes for comparing ecosystem properties into our studies. In particular, Odum (1971) postulated that the ratio between total primary productivity and total system respiration (TPP/TR) would approach unity in mature system, whereas systems in development would be characterized by smaller ratios. Total primary production per total biomass (TPP/TB) has also been used to indicate system maturity (Odum, 1971, Christensen, 1995). Systems in “developmental phase” have high TPP/TB ratios, while “mature” ones tends to have lower TPP/TB ratio,

associated with high biomass or lower production rate (Christensen, 1995). Similarly, the Total Biomass per Total System Throughput ratio (TB/TST) tends to be low in the developmental phase of an ecosystem and increase in values as the system matures and conserves energy by storing it in its components (Odum, 1971, Ulanowicz, 1986). The System Omnivory Index (SOI) is defined as the average omnivory index (variance of trophic levels of the consumers prey) of all consumers weighted by the logarithm of each consumer's food intake. The system omnivory index therefore characterizes the diversity of consumer – prey relationships (Pauly et al., 1993).

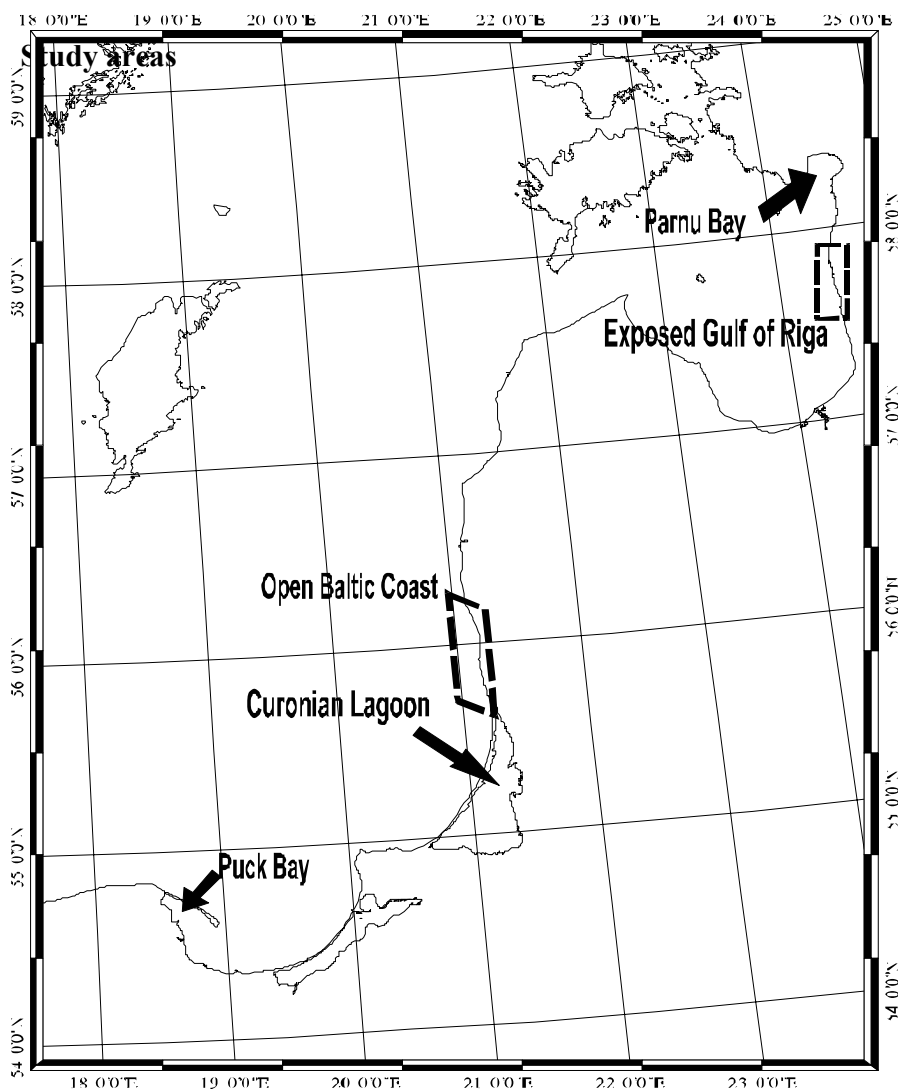


Figure1: South-Eastern Baltic Sea with location of the investigated areas – from south to north: Puck Bay, Curonian Lagoon Open Baltic Sea near Lithuanian Baltic coast, Exposed Gulf of Riga (Ananzi Denzi region) and Pärnu Bay

The study areas span the entire South-Eastern coast of the Baltic Sea (Fig. 1). The Open Baltic Coast site in the Lithuanian economic zone and the Exposed Gulf of Riga Coast represent exposed areas with relatively high wave energy. The Open Baltic Coast is located to the north of the Klaipeda strait. Hydrographic conditions at this site, located at water depths up to 20 m, are determined by the interaction between the south-eastern Baltic offshore waters and the nutrient rich freshwater runoff of the Curonian Lagoon. The Open Baltic Coast study area is mainly covered by hard (pebbles, stones and boulders), but also sandy, and mixed sediments (sand, gravel, stones). In large parts of the study area the red algae *Furcellaria lumbricalis* structures the biotic communities. The study site at the Exposed Gulf of Riga coast is the marine part of the North Vidzeme Biosphere reserve, located between Ainiži and Dzeņi in the North-Eastern part of the Gulf of Riga. Because of its high biological diversity, importance as fish spawning and nursery ground as well as bird feeding area, the area is nominated as a HELCOM Baltic Sea Protected area. The study area is delineated by the 10 m isobath and average depth is about 5 m. Bottom types range from soft bottoms to rocks and sustain high macrophyte biomass. The Gulf of Riga is an eutrophic area (Wasmund et al., 2001), but the study site is located relatively far from major river mouths. Puck Bay and Pärnu Bay are sheltered areas in the Gulf of Gdansk and Gulf of Riga, respectively. Puck Bay, the marine part of the Nadmorski Landscape Park and another designated HELCOM Baltic Sea Protected Area, comprises an area of 359 km<sup>2</sup> and forms a semi-closed part of the Gulf of Gdansk. It is a shallow bay, particularly in its inner part which is at most 8.5 m deep. Salinity ranges from 5.0 to 7.2 PSU, and water temperature from 1.4 to 19.2<sup>0</sup>C (Pelczarski 1999). Bottom sediments are mainly sandy, and in some parts (Kruk-Dowgiałło 1991) covered by seagrasses (*Zostera marina*, *Ruppia rostellata*, *Zannichaellia palustris*) and annual macrophytes (*Pilayella littoralis*, *Ectocarpus siliculosus*). Also physico-chemical parameters and the structure of the ichthiofauna differ from the general characteristic of the Gulf of Gdansk. Pärnu Bay is a shallow semi-enclosed basin in the NE Gulf of Riga, with surface area of about 700 km<sup>2</sup> and a volume of 2 km<sup>3</sup>. Its maximum depth increases gradually from 7.5 m in its inner part to 23 m. A complex interplay of meteorological processes, river discharge, and water exchange with the open part of the Gulf of Riga determine the hydrological conditions in the bay. Coastline morphology is relatively

simple and sand and silty sand dominate the bottom sediments. Macrophytes occur along the coast where the water depth is less than 2 m. The Pärnu River (annual runoff approximately 2 km<sup>3</sup>) falls into the NE part of the bay. Together with the Pärnu town, it is the major sources of eutrophication in the bay. In the eutrophied bay, biomass of mesozooplankton and nectobenthos is several times larger than in the open Gulf of Riga. Fish communities are dominated by cyprinids. The Curonian Lagoon is a hypertrophic freshwater transition zone, characterized by the flow of the Nemunas River into the shallow lagoon (area 1584 km<sup>2</sup>, average depth 3.5 m), with a very narrow connection to the Baltic Proper through the Klaipeda Strait. The southern part of the lagoon is freshwater, while in the northern part salinity varies between 0 and 7 PSU, depending on the water inflow from the open Baltic Sea. Due to the low salinity, phytoplankton communities are similar to temperate freshwaters with a diatom spring bloom followed by cyanobacteria dominating during summer. Zooplankton is mostly represented by freshwater species, with *Cyclops* spp., *Daphnia* spp. making up the majority of the biomass. During summer the predatory cladoceran *Leptodora kindtii* is quite abundant. Bottom sediments are mainly sandy with significant areas of muddy bottoms in the southern part. There is only very little macrophyte growth (at depths < 0.9 m) due to the high turbidity in the lagoon caused by the high primary production and bottom sediment resuspension. More shallow locations were excluded from the analysis, due to the low data availability. Bottom fauna is represented by sestonophagous species (chironomids, oligochaets) together with suspension feeders, of which the zebra mussel (*Dreissena polymorpha*) is the most abundant. Fish communities are dominated by roach (*Rutilus rutilus*), perch (*Perca fluviatilis*), redeye (*Scardinius erythrophthalmus*), white bream (*Blicca bjoerkna*) and common bream (*Abramis brama*). Planktivorous fish in the pelagic zone are represented only by ziege (*Pelecus cultratus*), while smelt (*Osmerus eperlanus*) is abundant only during the winter spawning migrations.

### Data aggregation and foodweb model structure

The five ECOPATH models show annual average carbon flows (Fig. 2), using an identical twelve compartment model structure to make the models comparable among each other (Abarca-Arenas, Ulanowicz, 2002). Phytoplankton was represented by a single model compartment, while benthic primary producers were split into annual and perennial macrophytes. Pelagic zooplankton was divided into mesozooplankton and macrozooplankton. Benthic consumers were represented as benthic deposit feeders and benthic filter feeders. The models included three ecological group of fish – planktivorous, benthivorous (including also omnivorous species), and piscivorous fish. Birds were included as a top predator group. Seals occur only infrequently in the investigated coastal systems and were therefore omitted. Fishing pressure is represented by a fishing fleet. The main species aggregated into each of the model components are listed in table 1.

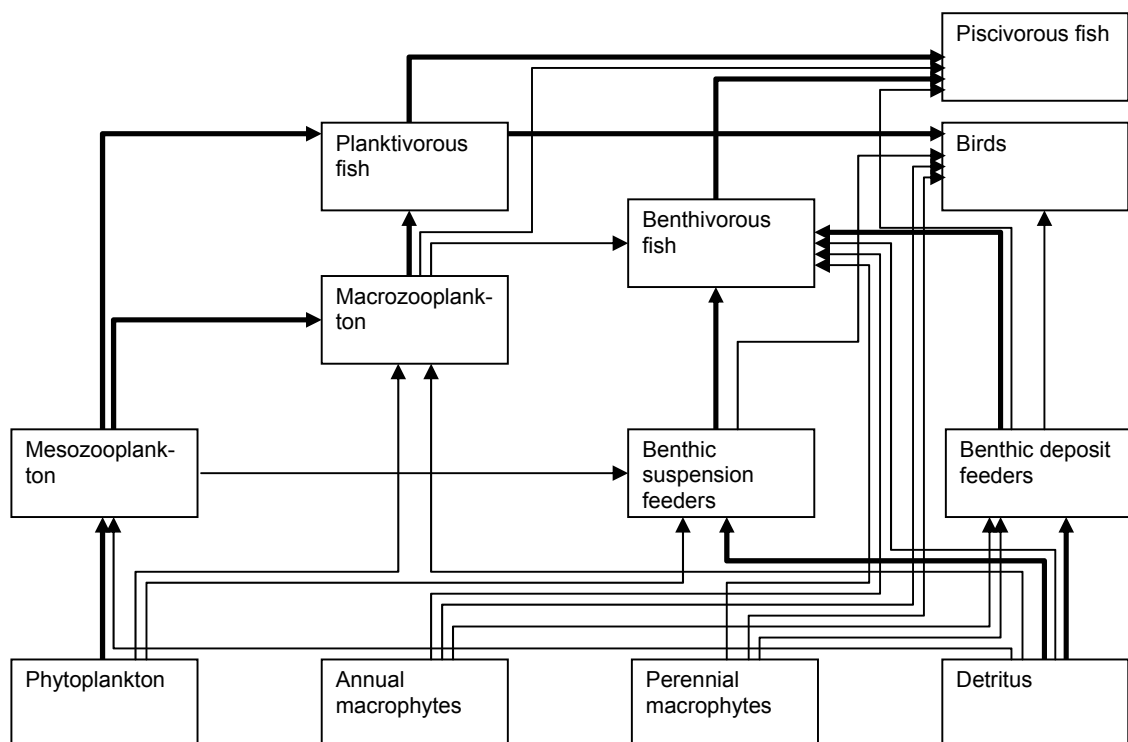


Figure 2: Foodweb structure of the ECOPATH models (fluxes to detritus are omitted, bold arrows denote main food flows for each consumer group).

# RESULTS

## Biomass

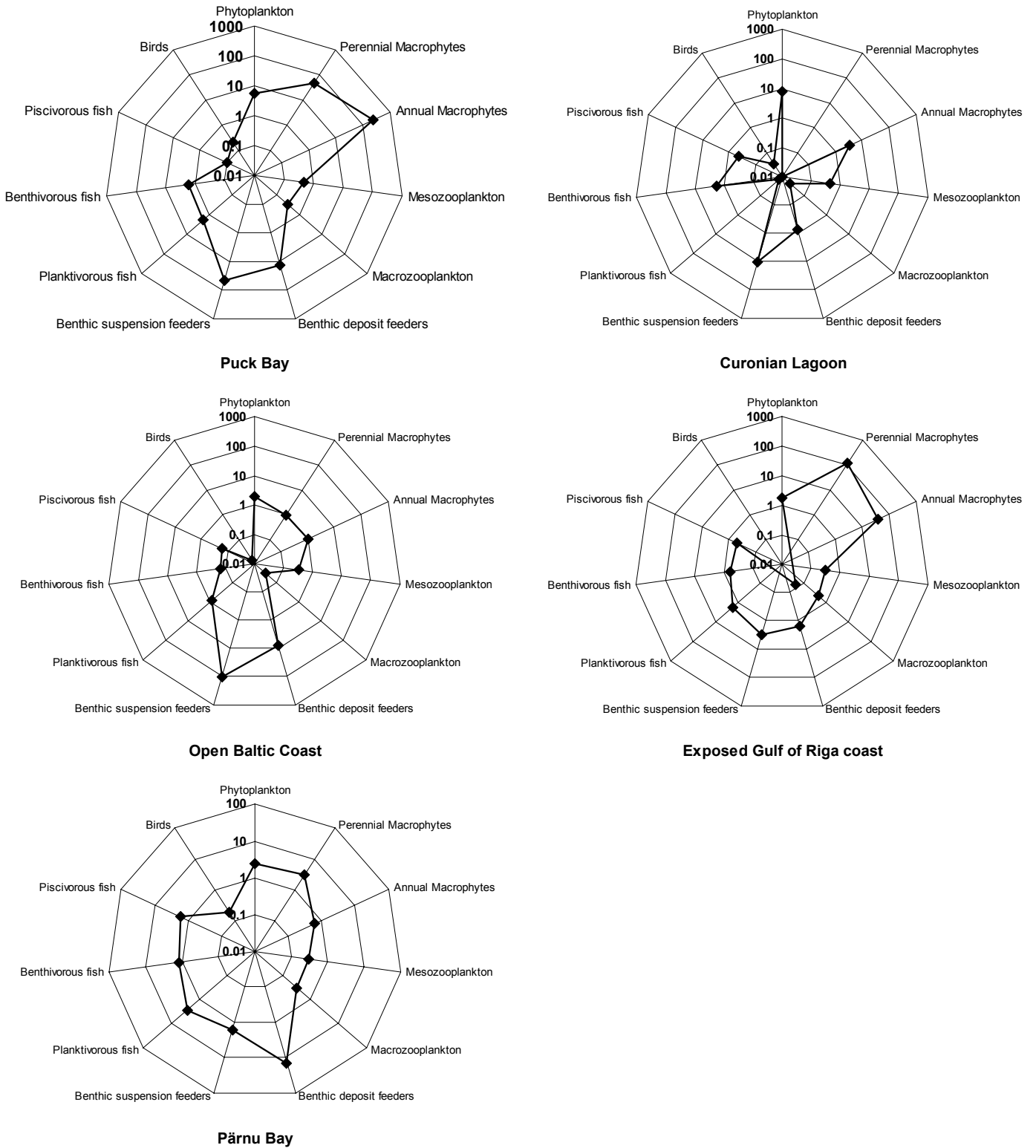


Figure 3: Annual average biomasses (g C m<sup>-2</sup>) in the modeled coastal ecosystems (note logarithmic scale!)

While pelagic component standing stocks - phytoplankton, mesozooplankton, and macrozooplankton – were similar in all areas, benthic macrophytes and benthic macrofauna showed large differences. Also fish and bird biomass varied between the investigated areas (Fig. 3). In all systems except the shallow, turbid Curonian Lagoon macrophytes dominated the primary producer biomass and especially Puck Bay and the exposed Gulf of Riga coast were covered by dense macrophyte beds. On the other hand, phytoplankton biomass was comparable in all investigated coastal systems, with slightly higher concentrations in the enclosed Puck Bay and Curonian Lagoon. Macrozooplankton was mostly present at similar concentrations than mesozooplankton, only in the Curonian Lagoon and at the Open Baltic Coast macrozooplankton biomass was low. In all systems, biomass of benthic fauna exceeded the biomass of pelagic consumers. Largest benthic suspension and deposit feeder biomasses were observed at Puck Bay and the Open Baltic Coast. Fish communities were – with the exception of the Curonian lagoon, dominated by planktivorous fish. Biomass of benthivorous and piscivorous fish were slightly lower. Pärnu Bay and Puck Bay had large bird communities, made up largely by cormorants and in the case of Puck Bay also by marine ducks.

## Carbon flows

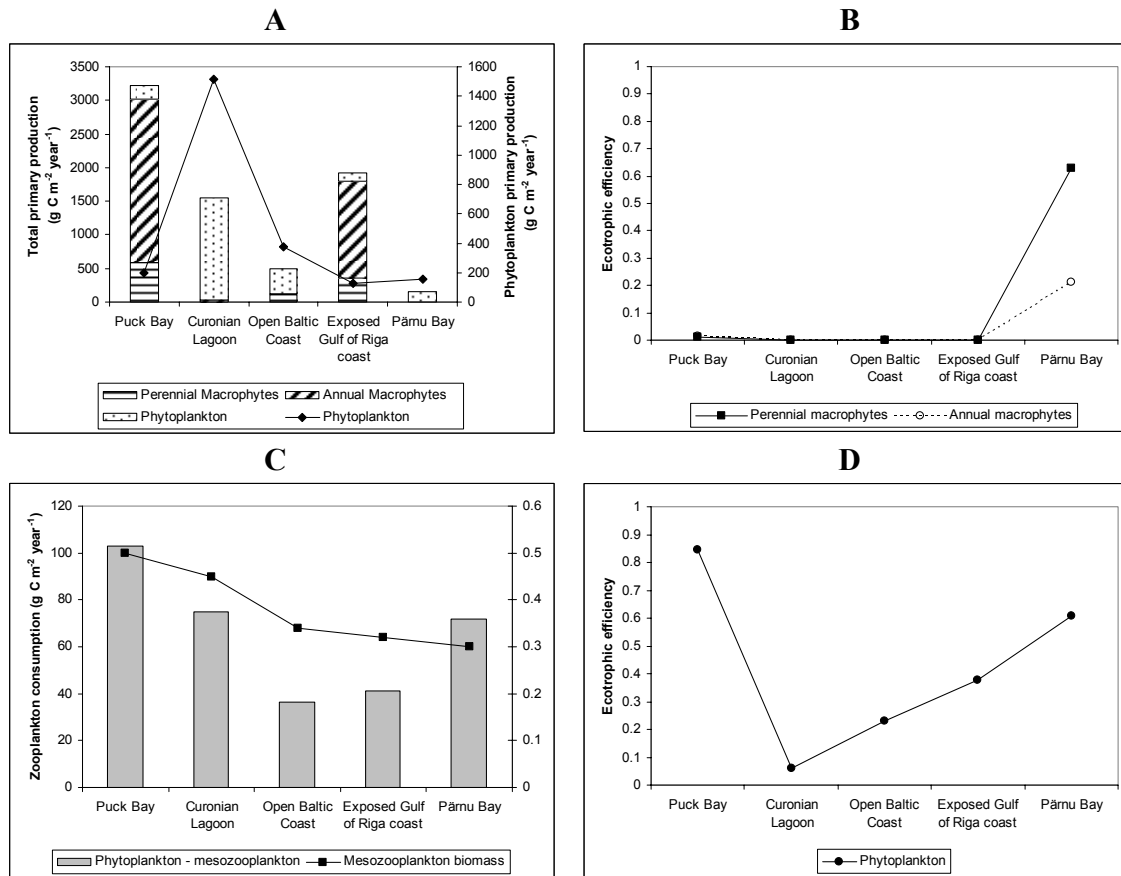


Figure 4: Estimated primary production (A) and fate of primary producers shown by the ecotrophic efficiency of macrophytes (B), mesozooplankton predation of phytoplankton (C) and ecotrophic efficiency of phytoplankton (D)

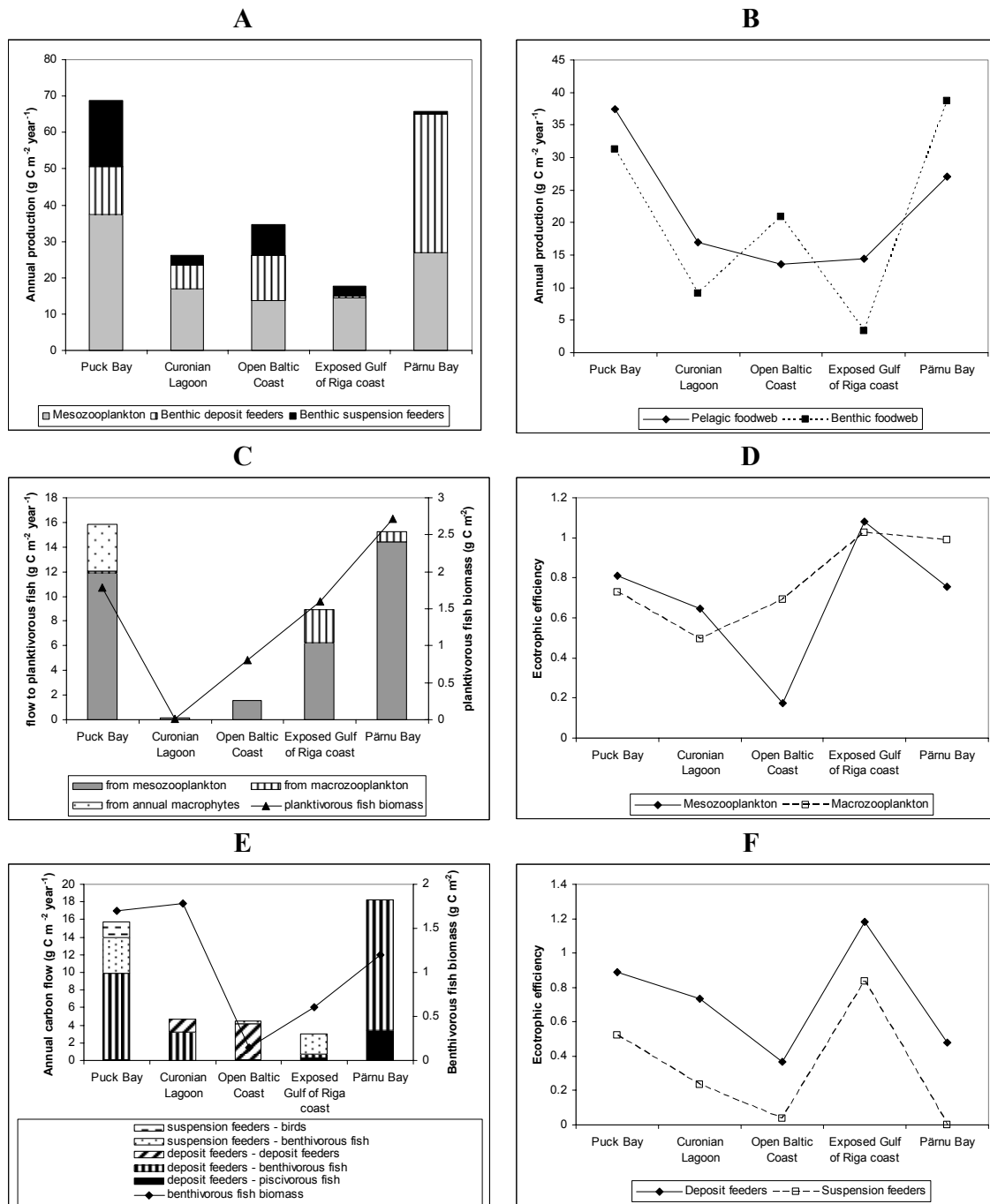


Figure 5: Annual production of primary consumers (A) and carbon flow channeled into benthic and pelagic foodwebs (B). Middle panels show food consumption of the main pelagic secondary consumer, planktivorous fish (C) and ecotrophic efficiency of its major prey items (D), while bottom panels show carbon flows in the benthic foodweb (E) and ecotrophic efficiency of benthic groups (F)

Three groups of primary producers - phytoplankton, annual and perennial macrophytes – were the sole source of carbon and energy for the coastal foodwebs. In systems with dense macrophyte growth, annual macrophytes strongly dominated the total primary production (Fig. 4 A), which varied widely from estimated 3200 g C m<sup>-2</sup> year<sup>-1</sup> in Puck Bay to 160 g C m<sup>-2</sup> year<sup>-1</sup> in Pärnu Bay. Because of their high P/B ratio, perennial macrophytes contributed less to the total primary production than annual macrophytes. With the exception of Pärnu Bay, where macrophytes were grazed by benthivorous fish – mainly cyprinids -, macrophyte production was not channeled into the foodwebs directly as shown by the low ecotrophic efficiency (Fig. 4 B). Rather, macrophytes provided a source of detritus for benthic communities.

Phytoplankton primary production was largest in the hypertrophic Curonian lagoon (1500 g C m<sup>-2</sup> year<sup>-1</sup>). Phytoplankton primary production for the other ecosystems investigated ranged from 370 g C m<sup>-2</sup> year<sup>-1</sup> in the Open Baltic Coast, which is affected by the outflow of nutrient rich water from the Curonian Lagoon, to 160 g C m<sup>-2</sup> year<sup>-1</sup> in Pärnu Bay (Fig. 4 A).

According to the foodweb structure (see Fig. 2), carbon flows to higher trophic levels can be roughly divided into pelagic fluxes, channelled from phytoplankton to meso- and macrozooplankton and further to planktivorous fish, as opposed to benthic fluxes. Benthic fluxes are based on detritus, which is generated by decaying phytoplankton and phytobenthos material. Detritus is consumed by benthic suspension and deposit feeders, which are in turn consumed by benthivorous fish. The basis of the pelagic foodweb – mesozooplankton production – was slightly larger in Puck Bay and Pärnu Bay than in the other systems investigated. The flow of carbon to planktivorous fish largely followed the pattern in planktivorous fish biomass (Fig. 5 C) and differed therefore widely between the investigated ecosystems. High ecotrophic efficiencies for meso- and macrozooplankton – around one – at the exposed Gulf of Riga coast and at Pärnu Bay show, that carbon was passed to planktivorous fish at close to maximum efficiency.

Following the differences in biomass, benthic production also varied strongly between the systems, decreasing from very high production at the Open Baltic Coast, intermediate production at Puck Bay and Pärnu Bay to very low values in the Curonian Lagoon and the exposed Gulf of Riga coast. Benthic deposit and suspension feeders were mainly preyed upon by benthivorous fish and – to a lesser degree – by birds. The flow of carbon from the benthic fauna to higher trophic levels therefore roughly followed the pattern in benthivorous fish biomass (Fig. 5 E), with the exception of the Curonian lagoon. Here the high biomass of benthivorous fish was also supported by import from the very productive shallow areas of the lagoon not included in the analysis, while in the central lagoon benthic production and the flows originating from the benthic fauna were low. Both benthic fauna production and predation pressure by benthivorous fish determined the ecotrophic efficiency of benthic suspension and deposit feeders. Ecotrophic efficiency was lowest at the open Baltic coast and Pärnu Bay, with high benthic production but low benthivorous fish biomass, while at the exposed Gulf of Riga coast the small benthic production caused high ecotrophic efficiency (Fig. 5 F).

Utilization of fish resources in the investigated costal Baltic ecosystems was caused by fisheries, and by predation from birds and piscivorous fish (Fig. 6 A). Lowest catches were found in the Curonian Lagoon, highest at the Open Baltic Coast. Also the structure of the catch differed markedly between the ecosystems. While fisheries focused on benthivorous fish in Puck Bay and the Curonian Lagoon, planktivorous fish were the dominant catch in the other systems. Predation by birds ranged from insignificant to exceeding the total catches, as in the case of the large bird colonies (cormorants) in Pärnu Bay. However, bird predation in Pärnu Bay mainly affected piscivorous fish (perch), while the fisheries targeted planktivores. Differences between bird predation on fish were consequently large and ranged from  $0.001 \text{ g C m}^{-2} \text{ year}^{-1}$  at the exposed Gulf of Riga coast to  $2.66 \text{ g C m}^{-2} \text{ year}^{-1}$  in Pärnu Bay. In some ecosystems with high piscivorous fish biomass, predation by piscivores constituted a significant loss for planktivorous and benthivorous fish, especially in Pärnu Bay, where piscivore predation on planktivorous fish exceeded the catch of planktivores and was also larger than bird consumption.

Catches in all areas peaked in trophic level (TL) III (Fig. 6 C). The mean trophic level of the catch was highest in the Open Baltic Sea area and lowest in Puck Bay (Fig 6 C, Tab. 2). The Ecotrophic Efficiency (Fig. 6 B) shows the utilization of fishes in the different ecosystems. Ecotrophic efficiency of planktivorous fish was much higher in the exposed Gulf of Riga coast and Pärnu Bay than in Puck Bay and the Curonian Lagoon, and reached extremely high values in the Open Baltic Coast. Ecotrophic efficiency of benthivorous fish had similar high values around 1 in all ecosystems, and also piscivorous fish had high ecotrophic efficiencies in most systems.

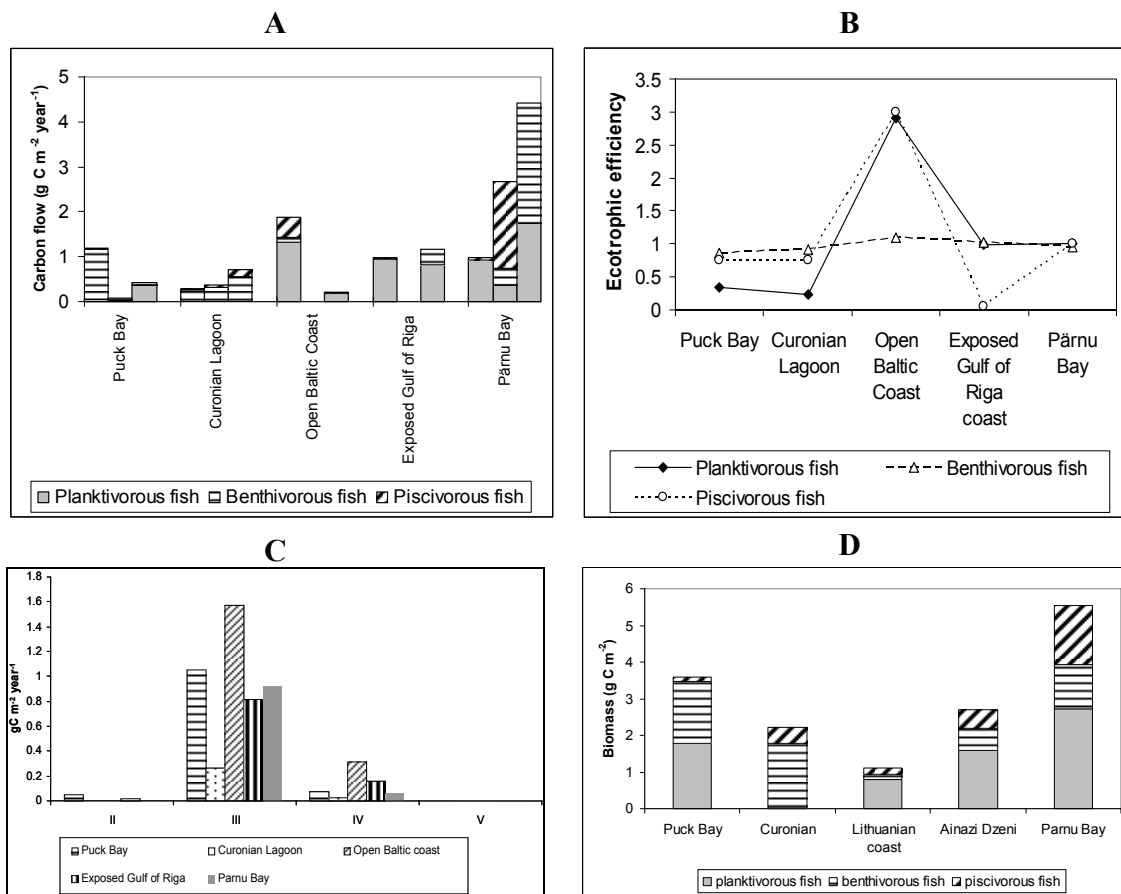


Figure 6: Fate of fish biomass (A, stacked bar groups for each ecosystem denote from left to right catches, consumption by birds, and consumption by piscivorous fish), ecotrophic efficiency of fish (B), trophic level of catches (C) and biomass composition of fish in the models (D)

### Trophic level structure and trophic transfers

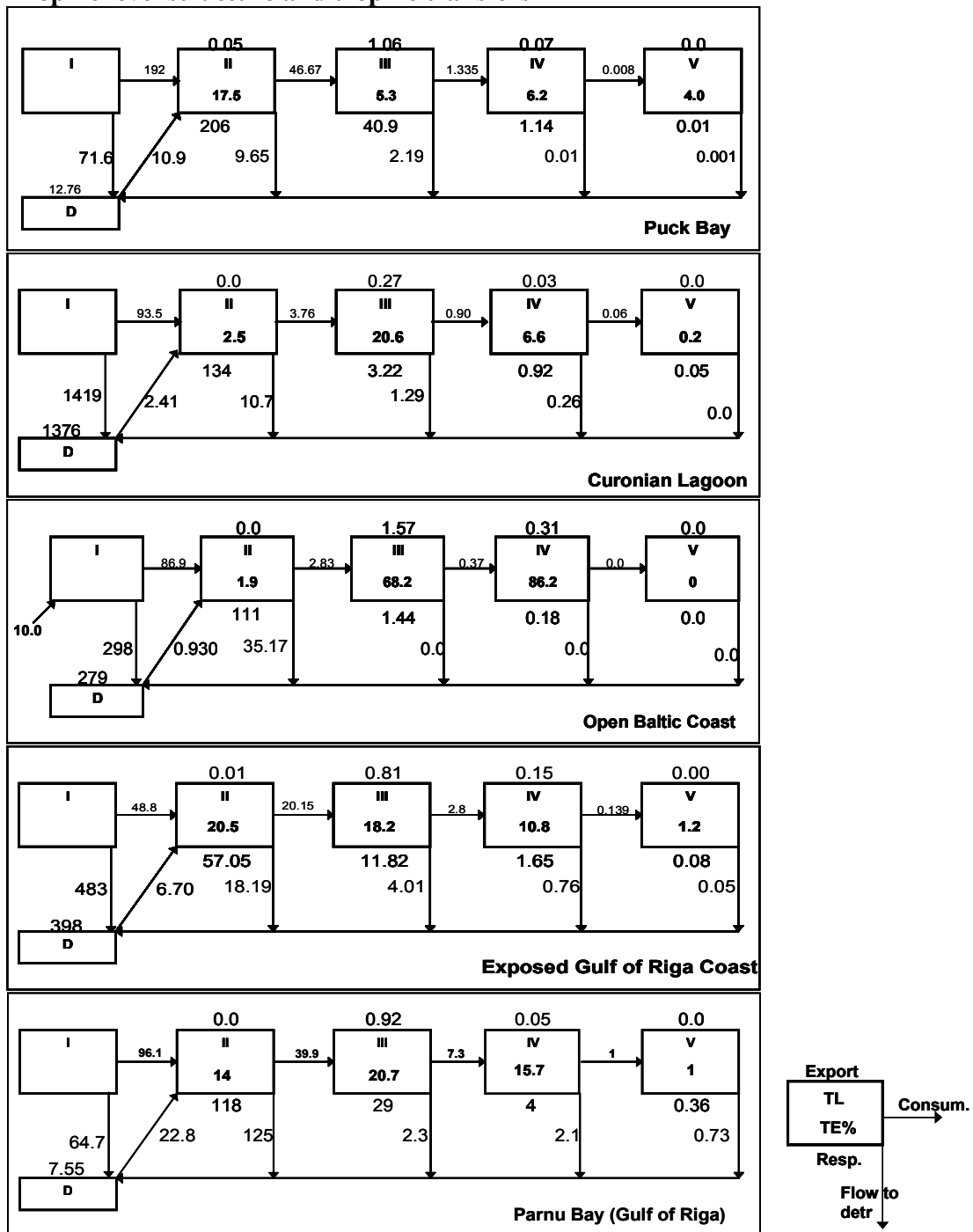


Figure 7. The aggregation of the flow ( $g C/m^2/year^{-1}$ ) web into a concentrated chain through five trophic levels (Ulanowicz 1995). (roman numbers inside boxes – TL, Arabic - TE%-Transfer Efficiencies in %)

Lindeman spine analysis revealed trophic pathways with up to 5 levels in all models (Fig. 7). Biomasses associated with the highest trophic levels (TL IV and V) were very small, especially in the Puck Bay and Open Baltic Coast models. In Puck Bay the most efficient trophic transfer occurred from TL I to TL II with a transfer efficiency (TE) of 17.5 %, but in the Curonian Lagoon and Pärnu Bay the most efficient transfer occurred between TL II and III (TE 20.6 % and 20.7 % respectively). Only in the open Baltic Coast the most efficient transfer occurred between TL III and IV (TE 86.2 %).

Despite of the same number of discrete trophic levels we found different trophic level composition between groups of organism (Tab. 2). The first trophic level in all ecosystems was, by definition, associated with primary producers (phytoplankton, perennial/annual macrophytes) and detritus. The second TL related mainly to benthic consumers and mesozooplankton. Macrozooplankton typically fed on a mixture of mesozooplankton (TL II), phytoplankton and detritus (TL I), giving them effective trophic levels between 2.22 and 2.68. Planktivorous fish mainly fed on trophic levels around 3, only in Puck Bay TL was lower (2.76), because planktivorous fish there also grazed on annual macrophytes. In the Curonian Lagoon and Pärnu Bay birds occupied the highest trophic level (TL 4.39 and 4.2, respectively), while in Puck Bay birds fed on trophic levels 2 and 3 (TL 2.78). Piscivorous fish fed on a combination of trophic levels 3 and 4 in all systems.

Table 2: Effective trophic level of model groups

	<b>Puck Bay</b>	<b>Curonian Lagoon</b>	<b>Open Baltic coast</b>	<b>Exposed Gulf of Riga</b>	<b>Pärnu Bay</b>
	<b>Average TL</b>	<b>Average TL</b>	<b>Average TL</b>	<b>Average TL</b>	<b>Average TL</b>
<b>Birds</b>	2.78	4.2	3.18	3.15	4.39
<b>Piscivorous fish</b>	3.67	3.91	3.72	3.56	3.55
<b>Planktivorous fish</b>	2.76	3.11	3	3.15	3.03
<b>Benthivorous fish</b>	3	3.05	3.32	2.5	2.91
<b>Benthic deposit feeders</b>	2	2.05	2.08	2	2
<b>Benthic suspension feeders</b>	2.1	2	2.01	2.1	2.05
<b>Macrozooplankton</b>	2.4	2.22	2.68	2.5	2.6
<b>Mesozooplankton</b>	2	2.11	2	2	2
<b>Perennial Macrophytes</b>	1	1	1	1	1
<b>Annual Macrophytes</b>	1	1	1	1	1
<b>Phytoplankton</b>	1	1	1	1	1
<b>Detritus</b>	1	1	1	1	1
<b>Mean TL of Catch</b>	3.02	3.14	3.19	3.15	3.06

Table 3: Transfer efficiencies (% of ingested food) between trophic levels and biomass ( $\text{g C m}^{-2}$ ) of each trophic level, based on the “Lindeman spine” analysis

	I	II	III	IV	V	Average per trophic step
<b>Puck Bay</b>						
Producer		18.2	4.8	6.3	4.1	8.2
Detritus		15.6	6.6	5.9	0	8.5
All flows		17.5	5.3	6.2	4	8.3
Biomass per TL	297.9	55.838	7.778	0.163	0.001	
<b>Curonian Lagoon</b>						
Producer		1.4	20.1	6.8	0.5	5.8
Detritus		4.4	20.8	6.5	0.1	8.4
All flows		2.5	20.6	6.6	0.2	7
Biomass per TL	8.018	3.747	1.854	0.39	0.004	
<b>Open Baltic Coast</b>						
Producer		2.2	64.5	86.2	0	23
Detritus		1.5	75.6	86.4	0	21.3
All flows		1.9	68.2	86.2	0	22.3
Biomass per TL	2.871	16.89	1.077	0.144	0	
<b>Exposed Gulf of Riga</b>						
Producer		27.6	19.4	11.5	1.2	18.3
Detritus		10.5	14.2	8.4	1.2	10.8
All flows		17.9	17.7	10.7	1.2	15
Biomass per TL	160.28	3.63	2.241	0.547	0.034	
<b>Pärnu Bay</b>						
Producer		17.8	22.1	17.3	1.7	18.9
Detritus		12.1	19.6	14.6	0.3	15.1
All flows		14	20.7	15.7	1	16.6
Biomass per TL	6.001	15.755	4.746	1.077	0.081	

### Ecosystem Properties

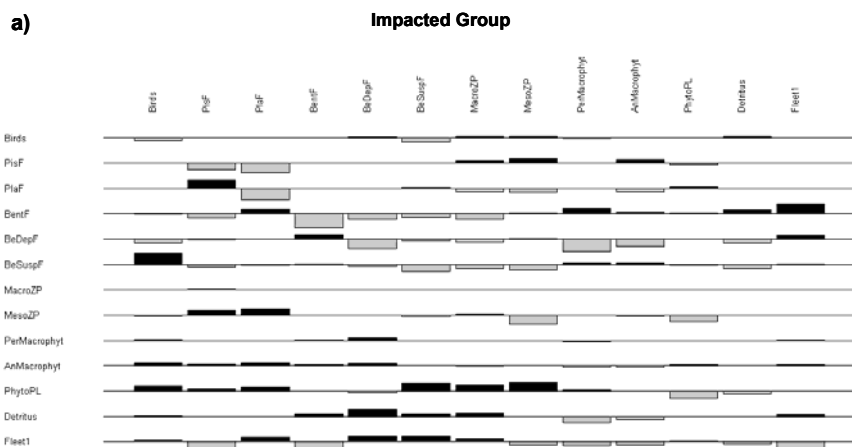
In reference to Odum's ecosystem properties and the classification in Christensen (1995) almost all the investigated southern Baltic coastal ecosystems were in the developmental phase, with the most mature being Pärnu Bay, because of the lowest TPP/TB and close to unity TPP/TR (Tab. 4). Taking into account the highest values of TB/TST the second mature ecosystem was Puck Bay, because of the larger biomass storage in ecosystem components. However, values of TPP/TR, as Christensen and Pauly (1993) concluded, might be overestimated in models excluding bacterial activity.

The values of SOI close to nil imply that consumers in all ecosystems were specialized and fed mainly on single trophic levels. Only the Curonian Lagoon SOI close to 0.2 suggest that food web structure in this basin is more omnivorous. In other areas, for example the Mediterranean Orbetello lagoon, values between 0.2- 0.3 (Brando et al., 2004) are reported.

Table 4: Ecosystem properties

	Puck Bay	Curonian Lagoon	Open Baltic Coast	Exposed Gulf of Riga	Pärnu Bay	Units
Sum of all consumption	310.729	167.803	156.982	135.556	332.731	gC*m <sup>-2</sup> /year
Sum of all exports	13.386	1376.469	281.668	417.834	8.31	gC*m <sup>-2</sup> /year
Sum of all respiratory flows	248.213	138.322	113.342	87.787	152.495	gC*m <sup>-2</sup> /year
Sum of all flows into detritus	83.586	1431.265	342.641	462.014	195.571	gC*m <sup>-2</sup> /year
Total system throughput	656	3114	895	1085	689	gC*m <sup>-2</sup> /year
Sum of all production	3296	1542	419	1942	239	gC*m <sup>-2</sup> /year
Calculated total net primary production	3222	1516.326	385.02	1918.127	160.8	gC*m <sup>-2</sup> /year
Net system production	2973.787	1378.004	271.678	1830.34	8.305	gC*m <sup>-2</sup> /year
Total catches	1.18	0.293	1.881	0.983	0.979	gC*m <sup>-2</sup> /year
Total biomass (excluding detritus)	361.68	14.013	20.981	166.732	27.659	gC*m <sup>-2</sup>
Connectance Index	0.24	0.23	0.207	0.182	0.165	
System Omnivory Index (SOI)	0.092	0.18	0.073	0.11	0.05	
Mean trophic level of the catch	3.02	3.14	3.19	3.15	3.06	
Gross efficiency (catch/net p.p.)	0.000366	0.000193	0.004885	0.000513	0.006088	
Total primary production/ total respiration (TPP/TR)	12.981	10.962	3.397	21.85	1.054	
Total primary production/ total biomass (TPP/TB)	8.908	108.212	18.351	11.504	5.814	
Total biomass/ total throughput (TB/TST)	0.551	0.004	0.023	0.154	0.04	

### Mixed Trophic Impact Analysis





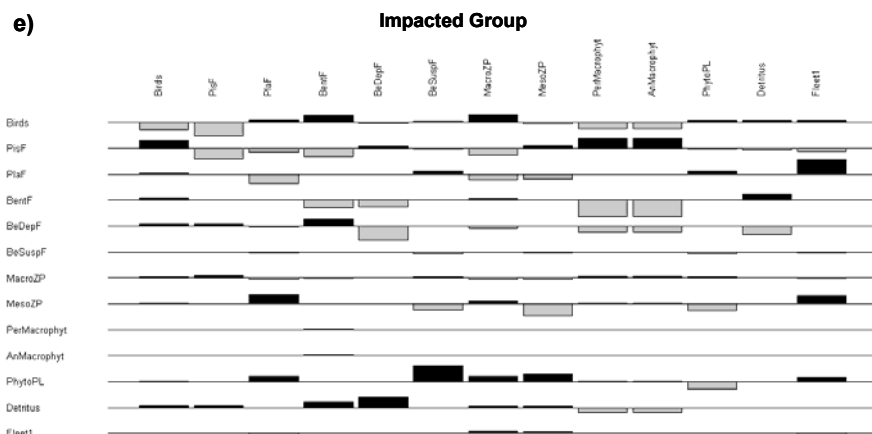


Figure 8: Mixed trophic impact plot for a) Puck Bay, b) Curonian Lagoon c) Open Baltic Coast, d) Exposed Gulf of Riga, e) Pärnu Bay.

Group acronyms: PisF – Piscivorous Fish, PlaF – Planktivorous Fish, BentF – Benthivorous Fish, BeDepF – Benthic Deposit Feeders, BeSuspF – Benthic Suspension Feeders, MacroZP – Macrozooplankton, MesoZP – Mesozooplankton, PerMacrophyt – Perennial Macrophytes, AnMacrophyt – Annual Macrophytes, PhytoPL – Phytoplankton.

In almost all ecosystems benthic primary producers had no impact on the other groups (Fig. 8 b, c, e), except for Puck Bay (Fig. 8 a), where annual macrophytes had a small positive impact on higher trophic levels, and the exposed Gulf of Riga (Fig. 8 d), where annual macrophytes increased benthivorous fish biomass, thereby negatively affecting benthic fauna and birds. Macrozooplankton had only very small impact on other groups, except in the exposed Gulf of Riga (Fig. 8 d), where the impact of macrozooplankton was relatively broad. Birds affected only the Curonian Lagoon and Pärnu Bay ecosystems, and to a small degree also Puck Bay. In the Curonian Lagoon and Pärnu Bay birds had a relatively high direct impact on fish stocks and an indirect effect on benthic invertebrates (Fig. 8 b, e), in Puck Bay birds affected mostly benthic fauna. In all models fisheries impacted almost all other ecosystem components. In the Gulf of Riga we found a surprisingly large fisheries impact on birds, which could not be explained by the small bird bycatch included in the model, but rather by the removal of piscivorous fish, thereby increasing the competition from benthivorous fish for benthic filter feeders, the main waterfowl prey in this area.

## **Discussion**

Our model results represent five Eastern Baltic Coastal foodwebs, which have been analyzed using an identical model structure. As Baird and Ulanowicz (1993) pointed out, similar model structure is crucial to make models comparable. However, species aggregated into the model groups differed between ecosystems, especially with respect to fish communities. Using a unified model structure also necessarily means simplifying the foodweb interactions in the investigated ecosystems to fit to a generic scheme. Aggregation might have affected model results (Abarca-Arenas and Ulanowicz 2002), in our case especially with respect to indexes measuring the diversity of carbon flows like the connectance index and the system omnivory index.

Due to lack of data our models did not include a microbial loop, but represent only the “classical food web”. As pointed out by Witek (1995), in the coastal pelagic zone bacteria and protozooplankton contribute the largest energy flow among heterotrophic organisms. However, carbon transfer efficiencies from the microbial loop to the “classical” foodweb can be low (Uitto, 1996) and as our models are focused on carbon fluxes to the higher trophic levels, we omitted bacteria and treated the microbial loop as part of the carbon flows originating from detritus.

Even though located in a narrow geographical region, ecosystems differed markedly from each other. While proximity to large river outlets, together with limited water exchange and the potential for internal nutrient loading drives phytoplankton primary production, bottom substrate type – together with hydrological conditions - determines the abundance of benthic flora and also influences benthic fauna. Hydrological conditions affect the composition of coastal fish communities in the investigated areas.

Morphometry, determining water exchange and sedimentation, influences the trophic state of coastal ecosystems together with local nutrient sources (Wallin and Hakanson, 1992, Nilsson and Jansson, 2002). By far the largest phytoplankton primary production was observed in the Curonian Lagoon. The Lagoon is affected by loading from the Nemunas River, has limited water exchange with the Baltic Proper, and soft bottom sediments capable of sequestering organic matter. Also in the sheltered Puck Bay

phytoplankton primary production is elevated, because of direct and indirect loading from the Reda and Vistula rivers, respectively, together with nutrient runoff from agriculture and atmospheric deposition (Korzeniewski 1993, Falkowska, Bolalek 1991). Similarly, within both Gulf of Riga systems, the sheltered Pärnu Bay, which is also affected by the Pärnu River, has the higher phytoplankton primary production.

Occurrence of macrophytes was restricted to sites with suitable substrate for growth or attachment in areas with sufficient light. Thus, in the relatively deep Open Baltic Coast, only 10 % of the area were covered by macrophytes, while dense macrophyte stands in the Exposed Gulf of Riga were supported by stony bottoms at average water depth of only 5 m. Contrary to the Open Baltic coast, the exposed Gulf of Riga coast and Pärnu Bay, where macroalgae (*Fucus*, *Furcellaria*) constitute the perennial macrophyte group, this group is composed by seagrasses in Puck Bay (*Zostera* sp. and *Zanichellia* sp.). Seagrasses are adapted to the soft bottoms prevailing in Puck Bay. However, they do not occur on the soft bottoms in the central Curonian Lagoon, most likely due to light limitation caused by bottom resuspension and high phytoplankton growth in the central part of the lagoon. *Zostera* might also be limited by the low salinity (Borum et al., 2004) and by wave action in exposed sandy areas.

Biomass of benthic consumers generally differed more between the investigated ecosystems than the biomass of pelagic compartments. This is also due to the fact that many benthic species have lifespans of several years, therefore differences in growth conditions become accentuated over a longer time period, whereas at least phytoplankton and zooplankton have turnover times of days to months. The difference in benthic invertebrate assemblages may be partially attributed to the type of bottom substrate and the intensity of water exchange. Pärnu Bay is characterized by high riverine nutrient input, relatively low water exchange and, thus, high sedimentation rate. Consequently, organic rich soft sediments support very high densities of deposit feeders whereas the suspension feeders are not so important in the system. In all other systems the biomass of suspension feeders exceeds that of the deposit feeders. In more saline areas the communities of suspension feeders are dominated by *Mytilus trossulus* whereas in more diluted areas such as in Curonian Lagoon and Pärnu Bay *Dreissena polymorpha* prevails. The biomass of suspension feeders increases with water exchange rate and in the exposed

coasts of the Baltic Proper and Puck Bay biomass of suspension feeders were highest. In these systems the mussels may control the development of phytoplankton and, hence, indirectly also mesozooplankton. In very dynamic coastal systems the biodeposits of mussels are at least partly used locally and are not flushed away to the open sea. As a consequence mussels enhance the growth of macrovegetation by increasing water transparency and fertilizing co-occurring algae. The fast growing filamentous algae are especially favoured owing to their higher competitiveness at higher nutrient concentrations. As mussels import large quantities of organic matter to the sediments, visible in the models by the flux from benthic suspension feeders to detritus, they might – if the deposited material is of sufficient nutritional quality - release deposit feeders from the food limitation otherwise common in low-trophic coastal marine ecosystems.

Different hydrological conditions also lead to different species compositions in fish groups, modified by fishing pressure. Despite fresh water species dominating fish communities in Pärnu Bay, herring also occurred in the bay because of suitable spawning grounds and the high abundance of the Gulf of Riga herring stock. In contrast, the Curonian Lagoon with very small perennial macrophyte biomass is not favourable to fish species preferring vegetated bottoms for spawning. Also the high turbidity might affect planktivorous species. Low biomass of herring in Puck Bay may be caused by two reasons: First, reduction of macrophyte coverage caused by eutrophication destroyed spawning grounds for commercially valuable fish species (Jackowski 1998, Andruliewicz et al., 2004). Second, migrations to other feeding or spawning areas might also contribute to the low herring biomass. During spawning season herring might have found more attractive spawning grounds, for example in the Vistula Lagoon (Jackowski, 2002). Also the very high biomass of three-spined stickleback (Sapota and Skóra, 1996, Lizińska, 2002) might have caused competition between fish in the basin. Three-spined stickleback are a “fish-pest”, as they feed on eggs of commercially important species (Andruliewicz et al., 2004) especially in the very shallow part of the bay, where the herring spawning grounds used to be located.

As opposed to phytoplankton primary production, phytobenthos production is not channelled directly into the investigated foodwebs, as indicated by the low ecotrophic efficiency of macrophytes. Also the MTI matrix indicated very low dependency of higher

trophic levels on benthic macrophytes, suggesting that changes in benthic primary production do not affect the trophic web. This finding is in contrast to other ecosystem, for example the Lagoon of Venice (Carrer and Optiz 1999). While perennial macroalgae are grazed on very low level in many systems (Duarte, 1995, Worm et al, 2000, Szyrmer and Ulanowicz, 1987), also in the Baltic Sea (Kautsky 1988; Kautsky and Kautsky 1995), annual macrophytes are a potential food source to benthic grazers (Duarte, 1995, Worm et al., 2000), and benthivorous fish. This has been taken into account in the foodweb of Pärnu Bay, where annual macrophytes are partially utilized. Also the very high biomass of annual macrophytes in Puck Bay, especially the pelagic form of *Pilayella* sp. (Florczyk in Korzeniewski 1993), should be exploitable by higher trophic levels. Treatment of macrophytes in the foodweb models might thus have been limited by studies available on local or similar ecosystems.

The low trophic transfer of macrophyte carbon into the foodweb also does not correctly reflect their significance for the Baltic ecosystem. Benthic macrophytes are important habitat forming species, providing shelter for benthic animals (Kautsky, 1988, Kruk-Dowgiałło et al. 2000, Martin, 2000), as well as spawning and nursery areas for fish (Kruk-Dowgiałło et al. 2000, Jackowski 1998, Skóra in Korzeniewski 1993).

The investigated ecosystems also differed in their trophic composition, especially for fish and birds. The number of five discrete trophic levels sensu Lindemman (Ulanowicz 1995) is in the range commonly found in marine coastal ecosystems (Christensen and Pauly 1993). However, assignment of groups to trophic level seems to be rather sensitive to the assumed diet composition. For example, the effective trophic level of piscivorous fish ranges from 3.55 to 3.91 for the Curonian Lagoon and the two Gulf of Riga systems, even though they feature the same species (perch and pike perch) in this group. Other differences, for example the low efficient trophic level of birds in Puck Bay can be easily linked to high consumption of benthic organisms by the marine ducks (Stempniewicz and Maisner, 1999), which are together with cormorants abundant in Puck Bay. Dependence of birds in Puck Bay on benthic organisms is also visible in the MTI analysis. Cormorants dominate bird biomass in the Curonian lagoon and in Pärnu Bay, where they act as top predators, consuming a mix of fish species, including also piscivores.

Because macrophyte production is largely unexploited, phytoplankton primary production is the dominating source of organic carbon to the coastal ecosystem. As shown by the ecotrophic efficiency, phytoplankton primary production is channelled into foodwebs with highly different efficiency. In the Curonian lagoon phytoplankton is dominated by the filamentous cyanobacteria *Aphanizomenon flos-aquae* and despite the large phytoplankton primary production, the amount of carbon transferred to zooplankton is below average. The low efficiency is also reflected in the transfer efficiencies calculated in the Lindeman spine. Despite the low abundance of macrozooplankton and planktivorous fish, the Curonian lagoon features only slightly above average mesozooplankton biomass. The reason might be that the dominating cyanobacteria are not grazed efficiently (Razinkovas and Gasunaite, 1999), and the high predation within the zooplankton of the lagoon, where *Leptodora kindtii* consume *Daphnia* and other species. The most complete phytoplankton - zooplankton transfer, and thus highest ecotrophic efficiency of phytoplankton, occurs in Puck Bay because of the high zooplankton biomass in the sheltered bay, and in Pärnu Bay because of the high Q/B ratio of the dominating small sized zooplankton.

Benthic ecosystems seem to be controlled mainly by food availability, modified by suitability of the bottom substrate and predation. Carbon fluxes into the benthic foodweb show the same pattern than the flows into the pelagic foodweb. This suggests that the amount of energy available for secondary production is characteristic for each ecosystem. In sheltered ecosystems like Puck Bay and Pärnu Bay, primary production is retained, while exposed systems like the Open Baltic and the exposed Gulf of Riga coasts tend to lose their production. Production is also lost from the transitory estuarine Curonian Lagoon. Divergences in the carbon flow pattern between benthic and pelagic foodweb seem to be linked to substrate properties, e.g. extremely low benthic secondary production in the exposed Gulf of Riga coast is likely due to low proportion of soft bottoms.

The role of primary production for benthic consumers is also confirmed by the MTI matrix, where phytoplankton enhances benthic production. However, since benthic fauna is the main food source of benthivorous fish in all ecosystems, the MTI matrix also predicts impacts of benthivorous fish on their prey in all ecosystems. The degree of

predation control on macrozoobenthos is difficult to assess, because in all ecosystems benthivorous fish are heavily exploited with ecotrophic efficiencies close to one. The reasons are fishery (especially in Puck Bay) together with predation by piscivores. The high pressure on benthivorous fish therefore indicates that they might not be able to control their prey, making zoobenthos production limited by food and ambient physical factors.

While carbon transfer into pelagic and benthic foodwebs seems to be related to the retention capacity of coastal ecosystems, mesozooplankton is further exploited with close to maximum ecotrophic efficiency in all ecosystems except the Open Baltic Coast. In Puck Bay, the exposed Gulf of Riga coast and Pärnu Bay large fluxes to pelagic fish follow, while in the Curonian Lagoon the high mesozooplankton ecotrophic efficiency seems to be caused by *Leptodora kindtii* predation on *Daphnia*. In Puck Bay and the Curonian lagoon hydrological conditions are unfavourable for commercially valuable planktivorous species, therefore planktivorous fish are not exploited further, resulting in low ecotrophic efficiency. The higher level predators, for example Cormorant (common in both areas) are trophic opportunists, and select prey that can be accessed with the lowest effort (Bzoma 2004). At the exposed Gulf of Riga coast and in Pärnu Bay planktivorous fish are pressured by fishing, predation from piscivores, and in the case of Pärnu Bay also by predation from birds. However, birds in Pärnu Bay mainly prey on piscivores, therefore the MTI matrix suggests that planktivorous fish and the fishery even benefit from bird predation.

Despite high catches of planktivorous fish, the MTI matrix suggests only very small (Pärnu Bay) or no impact of fisheries on planktivorous fish. Most likely, removal of planktivorous fish is balanced by increased mesozooplankton production. In Pärnu Bay, where benthic filter feeders compete with zooplankton for phytoplankton, fishing effects cannot be compensated so easily and the MTI suggests a small negative impact of the fishery on planktivorous fish. Negative impacts of fishing are very strong at the open Baltic Coast, where planktivorous fish are exploited so strongly, that they cannot control mesozooplankton biomass. The differing behaviour of both Gulf of Riga systems from the Open Baltic Coast is supported by the stable, growing herring population in the Gulf of Riga, as opposed to the overexploited population in the Baltic proper (ICES WGBFAS

2005). Also in Puck Bay ecosystem effects of fisheries are well known (Andrzejewicz et al., 2004) and obvious in the current model, affecting benthivorous and piscivorous fish, zooplankton, zoobenthos and macrophytes. In systems where fishing pressure is relatively high, most other ecosystem components are affected as well. The wide impact spectrum of fishing activities, causing direct and indirect effects on fish populations and the entire ecosystem, has been documented for example by Pauly et al. (2000).

Our findings suggest that the most efficient ecosystem is the Open Baltic Coast with average transfer efficiencies from II-IV TL from all flows of 22.3 %. However, this is because of the high fishery export, which is not balanced by the trophic transfers in the model itself (see Lindeman spine and  $> 1$  ecotrophic efficiency of planktivorous and piscivorous fish). Therefore, the very high transfer efficiencies for TL III and IV are erroneous and are most likely caused by difficulties in assigning catch data to coastal areas. Comparison of transfer efficiencies between higher trophic levels should be restricted to the other ecosystems, with balanced Ecopath models. Lowest efficiency in the Curonian Lagoon (average 7 %) is due to the inefficient use of primary production mentioned before, whereas Puck Bay, with similar low efficiency, shows a different pattern. Here zooplankton is used with low ecotrophic efficiency, leading to a low TL between TL II and III. Most efficient were systems with high piscivore and bird predation (Pärnu Bay) or high fishing pressure (exposed Gulf of Riga). These systems are slightly more efficient than the range of average TE for coastal areas – 10 to 15 % - given by Christensen and Pauly (1993). This is perhaps due to a tendency to overestimate herring biomass and catch in coastal sites, as data are mostly available for more open areas only. It is well known, that in “open” systems like the Open Baltic coast and the exposed Gulf of Riga coast piscivorous and planktivorous fish migrate between different feeding and spawning areas (Kompowski, 1994, Jackowski, 2002), making it difficult to estimate their food consumption and their catch in the coastal zone. Overestimated biomass of herring could also have exaggerated the differences in the zooplankton – planktivorous fish transfer efficiency, causing additional variation between herring dominated systems (open Baltic Coast, exposed Gulf of Riga, Pärnu Bay) and the Curonian Lagoon and Puck Bay, where the main component of the planktivorous fish group are Ziege (*Pelecus cultratus*) and three-spined stickleback (*Gasterosteus aculeatus*). However, there is no

doubt about the occurrence of herring outside the open Baltic Sea, as the Gulf of Riga is known to have a separate herring population and shoals of clupeids have been reported from Puck Bay (Jackowski 2002).

Average transfer efficiencies “from producers” were lower than “from detritus” in the Curonian Lagoon, showing difficulties in channelling phytoplankton into the foodweb and highlighting the relative importance of secondary production from detritus. In all other systems transfers from producers were more efficient. Especially the exposed Gulf of Riga site with its low zoobenthos biomass channelled detritus based flows inefficiently. In Puck Bay transfer efficiencies from producers and detritus were almost equal.

The gross efficiency (GE) of the system, defined as the catch per unit of net primary production, tends to be very low in system where the fishery is concentrated on top predators (Christensen et al., 2004). Gross efficiency ranged from 0.000193 in the Curonian Lagoon to 0.006088 in Pärnu Bay. The lowest GE in the Curonian Lagoon does not relate to fishing pressure on predatory fish as benthivorous fish with low TL dominate the catch, but is due to the inefficient use of the high primary production. Gross efficiency is also rather low in all systems with a high share of phytobenthos primary production (Puck Bay, exposed Gulf of Riga), because the latter is not used in the foodwebs. Still, except the Curonian Lagoon all systems had higher GE than the global average of 0.0002 (Christensen et al., 2004) calculated for a wide range of ecosystems. At the same time, TL of the catches was low, in all ecosystems lower than the TL of piscivorous fish. This suggests that the fisheries are harvesting fish down in the food web (Pauly et al., 2000, Christensen et al., 2004).

## Conclusions

The investigated south-eastern Baltic coastal ecosystems are highly productive, channelling a large proportion of their primary production into exploitable fishery resources. Local nutrient sources influence phytoplankton primary production, but retention of primary production in sheltered areas with favourable hydrographic conditions is the most important factor determining food availability to the pelagic and benthic foodweb.

While the second trophic level appears to be mainly food limited, further transfers in both benthic and pelagic foodwebs are affected by complex patterns of bottom-up and top-down control. In all ecosystems fisheries had far reaching impacts on their target species, on target species predators, as well as on lower trophic levels. In particular benthic foodwebs can be affected by indirect fisheries effects, as fisheries tend to change the biomass of piscivorous fish, therefore causing a cascading effect on benthivorous fish and macrozoobenthos. These cascades are ecosystem specific and have to be taken into account using benthic invertebrates as productivity and eutrophication indicators. In systems with high fishing of pelagic fish a similar cascade exists from pelagic fish over mesozooplankton to phytoplankton.

All models are to some extent affected by difficulties in estimating fish biomass and their food consumption in the coastal zone. Biomass and catch data are mainly available for more open areas and had mostly to be extrapolated to the coastal zone. However, all models are sensitive to the biomass of fish components and their diet composition. Because effects of fish groups channel through the foodweb, quantitative data on coastal fish communities and their food composition are important for assessing coastal carbon fluxes and interactions between different ecosystem components.

Our comparative flow and network analysis show marginal impact of macrophytes on trophic transfers in all investigated ecosystems and suggest that macrophyte biomass is mainly channeled into detritus. The role of macrophytes in the

trophic transfers of the coastal Baltic ecosystems is most likely underestimated in the models and reasons for that should be investigated thoroughly in future. At the same time low grazing levels on Baltic Sea macrophytes has been found by a number of authors and explains many distribution characteristics of different macrophyte communities in the Baltic. However, our modeling efforts also showed that the perception of the role of macrophytes depended on the knowledge available on their productivity and fate in each ecosystem.

Odum's maturity attributes and ECOPATH indexes allow a ranking of coastal ecosystems according to their level of maturity and development. Maturity and development decreases in the order Pärnu Bay > Puck Bay > Exposed Gulf of Riga > Open Baltic Coast > Curonian Lagoon.

Food web models are a suitable tool for ecosystem understanding and can give valuable information on the sensitivity and information content of productivity and eutrophication indicators. Present knowledge on ecosystem components should be extended by studies of ecosystem component biomasses and mass/energy import and export to ecosystems. Food web models are useful for ecosystem based management of the Baltic coastal areas, as they highlight interactions between trophic components that are specific for each area.

## **Acknowledgements**

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Table.1. Species composition in functional groups

	Puck Bay	Curonian Lagoon	Open Baltic Coast	Exposed Gulf of Riga	Parnu Bay
<b>Birds</b>	Long-tailed duck <i>Clangula hyemalis</i> Tufted duck <i>Aythya fuligula</i> Coot <i>Fulica atra</i> Mallard <i>Anas platyrhynchos</i> Golden eye <i>Bucephala clangula</i> Mute swan <i>Cygnus olor</i> Great crested grebe <i>Podiceps cristatus</i> Great cormorant <i>Phalacrocorax carbo</i> Wigeon <i>Anas penelope</i> Greater Scaup <i>Aithya marila</i> Velvet scoter <i>Melanitta fusca</i> Lesser Scaoter <i>Melanitta nigra</i> Pohard duck <i>Aythya fermia</i> Goossander <i>Mergus merganser</i> Merganser <i>Mergus serrator</i> Blagk-headed gull <i>Larus ridibanus</i> Herring gull <i>Larus argenatus</i> Common gull <i>Larus canus</i>	Great cormorant <i>Phalacrocorax carbo</i> Herring gull <i>Larus argenatus</i> Common gull <i>Larus canus</i> Great crested grebe <i>Podiceps cristatus</i>	Herring gull <i>Larus argenatus</i> Common gull <i>Larus canus</i> Great crested grebe <i>Podiceps cristatus</i>	Herring gull <i>Larus argenatus</i> Common gull <i>Larus canus</i>	Tufted duck <i>Aythya fuligula</i> Mallard <i>Anas platyrhynchos</i> Mute swan <i>Cygnus olor</i> Great cormorant <i>Phalacrocorax carbo</i> <i>Anas strepera</i> Merganser <i>Mergus serrator</i> Blagk-headed gull <i>Larus ridibanus</i> Herring gull <i>Larus argenatus</i> Common gull <i>Larus canus</i> <i>Anas querquedula</i>  <i>Anas clypeata</i>  <i>Tadorna tadorna</i>  <i>Sterna paradisaea</i>  <i>Sterna hirundo</i> <i>Haematopus ostralegus</i>

	Puck Bay	Curonian Lagoon	Open Baltic Coast	Exposed Gulf of Riga	Parnu Bay
<b>Piscivores fish</b>	Salmon <i>Salmo salar</i>	Perch <i>Perca fluviatilis</i>	Salmon <i>Salmo salar</i>	Perch <i>Perca fluviatilis</i>	Perch <i>Perca fluviatilis</i>
	Sea Trout <i>Salmo trutta trutta</i>	Pikeperch <i>Stizostedion lucioperca</i>	Cod <i>Gadus morrhua callarias</i>	Pikeperch <i>Stizostedion lucioperca</i>	Pikeperch <i>Stizostedion lucioperca</i>
	Cod <i>Gadus morrhua callarias</i>	Pike <i>Esox lucius</i>	Sea Trout <i>Salmo trutta trutta</i>		Pike <i>Esox lucius</i>
	Rainbow trout <i>Oncorhynchus mykiss</i>		Grayfish <i>Belone belone</i>		
	Perch <i>Perca fluviatilis</i>		Pikeperch <i>Stizostedion lucioperca</i>		
	Grayfish <i>Belone belone</i>		Rainbow trout <i>Oncorhynchus mykiss</i>		
<b>Planktivores fish</b>					
	Deep-snouted pipefish <i>Syngnathus typhle</i>	Three-spined stickleback <i>Gasterosteus aculeatus</i>	Sprat <i>Stratus spratus</i>	Herring <i>Clupea harengus</i>	Bleak <i>Alburnus alburnus</i>
	Pipe-fish <i>Nerophis ophidion</i>	Sichel <i>Pelecus cultratus</i>	Herring <i>Clupea harengus</i>		Whitefish <i>Coregonus lavaretus</i>
	Whitefish <i>Coregonus lavaretus</i>				Smelt <i>Osmerus eperlanus</i>
	Smelt <i>Osmerus eperlanus</i>				Thre-spined stickleback <i>Gasterosteus aculeatus</i>
	Sandeel <i>Ammodytes tobianus</i>				Herring <i>Clupea harengus</i>
	Herring <i>Clupea harengus</i>				
	Thre-spined stickleback <i>Gasterosteus aculeatus</i>				

	<b>Puck Bay</b>	<b>Curonian Lagoon</b>	<b>Open Baltic Coast</b>	<b>Exposed Gulf of Riga</b>	<b>Parnu Bay</b>
<b>Benthivores fish</b>	Black goby <i>Gobius niger</i> Vimba bream <i>Vimba vimba</i> Rouch <i>Rutilus rutilus</i> Common bream <i>Abramis brama</i> Flounder <i>Platichies flesus</i> Lumpfish <i>Cyclopterus lumpus</i> Eelpout <i>Zoarces viviparus</i> Sea Scorpion <i>Myxocephalus scorpius</i> Eel <i>Anquilla anquilla</i> Common goby <i>Pomatoschistus minutus</i> Sand goby <i>Pomatoschistus microps</i> Round Goby <i>Neogobius melanostomus</i>	Rouch <i>Rutilus rutilus</i> Common bream <i>Abramis brama</i> Silver bream <i>Abramis bjoerkna</i> Ruff <i>Gymnocephalus cernus</i>	Flounder <i>Platichies flesus</i>	Vimba bream <i>Vimba vimba</i> Rouch <i>Rutilus rutilus</i>	Vimba bream <i>Vimba vimba</i> Rouch <i>Rutilus rutilus</i> Silver bream <i>Abramis bjoerkna</i> Gibel carp <i>Carassius auratus</i> Flounder <i>Platichies flesus</i> Rudd <i>Scardinius eruthrophthalmus</i> Eelpout <i>Zoarces viviparus</i> Ruff <i>Gymnocephalus cernus</i> Dace <i>Leuciscus leuciscus</i>

	Puck Bay	Curonian Lagoon	Open Baltic Coast	Exposed Gulf of Riga	Parnu Bay
<b>Benthic deposit feeders</b>	<i>Hediste diversicolor</i> , <i>Harmathoe sarsi</i> , <i>Scorops armiger</i> , <i>Pygospio elegas</i> <i>Crangon crangon</i> , <i>Balanus improvisus</i> , <i>Gammarus sp.</i>	<i>Chironomidae</i> <i>Oligochaeta</i>		<i>Marenzelleria viridis</i> <i>Macoma balthica</i> <i>Bathyporeia pilosa</i> <i>Nereis diversicolor</i>	<i>Hediste diversicolor</i> , <i>Marenzelleria neglecta</i> <i>Oligochaeta</i> <i>Gammarus sp.</i> <i>Hydrobia ventrosa</i> <i>Chironomidae</i> <i>Theodoxus fluviatilis</i>
<b>Benthic deposit feeders</b>	<i>Pahalemon adspersis</i> <i>Hydrobia ulvae</i> <i>Bathyporeia pilosa</i> <i>Theodoxus fluviatilis</i>				<i>Corophium volutator</i> <i>Monoporeia affinis</i>
<b>Benthic suspension feeders</b>	Blue mussel <i>Mytilus edulis trossulus</i> <i>Mya arenaria</i> , <i>Cerastoderma glaucum</i> , <i>Macoma balthica</i>	<i>Dreissena polymorpha</i> <i>Unio spp.</i>	Blue mussel <i>Mytilus edulis trossulus</i> <i>Mya arenaria</i> , <i>Cerastoderma glaucum</i> , <i>Macoma balthica</i>	<i>Dreissena polymorpha</i> <i>Balanus improvisus</i> <i>Mytilus edulis trossulus</i>	<i>Mya arenaria</i> , <i>Cerastoderma glaucum</i> , <i>Macoma balthica</i> <i>Dreissena polymorpha</i>
<b>Macrozooplankton</b>	<i>Mysis mixta</i> , <i>Neomysis intiger</i>	<i>Paramysis lacustris</i>		<i>Neomysis integer</i> <i>Mysis relicta</i>	<i>Neomysis intiger</i>

	<b>Puck Bay</b>	<b>Curonian Lagoon</b>	<b>Open Baltic Coast</b>	<b>Exposed Gulf of Riga</b>	<b>Parnu Bay</b>
<b>Mesozooplankton</b>	<i>Acartia longiremis</i> <i>Acartia bifilosa</i> <i>Acartia tonsa</i> <i>Temora longicornis</i> <i>Centropages hamatus</i> <i>Eurytemora sp.</i> <i>Pseudocalanus elongatus</i> <i>Rotatoria</i>	<i>Chydorus sphaericus</i> <i>Daphnia longispina</i> <i>Bosmina coregoni</i> <i>Mesocyclops leuckartii</i>	<i>Acartia bifilosa</i> <i>Bosmina coregoni. maritima</i> <i>Pseudocalanus elongatus</i> <i>Eurytemora sp.</i> <i>Evadne spp.</i> <i>Podon polyphemoides</i>	<i>Eurytemora affinis</i> <i>Acartia bifilosa</i> <i>Bosmina o. maritima</i> <i>Keratella quadrata</i> <i>Keratella cochlearis</i>	<i>Acartia bifilosa</i> <i>Eurytemora affinis</i> <i>Bosmina coregoni maritima</i> <i>Pleopsis polyphemoides</i> <i>Cercopagis pengoi</i> <i>Rotatoria</i>
<b>Perennial Macrophytes</b>	<i>Zostera marina</i> <i>Zannichellia palustris,</i> <i>Rupia rostellata</i>			<i>Polysiphonia nigrescens</i> <i>Fucus vesiculosus</i>	<i>Potamogeton pectinatus</i> <i>Myriophyllum spicatum</i> <i>Furcellaria lumbricalis</i>
<b>Annual Macrophytes</b>	<i>Ectocarpaceae</i> <i>Pilayella littoralis.</i> <i>Cladophora sp.</i> <i>Enteromorpha sp.,</i>			<i>Ceramium tenuicorne</i> <i>Enteromorpha interstitialis</i> <i>Cladophora glomerata</i>	<i>Cladophora glomerata</i> <i>Ceramium tenuicorne</i> <i>Polysiphonia nigrescens</i>

	<b>Puck Bay</b>	<b>Curonian Lagoon</b>	<b>Open Baltic Coast</b>	<b>Exposed Gulf of Riga</b>	<b>Parnu Bay</b>
<b>Phytoplankton</b>	<i>Aphanizomenon flos-aquae</i> <i>Nodularia spumigena</i> <i>Skeletonema costatum</i> <i>Melosira nummuloides</i> <i>Achnanthes sp.</i> <i>Chaetoceros sp.</i> <i>Thalassiosira sp.</i> <i>Synedra tabulate</i> <i>Nitzhia closterium</i> <i>Cosinodiscus granii</i> <i>Scenedesmus sp.</i> <i>Pediastrum sp.</i>	<i>Aphanizomenon flos-aquae</i>	<i>Aphanizomenon flos-aquae</i>	<i>Melosira spp.</i> <i>Chaetoceros spp.</i> <i>Aphanizomenon flos-aquae</i> <i>Chrysochromulina spp.</i> <i>Skeletonema costatum</i> <i>Thalassiosira baltica</i>	<i>Thalassiosira baltica</i> <i>Achnanthes taeniata</i> <i>Monoraphidium contortum</i> <i>Cyclotella choctawatcheeana</i> <i>Chaetoceros wighamii</i> <i>Peridiniella catenata</i> <i>Heterocapsa rotundata</i> <i>Aphanizomenon sp.</i> <i>Nodularia spumigena</i> <i>Mesodinium rubrum</i>

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