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Summer dynamics of the coastal planktonic food web in the northern Baltic Sea

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ABSTRACT: Summer carbon flow in the pelagic food web was studied within the coastal region of the northern Baltic Sea. Heterotrophic nanoflagellates (HNAN) transferred carbon from picoplankton to ciliates, while ciliates linked nano- and metazooplankton. Hydrodynamic conditions affected the planktonic community, and 3 different periods characterised by distinct community structure and carbon flow dynamics could be distinguished. All trophic groups were largely omnivorous, but the role of herbivory and feeding on heterotrophs varied during summer. In early June, an upwelling mixed the upper water layer. The water column was rich in detritus, remnants from the preceding spring phytoplankton bloom. Phytoplankton was dominated by >10 µm phytoplankton, that was grazed by metazooplankton and heterotrophic dinoflagellates. At the same time HNAN were largely bacteriovorous, thus the microbial food web (MFW) could transfer bacterial carbon to ciliates and metazooplankton. In July during strong thermal stratification the biomass of <10 µm phytoplankton increased, and protists became the most important herbivores. In addition to grazing, metazooplankton gained nanophytoplankton carbon through the MFW by feeding on ciliates. Strong horizontal currents due to upwelling destroyed the stable mid-summer community in late July. Primary production, the biomass of phytoplankton and metazooplankton declined abruptly, whereas the detritus pool increased again. Because all trophic groups fed largely on heterotrophs, the efficiency of the MFW in transferring bacterial carbon to metazooplankton was estimated to be at its highest. When integrated throughout the summer, primary production was 20.5 g m^{-2}, from which sedimentation, herbivory by protists and herbivory by metazooplankton accounted for 27, 40 and 26%, respectively. Bacterial production was 8 g m^{-2}, from which HNAN and ciliates grazed approximately 60%. Excepting the sedimentation in early June, carbon was mostly recycled within the planktonic community during the summer

KEY WORDS: Primary production · Bacterial production · Sedimentation · Grazing food chain · Microbial food web · Trophic interactions

INTRODUCTION

Information regarding the basic trophic structure and functioning of the pelagial food web has advanced considerably, enabling the construction of schematic representations of the systems (Taylor & Joint 1990, Legendre & Rassoulzadegan 1995). Energy supplied to higher trophic levels is transferred through 2 main pathways: the herbivorous grazing food chain from larger phytoplankton to metazooplankton, and the microbial food web, in which mostly picoplanktonic carbon is transferred to protists and only a minor part of the carbon is available to higher trophic levels (Ducklow et al. 1986, Hagström et al. 1988, Wikner et al. 1990). However, the ability of many metazoan and protozoan species, traditionally grouped into separate trophic levels, to use particles from a very wide size range means that the models describing carbon pathways have become more complicated (Turner & Roff 1993). Copepods, cladocerans and rotifers are known to be largely omnivorous (Stoecker & Egloff 1987, Wiadnyana & Rassoulzadegan 1989, Stoecker & Capuzzo 1990). Thus, when metazooplankton species feed on protists of a wide size range, which in turn are known efficiently to consume pico- and nanoplankton, the

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energy transfer from the microbial loop (ML; including bacteria and protists) and from the microbial food web (MFW; including also autotrophic pico- and nanoplankton) (*sensu* Rassoulzadegan 1993) to higher trophic levels can be greater than previously assumed. However, even the simplest empirical quantification of ecological energetics requires a wide range of measurements on different possible interactions between the main species groups of different trophic status (Pomeroy & Wiebe 1988).

Seasonal dynamics of the pelagic community from primary producers to metazooplankton has been intensively studied in the field, as well as in mesocosm and laboratory experiments, in the Tvärminne sea area of the coastal northern Baltic Sea. In spring, phytoplankton is composed mostly of large diatoms that are sedimented (Lignell et al. 1993). During summer autotrophic and heterotrophic pico- and nanoplankton become dominant, while later in summer, the biomass of filamentous bluegreen algae increases (Niemi 1973, 1975, Forsskåhl & Sundberg 1981, Huttunen & Kuparinen 1986, Kuosa 1991, Kuuppo-Leinikki 1993, Kononen et al. 1996), and sedimentary losses gradually decrease (Heiskanen & Leppänen 1995). The summer net primary production is mainly limited by nitrogen and phosphorus (Tamminen et al. 1985), but productivity occasionally increases in the euphotic zone when wind-induced vertical mixing brings nutrient-rich water from the deeper water mass to the upper water layer (Kononen et al. 1996). Thermal stratification gives rise to the development of the summer metazooplankton community, dominated by copepods, cladocerans and rotifers (Viitasalo et al. 1995). Heterotrophic nanoflagellates (HNAN) are the main consumers of bacteria (Autio et al. 1988, Kuosa & Kivi 1989, Kuuppo-Leinikki 1990) and autotrophic picoplankton (Kuosa 1991). Nanoplankton is largely grazed by microprotists (>20 µm) dominated by ciliates and heterotrophic dinoflagellates (Kivi & Setälä 1995), and by metazooplankton dominated by calanoid copepods, cladocerans and rotatorians (Uitto 1996a). Bacterial production is limited by dissolved organic carbon and inorganic nutrients (Lignell et al. 1992, Kuparinen & Heinänen 1993)

In the present study, the structure and dynamics of the pelagic community in the euphotic zone were evaluated, combining data from different pelagic compartments mentioned above. All measurements were carried out in the Tvärminne sea area or a nearby archipelago area, and most of the studies were carried out during the summer of 1988. The study aims to empirically quantify the main carbon flow from primary and bacterial production to metazooplankton during summer, to assess the transfer efficiency of different trophic groups, and to construct a carbon budget for the study area.

MATERIAL AND METHODS

Sampling. The study area is located in the coastal area of SW Finland (59° 47' N, 23° 30' E), where water depth is around 46 m. Salinity varies from 6 to 8 psu and the water column lacks a permanent halocline. The thermocline is usually located at 10 to 30 m depth during the summer, but is interrupted by vertical mixing of water masses caused by irregular upwellings and downwellings. A more detailed description of the hydrography of the sea area during 1988 is presented by Haapala (1994).

Water samples were taken weekly between 2 and 16 June, and thereafter every other week until 24 August 1988. Temperature was measured from 0, 2.5, 5, 10, 15, 20, 30 and 40 m depth using a water sampler equipped with a thermometer. At the same time, the vertical distribution of salinity (Autosal Laboratory salinometer) was measured. Phytoplankton samples from 0, 2.5, 5, 10 and 15 m depth were pooled before phytoplankton enumeration. Samples for zooplankton enumeration were taken from 0, 5, 10 and 15 m depth. Phytoplankton and microprotists samples were preserved with acid Lugol's iodine solution (ca 0.5% final concentration). The metazooplankton samples were filtered through a 40 µm mesh net, and the retained material was rinsed to 1 l bottles and preserved with 4% buffered formalin. Sampling and staining of heterotrophic nanoflagellates are presented in Kuosa (1991). The bacteria samples were collected from 0, 2.5, 5, and 10 m depth.

Microscopy and biomass determinations. The samples of phytoplankton, metazooplankton and microprotists were prepared for counting according to Utermöhl (1958) and enumerated using an inverted microscope. At least 50 or 100 units (cells, chains or colonies) of the most abundant >2 µm phytoplankton species were counted. The phytoplankton plasma volume and carbon-biomass values were calculated according to Strathmann (1967) and Sicko-Goard et al. (1977), but modified as suggested by the Baltic Marine Biologists (Edler 1979) and Kononen et al. (1984). The genus *Protoperidinium* (Jacobson & Anderson 1986) and the species *Ebria tripartita* Lemmermann were grouped as heterotrophs. When possible, at least 50 counting units were enumerated for each taxon of metazooplankton and microprotists. The species-specific biovolumes were converted to carbon equivalents using carbon contents of 0.11 pg C μm^{-3} for protozoan microplankton (Edler 1979), and 0.05 pg C μm^{-3} for metazooplankton (Mullin 1969).

Bacterial cell numbers were measured according to Hobbie et al. (1977). Water samples of 10 ml were preserved with particle-free formalin (37% formaldehyde, 2% final concentration) and stored in a refrigerator. In

a few weeks' time subsamples of 1 ml were stained with acridine orange and collected on black 0.2 µm pore-sized polycarbonate filters. The filters were examined with an epifluorescence microscope. Bacterial biomass was estimated using a mean cell volume of 0.045 μm^3 and a mean carbon content of 0.27 pg C μm^{-3} (Kuparinen 1988), both measurements made in the Tvärminne sea area. The bacterial biovolume used is within the range of 16 to 46 pg C μm^{-3}, measured by Heinänen (1992) for the open sea area of the Gulf of Finland during late summer in 1988. The biomass of picoplanktonic cyanobacteria was obtained from the measurements by Kuosa (1991).

Primary and bacterial productivity. The incubation depths for the *in situ* primary productivity measurements were 0.2, 1, 2.5, 5, 7 and 9 m, approximately covering the entire euphotic layer. Primary productivity was measured by the ^{14}C method (Steemann Nielsen 1952). Duplicate light bottles were used at each incubation depth and duplicate dark bottles at 2.5 and 7 m. Light attenuation (Mavolux light meter, Germany) in the water column was measured. The incubations were started between 10:00 and 11:00 h and lasted for 5 to 6 h. A short incubation time was used to avoid the bias caused by intensified herbivorous feeding and the subsequent respiratory losses of algal ^{14}C; the primary production values from short incubations were transformed to daily values by correcting with the ratio of the corresponding cumulative irradiation values (Kipp & Zonen light meter, The Netherlands). Primary productivity (particulate plus dissolved organic ^{14}C) was measured by allowing an acidified 4 ml subsample to stand in uncapped 20 ml glass scintillation vials for 24 h (ventilation cupboard, no bubbling) before the scintillation cocktail (Lumac) was added (Niemi et al. 1983). Radioactivity was measured with a LKB Rackbeta 1215 liquid scintillation counter. In ^{14}C primary productivity calculations, the dark values were subtracted from the corresponding light values. Dissolved inorganic carbon was measured with an infra-red carbon detector (Elektro-Dynamo carbon analyser, Finland). Due to limited irradiation data, variations in the depth of saturating light levels during the day could not be taken into account. Simple calculations (assuming no light saturation of photosynthesis during the light period not covered by incubations) suggested, however, that our approach led to only a small (usually <10%) underestimate of the daily productivity values.

Bacterial production was estimated using the thymidine incorporation technique of Fuhrman & Azam (1980, 1982), with slight modifications. Duplicate 20 ml samples and a formalin-killed adsorption control were incubated with [methyl-^3H]-thymidine (10 nM final concentration, 40 to 42 Ci $mmol^{-1}$; Amersham International) for 1 h. The incubations were terminated with formalin (37% formaldehyde, 0.5% final concentration). The samples were stored in a refrigerator until macromolecule extraction, which was always done within 24 h. The samples were chilled below 3°C and extracted with TCA (5% final concentration). The macromolecules were collected on 0.2 µm pore-sized cellulose nitrate filters (Sartorius). The filters were placed into scintillation vials and soaked with PCS (Amersham) scintillation cocktail. In order to let the filters dissolve, counting was postponed for at least 12 h. The incorporated radioactive thymidine was assayed with a liquid scintillation counter. Daily bacterial carbon production was calculated using the thymidine conversion factor of 1.1×10^{18} cells mol^{-1} thymidine incorporated (Riemann et al. 1987). The growth yield of bacteria was 40% [measured with ^{14}C-labelled DOC (dissolved organic carbon, released from natural phytoplankton communities in the study area; R. Lignell pers. comm.].

Sedimentation. Settled material was collected at 5 to 9 d intervals from 2 to 15 June and thereafter at 2 wk intervals until 25 August by using cylindrical sediment traps (height:diameter = 10) moored at 15 and 30 m depth. Sediment trap samples were preserved with 50 ml of non-buffered, concentrated formaldehyde during deployment. Samples for particulate organic carbon (POC) were filtered in triplicate on acid-washed and precombusted (4 h at 450°C) glass-fiber filters (Whatman GF/F) and analysed with a Heraeus CHN analyser. Metazooplankton swimmers were removed from the filters under a stereomicroscope. A detailed description of sediment trap sampling, analysis, and corrections of the phytoflagellate migration contamination and resuspension are presented in Heiskanen (1995) and Heiskanen & Leppänen (1995).

Ingestion by heterotrophs. Grazing by mesozooplankton and metazoan microplankton was measured on respective sampling days by Uitto (1996a) in the study area, using a ^{14}C-tracer feeding technique and 2 cultures of autotrophic nanoflagellates. The biomass specific clearance rates of 0.7 to 3.9 ml μg^{-1} C d^{-1} on *Brachiomonas submarina* and 0.3 to 4.6 ml μg^{-1} C d^{-1} on *Pavlova lutheri*, were used to estimate the grazing of mesozooplankton on >10 µm and 2 to 10 µm sized natural phytoplankton, respectively. For metazoan microplankton the corresponding values were 1.1 to 6.5 ml μg^{-1} C d^{-1} and 1.3 to 6.7 ml μg^{-1} C d^{-1}. Cyanobacteria were not included in the larger phytoplankton group, because they are not grazed by metazooplankton in the study area (Sellner et al. 1994). All other species, dominated by nanoflagellates, were assumed to be palatable to zooplankton. Mesozooplankton and metazoan microplankton grazing on HNAN was calculated according to measurements made in a mesocosm experiment in the nearby archipelago area during the same summer (Uitto 1996b) using the average daily

biomass specific clearance rate of 1.02 ml μg^{-1} C for mesozooplankton and 3.3 ml μg^{-1} C for metazoan microplankton. Ingestion of ciliates, *Protoperidinium* sp. and *Mesodinium rubrum* by adult copepods were estimated using the clearance rates of 0.4 to 1.6 ml $ind.^{-1}$ h^{-1}. These rates had been measured for *Acartia* spp. found in the same study area, ingesting microplankton at a temperature of 13 to 18°C (Kivi 1996). The clearance rates of 3 smaller size categories of different developmental copepod stages were estimated by applying the allometric equation of Moloney & Field (1989).

Ciliate grazing on 2 to 10 µm phytoplankton and on HNAN was estimated using the clearance rate measurements of Kivi & Setälä (1995) made on natural communities in the same study area during the summers of 1987 and 1989. In their study, clearance rates of several oligotrich ciliate species were measured using starch particles as a food tracer. The size-specific clearance rate of each species of protozoan microplankton was estimated with the equation. $y = 2.67 + 47.57x$, where y stands for clearance rate (µl $cell^{-1}$ h^{-1}), and x for cell biovolume. Ciliates were assumed to graze only on phytoplankton <10 µm, as the optimal food size of ciliates in the study area is around 5 µm (Kivi & Setälä 1995). Ciliate grazing on bacteria and picocyanobacteria was estimated on the basis of the measurements of Kuuppo-Leinikki (1990) during the enclosure experiment conducted in the nearby archipelago area in 1988; the mean daily biomass-specific clearance rate of 1.2 ml μg^{-1} C was used.

The carbon requirement of *Ebria tripartita* and *Protoperidinium* spp. was estimated according to the highest growth rate (k) found between 2 and 9 June: $k = (\ln C_t - \ln C_0)/t$, where t is the sampling interval (7 d) and C_t and C_0 are the carbon biomass values on the 2 consecutive samplings. The daily production (P) was thus estimated using the formula: $P = k \times B$. The carbon requirement of these groups was estimated by assuming a growth yield of 40% (Fenchel 1982). Because these taxa are known to feed extracellularly on large diatoms (Jacobson & Anderson 1986), their feeding was assumed to be restricted to phytoplankton >10 µm.

Biomass, grazing on picoplanktonic cyanobacteria and production of HNAN were calculated using the abundance, grazing and daily growth rate measurements made by Kuosa (1991) in the same study area in 1988. Daily grazing by HNAN on bacteria was estimated from the grazing and growth measurements made by Kuosa (1991). Total carbon requirement of HNAN was calculated from production (P) assuming the growth yield of 40% (Fenchel 1982), from which the measured proportion of HNAN grazing on picocyanobacteria was subtracted to estimate the HNAN ingestion of bacteria.

Total particulate and dissolved detrital carbon. The proportion of POC in the form of detrital particulate carbon (DPC) was calculated by subtracting the amount of total autotroph and heterotroph biomass from POC. Non-ingested particulate carbon remained from the estimated daily production of different trophic groups and faecal pellets of metazooplankton were assumed to be usable detrital carbon (UDC) for bacterial production. DOC released directly to the water was assumed to come from phytoplankton exudation (about 10% of primary production in the study area; Lignell 1990) and from metazooplankton sloppy feeding (10% of total feeding; Lampert 1978). The production of faecal pellets was estimated by assuming an assimilation efficiency of 60% for metazooplankton (Laws et al. 1988), thus 40% of total ingested carbon would be transformed to faecal pellets. Other sources for UDC were estimated to originate from primary and secondary production of different trophic groups that was not consumed by heterotrophs.

Calculating food web dynamics. All biomass concentrations and rate measurements were integrated between 0 and 10 m. Food web efficiency was calculated assuming that the ration of different carbon sources in the secondary production of a trophic group will remain the same as in that ingested by the same group. Autotrophs were assigned to 3 size-classes; <2 µm, 2 to 10 µm, and >10 µm, an autotrophic ciliate *Mesodinium rubrum*. Heterotrophs were divided into bacteria, HNAN, ciliates, the heterotrophic dinoflagellate *Protoperidinium* spp., the ebrian *Ebria tripartita*, <140 µm metazoan microplankton and >140 µm mesozooplankton (cf. Sieburth et al. 1978). Pico-, nano-, micro- and metazooplankton were assumed to form 4 functional groups within the food web, thus the food web structure was composed of 1-step food chains (direct ingestion of autotrophs and bacteria) and 2- to 3-step food chains (ingestion of heterotrophs by different trophic groups).

$$I^{\bullet}2 = (I_{X_i}/TI_{X_i})\, I_{X_{i+1}}$$
$$I^{\bullet}3 = (I_{X_i}/TI_{X_i})\, (I_{X_{i+1}}/TI_{X_{i+1}})\, I_{X_{i+2}},$$

where $I^{\bullet}2$ is the daily amount of carbon (mg C m^{-2}) transferred through the 2 food steps to be ingested by microprotists or metazooplankton, $I^{\bullet}3$ is the corresponding carbon transferred through the 3 food steps to be ingested by metazooplankton, I is the ingestion of a lower trophic group by a 1-step higher trophic group (i.e. the ingestion of bacteria and picocyanobacteria by HNAN or microprotists; ingestion of HNAN and 2 to 10 µm phytoplankton by microprotists or metazooplankton; ingestion of microprotists and >10 µm phytoplankton by metazooplankton), TI is the total ingestion by a 1-step higher trophic group, and X_i, X_{i+1} and X_{i+2} are 3 different trophic groups corre-

sponding to nanoheterotrophs, microprotists (ciliates and *Protoperidinium* spp.) and metazooplankton (mesozooplankton and metazoan microplankton).

RESULTS

Hydrography

Three different periods of hydrodynamic events occurred in the study area. In the beginning of June, a strong upwelling mixed the water column (cf. Lignell et al. 1993, Haapala 1994), after which thermal stratification began to develop (Fig. 1A). The second period was characterised by thermal stratification which prevailed from late June until the end of July. The third period began in late July, when the wind induced strong surface currents directed towards the coast, causing a downwelling in the study area (Haapala 1994). This event was concurrent with a decrease in surface layer temperature and salinity (Fig. 1A, B). The downwelling was soon followed by an upwelling and simultaneous strong off-shore current of the surface layer, which was followed by a weakening of thermal stratification and a further fall in temperature and increase of salinity in August.

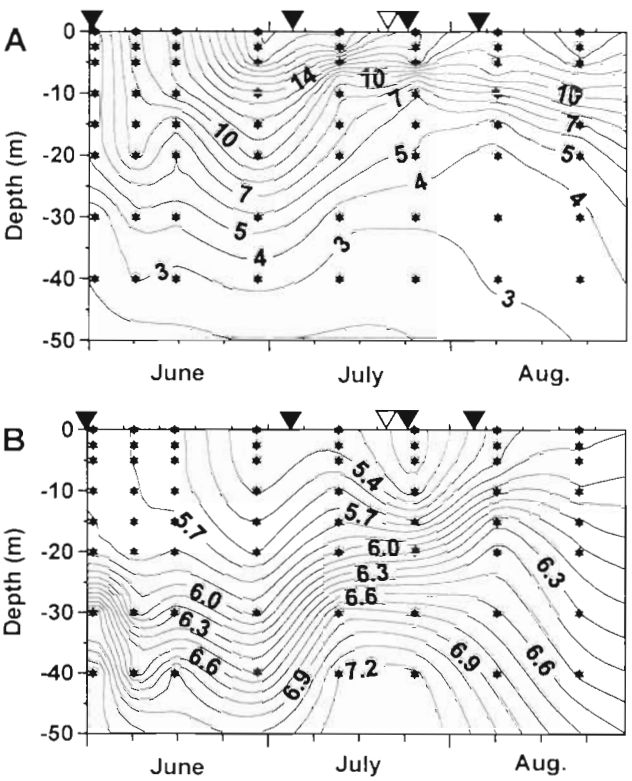

Fig. 1 (A) Temperature and (B) salinity variations in the sea area off Tvärminne in summer 1988. (▼) Upwelling; (▽) downwelling (cf. Haapala 1994)

Succession and biomass development of different trophic groups

Phytoplankton biomass varied from 375 to 1200 mg C m^{-2}, being largest in June (Fig. 2A). In early June, it was composed mostly of >10 µm phytoplankton, dominated by the diatoms *Skeletonema costatum* (Greville) Cleve and *Chaetoceros wighamii* Brightwell; the dinoflagellates *Peridiniella catenata* (Levander) Balech, *Dinophysis acuminata* Claparède & Lachmann; *Gymnodinium* sp. and and by an euglenoid flagellate *Eutreptiella* sp. After mid-June the remains of the vernal phytoplankton community (i.e. *S. costatum* and *P. catenata*) disappeared. The warm and relatively stable period from late June until mid-July was characterised by the dominance of 2 to 10 µm nanoflagellates, especially *Chrysochromulina* spp., *Cryptomonas* spp. and *Pedinella* spp. (Fig. 2A). The biomass of picoplanktonic cyanobacteria, mostly *Synechococcus*, also increased (Kuosa 1991). Blue-green algae were dominated by *Aphanizomenon* cf. *flos-aquae* (L.) Ralfs during the summer.

Biomass of metazooplankton was 165 mg C m^{-2} on 2 June, but increased within 2 wk to the maximum 1110 mg C m^{-2}, due to the growth of *Synchaeta* spp. and meroplanktonic bivalvia larvae (Fig. 2B). *Eurytemora affinis* (Poppe) CI–CVI became dominant in June and July, in August the share of *Acartia* spp. and *Bosmina longispina maritima* (P. E. Müller) increased, causing another biomass maximum. Metazoan microplankton, composed mostly of copepod nauplii and small rotifers *Synchaeta* spp. and *Keratella* spp., accounted for 1 to 20% of the total metazooplankton biomass. Biomass of heterotrophic microprotists was 52 to 126 mg C m^{-2}, being dominated by *Ebria tripartita* and heterotrophic dinoflagellates *Protoperidinium* spp. in June. From July on, the share of oligotrich ciliates, especially *Strobilidium spiralis* Leegaard and *Strombidium* spp., increased (Fig. 2C). In August, the biomass of the autotrophic ciliate *Mesodinium rubrum* Lohmann (Fig. 2A) was as large as that of ciliates, being 125 mg C m^{-2}. Bacterial biomass was 560 mg C m^{-2} on 2 June, but later in the summer it varied between 700 and 1100 mg C m^{-2} (Fig. 2C).

Primary production, herbivory and sedimentation

Primary productivity was 80 to 370 mg C m^{-2} d^{-1} (Fig 3), increasing steadily during June and the first half of July, whereafter it decreased strongly at the

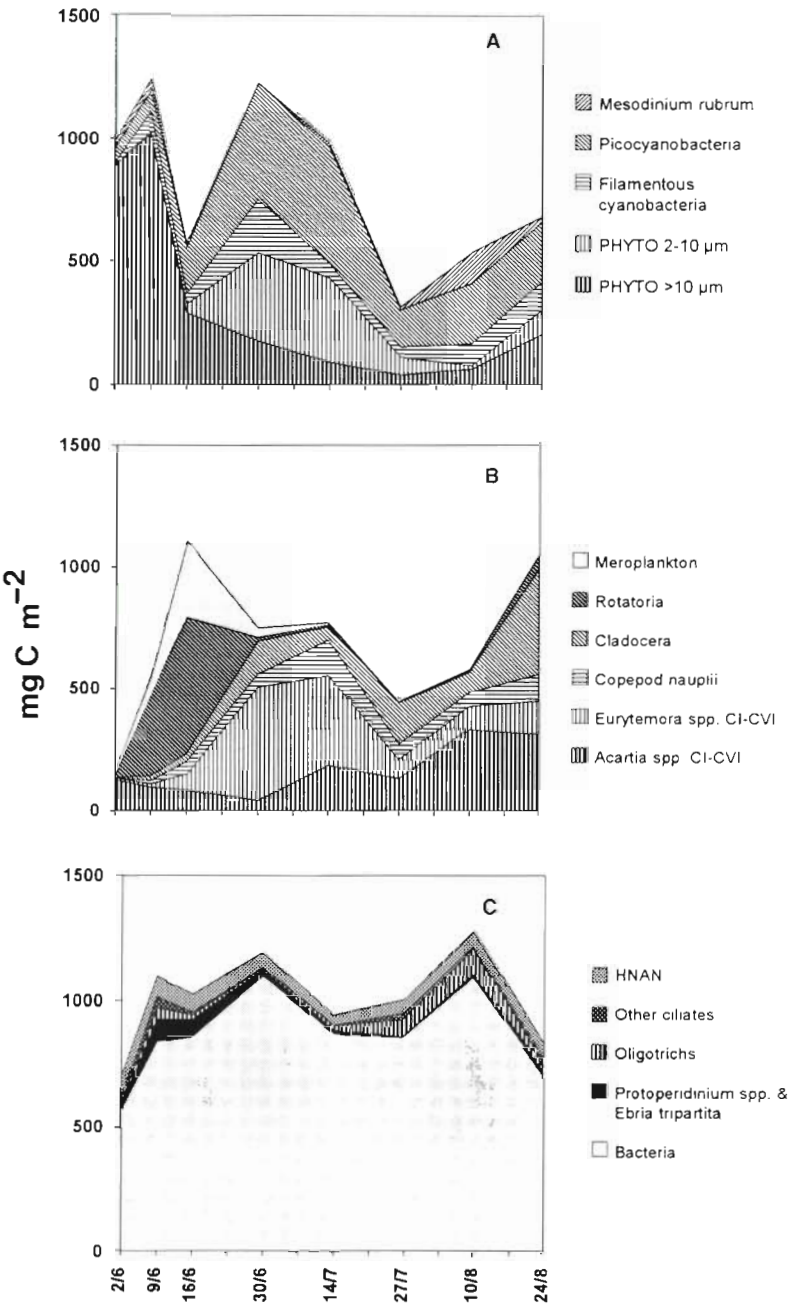

Fig. 2. Succession and development of (A) phytoplankton, (B) metazooplankton, and (C) protozooplankton and bacteria at the sea area off Tvärminne in summer 1988

same time as phytoplankton biomass declined. A higher rate was found again in August, along with a phytoplankton biomass increase. The estimated primary sedimentation rate was 10 to 350 mg C m^{-2} d^{-1}, reaching its maximum in mid-June, after which it decreased to the end of the summer.

Daily grazing by different trophic groups varied widely during the summer (Fig. 4). HNAN and ciliates grazed most in July, when picocyanobacteria and nanoflagellates dominated the phytoplankton biomass (Figs. 4A, B). *Protoperidinium* spp. and *Ebria tripartita* together were estimated to graze most in early June, when phytoplankton >10 µm predominated. Mesozooplankton grazed most in early June, but metazoan microplankton grazed most in July. Grazing on autotrophic *Mesodinium rubrum* by metazooplankton was estimated to be greatest in August. Total herbivory was 30 to 330 mg C m^{-2} d^{-1}

Heterotrophy and food web dynamics

Bacteria were estimated to account for 20 to 90% of the daily HNAN nutrition. Among ciliates, bacteria were estimated to comprise 2 to 34% of the daily nutrition, the largest percentage occurring in August (Fig. 4B). In June, up to 80% of total ciliate nutrition was composed of HNAN, and at the same time the efficiency of the MFW in transferring bacterial carbon to ciliate nutrition was estimated to be 74% (Table 1). The efficiency of the MFW varied during the summer, but ciliates were estimated to gain a greater amount of bacterial carbon through this 2-step food chain than through direct grazing on bacteria (Fig. 4, Table 1).

Metazooplankton predation on ciliates increased during the summer, accounting for up to 60% of total ingestion (Fig. 4). In the 2-step MFW ciliates were most important in transferring nanoplanktonic carbon to metazooplankton; as much as 24% and 21% of metazooplankton nutrition was composed of 2 to 10 µm phytoplankton and HNAN transferred by ciliates in August, respectively (Table 1). Direct grazing on HNAN was more inefficient, corresponding at most to 17% of metazooplankton total nutrition in June (Fig. 4C). The contribution of picocyanobacterial carbon to metazooplankton nutrition was no more than 5 and 3%, when estimated to have been transferred through the 2-step food chains through ciliates and HNAN, respectively. The contribution of bacteria transferred through the same routes was estimated to be at most 14 and 15% In addition, as much as 17 and 16% of picocyanobacterial and bacterial carbon was estimated to have been transferred to metazooplankton nutrition through the 3-step linkage of HNAN and ciliates, respectively (Table 1).

Detrital carbon and bacterial production

Total POC varied between 3.8 and 5.6 g C m^{-2}, DPC accounting for 31 to 62% of the total (Fig. 5A). The formation ofUDC through the functioning of the pelagic food web was estimated to be highest in August. Primary production (non-consumed phytoplankton + exudation by phytoplankton) was estimated to comprise ca 10 to 70% of UDC formation, the lowest percentages occurring in July. The respective contribution of metazooplankton (faecal pellets + sloppy feeding) was estimated to be 10 to 60%, being largest in June, when metazooplankton grazed on >10 µm phytoplankton. Non-consumed secondary production of HNAN, microprotists and bacteria was estimated to account for 10 to 50% of UDC formation, being largest in July when protists were estimated to be most productive. The carbon demand of bacteria was estimated to be 110 to 325 mg C m^{-2} d^{-1}. The formation of UDC was estimated to usually meet the daily bacterial carbon requirement, if loss by sedimentation was not taken into account. Bacterial production was 45 to 130 mg C m^{-2} d^{-1} and both the highest and lowest rates were measured in August (Fig. 5B).

Carbon budget

The grazing impact of different herbivorous groups varied during the summer (Fig. 6). HNAN were important in late July, when they grazed approximately half of the total daily primary production. The combined daily carbon requirement of microprotozoan *Protoperidinium* spp. and *Ebria tripartita* was largest in June when it accounted for one quarter of the daily primary production, but at other times <5% of was grazed. Ciliates were estimated to directly graze approximately one half of the primary production in mid-July, and up to 11% was estimated to have been transferred from picocyanobacteria through HNAN to ciliates in August. Metazooplankton directly grazed as much as 64% of the primary production in June, but up to one quarter of the daily phytoplankton production could be transferred to metazooplankton via 2- and 3-step food chains through HNAN and ciliates from <10 µm phytoplankton during late summer, the nanoalgae→ciliate→metazooplankton linkage being the most important pathway. Metazooplankton grazing on *Mesodinium rubrum* was estimated to account for up to 40% of primary production in August (Fig. 6).

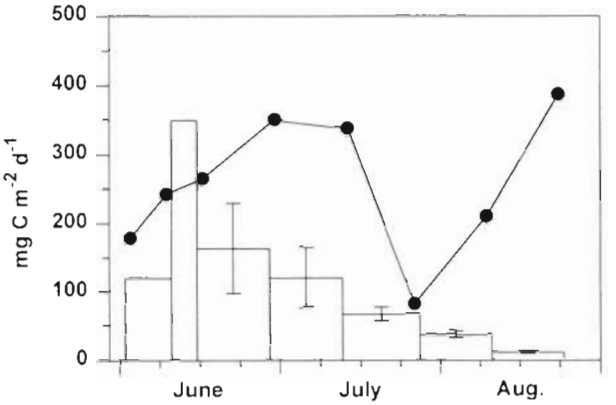

Fig. 3. Primary productivity (line) and mean primary sedimentation (columns); vertical bars show the range between the traps at 15 m (upper limit) and 30 m (lower limit) depth

Table 1. Potential efficiency of the 2- and 3-step pelagic food chains in transferring phytoplankton and bacterial biomass to higher trophic levels, expressed as a percentage of carbon transferred to ciliate and metazooplankton nutrition in the sea area during summer 1988. Picocyano: picocyanobacteria; HNAN: heterotrophic nanoflagellates; meta: metazooplankton

Hydrodynamic period:	I			II		III			Mean	SD
Date:	2/6	9/6	16/6	30/6	13/7	27/7	10/8	24/8		
Ciliates										
Picocyano → HNAN → ciliates	7	7	10	8	7	7	39	27	14	12
Bacteria → HNAN → ciliates	74	59	46	6	4	27	9	6	29	26
Metazooplankton										
Picocyano → HNAN → meta	<1	<1	3	2	2	1	2	5	2	1
Picocyano → ciliates → meta	<1	<1	1	<1	<1	2	3	1	1	1
Picocyano → HNAN → ciliates → meta	<1	1	2	<1	<1	4	17	7	4	5
Total	1	1	6	3	3	7	22	13	7	7
2–10 µm algae → ciliates → meta	<1	<1	5	5	13	24	4	15	8	8
>10 µm algae → *Protoperidinium* → meta	1	3	2	<1	1	<1	1	<1	1	1
Total	1	4	7	5	13	24	5	16	9	7
Bacteria → HNAN → meta	3	2	14	2	1	5	1	1	4	4
Bacteria → ciliates → meta	<1	2	2	<1	<1	12	15	2	4	5
Bacteria → HNAN → ciliates → meta	3	5	8	<1	1	16	4	2	5	5
Total	6	9	24	2	2	33	20	5	13	11

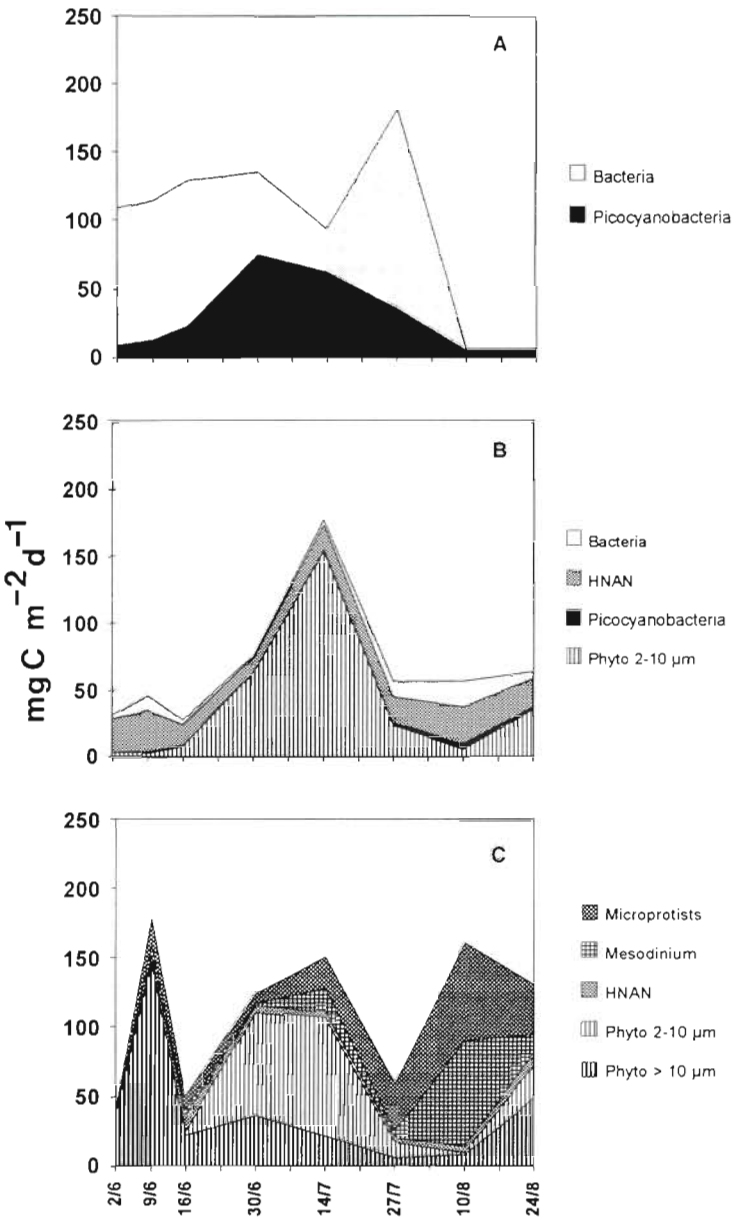

Fig. 4. Ingestion rates of various food sources by (A) HNAN, (B) ciliates and (C) metazooplankton

HNAN were important grazers on bacteria in early June and late July, when their grazing was estimated to exceed the measured bacterial production. Ingestion of bacteria by ciliates was estimated to account for at its highest only 15% of the bacterial production in late August. On average, the amount of algal and bacterial carbon that was estimated to have been transferred through the MFW to the daily nutrition of ciliates corresponded to 4 and 16% of the daily primary and bacterial production, respectively. The corresponding percentages for metazooplankton were as much as 9 and 7%, due to the metazooplankton feeding on HNAN and ciliates.

The summer carbon budget was constructed for the period between 2 June and 27 August (Fig 7) by integrating the daily rate measurements. In this carbon budget, primary production was 20.5 g C m^{-2}, total herbivory 13.6 g C m^{-2} and estimated primary sedimentation 8.5 g C m^{-2}. If the sedimentation loss of early June, composed of mostly the sinking senescent phytoplankton bloom, was excluded from the calculations, summer sedimentation would be 5.7 g C m^{-2}. Bacterial production was 8 g C m^{-2}, from which protists were estimated to have grazed 5.1 g C m^{-2} (Fig. 7) Carbon release from phytoplankton production to the UDC pool was estimated to be 8.5 g C m^{-2} during the summer, from which non-consumed phytoplankton, phytoplankton exudation and metazoplankton sloppy feeding accounted for 64, 25 and 12%, respectively. Formation of metazooplankton faecal pellets was estimated to be 3.9 g C m^{-2} and the release from other trophic groups 5.2 g C m^{-2}. If metazooplankton biomass elimination was calculated using the equation $B_1 + P - B_2$, where B_1 is metazooplankton biomass at time t_1, P is the integrated production between times t_1 and t_2, and B_2 is metazooplankton biomass at time t_2, total elimination would be 2.3 g C m^{-2}, i.e. the carbon potentially available to zooplanktivores or recycled within the community in summer.

DISCUSSION

Hydrodynamic periods and food web dynamics

Hydrodynamic conditions, mainly the degree of stratification and upwellings in late July and early August, strongly affected the planktonic community, consequently 3 different stages of food web dynamics could be distinguished. All trophic groups were largely omnivorous, but the role of different carbon pathways varied during the summer In early June, the remains of the vernal phytoplankton community and large amounts of detrital carbon prevailed in the water column. Assuming a rough growth yield of 30 to 40% for metazooplankton (Mullin & Brooks 1970, Durbin & Durbin 1992), the integrated total ingestion of naturally occurring phytoplankton and protists could meet approximately 30 to 50% of the community's carbon demand, the rest being possibly fulfilled by ingestion on detritus in early June. Bacterial carbon was important for HNAN nutrition,

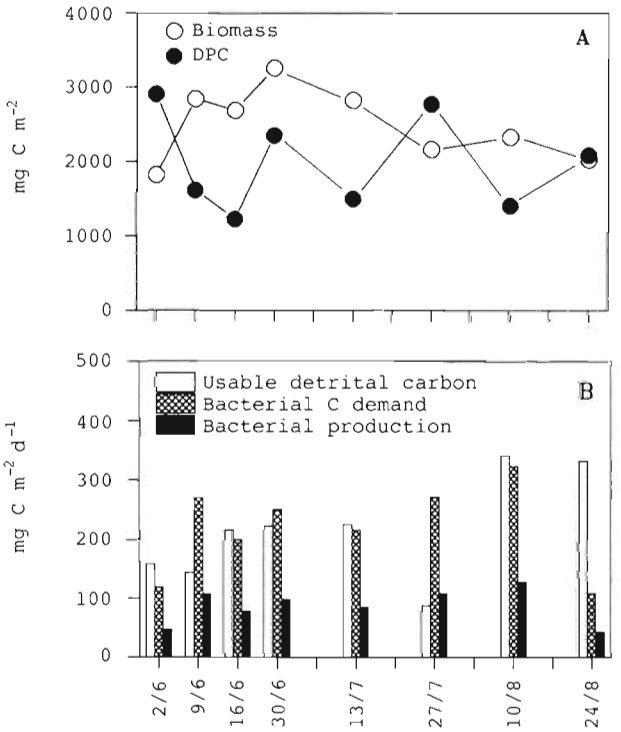

Fig. 5. (A) Development of total biomass and detrital particulate carbon (DPC), and (B) estimated usable detrital carbon (UDC) released from the food web, estimated bacterial carbon demand and measured bacterial production

which is in accordance with previous studies done in the area (Kuosa & Kivi 1989, Kuuppo-Leinikki 1990) and with the studies from other marine areas (Wigner & Hagström 1988, Sanders et al. 1992). A considerable amount of bacterial carbon was also transferred to ciliate nutrition through the MFW. The large amount of DPC probably provided usable compounds for bacteria, whose biomass increased in spite of a severe predation pressure by HNAN.

In late June and in July, the warm and stratified period was characterised by the dominance of autotrophic picoplankton and nanoflagellates, and microprotozoan biomass was at its lowest level, whereas mesozooplankton biomass increased. Unlike early June, all trophic groups were largely herbivorous. Metazooplankton fed also on ciliates, that transferred nanoplanktonic carbon. There seemed to be a balance between the formation of UDC and bacterial carbon requirements, indicating that the mid-summer community recycled carbon within the pelagic ecosystem.

The third period began when surface water currents and wind-induced upwellings in late July weakened thermal stratification and strongly affected the planktonic community. Primary productivity, the biomass of phytoplankton and the biomass of metazooplankton decreased. Ciliates and metazooplankton fed largely on heterotrophs, thus both bacterial and algal carbon were transferred to metazooplankton with the highest rate. After the first part of August, no major perturbations occurred and stratification was re-established. The formation of UDC exceeded the carbon demand of bacteria at the end of August, but no increase in sedimentation was observed. The biomass of *Aphanizomenon* cf. *flos-aquae* increased in August. This filamentous cyanobacteria is not palatable to metazooplankton (Sellner et al. 1994), hence the degradation of this species could have caused the increase in UDC.

Picoplankton was not an important food source for ciliates, accounting on average for 17% of the their total nutrition. However, picocyanobacteria are known to form colonies of approximately 10 cells (Kuosa 1988), which may be eaten by ciliates. Herbivory was the major feeding mode for metazooplankton, but feeding on ciliates increased throughout the summer, reflecting the increasing role of the MFW in metazoan nutrition. Ingestion by metazooplankton of carbon originating from picoplankton was small, depending mostly on the percentage of ciliates in metazooplankton food, and on the concurrent ciliate diet. The daily efficiency of picoplanktonic carbon transfer through the 3-step food chain was low; on average 4 and 5% of metazooplankton nutrition was composed of transferred picocyanobacterial and bacterial carbon respectively, which is in accordance with other studies on the MFW efficiency (Ducklow et al. 1986, Hagström et al. 1988, Wikner & Hagström 1988). However, a slightly smaller amount of picoplanktonic carbon was also

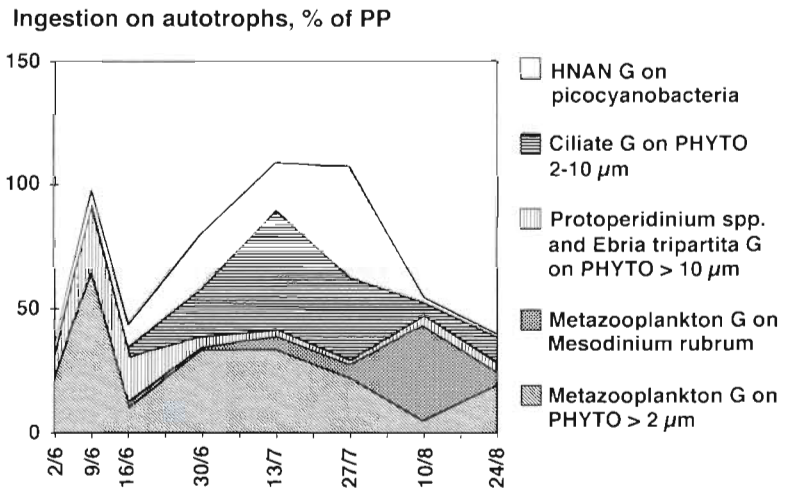

Fig. 6. Estimated ingestion of autotrophs by herbivorous trophic groups, expressed as a percentage of the daily primary production. G: grazing

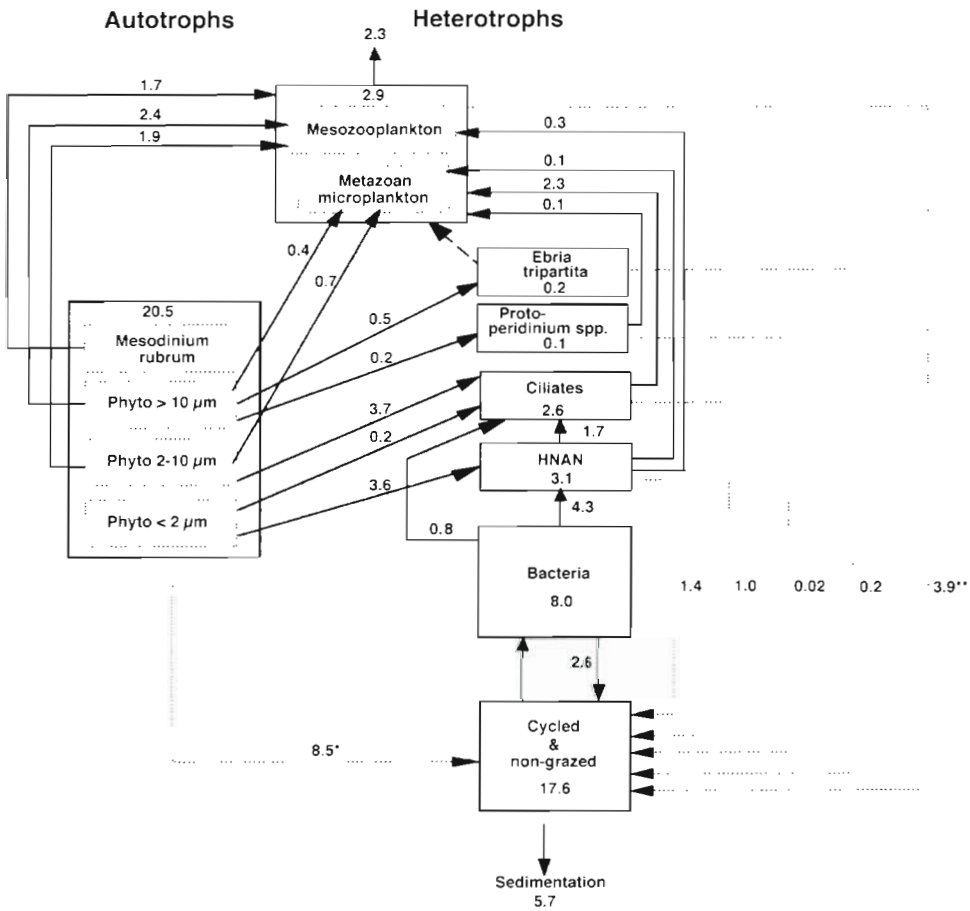

Fig. 7. Carbon flow analysis of the pelagic community in the Tvärminne sea area, integrated values between 2 June and 28 August 1988. Values in boxes: production; continuous line with arrow: ingestion; dotted line: recycled carbon (g C m^{-2} $period^{-1}$). *non-grazed phytoplankton carbon + phytoplankton exudation + metazooplankton sloppy feeding; **metazooplankton faecal pellets

transferred through 2-step chains, i.e. through HNAN and ciliates, thus increasing total picocyanobacterial and bacterial carbon transfer to 7 and 13% of metazooplankton nutrition, respectively.

Alternative carbon pathways

HNAN were estimated to satisfy 56% of their carbon demand with picophytoplankton, which agrees with values previously measured by Kuosa & Kivi (1989). Flagellates >5 µm are also known to ingest small nanoplanktonic organisms (Kuosa 1990, Sherr & Sherr 1992), whose role, however, could not be estimated in this study. In addition, choanoflagellates at least are also known to utilise detrital particles as food (Marchant & Scott 1993, Tranvik et al. 1993), which is also an alternative carbon pathway to higher trophic groups.

In many recent studies, athecate phagotrophic gymnodinoid and katodinoid dinoflagellates have been found to be efficient grazers of nanoplankton (Bjørnsen & Kuparinen 1991, Hansen 1991, Strom 1991, Neuer & Cowles 1994). Unfortunately, phagotrophic species could not be distinguished from autotrophic dinoflagellates in this study, and only a rough estimation of the role of the potentially phagotrophous genera *Gymnodinium*, *Gyrodinium*, *Glenodinium* and *Katodinium* (Neuer & Cowles 1994, Sherr & Sherr 1994) could be carried out. The combined biomass of these dinoflagellates was ca 100 to 400 mg C m^{-2} in June, but decreased to <20 mg C m^{-2} in late summer. That biomass accounted for as much as 30% of the total phytoplankton biomass and 150% of the microprotozoan biomass in early June. Assuming that all species of these genera were heterotrophic, their daily carbon ingestion would be 20 to 110 mg C m^{-2} in June, if the carbon demand was calculated in the same way as for *Protoperidinium* spp. This emphasises the large potential grazing impact of these potentially heterotrophic dinoflagellates, being similar to that of *Protoperidinium* spp. As most of these dinoflagellates were 20 to 30 µm in size, they were likely to use the same food as ciliates (Sherr & Sherr 1992). Potentially heterotrophic dinoflagellates contributed 20 to 40% to the edible phytoplankton biomass in June, and unlike *Ebria tripartita* (Kivi et al. 1996), athecate species were probably grazed by metazooplankton. Thus the efficiency of

the MFW in transferring bacterial and algal carbon to metazooplankton could have been higher than was estimated in June. In late summer, the percentage of athecate dinoflagellates was usually <10% of the edible phytoplankton biomass, and thus their role in the carbon transfer was apparently minor.

Mixotrophic nanoflagellates may also have increased ingestion on picoplankton and small nanoplankton during the summer minimum stage. From July onwards, phytoplankton biomass was composed mostly of the potentially mixotrophic species *Chrysochromulina* spp., unidentified cryptomonads and *Pseudopedinella* sp. (Kuosa 1990, Turner & Roff 1993). According to Andersson et al. (1994), the growth of mixotrophic algae may explain flagellate peaks coinciding with the late summer peak in bacterial production in coastal areas of the northern Baltic. If mixotrophic organisms are able to graze at significant rates, the efficiency of the MFW in transferring picoplanktonic carbon to higher trophic levels is likely to be higher than previously stated.

Carbon budget

Generally, seasonal succession of phytoplankton, protists and metazooplankton followed the pattern described in previous studies of this area (Niemi 1975, Forsskåhl & Sundberg 1981, Huttunen & Kuparinen 1986, Viitasalo 1992, Kuuppo-Leinikki 1993). Primary productivity and bacterial production were also found to be at the levels measured earlier by Kuparinen (1984), Kuosa & Kivi (1989) and Lignell (1990). This indicates that the general pattern of the summer carbon budget of this study was representative for this coastal area of SW Finland.

On a seasonal basis, differences in the structure of the pelagic community and in the main carbon flows were large. In the study carried out during the preceding cooler and non-stratified spring period, phytoplankton was dominated by large diatoms and 70% of primary production was estimated to sink, whereas the role of grazing was minor in the study area (Lignell et al. 1993). During summer, temperature, stratification and upwellings influenced community composition and dynamics, and most of the primary production was recycled. When the 2 first sampling periods in early June were left out from the calculations, the total integrated primary sedimentation corresponded to 27% of the integrated primary production (Fig. 7), which is slightly higher than the other summer estimates in the Baltic Sea (Kuparinen et al. 1984, Smetacek et al. 1984, Heiskanen & Leppänen 1995). Sedimentation did not correlate with the amount of total metazooplankton ingestion and with the estimated formation of faecal pellets, which implies that faecal material was mostly recycled within the water column. However, sedimentation correlated significantly with metazooplankton grazing on phytoplankton >10 µm, and it is possible that pellets formed during June sank. If coprophagy is not important, faecal pellets can sink quickly, which has also been noticed in POC sedimentation rates (Voss 1991). Faecal material of cladocerans is usually recycled within the pelagic community (Elser et al. 1995).

Using integrated values, HNAN grazing on cyanobacteria accounted for 19% of primary production in summer 1986 (Kuosa 1991), being similar to the 18% of this study. HNAN are known to also use picoeucaryotic algae as food, and the total grazing by HNAN was estimated to account for 32% of summer primary production by Kuosa (1991). No previous measurements on summer herbivory of the microprotist community were available from our study area. The estimated 23% grazing of primary production is within the range found in coastal waters off Washington, USA (17 to 52%; Landry & Hassett 1982) but lower than the 37 to 115% found in the coastal area of the eastern Canadian Arctic (Paranjape 1987). As a whole, HNAN and microprotists were estimated to graze on total phytoplankton more than metazooplankton, emphasising their importance in controlling phytoplankton and in the functioning of pelagic food webs in general (Azam et al. 1983). For metazooplankton, the 26% grazing of primary production is close to the 19% measured by Uitto (1996a) at 5 m depth in the same study area, and within the range of 5 to 48% found in the southern Baltic (Tiselius 1988) or the 14 to 31% in the Dogger Bank area of the North Sea (Nielsen et al. 1993).

Production by bacteria, HNAN, microprotists and metazooplankton was estimated to account for 39, 15, 14 and 14% of primary production, respectively, when integrated throughout the summer. If the results of this study are combined with those measured the previous spring (Lignell et al. 1993), the integrated metazooplankton production would be 4 g C m^{-2} for the period from March to August, which is 2 times larger than that estimated by Koski (1995) in 1992 for copepods only, in the same study area. The integrated metazooplankton production for the whole spring and summer period would be 6% of primary production, which is similar to the earlier estimates for copepods in the northern Baltic (Johansson 1992). Pelagic clupeid fish and mysid shrimp are the most important predators of metazooplankton in the northern Baltic (Rudstam et al. 1992, Uitto et al. 1995), although their grazing impact is largely restricted to the late summer-autumn period (Rudstam et al. 1992).

HNAN were practically the only grazers on bacteria; approximately 53% of bacterial production was estimated to have been grazed by HNAN, the contribution

of ciliates being only 11%. On the other hand, Kuosa & Kivi (1989) estimated that summer bacterial production was not able to sustain the total carbon demand of HNAN, which suggests large interannual variability. Calculated as a percentage of primary production, 25% of the cycled carbon re-entered the food web as bacterial carbon, mostly as food of HNAN (Fig. 7). On average, the produced and recycled carbon within the food web could sustain daily bacterial carbon demand. UDC can be released from algae and protists by passive diffusion or egestion through cell membranes, by sloppy feeding of metazooplankton and by protists that can produce nonliving sub-micrometer particles during grazing (Hagström et al. 1988, Jumars et al. 1989, Lignell 1990, Nagata & Kirchman 1992). Autolysis caused by abiotic factors (Cole et al. 1984) and by viral infections (Bratbak et al. 1992) is another potential source of UDC. In the more open sea area of the Baltic Sea, autochthonous carbon released by heterotrophic organisms is considered to form the dominant carbon source for bacterial production (Kuparinen & Heinänen 1993).

Reliability of the estimates

The carbon budget and estimated flow dynamics are exposed to some error factors due to the use of constant carbon conversion factors and growth yields. The food web structure is also likely to be more complicated than presented in this study, especially within protists. Spatial and temporal patchiness of plankton, as well as variations in the feeding behaviour of planktonic organisms, can cause undetectable error in the carbon flow estimation within the euphotic layer. However, daily differences in the food chain efficiency (Table 1) were large enough to suggest temporal variation in the carbon flow dynamics during summer, at least between different hydrodynamic periods.

Most of the grazing measurements were carried out during the same summer, which improves the reliability of the daily flow analysis. One indication of the rough balance of the carbon budget is that the summer primary production was estimated to meet the loss factors caused by herbivory and sedimentation. However, 20 to 40% of the bacterial carbon demand remained unresolved, depending on whether the summer sedimentation was integrated at 15 m (9.7 g C m^{-2} $period^{-1}$) or 30 m trap measurements (4.5 g C m^{-2} $period^{-1}$), and whether the whole metazooplankton production was assumed to have been recycled or consumed by zooplanktivores. Allochthonous carbon is a potential reason for high bacterial production in the coastal area off Tvärminne (Kuosa & Kivi 1989, Lignell 1990, Lignell et al. 1993), but its importance has not been studied.

This study has produced evidence to support the conclusion that the summer structure and dynamics of the pelagic food web are largely 'multivorous' (*sensu* Legendre & Rassoulzadegan 1995), where both herbivory and MFW have significant roles, and where picoplankton is mostly consumed by HNAN and nanoplankton by ciliates and metazooplankton. Ciliates appeared to be an important food source for metazooplankton during summer, which is in accordance with the study of Painting et al. (1993), which found mesozooplankton to be equally dependent on microprotists and phytoplankton during periods when phytoplankton was predominated by small cells, unavailable to metazooplankton. The pelagic food steps seemed to be loosely coupled and usable detrital carbon released from different trophic groups could sustain bacterial production. Upwellings seemed to have the most powerful effect on the stabile summer pelagic community, emphasising the important role of hydrodynamic events, regulated mainly by regional weather conditions, in modifying the functioning of the whole pelagic ecosystem.

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