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Contribution of Zooplankton to Vertical Carbon Fluxes in the Kara and White Seas

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Abstract: Data on the zooplankton community structure, gut evacuation rate and carbon content of zooplankton faecal pellets were used for assessing the contribution of zooplankton to vertical carbon fluxes in the White and Kara Seas. The results revealed strong regional and seasonal variations of pellet carbon input related to differences in structure and dynamics of the zooplankton communities in the regions studied. In the deep regions of the White Sea, maximum daily pellet carbon flux from the 0-50 m layer was observed in the spring. It reached 98 mg C_{org} m^{-2} day^{-1} and coincided with a strong predominance of the large arctic herbivorous copepod *Calanus glacialis* in the surface layers. In summer and fall, it decreased by 1 to 2 orders of magnitude due to migration of this copepod to its overwintering depths. In contrast, in the shallow coastal regions, the pellet production was low in spring, gradually increased during summer and reached its maximum of 138 mg C_{org} m^{-2} day^{-1} by late summer to beginning of autumn. Such a seasonal pattern was in accordance with the seasonal variation of abundance of major pellet producers, the small boreal copepods *Acartia bifilosa, Centropages hamatus,* and *Temora longicornis.* In the estuarine zone of the Kara Sea, the pellet flux was mostly formed by pellets of brackish-water omnivorous copepods. It varied from 35 mg C_{org} m^{-2} day^{-1} in 1997 to 96 mg C_{org} m^{-2} day^{-1} in 1999. In the central Kara Sea with its typical marine community, the daily flux reached 125 mg C_{org} m^{-2} day^{-1} in summer. The results of our calculations indicate that both in the White and Kara seas zooplankton pellet carbon contributes up to 30 % to the total carbon flux during particular seasons.

Zusammenfassung: Struktur der Zooplankton-Gemeinschaft, Darmdurchsatz-Rate und Kohlenstoffgehalt von Kotballen des Zooplanktons wurden genutzt, um den Beitrag des Zooplanktons zum vertikalen Kohlenstoff-Fluss im Weißen Meer und der Karasee abzuschätzen. Die Ergebnisse zeigen starke regionale und saisonale Schwankungen im Kohlenstoffeintrag durch Kotballen in Abhängigkeit von Struktur und Dynamik der Planktongemeinschaften in den Untersuchungsgebieten. In den tiefen Bereichen des Weißen Meeres wurde ein maximaler Kohlenstoff-Fluss aus dem Oberflächenwasser (0-50 m) im Frühjahr beobachtet. Er erreichte 98 mg C_{org} m^{-2} Tag^{-1} zusammen mit einer starken Dominanz des großen, herbivoren arktischen Copepoden *Calanus glacialis* in der Oberflächenschicht. Im Sommer und Herbst verringerte sich der Fluss um ein bis zwei Größenordnungen in Abhängigkeit zur Wanderung dieses Copepoden in seine Überwinterungstiefen. Im Gegensatz dazu war die Kotballenproduktion in den flachen Küstenbereichen niedrig im Frühjahr, nahm während des Sommers allmählich zu und erreichte ihr Maximum von 138 mg C_{org} m^{-2} Tag^{-1} im Spätsommer im Übergang zum Herbst. Dieses saisonale Muster war im Einklang mit der saisonalen Häufigkeitsvariation der hauptsächlichen Kotballen-Produzenten, den kleinen borealen Copepoden *Arcartia bifilosa, Centropages hamatus* und *Temora longicornis.* In den ästuaren Bereichen der Karasee bestand der Kotballen-Fluss vorwiegend aus den Kotballen omnivorer Brackwasser-Copepoden. Er schwankte zwischen 35 mg C_{org} m^{-2} Tag^{-1} 1997 und 96 mg C_{org} m^{-2} Tag^{-1} 1999. In der zentralen Karasee mit ihrer typischen marinen Ge meinschaft wurde im Sommer eine Flussrate von 125 mg C_{org} m^{-2} Tag^{-1} erreicht. Die Ergebnisse unserer Abschätzung zeigen, dass sowohl im Weißen Meer wie in der Karasee der Kotballen-Kohlenstoff des Zooplanktons bis zu 30 % des Kohlenstoff-Flusses in bestimmten Jahreszeiten ausmachen kann.

INTRODUCTION

Zooplankton organisms are active agents, consuming organic matter produced in the pelagic zone through photosynthetic activity by phytoplankton. Therefore, they strongly modify the vertical carbon flux in the sea. On the one hand, zooplankton significantly reduces the amount of settling particulate organic matter by grazing on phytoplankton. On the other hand, it contributes to the flux by production of the faecal pellet material after digestive transformation. The faecal pellets are important components of settling matter and principal conveyors in the vertical flux of particulate and dissolved material (FOWLER & KNAUER 1986). Settling of faecal pellets is accompanied by multiple processes, such as re-ingestion or break-down by producers (LAMPITT et al. 1990), microbial degradation and release of particulate and dissolved matter into the water column. As life at the seafloor mainly depends on the input of organic material from the euphotic zone (GRAHL et al. 1999), vertical transport of pellets and processes of transformation of their organic content are of great importance.

In polar seas, pellet production is largely restricted to the summer season when phytoplankton is available and zooplankton organisms are feeding actively (HARGRAVE et al. 1994, GAYE-HAAKE et al. 2002). Unfortunately, seasonal variations of the zooplankton pellet flux remain poorly studied in the Arctic seas due to their restricted accessibility during most of the year, and especially in the winter. Other reasons are insufficient knowledge on seasonal variations of the phyto- and zooplankton communities in the Arctic seas and lack of information on pellet transformation during sinking to the bottom. Consequently, the linkage between biological and biogeochemical processes and contribution of the pelagic inhabitants to the sedimentation remain largely unknown.

The major goal of this paper is to improve our understanding of contribution of zooplankton to the vertical carbon fluxes in the White and Kara seas using the results of our seasonal observations on the zooplankton community structure in both seas and experimental studies of the faecal pellet production of zooplankton in the White Sea. The Kara and White seas are inhabited by zooplankton fauna of low diversity. In both seas, a few zooplankton species contribute up to 95 % of the zooplankton biomass and abundance and, therefore, hold a key position in the pelagic food web (PERTZOVA 1980, VINOGRADOV et al. 1994, PERTZOVA & PRYGUNKOVA 1995, FETZER et al. 2002, DEUBEL et al. 2003, PERTSOVA & KOSOBOKOVA 2003, 2005, KOSOBOKOVA & PERTZOVA 2005, HIRCHE et al. 2006). The composition of the key species in these seas is quite similar, and therefore our major approach was to use results of experimental studies conducted at the White Sea for assessing the pellet contribution of the Kara Sea zooplankton, where it was difficult to carry out the experimental studies.

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MATERIAL AND METHODS

In order to identify and quantify zooplankton pellets in the water column, experimental studies of feeding of the dominant copepod species were carried out in the coastal waters of the White Sea at the biological station, RAS, Cape Kartesh, 66°20.2 N, 33°38.9 E (for further details, see MARTYNOVA 2003, 2005). Three abundant boreal copepod species *Acartia bifilosa, Centropages hamatus,* and *Temora longicornis* were used for feeding experiments. Copepods were collected from the surface water layer 0-10 m, sorted out immediately after collection, and transferred into 150 ml glass vials filled with pre-filtered seawater. After 24 h incubation in the laboratory, their pellets were gently collected from the bottom of the vials, enumerated and measured under a stereomicroscope. Pellet organic carbon (C_{org}) and nitrogen (N) content was measured using pre-weighed pre-combusted GF/C filters dried at +50 °C for 24 hours. Carbon and nitrogen content was measured by standard methods with Carlo Erba NA 1500 Analyzer at the AWI, Bremerhaven. The gut evacuation rate (GER) was measured for all three target species (for details, see MARTYNOVA & BATHMANN, submit.).

The study of the White Sea zooplankton community structure was carried out in the shallow and deep regions. The shallow-water communities were studied in the Chupa Inlet of the Kandalaksha Bay. Zooplankton was collected from the upper 0-10 m water layer with a Juday net (mouth opening 37 cm, mesh size 200 µm) with 10 d intervals throughout the ice-free season, from 05 June to 11 September 2002. The structure of communities of the deep regions was studied at three stations, A, B, and C, along a transect crossing the Kandalaksha Depression, the area of the maximum depths of the White Sea (270-340 m). Zooplankton was collected in 1999 and 2001 during different seasons from early spring (end of May) to late autumn (end of November, for the expeditions list, see PERTZOVA & KOSOBOKOVA 2003, 2005). At all the three stations stratified sampling of standard water layers 0-10, 10-25, 25-50, 50-100, 100-150, 150-200, 200 m to bottom was carried out using a closing Juday net (mouth opening 37 cm, mesh size 200 μm).

The data on the zooplankton community structure of the Kara Sea were collected in the southern, fresh-water influenced, and central open, more marine, area, during several summers by Russian-German expeditions between 1997 and 2001 (for the expeditions list and sampling procedures, see HIRCHE et al. 2006).

Zooplankton samples were preserved in 4 % formaldehyde. All meso-zooplankton organisms (>1 mm) from the samples were counted and identified to the species level under a stereo microscope. For the small plankton (<1 mm), an aliquot (1:8, 1:10) of the sample was counted after fractionation with a stempel-pipette.

The impact of carnivorous zooplankton on copepods and other plankters was assessed from experimental observations on feeding of three species of hydromedusae, *Aglantha digitale, Bougainvillia superciliaris,* and *Sarsia tubulosa* (PRUDKOVSKY 2006). The live material was collected in vicinity of the White Sea biological station of Moscow State University (MSU) (Kandalaksha Bay) in June 2003 and 2004. Additionally, formalin preserved zooplankton samples collected during the 49 cruise of RV "Professor Schtockmann" in the Dvina and Onega bays in August 2001 were used to study feeding spectra of the target hydromedusas. All specimens of the three species were measured under a stereomicroscope, and their gut content was examined after dissection. Carbon content of two species, A. *digitale* and *S. tubulosa,* was measured using the C/N analyzer VARIO EL III at the analytical laboratory of the Otto Schmidt Laboratory (OSL, St. Petersburg).

The potential faecal pellet production was calculated using original data on abundance and stage composition of dominant zooplankton organisms. For shallow-water regions of the White Sea, the pellet production was assessed for the upper 0-10 m water layer using data on the pellet organic carbon content (C_{org}) and gut evacuation rates (GER) of the three boreal copepod species *Acartia bifilosa, Centropages hamatus,* and *Temora longicornis* from MARTYNOVA & BATHMANN (submit.). For the deep regions of the White Sea and two different regions of the Kara Sea, potential fecal pellet production was assessed for the upper 0-50 m water layer using original data on abundance and stage composition of zooplankton and literature data on GER and pellet size (ARASHKEVICH & SERGEEVA 1991). The assessments were made taking into consideration the impact of predators, and assuming that food was not a limiting factor for grazers. The published conversion rates (C_{org} = 26.8 % dry weight) were applied to calculate carbon content of pellets of arctic copepods *Calanus glacialis* and *Metridia longa* and the arctic-boreal *Pseudocalanus minutus* (URREERE & KNAUER 1981).

RESULTS AND DISCUSSION

Examination of morphology of the faecal pellets during this study indicated that pellets of different zooplankton organisms differ in size and shape, and their color depends on the consumed food. The pellet size correlates positively with the individual plankter's body size (for details, see MARTYNOVA 2003). The gut evacuation rate (pellet production time) varied from 18 to 38 min in copepodite stages CIII to CVI of *Acartia bifilosa,* from 30 to 60 min in CIII to CVI of *Centropages hamatus,* and from 28 to 50 min in CIII to CVI of *Temora longicornis.* According to our measurements, pellets of omnivorous boreal copepods *Acartia bifilosa, Centropages hamatus,* and *Temora longicornis,* pellets contained only 50 % of the organic carbon compared to the carbon content of seston. The nitrogen content of pellets was low and resulted in a 20 % higher C/N ratio of pellets compared to natural seston (MARTYNOVA & BATHMANN, submit.). As carbon content of pellets produced by different plankters was substantially different (MARTYNOVA 2003), we used species-specific pellet size, dry weight, and carbon content from MARTYNOVA & BATHMANN (submit.) for calculating the pellet carbon fluxes.

The comparative description of structure of the zooplankton communities of the shallow and deep regions of the White Sea was presented by PERTZOVA & PRYGUNKOVA (1995) and PERTZOVA & KOSOBOKOVA (2003, 2005). These authors showed that the coastal regions of the White Sea with depths <50 m are characterized by strong variation of the zooplankton composition during the year resulting in dramatic seasonal variation of abundance and biomass. In the summer, small-sized copepod species of the boreal thermophilic assemblage and meroplankton (larvae of benthic animals) build most of the zooplankton stock in these regions (PERTZOVA & PRYGUNKOVA 1995). The dominant copepod species are the boreal omnivoures *Temora longicornis, Centropages hamatus, Acartia longiremis/bifilosa,* and the arctic-boreal filter-feeding *Pseudocalanus minutus.* In the winter, the first three species and meroplankton disappear from the water column almost completely, resulting in dramatic decrease of the zooplankton abundance, and in 10 to 20-fold decrease of biomass in the coastal regions (PERTZOVA & KOSOBOKOVA 2003, 2005).

Table 1 presents our original data on variation of abundance of the three boreal copepod species in area of our studies, the shallow-water Chupa Inlet, Kandalaksha Bay, in 2002. These data confirm general conclusions on the zooplankton dynamics in the coastal zone of the White Sea (PERTZOVA & KOSOBOKOVA 2003, 2005). They demonstrate that during the ice-free season, from June to September, abundance of *Acartia bifilosa* varied within two orders of magnitude, while in *Temora longicornis* and *Centropages hamatus* abundance variations reached three orders of magnitude. The calculated daily pellet carbon production of these species, subsequently, also showed a broad range of variability (Tab. 1). The lowest values were observed at the beginning of June, when abundance of all the three boreal species was very low. The maximum pellet production reached 13.7 mg C_{org} m^{-2} day^{-1} by the end of August, coinciding with the seasonal abundance maximum of these copepods (Tab. 1).

Contrary to the shallow-water regions, deep regions of the White Sea are characterized by all year-round dominance of the large cold-water arctic and arctic-boreal zooplankton species and negligible contribution of small-sized species of the boreal assemblage (PERTZOVA & KOSOBOKOVA 2003). In terms of abundance and biomass, dominant components of this community are large filter-feeding copepods *Calanus glacialis,* and *Metridia longa* and a smaller *Pseudocalanus minutus.* Seasonal variability of the total zooplankton biomass in the entire water column of the deep region is only twofold in comparison to 10 to 20-fold variations in the coastal waters (PERTZOVA & KOSOBOKOVA 2005). At the same time, seasonal vertical migrations of the arctic and arctic-boreal copepods result in a strong vertical translocation of the zooplankton stock within the water column during the annual cycle (Fig. 1). Consequently, seasonal variations of the zooplankton abundance and biomass in the particular water layers are very strong (PERTZOVA & KOSOBOKOVA 2005). Thus, the biomass of the upper 0-10 m water layer varied almost 150-fold from the spring to fall of 1999 (Fig. 1).

Date	*Acartia bifilosa* PD	*Acartia bifilosa* PC_{org}	*Temora longicornis* PD 1	*Temora longicornis* PC_{org}	*Centropages hamatus* PD	*Centropages hamatus* PC_{org}	Total PC_{org} 10 d
05 June	1	0.02	0	0.00	0	0.00	0.2
14 June	49	0.33	0	0.00	11	0.04	3.7
22 June	706	2.68	0	0.00	2	0.01	26.9
27 June	218	2.00	0	0.00	16	0.08	20.8
11 July	65	0.45	12	0.10	1300	2.79	33.4
22 July	144	1.40	48	0.34	304	1.25	29.9
1 Aug	146	0.36	448	0.88	2161	5.35	65.9
11 Aug	79	0.41	329	1.95	948	3.24	56.0
22 Aug	301	1.64	718	2.32	1023	2.75	67.1
31 Aug	180	0.75	930	4.22	2541	8.90	138.7
11 Sept	757	4.07	1337	5.69	990	3.95	137.1
Total PC_{org}, from 5 June to 21 September, 2002							579.7

Tab. 1: Chupa Inlet, Kandalaksha Bay of the White Sea. Population density of the dominant boreal copepod species, ind m^{-3} (PD) and daily pellet carbon flux from the upper 0-10 m water layer, mg C_{org} m^{-2} day^{-1} (PC_{org}).

Tab. 1: Chupa-Einlass, Kandalaksha-Bucht, Weißes Meer. Populationsdich-te der dominanten, borealen Copepoden-Spezies als Individuen m^{-3} = PD; PC_{org} = Kohlenstoff-Fluss aus Kotpillen aus dem Oberflächenwasser 0-10 m (mg C_{org} m^{-2} day^{-1}).

Both in the coastal and deep regions, herbivorous and omnivorous copepods experience pressure of the plankton predators (chaetognaths, medusas and ctenophores), which reduce their abundance and, consequently, the number of the pellets produced. Our results indicate that impact of hydromedusae is at maximum during the spring, when it reaches 9 to 16 % of the total prey abundance per day (Tab. 2).

The results of calculations of the potential fecal pellet production by dominant copepod species in the deep regions of the White Sea (Fig. 1) show that it was at maximum in early spring, end of May to beginning of June. During this period almost entire population of predominantly herbivorous

Prey organisms	*A. digitale*	*B. superciliaris*	*S. tubulosa*
Pseudocalanus minutus nauplii	18	17.6	19
Pseudocalanus minutus copepodites	30	1.2	19.4
Oithona similis	33.4	41.6	11
Microsetella norvegica	+	13	6.5
Acartia spp.	+	+	20
Temora longicornis	+	+	+
Centropages hamatus	+		+
Oncaea borealis	+	+	+
Metridia longa	+		
Calanus glacialis	+	+	+
Calanus glacialis ova	5.5		
Unidentified Copepoda	8.3	+	4.7
Evadne nordmanni	+	+	
Podon leuckarti	+	+	
Euphausiacea larvae	+		
Gammaroidea			+
Cirripedia larvae	+	22.1	12.7
Polychaeta larvae	+	+	
Mollusca larvae	+	+	+
Bryozoa larvae	+		
Fritillaria borealis	+	+	
Parasagitta elegans			+
Harpacticoidae	+	+	+
Polychaeta			+
Tintinnida	+		+
Littorina littorea ova	+		+

Tab. 2: : Feeding spectra of hydromedusae species and relative abundance (%) of zooplankton taxa in the medusae guts in June 2004.

Tab. 2: Fraßspektrum der Hydromedusen-Arten und relative Häufigkeit (%) der Zooplankton-Taxa im Medusendarm im Juni 2004.

copepod *Calanus glacialis* concentrated near the surface (Fig. 1), and the pellet flux from the upper 50 m water layer reached 98 mg C_{org} m^{-2} day^{-1} (Fig. 1). At sinking rates of 80 m day^{-1} reported by ARASHKEVICH & SERGEEVA (1991), this material could reach the bottom of the White Sea within two days. In mid-summer, early August, when *Calanus glacialis* descended from the upper layers and was replaced by the smaller species *Pseudocalanus minutus* and *Metridia longa,* the flux decreased by one order of magnitude to 5-7 mg C_{org} m^{-2} day^{-1} (Fig. 1). In fall, late November, feeding activity of the planktonic herbivores decreased significantly. They descended into the deep-water layers (Fig. 1) and, therefore, the pellet flux

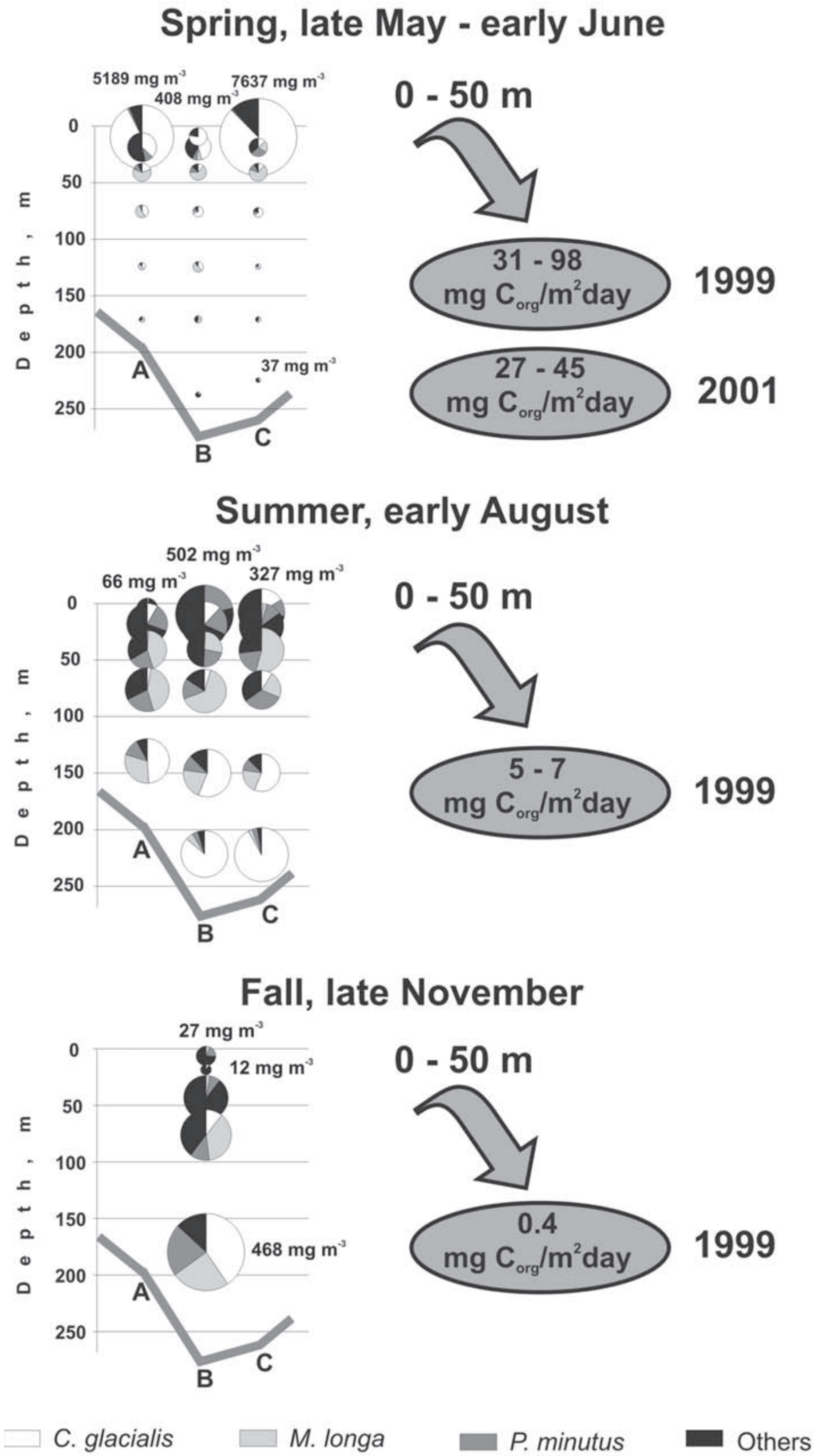

Fig. 1: Deep stations A, B, C in the Kandalaksha Bay of the White Sea. Vertical distribution of zooplankton biomass (left) and daily pellet carbon flux (mg C_{org} m^{-2} day^{-1}) from the 0-50 m water layer in spring, summer, and fall. Broken lines A-B-C show the bottom profile.

Abb. 1: Vertikale Verteilung der Zooplankton-Biomasse (links) und der Kohlenstoff-Fluss in Kotballen (mg C_{org} m^{-2} Tag^{-1}) aus 0-50 m Tiefe in Frühling, Sommer und Herbst an den Tiefwasserstationen A, B, C in der Kandalaksha-Bucht, Weißes Meer. Linien A-B-C beschreiben das Bodenprofil.

hardly reached 0.4 mg C_{org} m^{-2} day^{-1} (Fig. 1).

The pelagic system of the Kara Sea is shaped by freshwater input in its southern estuarian zone (HIRCHE et al. 2006) and by the Barents Sea waters entering via the Kara Strait from the west and via deep troughs from the north. The brackish-water community in the estuarian zone represents a combination of the self-sustaining populations of the brackish-water species in the upper low-saline layer and the marine fauna trapped in the counter current below the pycnocline (HIRCHE et al. 2006). The communities over the rest of the sea are marine, they are similar to the communities over the deep regions of the White Sea.

Calculation of the potential faecal pellet production of the Kara Sea zooplankton was carried out for the estuarian and deep open-sea regions for the summer season. In the estuarine zone, the pellet flux was mostly formed by pellets of brackish-water omnivorous copepods. It varied from 35 mg C_{org} m^{-2} day^{-1} in 1997 to 96 mg C_{org} m^{-2} day^{-1} in 1999 due to quite different abundance of two major pellet producers, the omnivorous copepods *Drepanopus bungei* and *Limnocalanus macrurus* (Tab. 3). In the central Kara Sea with typical marine community, the daily flux reached 125 mg C_{org} m^{-2} day^{-1}. In this region, the herbivorous copepods *C. glacialis* and *P. minutus* were the major pellet producers, similar to the deep open regions of the White Sea in the spring (Tab. 3).

CONCLUSION

The results of this study indicate that the faecal pellet production by zooplankton in the Arctic seas is strongly related to the structure and seasonal state of the zooplankton communities. The pellet production has a pronounced seasonal pattern due to seasonal variations of the composition and spatial distribution of zooplankton. The seasonal patterns may differ considerably between different regions of the same sea due to regional differences in the zooplankton dynamics. In the open deep regions of the White Sea, with strong predominance of large arctic herbivorous copepods, the maximum pellet carbon flux was observed in the spring, when these copepods fed near the surface and consumed the spring phytoplankton bloom. In the summer and fall, carbon flux decreased dramatically by one to two orders of magnitude due to downward vertical migration of herbivores to their over-wintering depths. In the shallow coastal regions, pellet production had a different pattern. It was low in the spring, gradually increased throughout the summer, and reached its maximum by beginning of autumn, when major producers of pellets, small boreal copepods, reached their highest abundance in the water column (Tab. 1). The seasonally restricted occurrence of species of the boreal assemblage, thus, was an important factor shaping contribution of the zooplankton pellet material in the coastal zone.

Regional variations of the faecal pellet fluxes in the Kara Sea were also correlated with the structure of the zooplankton community (Tab. 4). The seasonal patterns of pellet production were not assessed for this sea due to the absence of seasonal observations on the zooplankton composition. However, data from the White Sea suggest that in the Kara Sea seasonal variations in the zooplankton community should also be reflected in its contribution to the matter flux in the pelagic.

With sinking rates of 2.5 m h^{-1} or 60 m day^{-1} (MARTYNOVA 2003) pellets of the boreal copepods could reach the seafloor within one day in well-mixed coastal areas of the White Sea. The microbial destruction seems to hardly take place during such a short sinking time because of low temperature below 25 m depth (BABKOV 1998, PANTIULIN 2003). In the deep regions with depths of 150-250 m, zooplankton pellets may reach the

Region	Southern Sea: freshwater influenced area, including river mouths, 7-40 m bottom depth		Central Sea: east of Yamal Peninsula, 60-80 m bottom depth
Expedition, year	BP-1997	BP-1999	DZ-2000
Calanus glacialis	9.6 (1.4)	3.5 (2.3)	112.1 (5.1)
Drepanopus bungei	24.1 (58.7)	8.7 (44.7)	9.7 (2.6)
Limnocalanus macrurus	< 0.1	83.0 (10.6)	< 0.1
Metridia longa	< 0.1	< 0.1	< 0.1 (0.3)
Pseudocalanus acuspes/minutus	0.34 (7.1)	0.03 (3.5)	3.0 (11.4)
P. major	0.2 (3.5)	0.17 (12.6)	< 0.1 (0.5)
Total fecal pellet carbon, mg C_{org} $m^{-2}day^{-1}$	34.9	95.6	124.8

Tab. 4: : Daily faecal pellet production (mg C_{org} m^{-2} day^{-1}) and relative abundance (% of total abundance, in brackets) of zooplankton in different Kara Sea areas in summer. BP = RV "Boris Petrov"; DZ = RV "Dalnie Zelentsye"

Tab. 4: Tägliche Kotpillen-Produktion (mg C_{org} m^{-2} day^{-1}) und relative Häufigkeit (% der Gesamthäufigkeit in Klammern) des Zooplankton in verschiedenen Gebieten der Karasee im Sommer. BP = RV „Boris Petrov"; DZ = RV „Dalnie Zelentsye".

Species	*Bougainvillia superciliaris**		*Sarsia tubulosa**		*Aglantha digitale***	
	number of consumed prey	consumed biomass C_{org} (µg)	number of consumed prey	consumed biomass C_{org} (µg)	number of consumed prey	consumed biomass C_{org} (µg)
Daily ration	57.6 ± 34.6	50.2 ± 41.3	91.5 ± 77.2	103 ± 43.4	5.9 ± 3.6	5.9 ± 3.8
Daily impact (%)	1	1.1	9.1	15.8	3.3	5.1

Tab. 3: : Mean daily rations (No. of prey ind. day^{-1} and μg C_{org} day^{-1}) and daily impact on copepod populations (prey abundance or biomass consumed during 24 h: total prey abundance or biomass, %) of the three hydromedusae species in the White Sea in June 2004. * = calculated for the upper 10 m, ** = calculated for the entire water column.

Tab. 3: Einfluss dreier Hydromedusenarten auf die Copepodenpopulation im Weißen Meer. Durchschnittliche tägliche Nahrung (als Individuenzahl je Tag bzw. Copepodenbiomasse in μg C_{org}) und täglicher Einfluss der drei Hydromedusenarten auf die Copepodenpopulation (bezogen auf Nahrungsindividuen bzw. auf Biomasse) . * = berechnet für die oberen 10 m Wasser-säule; ** = berechnet für die gesamte Wassersäule.

seafloor within two or three days if they sink directly (Arashkevich & Sergeeva 1991). However, in the stratified areas of the White and Kara seas with pronounced pycnocline, direct sinking may not take place. Consequently, the processes of sinking of pellets, their destruction and degradation require further investigation to understand their fate in such areas.

Our assessment of the potential zooplankton pellet carbon in both seas showed that zooplankton can contribute up to 30 % to the total carbon flux during particular seasons. Such a value is in good agreement with results based on data from sediment trap collections (Gaye-Haake et al. 2002, Novigatsky, pers. comm.).

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