

Copepod faecal pellets and their role in organic matter flux in the White Sea

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The faecal pellets of zooplankton species, especially copepods, play a significant role in organic and inorganic matter flux in marine and freshwater ecosystems (Fiadeiro, 1980; Summerhayes & Thorpe, 1996). The main parameters determined the pellets' amount are the pellet size, egestion time, sinking velocity and organic carbon content (Arashkevich & Sergeeva, 1991).

The main ideas of the present investigation are to determine some parameters of pellets, produced by the common boreal copepod species, and to evaluate the pellet carbon flux in the White Sea.

Materials and methods

The experiments were conducted on the White Sea Biological Station in 2001-2002 and during the 52nd cruise of RV "Ivan Petrov". Seston samples were taken every 7-10 days from June through September, 2002, at 0 and 5 m depth. The experiments were performed with animals of three boreal species common in the White Sea - *Acartia bifilosa* (Giesbrecht, 1882), *Centropages hamatus* (Lilljeborg, 1853) and *Temora longicornis* (O.F. Müller, 1792), and copepods of the arctic *Pseudocalanus* species. Fresh taken zooplankton sample (0-10 m) was immediately transported to the shore laboratory. Copepods were sorted by species and stage and then adapted to the experimental temperature during 18-24 hours in the filtered seawater (GF/C filters). Duration of experiment was 24 h. Copepods were maintained in the 150 ml glass vials in filtered seawater (76 µm mesh gauze) taken from 5-7 m depth. The average egestion time was calculated as the quotient obtained dividing the experiment duration by the number of pellets. In the end of the experiment pellets were gently picked up with glass pipette and then placed into Petri dishes with filtered seawater (GF/C filter). One or two drops of alcohol solution of KJ were then added to colour the pellets. In 3-4 minutes pellets were measured and placed in the clean filtered seawater (GF/C filters). Also the length of copepod prosome was measured. Volume of pellet was cal-

culated as cylinder volume, where the pellet width was the diameter of cylinder. The length of pellets used to determine their sinking velocity was not less than 70-80 μm . Measured pellets one by one were gently placed into the glass graduated vial with filtered seawater with constant temperature. After sinking to 50 mm depth the time of passing through the first and the second 100 mm water column was recorded. Not less than 30 measurements were performed for each stage of each species for two water temperatures (Table 1). Influence of species (*A. biflosa*, *C. hamatus* и *T. longicornis*) and stage on the pellet production time was calculated with two-way ANOVA.

Table 1. Size and sinking velocity of pellets

Species	Stage	Number of measurements	Pellet length, μm , ($m \pm s$)	Water temperature, $^{\circ}\text{C}$	Pellet sinking velocity, m/h ($m \pm s$)
<i>Pseudocalanus</i> spp.	CV	30	120 ± 7.53	8	2.34 ± 0.36
<i>Acartia biflosa</i>	females	32	115 ± 6.63	9	2.41 ± 0.36
		30	142 ± 10.74	7	2.42 ± 0.41
		30		12	2.69 ± 0.54
<i>Centropages hamatus</i>	females	29	168 ± 8.93	7	2.09 ± 0.25
		30		12	2.46 ± 0.27
<i>Temora longicornis</i>	females	30	122 ± 8.00	7	2.53 ± 0.31
		30		11	2.89 ± 0.39

Dry weight, organic C and N and content of chlorophyll *a* were measured in pellets and seston. Samples of seston or pellets were placed to the precombusted GF/C filters. Then filters were dried at $+50^{\circ}\text{C}$ during 24 h and then cooled with silica-gel to the constant weight. Content of organic C and N was measured by standard technique with Carlo Erba NA 1500 Analyser. Phytopigments were fixed in 90% aqua acetone. Their content was measured with fluorometer Turners Design TD-700 before and after acidification by standard technique. These analyses were carried out at Alfred Wegener Institute for Polar and Marine Research (Bremerhaven, Germany).

The pellet flux was calculated as the product of copepod population density and daily produced dry weight (organic carbon) of pellets (Table 2).

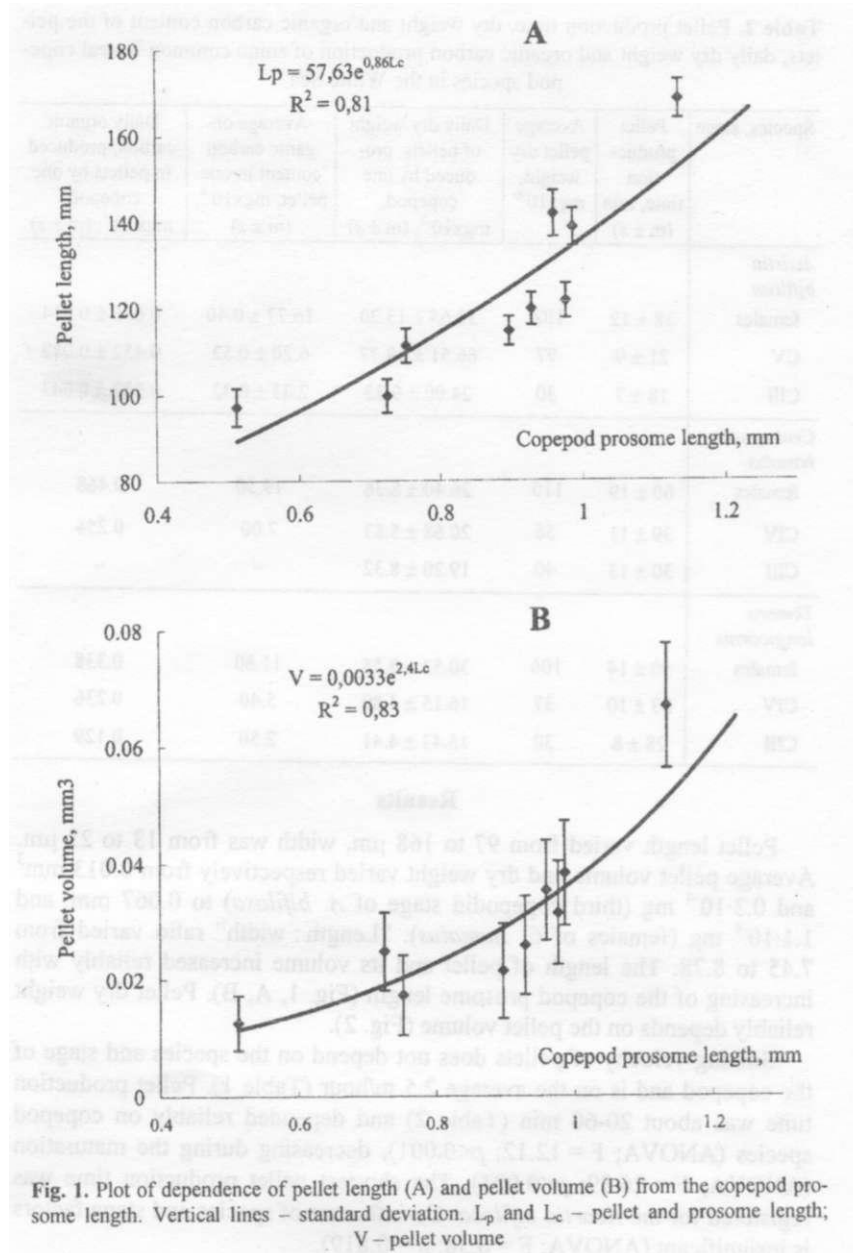
Table 2. Pellet production time, dry weight and organic carbon content of the pellets, daily dry weight and organic carbon production of some common boreal copepod species in the White Sea

Species, stage	Pellet production time, min (m ± s)	Average pellet dry weight, mgx10 ⁻⁶	Daily dry weight of pellets, produced by one copepod, mgx10 ⁻³ , (m ± s)	Average organic carbon content in one pellet, mgx10 ⁻⁶ , (m ± s)	Daily organic carbon, produced in pellets by one copepod, mgx10 ⁻³ , (m ± s)
<i>Acartia bifilosa</i>					
females	38 ± 12	102	38.65 ± 13.20	16.77 ± 0.40	0.636 ± 0.014
CV	21 ± 9	97	66.51 ± 18.77	6.20 ± 0.52	0.452 ± 0.082
CIII	18 ± 7	30	24.00 ± 9.33	2.33 ± 0.32	0.233 ± 0.043
<i>Centropages hamatus</i>					
females	60 ± 19	110	26.40 ± 8.36	19.50	0.468
CIV	39 ± 11	56	20.68 ± 5.83	7.00	0.258
CIII	30 ± 13	40	19.20 ± 8.32	–	–
<i>Temora longicornis</i>					
females	50 ± 14	106	30.53 ± 8.55	11.80	0.338
CIV	33 ± 10	37	16.15 ± 4.89	5.40	0.236
CIII	28 ± 8	30	15.43 ± 4.41	2.50	0.129

Results

Pellet length varied from 97 to 168 µm, width was from 13 to 23 µm. Average pellet volume and dry weight varied respectively from 0.013 mm³ and 0.3·10⁻⁴ mg (third copepodid stage of *A. bifilosa*) to 0.067 mm³ and 1.1· 10⁻⁴ mg (females of *C. hamatus*). "Length : width" ratio varied from 7.45 to 8.78. The length of pellet and its volume increased reliably with increasing of the copepod prosome length (Fig. 1, A, B). Pellet dry weight reliably depends on the pellet volume (Fig. 2).

Sinking velocity of pellets does not depend on the species and stage of the copepod and is on the average 2.5 m/hour (Table 1). Pellet production time was about 20-60 min (Table 2) and depended reliably on copepod species (ANOVA; F = 12.12; p<0.001), decreasing during the maturation (ANOVA; F = 26.89; p<0.001). The shortest pellet production time was registered for the *Acartia bifilosa*. Co-influence of species and stage factors is insignificant (ANOVA; F = 0.38; p = 0.819).



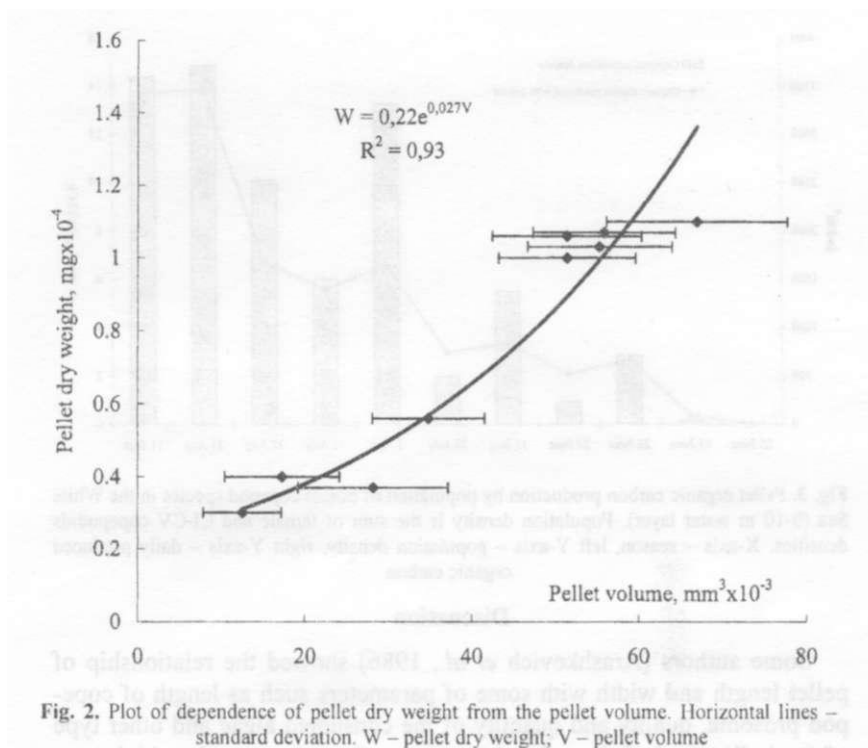


Fig. 2. Plot of dependence of pellet dry weight from the pellet volume. Horizontal lines – standard deviation. W – pellet dry weight; V – pellet volume

Chlorophyll *a* content in seston varied from $3.4 \cdot 10^{-3}$ to $27.8 \cdot 10^{-3}$ $\mu\text{g Chl. a}/\mu\text{g C}_{\text{org}}$, in pellets - from $0.14 \cdot 10^{-3}$ to $2.41 \cdot 10^{-3}$ $\mu\text{g Chl. a}/\mu\text{g C}_{\text{org}}$. The low content of phytopigments is usual to all the pellets and varies from 0.9% to 19.1% of its initial concentration in seston. The pellets also had very low organic N content as compared to seston. The C : N ratio for pellets varied from 6.6 to 20.5 (10.4 on the average); for seston - from 4.8 to 10.3 (7.1 on the average). Relative content of organic carbon in pellets varied from 2.8 to 18.3% of pellet dry weight, constituting on the average 9.7%. Organic carbon content in the seston was relatively high, i.e. $19.5 \pm 3.9\%$ of dry weight.

Population density of different stages of boreal copepod species reached up to 1987 ind/m³ in the inshore waters in the Kandalaksha Bay in August in 0-25 m depth water layer, in the offshore waters - about 100 ind/m³ (Prygunkova, 1977a, 1977b; original data of 1999-2000). Pellet flux, produced by *A. bifilosa*, *C. hamatus* and *T. longicornis*, in the small inlets reached up to 133 mg dry weight/m²/day, in the offshore waters - 0.5 mg dry weight/m²/day. Pellet organic carbon flux varied from $16.7 \cdot 10^{-3}$ to 13.7 mg C_{org}/m²/day (Fig. 3).

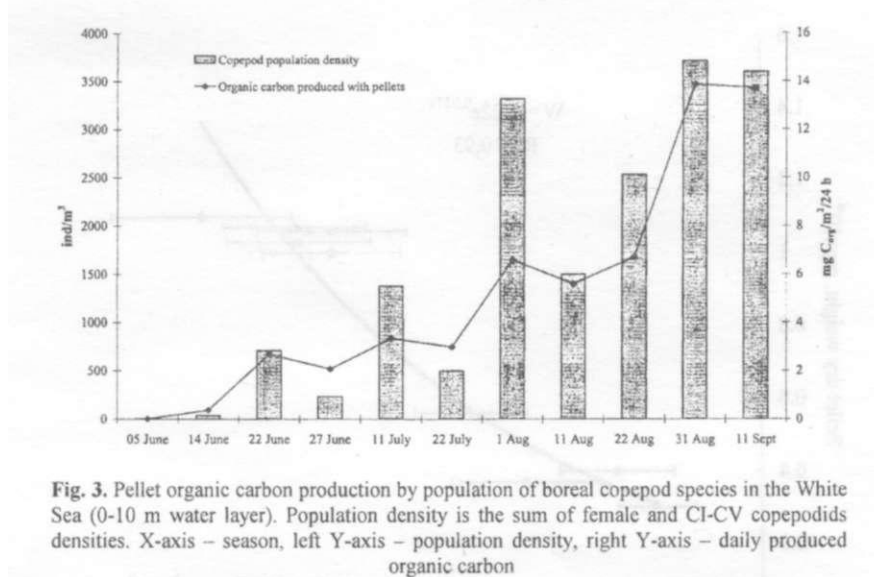


Fig. 3. Pellet organic carbon production by population of boreal copepod species in the White Sea (0-10 m water layer). Population density is the sum of female and CI-CV copepodids densities. X-axis – season, left Y-axis – population density, right Y-axis – daily produced organic carbon

Discussion

Some authors (Arashkevich *et al.*, 1986) showed the relationship of pellet length and width with some of parameters such as length of copepod prosome, quality and quantity of the consumed algae and other type of food. Copepods fed on the algae monoculture in normal or high concentration produced larger pellets than animals having insufficient food (Gaudy, 1974; Dritz, 1985). It goes without saying that the pellet size is "natural" in the case of using in experiments native seawater. In our experiments we used seawater taken from the depth where zooplankton was sampled. The variety of pellet length, volume and dependence of these parameters on the copepod prosome length are nearly the same as those characteristics given by the other authors (Corner *et al.*, 1986). The pellet "length : width" ratio has no relation with the copepod species. Thus, we cannot use this coefficient for the specification of pellets processing the *in situ* samples.

Dry weight of the pellet depends on its volume. The pellet density is equal for all the pellets and averages about 0.157 mg dry weight/mm³. This fact is proved by nearly the same sinking velocity of pellets - 2.5 m per hour or 60 m per day. On the Norwegian shelf sinking velocity of pellets is from 12 to 77 m per 24 hours (Wassmann *et al.*, 1999). Large pellets of

Calanus glacialis pass 84 m a day in the White Sea (Arashkevich & Sergeeva, 1991). It is necessary to say that we calculate the sinking velocity only under particular temperature conditions. For the more accurate calculation one has to take into account the different water density in changes of temperature and salinity, and also the possible influence of currents. Pellet production time, calculated under the experimental conditions, varied from 20 to 60 min. Mauchline (1998) points out the same order of magnitude for the other arctic species. The low pellet production time of *Acartia* in comparison to other copepods could be explained, on the one hand, by the size of the copepods (*A. bifilosa* has the smaller prosome length than *T. longicornis* и *C. hamatus*) and, on the other hand, by the fact that *Acartia* consumes more phytoplankton (Poulet, 1978). Gaudy (1974) pointed out that the herbivorous copepods had the lowest pellet production time than carnivorous and omnivorous animals.

The low content of chlorophyll *a* in pellets shows high destruction of phytopigments in the copepod gut. This is also proved by the brownish colour of produced pellets. Head (1988) showed, that in the pellets produced by *Pseudocalanus* sp. chlorophyll *a* content is 5-16% of the consumed chlorophyll *a*. Pellet production of organic carbon by the *Centropages* is 0.1-0.3 $\mu\text{g C}_{\text{org}}/\text{ind}/\text{day}$ in the Central Atlantic (Lane *et al.*, 1994).

In the White Sea the population of *C. glacialis* produces with pellets up to 180 mg dry weight/m²/day (Arashkevich, Sergeeva, 1991), the boreal copepods produces up to 133 mg dry weight/m²/day (original data). The dry weight of particulate organic matter varies from 0.2×10^3 to 10.9×10^3 mg/m³ during the iceless season, averaging 3.5×10^3 mg dry weight/m³ (Romankevich, Vetrov, 2001; Dolotov *et al.*, 2002; original data 2001-2002). So, the pellet flux averages about 0.13% of the particulate matter flux, reaching up to 1%. Organic carbon flux, calculated via its content in the faecal pellets, averages about 0.1% of the total C_{org} in particulate matter and 1% during the high population density of boreal species. In the Barents Sea in May faecal pellet organic matter flux averages 1.3% of the total organic matter flux (Wassmann *et al.*, 1999).

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