ISSN 0001-4370, Oceanology, 2017, Vol. 57, No. 1, pp. 122–129. © Pleiades Publishing, Inc., 2017.
Original Russian Text © A.F. Pasternak, A.V. Drits, M.V. Flint, 2017, published in Okeanologiya, 2017, Vol. 57, No. 1, pp. 137–145.

MARINE BIOLOGY

Feeding, Egg Production, and Respiration Rate of Pteropods *Limacina* in Arctic Seas

A. F. Pasternak*, A. V. Drits, and M. V. Flint

Shirshov Institute of Oceanology, Russian Academy of Sciences, Moscow, 117218 Russia

**e-mail: pasternakanna@hotmail.com*

Received September 23, 2016

Abstract—The feeding, egg production, and respiration rate of the dominant pteropod *Limacina helicina* have been studied in Russia's Arctic seas. The sinking rates of fecal pellets and dead individuals have been measured to estimate their role in vertical carbon flux. As has been shown, the rate of ecophysiological processes taking place in the pteropods is higher than that of copepods, the main consumers of phytoplankton. The gut pigment content in *Limacina* (3084 ng ind^{-1} as a maximum) was two orders of magnitude higher than in copepods. The egg production rate in *Limacina* even without feeding reached 4000 eggs ind^{-1} versus 350–450 egg ind^{-1} typical of the dominant copepods even with excess food. A close correlation between the pteropod feeding rate and individual body weight was observed for *Limacina* rather than a correlation with food concentration. The experimentally estimated sinking rate of *Limacina* fecal pellets was 270 m day^{-1}, higher than for most copepods. The sinking rate of dead pteropods reaches 2000 m day^{-1}. According to the literature, discarded mucous feeding nets sink at a rate of 80 to 1080 m day^{-1}. Evidently, pteropods play a significant role in biogeochemical cycles by accelerating sedimentation. High rates of all studied processes suggest that *Limacina* are an important component of plankton communities and play the most important role in trophodynamics at sites of their accumulation.

DOI: 10.1134/S000143701701012X

INTRODUCTION

Copepods are typically prevalent in abundance and biomass in pelagic communities of high latitudes, which has been convincingly demonstrated by many macroscale studies [1, 22]. As a rule, copepods play a leading role in grazing of phytoplankton, sedimentation and secondary production. However, the dominance of other, "ephemeral," groups of organisms, are frequently revealed in mesoscale studies due to the specific features of changes in the properties of the pelagic environment at distances of several kilometers to several tens of kilometers. Situations when pelagic pteropods take on the role of major phytoplankton consumers are observed in Arctic and Antarctic seas on a regular basis [7, 8].

An ever increasing number of studies recently deal with pteropods, in particular, their most abundant and widespread genus *Limacina*. These mollusks form local aggregations with high concentrations [3]; moreover, their role in grazing of suspended matter and in fluxes of organic matter in such aggregations can exceed the role of copepods [2] because of the high rate of food consumption [7, 8]. The second reason for researchers' increased interest in the ecology and physiology of thecosomatous pteropods is in possible alterations in their development caused by climate warming and forecasted decrease in seawater pH. Most of the current studies focus on the latter [11, 27], while the life cycle and ecological–physiological characteristics of pteropods are rather vague.

Limacina feed with a large mucous net trap [17]. The juveniles mainly consume phytoplankton but can also use other suspended particles (for example, nauplii and infusoria) of a suitable size [23]. Larger-sized *Limacina helicina* are regarded as omnivores [18]; in any case, juveniles are also able to switch from prevalently herbivorous to omnivorous feeding at a low phytoplankton concentration [15]. Mollusks lay eggs in mucous ribbons, as described for both closely related species *L. helicina* [24, 32] and *L. retroversa* [25]. A few estimates demonstrate the high fecundity of pteropods [24, 32]; however, daily egg production rate has not been studied.

Limacina fecal pellets and discarded mucous webs with particles stuck to them accelerate organic matter flux to depth [28, 30]. The shells of dead pteropods are also an important component of the vertical carbon flux in pelagic ecosystems [6, 35].

Quantitative estimates of energy fluxes on different spatiotemporal scales require the data on pteropod feeding, respiration, egg production, and fecal pellet sinking rate. As for the Arctic communities, only fragmented data on the *Limacina* diet [17, 23], feeding rate

of juveniles [2], and lipid content of their body [15] are available.

The main goals of the work were to

—study the feeding of *Limacina* (*L. helicina*) of different size;

—measure the respiration rate of *L. helicina*;

—assess the sinking rates of fecal pellets and dead mollusks; and

—assess the egg production rate in *Limacina*.

MATERIALS AND METHODS

The material was collected in several voyages to the Kara Sea, namely, cruises 59 and 63 of the R/V *Akademik Mstislav Keldysh* (September 2011 and September–October 2015) and cruises 125, 128, and 129 of the R/V *Professor Shtokman* (September 2013, August and September 2014, and October 2014, respectively). Figure 1 shows the positions of the stations where pteropods were sampled. The study was based mainly on *L. helicina* from the Kara and Laptev seas. Three stations used to analyze the trophic and production characteristics of *L. retroversa* were in the Barents Sea.

A Juday plankton net 37/50 was used for sampling (filter cone mesh, 180 μm) from the upper 0–20 or 0–50 m layers of the water column. The shell diameters of the sampled mollusks were measured. Feeding was assessed for pteropods of all sizes; other estimates were obtained only for adult animals with a size >3.5 mm. Animal weight was calculated as

$$DW = 0.257D^{2.141}, \text{ obtained for } L.\ helicina\ [15],$$

where DW is dry weight (mg ind^{-1}) and D, shell diameter (mm).

The diet of *Limacina* was assessed by microscopic examination of the contents of freshly sampled fecal pellets.

The feeding rate was estimated by a fluorescence technique according to the content of plant pigments (Chl *a* and pheopigments) in the gut and gut passage time [26]. In order to prevent food excretion from the gut, the animals were narcotized immediately after sampling with carbonated filtered seawater. The immobilized animals were sorted according to the shell size under a dissecting microscope and placed into 90% acetone for extraction of pheopigments. For each assay, 15–30 mollusks with shell diameters of <0.6 mm and 1–7 mollusks of large size were selected. Pigments were extracted at a temperature of 7°C for 24 h and quantified according to Strickland and Parsons [34]:

$$\text{chl}a = k(Fb - Fa)(V_{extr}/n)$$

$$\text{and pheopigment} = k(RFa - Fb)/(V_{extr}/n),$$

where k is the calibration coefficient of the measuring device; Fb and Fa, the fluorescence values of the analyte before and after acidification, respectively; R, the acidification coefficient; V_{extr}, the volume of acetone extract (mL); and n, the number of individuals in the extract.

The total content of pigments in the gut (G, ng chl *a*/ind) was calculated as [5]

$$G = (\text{chl}a + 1.51\,\text{pheopigment}).$$

In order to estimate the gut passage time, the freshly caught mollusks were placed into experimental 50–100 mL containers and examined every 5 min under a dissecting microscope. The time of excretion of the first three fecal pellets was recorded to obtain the mean interval between disposal of two successive pellets t. Then the fluorescence of pellets was recorded as well as the residual fluorescence of mollusk. The digestion time T was calculated as

$$T = Fl_{tot}/Fl_{pel}t,$$

where Fl_{tot} is the total fluorescence of plant pigments in the mollusk and the excreted pellets and Fl_{pel} is the content of pigments in pellets.

The daily Chl*a* consumption (I, ng Chl *a*/ind day) was calculated as

$$I = G \times 24/t.$$

Egg production. In order to assess the rate of egg production, adult *L. helicina* mollusks 4–4.5 mm in size were placed individually into 30–50-mL containers with filtered seawater. *Limacina* were kept in the dark at a temperature of 4–5°C. The presence of egg clutches and the number of eggs in a clutch was recorded twice a day, in the morning and evening. The rate of egg production was assessed for 2 days after sampling in 15 *L. helicina* individuals, and for comparison, in 17 *L. retroversa* individuals 1.3–2 mm in size. The preliminary data on the total *L. helicina* fecundity were obtained for two females during long-term keeping (16 days) in 50-mL containers. The water in containers was changed on a daily basis.

The sinking rate of fecal pellets and dead *Limacina* individuals were assayed during their sedimentation in a biological cylinder with a height of 25 cm and a volume of 1 L filled to the top with filtered seawater at a temperature of 5–6°C. Pellets or shells were gently placed in the surface layer and the time over which they covered the distance from surface to bottom was recorded. In total, sinking rate was measured 15 times for fecal pellets and 5 times for dead mollusks.

The respiration rate of *Limacina* with shell diameters of 3.5–4.5 mm was assessed in incubation experiments at a temperature of 6°C. Pteropods were placed individually in 30–40-mL containers. The oxygen content in water at the beginning and end of experiments, conducted for 20 h, was estimated by Winkler's method. In total, five experiments with *Limacina* were conducted with three controls (containers without animals).

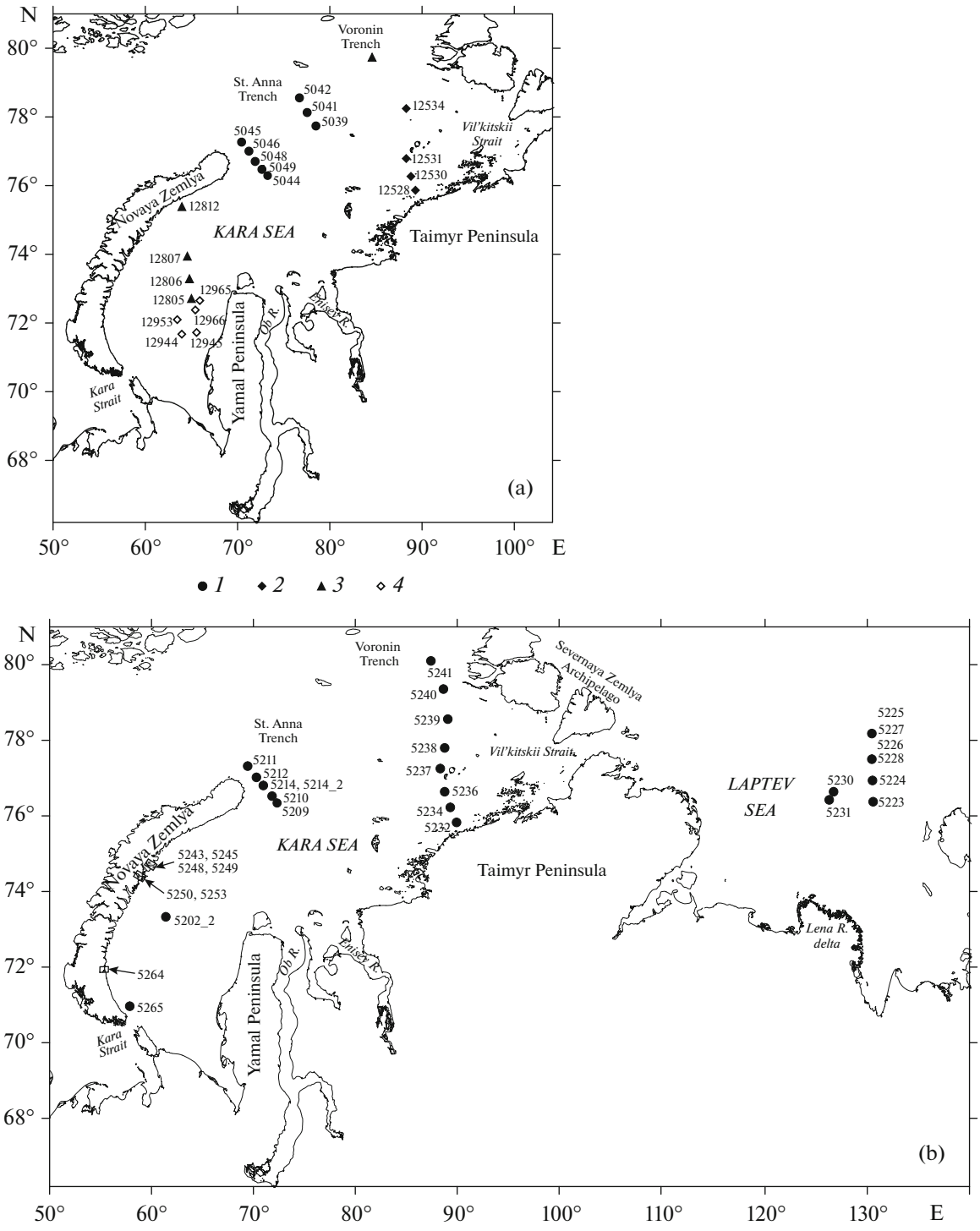

Fig. 1. Stations of *Limacina* sampling: (a) stations of (*1*) cruise 59 of R/V *Akademik Mstislav Keldysh* (2011), (*2*) cruise 125 of R/V *Professor Shtokman* (2013), (*3*) cruise 128 of R/V *Professor Shtokman* (2014), and (*4*) cruise 129 of R/V *Professor Shtokman* (2014) and (b) stations of (*1*) cruise 63 of R/V *Akademik Mstislav Keldysh* (2015).

RESULTS

Remains of diverse prevalently plant food were detected in fecal pellets of *Limacina* from the Kara, Barents, and Laptev seas (table). Tintinninds were regularly observed; however, no large prey was found except for a solitary finding a of copepod mandible. The size of the consumed particles varied from 2 to ~220 μm. The view of a *L. helicina* fecal pellet is shown in Fig. 2.

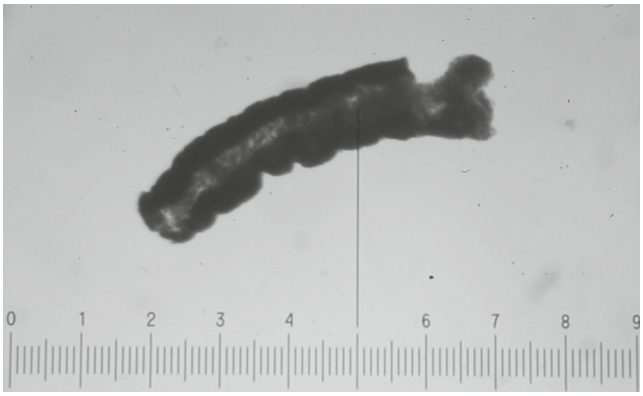

Fig. 2. View of *Limacina helicina* fecal pellet (small scale, 0.04 mm).

Feeding rate. The size (shell diameter) of *Limacina* individuals varied from 0.25 to 5.9 mm and the gut pigment content, from 0.14 to 3084 ng Chl*a* ind^{-1}. A high correlation between the content of pigments in the gut and the mollusk weight was observed (Fig. 3; R^2 = 0.976, $p < 0.0001$). For comparison, our data obtained in the 129th cruise of the R/V *Professor Shtokman* in the Barents Sea for another *Limacina* species, *L. retroversa,* are superimposed on this dependence. Addition of these data does not change the obtained dependence. The content of pigments in the gut can depend on the chlorophyll concentration in the environment; however, this concentration did not considerably change in the examined water layer, varying from 0.12 to 1.35 mg L^{-1}. Multiple regression has shown a pronounced dependence on weight ($\beta = 0.91$, $p < 0.0000$) and no correlation with the chlorophyll in the environment ($\beta = 0.06$, $p < 0.09$).

Identified food particles in fecal pellets

Food particle	Size	Rate
Small flagellates (*Micromonas* sp.?)	2 μm	+++
Archaemonas sp.	6–12 μm	++
Actinocyclus sp.	30 μm	+
Chaetoceros socialis	2–14 μm	++
Prorocentrum sp.	25–35 μm	+
Rhizosolenia setigera	30 μm	++
Thalassionema sp.	50–60 μm	+++
Thalassionema nitzschioides	40–100 μm	++
Thalassiosira sp.	20–30 μm	+++
Ceratium arcticum	200–300 μm (body of 50–60 μm)	++
Dinophysis acuminata	30–50 μm	+
Dinophysis rotundata	35–60 μm	++
Heterocapsa sp.	20 μm	+
Protoperidinium sp.	20–30 μm	+
Dicthyocha speculum	20–30 μm	++
Cysts	5–10 μm	++
Tintinnida	38–220 μm	++
Acanthostomella sp.	30–40 μm	++
Parafavella denticulata	130 μm	++
Copepod mandible	70 × 30 μm	1

(+) Observed at a rate of 1–25%; (++), 26–50%; and (+++) over 50% (based on examination of 20 fecal pellets); one solitary case is marked by 1.

The gut passage time for *Limacina* individuals with shell diameters of 4.5–5.5 mm was on average 14.4 ± 4.9 h, and with shell diameters of 1.3–1.6 mm, 8.7 ± 0.5 h. Taking into account the content of pigments and digestion time, each *Limacina* individual consumed 161 to 5149 ng Chl*a* day^{-1}.

Egg production. Similar to *L. retroversa, L. helicina* eggs are enclosed in a mucous envelope (Fig. 4). A *L. helicina* clutch typically contained 120–350 eggs with diameters of about 100 μm; each female laid one or two clutches daily. The average rate of egg-laying by *L. helicina* individuals with a size of 4–4.5 mm was 380 ± 142.4 eggs ind^{-1} day^{-1}, and by *L. retroversa* females with a size of 1.3–2 mm, 74.8 ± 39.7 eggs ind^{-1} day^{-1}. A long-term (16 days) observation of the egg-laying by *L. helicina* demonstrated that each female laid about 4000 eggs even in the absence of food. The rate of egg production decreased with time (Fig. 5) owing to a decrease in clutch size, most likely because of a deficiency in energy; however, one of the females continued egg-laying to the very end of the experiment (16 days). Thus, each individual in the absence of food is able to lay at least 4000 eggs. Veligers emerged on day 7.

Oxygen consumption by pteropods with shell diameters of 3.5–4.5 mm amounted to 220.25 ± 87.88 μL ind^{-1} day^{-1}.

The sinking rates of *L. helicina* fecal pellets and dead individuals measured in laboratory depended on the volume/weight of pellets ($R_S = 0.70$, $p = 0.004$) and mollusks ($R_S = 0.90$, $p = 0.037$). The correlation between the sinking rate of fecal pellets and their volume was described by a linear regression ($y = 11.28 + 0.08$, $R^2 = 0.50$, $n = 15$; Fig. 6). The correlation between the sinking rate of fecal pellets and their volume is also described by a linear regression ($y = 0.05 + 1.22$, $R^2 = 0.74$, $n = 5$; the corresponding figure is omitted because of the small number of replicates and the small range of weights). The sinking rate of fecal pellets in the studied volume range (0.001 to 0.02 mm^3) varied from 0.08 to 0.35 m min^{-1}, and the sinking rate of dead mollusks, from 1.3 to 1.9 m min^{-1} (at a weight of 5 to 15 mg).

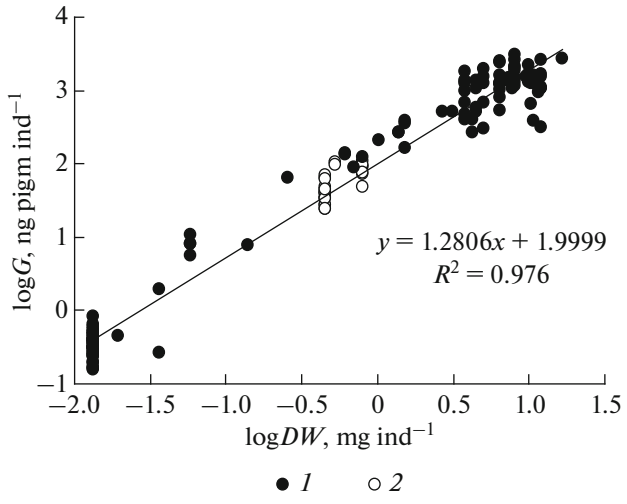

Fig. 3. Dependence of plant pigment concentration (ng Chl *a* ind^{-1}) in gut on *Limacina* dry weight (mg ind^{-1}): (*1*) *L. helicina* and (*2*) *L. retroversa*.

DISCUSSION

The obtained ecological and physiological characteristics of *L. helicina* suggest that the rates of the major studied processes are high and can be higher than in the other zooplankton consumers of phytoplankton in the Arctic. Omnivory, high feeding and reproductive rates, and rapid sinking of dead mollusks and their fecal pellets suggest that *Limacina* is among the key players in the organic matter flux in the pelagic zone when these mollusks are sufficiently abundant.

The contents of fecal pellets in general confirm the earlier data on *Limacina* omnivory [17, 23]. The shape of *Limacina* pellets excreted in the experimental containers considerably differed from the pellets described for Antarctic *Limacina* [28]. Nor did we observe the high share of animal food described by Gilmer and Harbison [17]. In this study, the authors assessed the share of animal food as 50%; this food contained tintinnids, small copepods, and *L. helicina* juveniles. While we also frequently observed tintinnids, copepod remains were recorded only once and *L. helicina* juveniles were absent altogether. Gilmer and Harbison [17] believe that large-sized *Limacina* individuals switch to prevalent consumption of mobile animal food after the bloom when phytoplankton abundance decreases. However, no bloom was either recorded during our field studies and the chlorophyll *a* concentration, an indicator of phytoplankton abundance, in the upper sea level was rather low, typically less than 1 mg chl *a* m^{-3}. Moreover, large adult individuals and juveniles were not observed concurrently in our samples; presumably, that is why any *Limacina* juveniles were undetectable in the food of large individuals. Perhaps, the difference between [17] and our data lies in the large 5–13-mm sizes of individuals analyzed by Gilmer and Harbison, different sampling seasons (midsummer), and the regional specificity of the *Limacina* diet (Barents and Greenland seas). The abundance of early developmental stages of both copepods and pteropods in midsummer could provide more favorable conditions for feeding on these objects.

The content of plant pigments in *Limacina* guts was high (maximum, 3084 ng ind^{-1}), two orders of magnitude higher than in other zooplankton organisms. Among copepods, the maximum values were observed in *Metridia longa* (to 39.3 ng ind^{-1}) and *Calanus glacialis* CV (to 24.4 ng ind^{-1}). As for the other plankton animals, the gut content was significant only in Decapoda larvae (22.6 ng ind^{-1}; our unpublished data). However, our experiments demonstrate that it takes much longer for *Limacina* to digest food than it does for copepods (8–14.5 versus 0.7–1.5 h) [33]; thus, the daily food consumption of *Limacina* and large-sized copepods does not differ as drastically as the food content in the gut, namely, by "only" one order of magnitude. The long digestion period characteristic of the Arctic *Limacina* species has been described by other researchers. In particular, it took *L. helicina* at least 10 h to clear the gut according to [17] or 13 h according to [12]. Of interest is the large difference in the estimates of the gut pas-

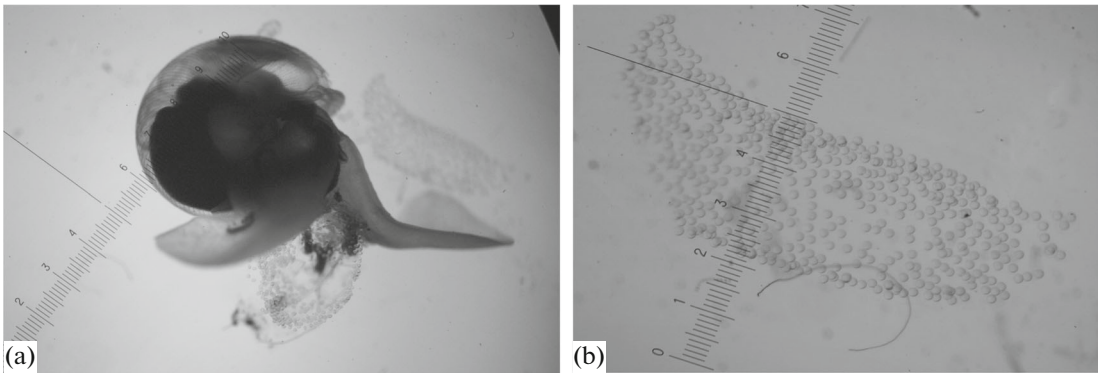

Fig. 4. (a) *Limacina helicina* laying eggs (small scale, 1 mm) and (b) *L. helicina* clutch (small scale, 0.1 mm).

sage time cited above and the data for the sub-Antarctic *L. retroversa,* amounting to 45 min [9] or 2 h [31]. The authors used another method for assessing the time of food passage: a decrease in the pigments in animals placed in filtered water [14]. However, it is unlikely that the difference between methods could yield such drastic differences. The same approach as in [14] was used earlier with *L. helicina* from the Kara Sea, and the gut passage time was assessed as 19 h [2], i.e., rather close to our estimates. This suggests that this characteristic may considerably vary between closely related pteropod species from different regions of the World Ocean. Different sizes of consumers, different food compositions, and different concentrations are among the factors that determine these distinctions. In our experiments, the gut passage time for small-sized *Limacina* (1.3–1.6 mm) was almost two times shorter than for larger individuals (4.5–5.5 mm). Bernard and Froneman [9] did not indicate exact *Limacina* sizes, stating that they were "medium-sized" (according to the classification by the authors, 0.5 to 1.5 mm). The daily consumption assessed by us and that reported by Bernard and Froneman [9] are rather close, up to 5104 ng ind^{-1} day^{-1} and an average of 4245 ng ind^{-1} day^{-1}, respectively.

Of interest is the close correlation between pteropod food consumption and weight, on the one hand, and the absence of a correlation between food consumption and concentration, on the other hand. This suggests two things. First, the mollusks were able to feed at a rate close to maximum even at a rather low concentration observed in our studies; otherwise, the differences in gut pigment content of mollusks with the similar weight would be more pronounced and the correlation between food consumption and body size/weight would not be as tight. Second, it is likely that even in the case of a vertically fractional sampling for chlorophyll (sampled every 10–15 m, sometimes even more frequent) and subsequent data integration for the layer used to sample *Limacina*, the resulting values are not completely adequate for assessing the feeding conditions in nature. Presumably, *Limacina* are able to find narrow layers with maximum food concentration and feed there at a maximal rate.

Having recalculated the food amount into carbon units with the help of a frequently used ratio, C_{org} : Chl a = 50, and having converted oxygen consumption into C_{org} units as well, we assessed that the mollusks spent approximately 60–70% of energy obtained from food for metabolism. Thus, 30–40% of energy remains for growth and egg production.

The *L. helicina* egg production rate and fecundity even in the absence of food is extremely high. Each female over 2 weeks laid approximately 4000 eggs in the absence of food. The *L. helicina* individuals sampled in the northern part of the Davis Strait showed an even higher fecundity (about 6000 eggs) [24]. These differences in fecundity estimates may stem from the

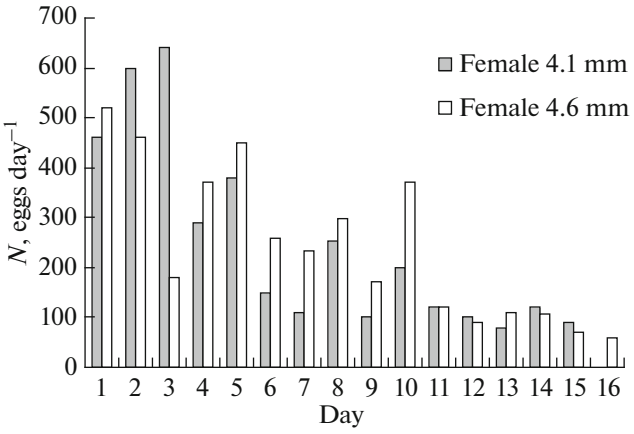

Fig. 5. Dynamics of egg-laying by two *Limacina helicina* females kept for long period without food.

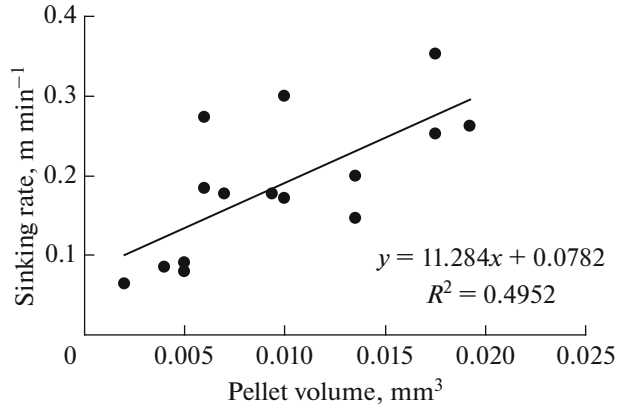

Fig. 6. Dependence of sinking rate of *Limacina helicina* fecal pellets on their volume.

egg counting technique. Lalli and Wells [24] directly counted eggs only in the first five clutches, measured the area of clutches, and multiplied this by the average number of eggs in clutch, which may give a certain error. However, the larger sizes of the females from the Davis Strait are a more likely reason for the observed difference. The diameters of their shells were 6–10 mm, while the mollusks we used to assess egg production and fecundity were considerably smaller (4–4.5 mm). Presumably, significantly lower estimates for the daily egg production rate of *L. retroversa* obtained in this study (75 eggs day^{-1}) versus 260 eggs day^{-1} [24] for *L. retroversa* are related to animal size. In our experiments, we used animals with shell sizes of 1.3–2 mm versus 1.8–2.0 mm in [24].

The fecundity of *L. helicina* can significantly exceed that of copepods laying eggs in water, which is 100–800 eggs over an entire life span [29]. However, very high values, up to 3800 eggs (*Calanus hyperboreus*) [13] and 1247 eggs (*C. glacialis*) [19], have been observed during long-term laboratory keeping of these

species with excess food. Note that these are the maximum values on the background of constant feeding over an entire life span, while the mean values for these copepods under the same conditions were 450 and 340 eggs, respectively.

Pteropods are known to play a significant role in biogeochemical cycles by accelerating sedimentation, especially due to rapidly sinking dead mollusks with aragonite shells, as well as their fecal pellets and mucous feeding nets with adhered suspended particles [11, 16, 20]. The sinking rate of *Limacina* pellets, which we assessed as 0.188 ± 0.087 m min^{-1}, i.e., 270 m day^{-1}, is somewhat lower than the value for the pteropod *Corolla spectabilis* (440–1800 m day^{-1}) [10], but it is still higher than in the majority of copepods [21]. According to Noji et al. [30], the mucous nets discarded by pteropods sunk at a rate of 80 to 1080 m day^{-1} (average, 301 m day^{-1}). The sinking rate of dead mollusks according to our estimates may be over 2000 m day^{-1}. Evidently, dead pteropods are a major contributor to the vertical flux of organic matter in Arctic seas by the end of the seasonal population cycle at sites of their mass accumulation [4, 11, 16, 35], where the pteropod biomass reaches 20–45 g/m^2 and the contribution to the total mesoplankton biomass exceeds 50–70% [3].

Thus, our study has shown that *L. helicina* in epicontinental Arctic seas are not only efficient consumers of suspended particles (phytoplankton), but also the producers of the most numerous offspring; note that their reproduction and the volume of consumed food are well synchronized. An unusually tight correlation between *Limacina* gut content and body weight, evident when examining field samples, drastically differs from the corresponding correlation typically obtained for copepods. The variability of the feeding rate is considerably higher among copepods. This implies that the contributions of copepods and pteropods to the plankton trophodynamics are significantly different: the vital activities of pteropods in dense local aggregations are much more synchronized compared to the copepod populations. Pteropods, with their high feeding and reproduction rates, and significant role in the sedimentation of organic matter, are a major contributor to the local mesoscale trophodynamics of plankton communities. Assessment of the role of pteropods in the fluxes of matter for the entire ecosystem of the basin requires knowledge about spatial characteristics and frequency of occurrence of the aggregations of these pelagic mollusks.

ACKNOWLEDGMENTS

The field work was supported by the Russian Science Foundation (project no. 14-17-00681), and the Russian Foundation for Basic Research (project no. 14-05-05003) and experiments on feeding rate assessment and data analysis, as well as the experiments on sinking rate and fecundity, were supported by the Russian Foundation for Basic Research (project nos. 16-04-00064 and 16-05-00037, respectively).

REFERENCES

1. N. M. Voronina, *Ecosystems of Pelagial of the Southern Ocean* (Nauka, Moscow, 1984) [in Russian].
2. A. V. Drits, E. G. Arashkevich, A. B. Nikishina, V. M. Sergeeva, K. A. Solovyev, and M. V. Flint, "Mesozooplankton grazing impact on phytoplankton in the northern regions of the Kara Sea in autumn," Oceanology (Engl. Transl.) **55**, 595–605 (2015).
3. M. V. Flint, S. G. Poyarkov, A. G. Timonin, and K. A. Soloviev, "The structure of the mesoplankton community in the area of the continental slope of the St. Anna Trough (Kara Sea)," Oceanology (Engl. Transl.) **55** (4), 583–594 (2015).
4. A. Accornero, C. Manno, F. Esposito, et al., "The vertical flux of particulate matter in the polynya of Terra Nova Bay. Part II. Biological components," Antarct. Sci. **15**, 175–188 (2003).
5. U. Båmstedt, D. J. Gifford, X. Irigoien, et al., "Feeding," in *ICES Zooplankton Methodology Manual*, Ed. by R. Harris, , (Academic, London, 2000), pp. 297–380.
6. N. Bednaršek, G. A. Tarling, S. Fielding, et al., "Population dynamics and biogeochemical significance of *Limacina helicina antarctica* in the Scotia Sea (Southern Ocean)," Deep Sea Res., Part II **59–60**, 105–116 (2012).
7. K. S. Bernard, PhD Thesis (Rhodes University, Grahamstown, 2006).
8. K. S. Bernard and P.W. Froneman, "Trophodynamics of selected mesozooplankton in the west-Indian sector of the Polar Frontal Zone, Southern Ocean," Polar Biol. **28**, 594–606 (2005).
9. K. S. Bernard and P.W. Froneman, "The sub-Antarctic euthecosome pteropod, *Limacina retroversa*: Distribution patterns and trophic role," Deep Sea Res., Part I **56**, 582–598 (2009).
10. K. W. Bruland and M. W. Silver, "Sinking rates of fecal pellets from gelatinous zooplankton (salps, pteropods, doliolids)," Mar. Biol. **63**, 295–300 (1981).
11. R. Collier, J. Dymond, S. M. Honjo, et al., "The vertical flux of biogenic and lithogenic material in the Ross Sea: moored sediment trap observations 1996–1998," Deep Sea Res., Part II **47**, 3491–3520 (2000).
12. S. Comeau, R. Jeffree, J.-L. Teyssié, et al., "Response of the Arctic pteropod *Limacina helicina* to projected future environmental conditions," PLoS One **5** (6), e11362 (2010). doi 10.1371/journal.pone.0011362
13. R. J. Conover, "Reproductive cycle, early development, and fecundity in laboratory populations of the copepod *Calanus hyperboreus*," Crustaceana **13**, 61–72 (1967).
14. H. G. Dam and W. T. Peterson, "The effect of temperature on the gut clearance rate constant of planktonic copepods," J. Exp. Mar. Biol. Ecol. **123**, 1–14 (1988).
15. C. Gannefors, M. Böer, G. Kattner, et al., "The Arctic sea butterfly *Limacina helicina*: lipids and life strategy," Mar. Biol. **147**, 169–177 (2005).

16. W. D. Gardner, M. J. Richardson, and W. O. Smith, "Seasonal patterns of water column particulate organic carbon and fluxes in the Ross Sea, Antarctica," Deep Sea Res., Part II **47**, 3423–3449 (2000).
17. R. W. Gilmer and G. R. Harbison, "Morphology and field behavior of pteropod mollusks: feeding methods in the families Cavoliniidae, Limacinidae and Peraclididae (Gastropoda: Thecosomata)," Mar. Biol. **91**, 47–57 (1986).
18. R. W. Gilmer and G. R. Harbison, "Diet of *Limacina helicina* (Gastropoda: Thecosomata) in Arctic waters in midsummer," Mar. Ecol.: Progr. Ser. **77**, 125–134 (1991).
19. H.-J. Hirche, "Egg production in the Arctic copepod *Calanus glacialis*: laboratory experiments," Mar. Biol. **103**, 311–318 (1989).
20. W. R. Howard, D. Roberts, A. D. Moy, et al., "Distribution, abundance and seasonal flux of pteropods in the Sub-Antarctic zone," Deep Sea Res., Part II **58**, 2293–2300 (2011).
21. P. D. Komar, A. P. Morse, L. F. Small, et al., "An analysis of sinking rates of natural copepod and euphausiid fecal pellets," Limnol. Oceanogr. **26**, 172–180 (1981).
22. K. N. Kosobokova and R. R. Hopcroft, "Diversity and vertical distribution of mesozooplankton in the Arctic's Canada Basin," Deep Sea Res., Part II **57**, 96–110 (2010).
23. C. M. Lalli and R. W. Gilmer, *Pelagic Snails: The Biology of Holoplanktonic Gastropod Mollusks* (Stanford University Press, Stanford, CA, 1989).
24. C. M. Lalli and F. E. Wells, "Reproduction in the genus *Limacina* (Opisthobranchia: Thecosomata)," J. Zool. London **186**, 95–108 (1978).
25. M. V. Lebour, "*Limacina retroversa* in Plymouth waters," J. Mar. Biol. Ass. U.K. **18**, 123–129 (1932).
26. D. L. Mackas and R. N. Bohrer, "Fluorescence analysis of zooplankton gut contents and investigation of diel feeding patterns," J. Exp. Mar. Biol. Ecol. **25**, 77–85 (1976).
27. D. L. Mackas and M. D. Galbraith, "Pteropod time-series from the NE Pacific," ICES J. Mar. Sci. **69** (3), 448–459 (2012). doi 10.1093/icesjms/fsr163
28. C. Manno, V. Tirelli, A. Accornero, et al., "Importance of the contribution of *Limacina helicina* faecal pellets to the carbon pump in Terra Nova Bay (Antarctica)," J. Plankton Res. **32** (2), 145–152 (2010).
29. J. Mauchline, *The Biology of Calanoid Copepods* (Academic, San Diego, 1998).
30. T. Noji, V. Ulrich, U. V. Bathmann, B. von Bodungen, et al., "Clearance of picoplankton-sized particles and formation of rapidly sinking aggregates by the pteropod, *Limacina retroversa*," J. Plankton Res. **19** (7), 863–875 (1997).
31. E. A. Pakhomov and R. Perissinotto, "Mesozooplankton community structure and grazing impact in the region of the Subtropical Convergence south of Africa," J. Plankton Res. **19**, 675–691 (1997).
32. M. A. Paranjape, "The egg mass and veligers of *Limacina helicina* Phipps," Veliger **10**, 322-326 (1968).
33. A. Pasternak, E. Arashkevich, M. Reigstad, et al., "Dividing mesozooplankton into upper and lower size groups: Applications to the grazing impact in the Marginal Ice Zone of the Barents Sea," Deep Sea Res., Part II **55**, 2245–2256 (2008).
34. J. D. H. Strickland and T. R. Parsons, "A practical handbook of seawater analysis. Pigment analysis," Bull. Fish. Res. Bd. Can. **167**, 1–311 (1968).
35. M. Tsurumi, D. L. Mackas, F. A. Whitney, et al., "Pteropods, eddies, carbon flux, and climate variability in the Alaska Gyre," Deep Sea Res., Part II **52**, 1037–1053 (2005).

Translated by G. Chirikova