Vol. 77: 125–134, 1991 | MARINE ECOLOGY PROGRESS SERIES Mar. Ecol. Prog. Ser. | Published November 26

Diet of *Limacina helicina* (Gastropoda: Thecosomata) in Arctic waters in midsummer

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ABSTRACT: The diet of *Limacina helicina* (Phipps) was examined from in situ collections of adult individuals made during 2 cruises in Arctic waters. Zooplankton, consisting mainly of small copepods and juvenile *L. helicina*, made up almost half of the mass of material found in digestive tracts of the 28 individuals examined. In contrast, these prey made up a much smaller fraction of the total mass of material in water samples and were only occasionally found as fragments in fecal pellets. A high percentage of diatoms appeared to pass intact through the guts of these pteropods. It appears that motile prey, including tintinnids, copepods, and juvenile *L. helicina*, are major constituents of the diet of adult *L. helicina* in midsummer in Arctic waters. This provides additional evidence that thecosome pteropods trap large, fast-moving prey in addition to feeding on fine suspended material.

INTRODUCTION

The euthecosome pteropod *Limacina helicina* (Phipps 1774), first described from Arctic waters by Martens (1675), is now known to be a common inhabitant of both the Arctic and the Antarctic (van der Spoel 1967, Bé & Gilmer 1977). Despite its abundance there and its excursions into lower latitudes, such as off the coast of California in the California Current (McGowan 1963), little is known of its biology and natural history.

Limacina helicina has a sinistrally coiled shell, which reaches a diameter of 14 mm. As with members of the Cavoliniidae, limacinids use a large, spherical external mucous web (Gilmer & Harbison 1986) to collect a wide range of different food types (Lalli & Gilmer 1989). These delicate webs are difficult to see. During the daytime, they can only be observed in strobe-lit photographs, or made visible by the gentle application of dye. These mucous webs have never been collected, so there is not even a qualitative description of their contents. The webs are difficult to collect, because euthecosomes are easily disturbed, and quickly withdraw or destroy them (Gilmer & Harbison 1986).

Dietary studies of thecosome pteropods are difficult since they do not feed normally in the laboratory. Previous analyses have largely been limited to gut content studies of preserved, net-collected specimens (e.g. Boas 1886, Meisenheimer 1905, Tesch 1913, Morton 1954, Mironov 1977, Richter 1977, Hopkins 1987, Ishumaru et al. 1988) or to studies of the composition of fecal pellets (Silver & Bruland 1981). Large metazoan prey such as veligers and juvenile gastropods, small crustaceans, and even eye parts from heteropods and alciopid worms have been found in their guts (see review in Lalli & Gilmer 1989). These larger prey are usually sparse and are mixed with many intact phytoplankton cells and protozoans. Meisenheimer (1905) believed that the appearance of large food items in the guts was at best due to chance. The only readily identifiable material in fecal pellets consists primarily of hard-bodied phytoplankton and small thecate protozoa (mostly dinoflagellates and Sarcodina). Based on these studies of gut and fecal material and an erroneous description of their feeding mechanism (e.g. Yonge 1926, Morton 1954, Gilmer 1974), thecosomes have been generally regarded as strict herbivores, feeding on fine suspended particles.

Richter (1977) pointed out that, on a volume basis, large zooplankton form a significant part of the diet of many euthecosomes. This led him to suggest that thecosomes should more appropriately be regarded as mucous trappers ('Fallensteller') rather than collectors or suspension feeders ('Sammler'). The discovery that all euthecosomes feed with a large external mucous web revealed an obvious mechanism for entrapping large, fast-moving prey (Gilmer & Harbison 1986). In contrast to other suspension feeders, euthecosomes lack a mechanism for moving water through their mucous webs (Gilmer 1990).

On night dives, the absence of diffused surface

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illumination makes the feeding webs easier to observe, but lights held by divers appear to affect the behavior of the pteropods. Some species, particularly the vertically migrating *Cuvierina columnella*, quickly ingest the webs and sink. On several such occasions, we have seen numerous small crustaceans (ca 1 mm) trapped inside the webs as they were ingested. Larger hyperiid amphipods (3 to 4 mm in length), attracted by our dive lights, could also become entangled, but were usually able to break free before they were eaten. The smaller crustaceans were unable to escape, however, and were ingested. Those cavoliniids that we have hand-collected at night all contained copepods in their guts (Gilmer 1990).

At the time of this study, the sun did not set, so night dives were not possible. Nevertheless, large zooplankton comprised a large fraction of the diet of *Limacina helicina*. In this paper, we will show that, at least during the summer months, larger zooplankton represented an important fraction of the diet of this species. This study adds credence to Richter's speculation, and provides the first information on the diet of this important pteropod in Arctic waters during summer.

MATERIALS AND METHODS

Limacina helicina was investigated on 2 cruises aboard RV 'Endeavor': Cruise 133 in August 1985 from Iceland to Newfoundland via the Greenland and Labrador currents, and Cruise 182 in August 1988 from Iceland to Norway via Spitsbergen. On Cruise 182 temperature salinity profiles were made of the upper 65 m at most stations using a portable CTD (SeaCat

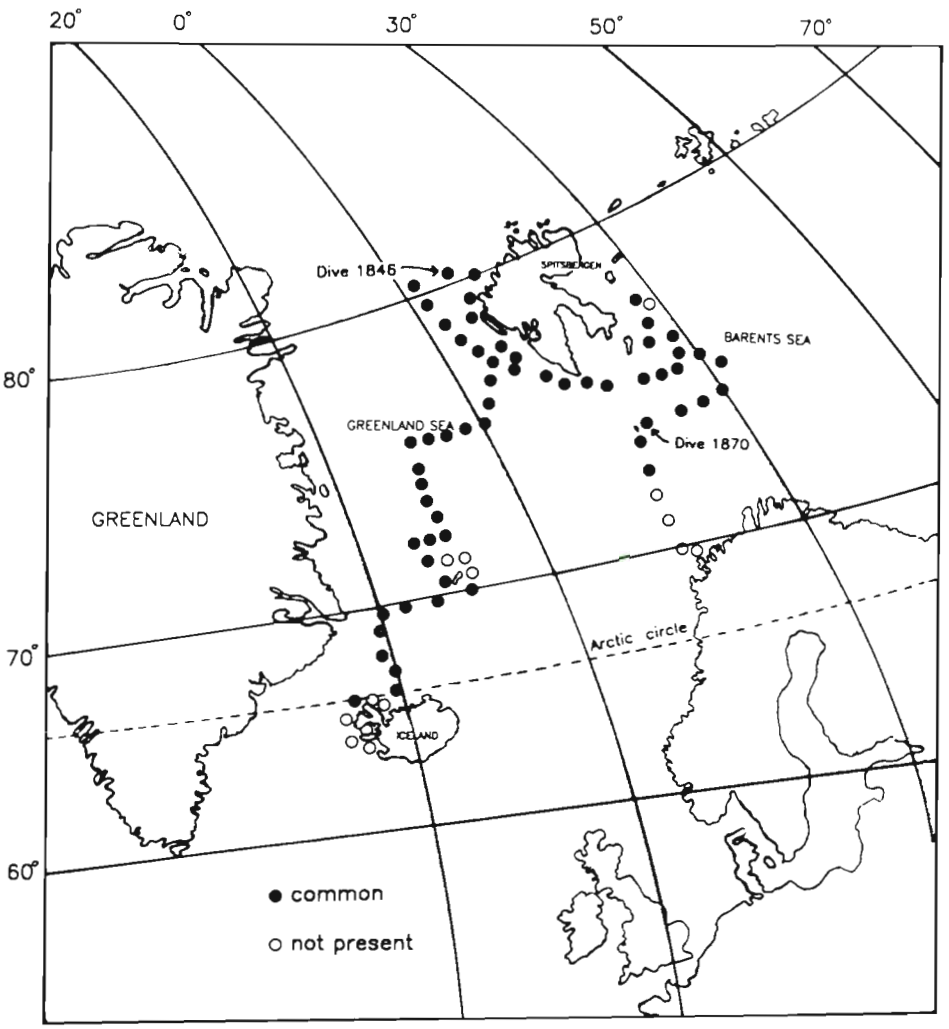

Fig. 1. *Limacina helicina*. Distribution of pteropods during RV 'Endeavor' Cruise 182

Profiler: SeaBird Electronics) lowered over the side of the ship. Chlorophyll measurements were provided by M. Putt (methodology given in Putt 1990) from water casts taken at dive stations. Locations of the dive stations for Cruise 182 are shown in Fig. 1. In situ collections using hand-held glass jars were made with standard blue-water diving techniques (Hamner 1975). We observed and collected specimens of *L. helicina* with shell diameters between 5 and 13 mm, which divers could easily see. The abundance of *L. helicina* in this size category was estimated by measuring the nearest neighbor distance between individuals (Hamner & Carlton 1979). Visual reference markers (5 cm intervals) placed on the diver tether line or on a separate piece of quarter-inch nylon rope were used to estimate distances. Since *L. helicina* is easily disturbed, measurements were made quickly. Nearest neighbor distances were rounded to the nearest 5 cm, producing a standard error of $\pm$ 0.25 ind. m^{-3}. The distances between 20 to 50 pteropods at each depth were measured. To assess the activities of *L. helicina*, a diver swam through the zone of highest density and observed individuals at random until 6 to 10 active individuals were counted. Most individuals were not swimming but were motionless in the water.

From previous observations on other species (Gilmer & Harbison 1986, Gilmer 1990), we assume that motionless *Limacina helicina* were feeding. Inactive individuals were collected in small jars (100 to 250 ml capacity) in 3 ways: (1) some were fixed in situ immediately upon capture by injecting several ml of 10 % formaldehyde (buffered with sodium borate and diluted with seawater) through a rubber serum stopper fitted to the jar lid; (2) others were returned to the laboratory and kept for up to 12 h to produce fecal pellets; or (3) some were collected in situ but preserved at various intervals over 12 h to determine the effect of time on gut contents. Pteropods preserved in the laboratory were first relaxed in dilute MS-222 (Ethyl m-aminobenzoate, Sigma) and carefully observed to be sure that material in the guts was not voided during preservation.

Water samples of 1 l were collected with plastic bottles by divers in the layer of maximal pteropod abundance to estimate the number of potential food items in the water. These water samples were preserved on board with filtered (0.45 µm) 10 % formaldehyde buffered with sodium borate to make a 3 % final solution. The samples were allowed to settle for 1 wk and concentrated into 50 ml jars. The entire sample was examined later for zooplankton under a dissecting microscope. Protozoa and phytoplankton were counted by resuspending the sample and counting ten 1 ml subsamples with a Segwick-Rafter chamber and Olympus compound microscope (fitted with both bright-field and chlorophyll epifluorescence illuminators with blue 490 IF exciter filter).

We removed the gizzard sac and esophagus under a dissecting microscope and examined the entire contents at 100 or 200× with a compound microscope. All food items larger than 10 µm were counted and classified. Cell volume was determined by calculating approximate cell shape from standard geometric forms and applying average values to all particles in each size category (see Table 1). For tintinnids, estimates of volumes were often made from measurements of empty loricae. Carbon values were based on values reported in the literature or calculated from published equations that best represented the size categories of food items (Table 1). Values used for volume $ind.^{-1}$ were obtained from the mean dimensions for each taxon and size category in Table 1. Particles smaller than 20 µm were counted but not classified. A spherical volume assuming a diameter of 15 µm for each particle of this fraction was used to estimate their volume (Table 1) and carbon. Counts of particles under 10 µm were not attempted after initial examinations. These particles were present in all samples, but their contribution to the total volume was always minimal. Total volume was calculated by summing the volumes of all particles greater than 10 µm.

Animals held to produce fecal pellets were kept in their collection jars at field temperature on board ship and were examined hourly. Pellets were removed as soon as they were produced and either examined immediately or frozen and examined from 1 to 8 mo later. The entire pellet was examined (200 or 400×) and all items larger than 10 µm were counted and classified. The presence of red fluorescence was used as a criterion to determine if a cell was intact in cases where the cell walls appeared to be disrupted. To check the way in which preservation and storage time affected epifluorescence, both frozen and preserved fecal pellets from *Limacina helicina* collected in 1985 (Cruise 133) were examined prior to Cruise 182 (35 mo later). Both types of material had comparable numbers of fluorescent cells. Because a high percentage of the pellet consisted of cells between 10 and 20 µm, an ocular grid divided into 100 squares was used as a reference to count them. Five to ten grid counts were made randomly for each pellet. The counts were then averaged and extrapolated to obtain values for the total pellet area. Total volumes of both the gut contents and fecal pellets were calculated by summation of these counts.

At our 2 study stations (see Fig. 2), hand-held net tows were made by a diver at 3 depths to compare the abundance of potential prey with amounts of prey in the guts of the pteropods. Samples were taken above (4 to 9 m), in (12 to 20 m), and below (25 to 30 m) the depth of maximum *Limacina helicina* densities. Each 100 µm mesh net had a 15 cm opening. A separate net

was used at each depth and the cod ends were tied off under water after the tow, in order to insure that none of the sample was lost. Each net was pushed through the water by the diver for a distance of 20 m. The volume sampled at each depth was ca 0.35 m^3. Samples were preserved in 4 % buffered formaldehyde and counted in their entirety.

RESULTS

On both cruises, *Limacina helicina* usually occurred in dense layers at depths between 5 and 25 m (Fig. 2a, b). Temperature/salinity profiles were extremely variable (Fig. 3a, b), but the occurrence of *L. helicina* was generally in the mixed zone between the surface and the deeper, more stable water. The pteropods tended to avoid the upper 4 m (possibly because of turbulence) and were usually present in highest concentrations above the thermocline. On Cruise 182, *L. helicina* occurred at 87 % of the stations where the surface temperature was below 8 °C. It was particularly abundant in the Greenland and Barents Seas and at most stations around Spitsbergen (Fig. 1). Nearest neighbor measurements indicated that the near-surface abundance maximum was usually between 10 and 24 m. Densities ranged between 1.5 and 2.5 ind. m^{-3} (Fig. 1a, b). More than 97 % of the ca 1200 individuals we counted were neutrally buoyant and motionless. Net tows indicated that copepods were also abundant in these layers (Fig. 2a, b). Chlorophyll levels were uniformly low in the surface waters at most stations (Fig. 2).

Gut contents

Small crustaceans (mostly copepod nauplii; Table 1) and *Limacina helicina* juveniles (Table 1) accounted for an average of 46 % of the total volume (Fig. 4a) and an average of 40 % of the estimated carbon (Fig. 4b) in the guts of specimens preserved in situ (n = 30), yet contributed a negligible amount to the total particle count (Table 2). Large thecate dinoflagellates (Group II; Table 1) accounted for an average of 7 % of the volume and 4 % of the available carbon. Tintinnids comprised 15 % of the volume and 19 % of the estimated carbon. At least 5 species of tintinnids were found in the gut contents but were not identified (Fig. 5a shows some of these species).

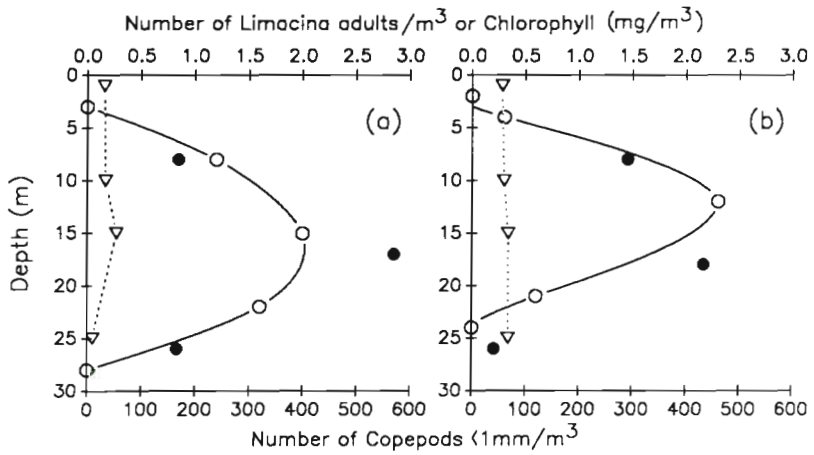

Fig. 2. Comparison of abundance of large (5 to 13 mm) *Limacina helicina* (○), of small (≤ 1 mm) crustacean zooplankton (●), and chlorophyll concentration (▽). (a) Dive 1846: 7 August 1988, 80° 39.88' N, 14° 27.15' E; (b) Dive 1870: 16 August 1988, 74° 43.88' N, 20° 37.53' E. Abundance of *L. helicina* calculated from nearest neighbor distances; abundance of zooplankton obtained from plankton tows; chlorophyll concentration determined fluorometrically

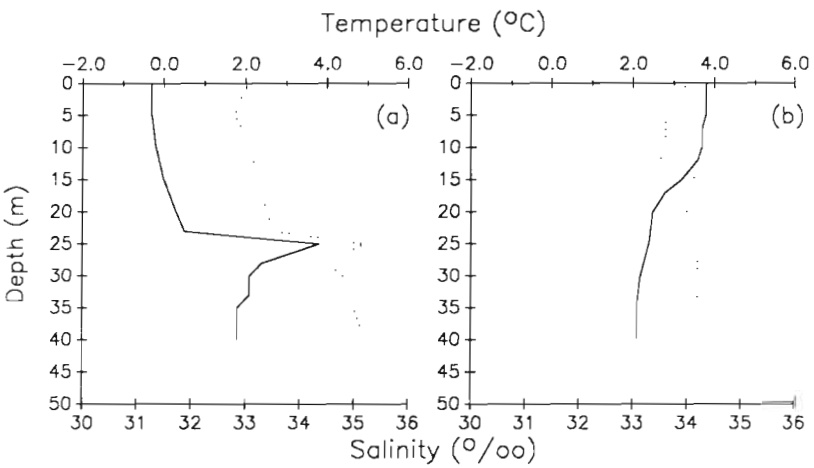

Fig. 3. Temperature (——) and salinity (·····) profiles at Dive Stations 1846 (a) and 1870 (b). Compare with Fig. 2

Table 1. *Limacina helicina*. Volume and carbon values assigned to food items shown in Table 2 and Figs. 4 & 6. For each food item, average dimensions ± SD are given, as well as the size range (in parentheses)

Food item	Avg. dimensions (μm)	Avg. vol. ind.$^{-1}$ (μm^3)	Avg. C ind.$^{-1}$ (ng)	Source
Copepod nauplii (thorax length)	180 ± 65 (100–650)	3×10^6	90	Mullin & Brooks (1970)
L. helicina juveniles (shell diameter)	160 ± 35 (130–270)	2×10^6	75[a]	Conover & Lalli (1974)
Tintinnids (lorica)	100 ± 35 × 45 ± 16 (40–300) × (30–85)	2×10^5	10	Verity & Langdon (1984)
Dinoflagellates				
Group I	34 ± 8 (25–58)	2×10^4	1	Mullin et al. (1966)
Group II	90 ± 5 (75–102)	4×10^5	9	
Diatoms				
Centric	47 ± 13 × 25 ± 3 (28–60)	4×10^4	1.6	
Pinnate Group I	86 ± 12 × 30 ± 3 (66–98)	8×10^4	2.7	
Pinnate Group II	154 ± 5 × 35 ± 4 (104–188) × (28–40)	2×10^5	5.5	
Cells 10–20 μm		2×10^3	0.2	

[a] Excludes C of shell

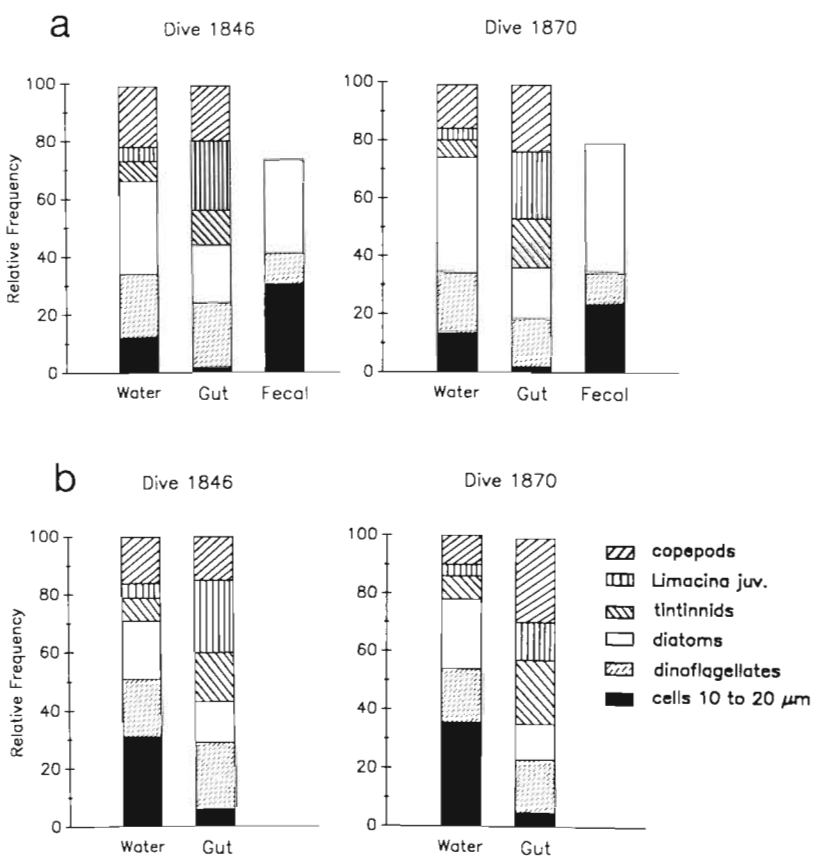

Fig. 4. *Limacina helicina*. Relative frequency (%) of intact food items in water samples, gut contents, and fecal pellets, for pteropods collected in situ at the 2 dive sites (a) by volume and (b) by carbon, using values from Table 1. Although fragments of pteropod shells, copepod exoskeletons and empty tintinnid loricae were found in guts and pellets, this material was not scored for this figure

Table 2. *Limacina helicina*. Comparison by taxa of total number of intact food items in water samples, guts and fecal pellets for pteropods sampled at 2 dive sites (see legend to Fig. 2). n: total numbers of guts or pellets examined; numbers in parentheses in gut content columns refer to the number of specimens with intact food items in their guts. Although fragments of pteropod shells, copepod exoskeletons and empty tintinnid loricae were found in guts and pellets, this material was not scored in this table

Taxon	Dive 1846			Dive 1870		
	Water (no. l^{-1})	Guts (n = 18)	Pellets (n = 11)	Water (no. l^{-1})	Guts (n = 10)	Pellets (n = 9)
Cells 10–20 μm	6870	4592 (18)	9740	7390	2894 (10)	8310
Thecate dinoflagellates						
Group I ($\bar{x}$ = 34 μm)	552	2851 (18)	327	480	1574 (10)	362
Group II ($\bar{x}$ = 90 μm)	35	97 (15)	0	28	36 (9)	0
Diatoms						
Centric ($\bar{x}$ = 47 μm)	216	835 (18)	203	244	283 (10)	244
Pinnate I ($\bar{x}$ = 86 μm)	126	171 (18)	131	106	181 (10)	169
Pinnate II ($\bar{x}$ = 154 μm)	63	86 (18)	60	167	107 (10)	77
Tintinnids	37	273 (18)	0	33	239 (10)	0
Limacina spp. (< 300 μm)	3	53 (12)	0	2	33 (10)	0
Copepods (thorax < 500 μm)	8	29 (14)	0	5	24 (8)	0
Ratios between taxa:						
Small cells/Dinoflagellates	11.7	1.6	29.8	14.5	1.8	23.0
Small cells/Diatoms	17.0	4.2	24.7	14.6	5.1	17.0
Dinoflagellates/Diatoms	1.4	2.6	0.8	1.0	3.2	0.7
Dinoflagellates/Tintinnids	15.8	10.8	–	15.4	6.7	–
Tintinnids/*Limacina* spp.	12.3	5.2	–	16.5	7.2	–
Tintinnids/Copepods	4.6	9.4	–	6.6	10.0	–
Limacina spp./Copepods	0.4	1.8	–	0.4	1.4	–
Diatoms/Copepods	50.6	31.7	–	101	20.9	–
Diatoms/Tintinnids	10.9	4.1	–	15.4	2.1	–
Dinoflagellates/Copepods	73.4	102	–	102	67.1	–

Ingested diatoms were scored into 4 size categories: 1 large centric type (Table 1; Fig. 5d); 2 large pinnate forms (Pinnate Groups I and II in Table 1; Fig. 5d); and numerous small centric forms (ca 15 μm average dimensions). Collectively the first 3 groups of diatoms contributed about 16 % to total volume and 17 % to estimated carbon in the gut contents.

The smallest cells categorized were small thecate dinoflagellates (Group I in Table 1; Fig. 5a). They contributed 11 to 12 % of the total volume and 15 to 18 % to the estimated carbon. Numerically they were the most abundant items identified (Table 2).

Five *Limacina helicina* had ingested fecal pellets produced by other zooplankton. These partially disrupted pellets measured 100 × 400 μm and contained many intact dinoflagellates and smaller cells (Fig. 5c). The identifiable intact material contained in these pellets was included in our cell counts.

Both water and net samples contained several taxa that were absent from the gut contents of *Limacina helicina*. These included small larvaceans (ca 300 to 400 μm), larval ctenophores, several different kinds of coelenterate larvae and small medusae. We did not find sarcodines in the gut contents either, but they were sparse in both the net tows and water samples. All of these organisms are soft-bodied, so they may have been rendered unrecognizable in the gut contents. Nevertheless, the comb plates of ctenophores are very resistant to degradation, and should have been observed in the gut contents had they been present.

Fecal pellets

Pellets from pteropods collected on the same dives as those used for gut content studies contained no whole items larger than 50 μm (Fig. 4a). Diatoms appeared least affected by passage through the gut. Many appeared to be intact or had small irregular holes in the cell walls. About two-thirds of all the diatoms in the fecal pellets displayed bright red fluorescence, in all probability due to chlorophyll or its degradation products. Diatoms contributed twice as much to the volume of fecal material as they did to the volume of gut contents (Fig. 4a).

Less than half of the intact dinoflagellates in the pellets fluoresced. Many were broken into smaller fragments, but intact thecae were split about evenly

between red-fluorescing and non-fluorescing cells. While cells between 10 and 20 μm in diameter contributed as much as 91 % of the total number of particles counted in fecal pellets, they constituted only about a third of the volume (Fig. 4a).

Small cells (10 to 20 μm) were much more abundant in the water samples and fecal material than in the gut contents. The small 'cells' in the fecal material consisted mainly of partially digested or degraded material, similar in appearance to that reported by Silver & Bruland (1981).

Recognizable debris was present and consisted of distal points from tintinnid loricae and large fragments of crustacean exoskeleton segments (Fig. 5d, e). These

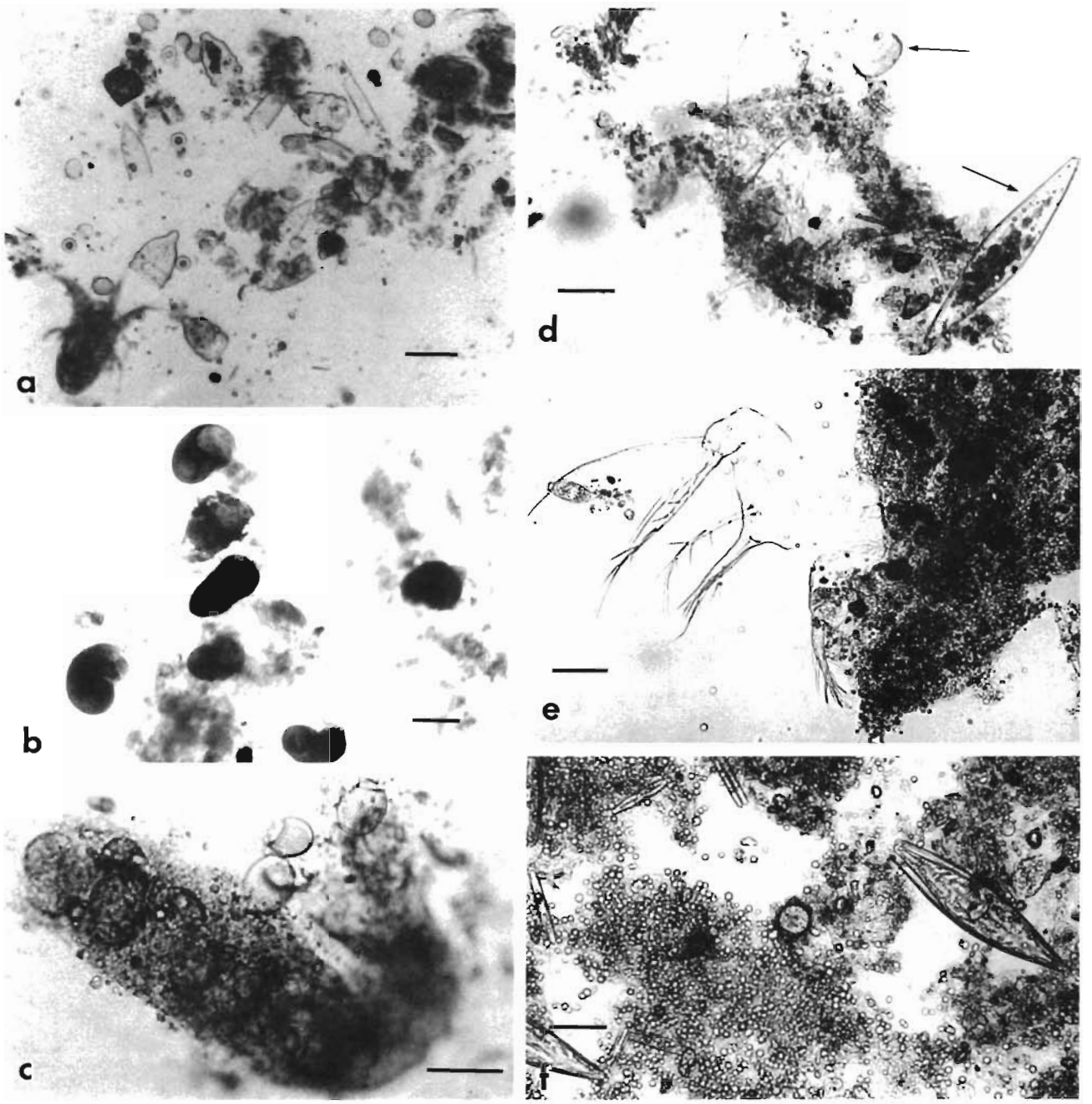

Fig. 5. *Limacina helicina*. Representative photographs of the contents of guts and fecal pellets. (a) Gut contents showing relative sizes of common prey items: copepod nauplii, tintinnids, and dinoflagellates. (b) Seven juvenile *L. helicina* in gut of an adult specimen. (c) Ingested fecal pellet with dinoflagellates, from gut contents of *L. helicina*. (d) Two kinds of diatoms commonly found in gut contents. (e) Fecal pellet containing large fragment of a copepod thorax. (f) Fecal pellet with diatoms containing chloroplasts. Scale bars: (a) 120 μm, (b) 100 μm, (c) 325 μm, (d) 230 μm, (e) 120 μm, (f) 200 μm

fragments were tallied and measured, and we estimated them to occupy between 21 and 27 % of the total pellet volumes. They were not included in the volume summations in Fig. 4 or Table 2, however. No intact tintinnid loricae were found in any of the fecal material. Intact shells or large shell fragments of *Limacina helicina* juveniles and intact crustaceans were absent in the fecal matter, although both were present in the gut contents.

Effect of residence time on gut contents

No intact crustaceans were found in the digestive tracts of specimens held for 4 h before preservation (n = 11), although fragmentary material was present. In contrast, intact *Limacina helicina* juveniles were found in the guts of these pteropods and in the guts of those held for 10 h (Fig. 6). The contribution of *L. helicina* juveniles to the total volume of gut contents was approximately the same (ca 25 %) for specimens held for 4 and 10 h. In the latter, however, the soft parts appeared to be more degraded. The overall volume of food in the guts of specimens was noticeably reduced in pteropods held for 10 h, and 2 specimens had totally empty guts. From Fig. 6, it appears that tintinnids and copepods are digested more rapidly than diatoms.

Numerical considerations

A comparison of ratios between taxa in the water samples with ratios between taxa in the gut contents (Table 2) revealed a significant difference ($p = 0.01$) at both sampling stations (Chi-square or Kolmogorov-Smirnov 2-group test). Fecal pellets contained much higher numbers of small cells relative to either dinoflagellates or diatoms when compared either to water samples or to gut contents. Dinoflagellates were 2 to 3 times more abundant than diatoms in the gut contents, yet were about equal in abundance in both water samples and fecal pellets (Table 2). This suggests either that dinoflagellates may be more easily digested than diatoms, or that diatoms are less susceptible to mechanical degradation by the gizzard. The frequency with which these cells occur relative to each other in water and gut samples also implies that dinoflagellates are collected at 3 times the rate of diatoms. The 8-fold decrease in small cells compared with dinoflagellates in the gut contents (Table 2) may simply reflect the difficulty of identifying smaller cells.

The ratios also showed that juvenile *Limacina* spp. were ingested at about 4 times the rate of crustaceans. Tintinnids were ingested at up to 7 times the rate of diatoms and up to 2.3 times the rate of dinoflagellates. Copepods were collected at 50 to 80 % lower rates than *Limacina* spp. juveniles, and 50 to 66 % lower rates than tintinnids.

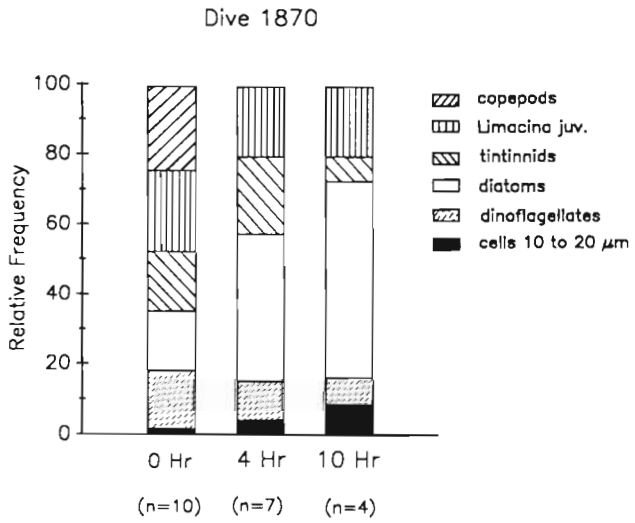

Fig. 6. *Limacina helicina*. Composition of gut contents as a function of residence time. Frequency (as % total volume) shown for specimens preserved in situ (0 h), held for 4 h before preservation, or held for 10 h before preservation

DISCUSSION

The *Limacina helicina* in our study acquired almost half of their diet by cannibalism and ingestion of small crustaceans. This obviously important fraction was not evident in either fecal pellets or guts of pteropods kept alive for more than a few hours before preservation. *L. helicina* defecates or regurgitates food when rapidly preserved, or if left confined in a collection jar. Some specimens defecated within 1 min of capture. In addition, large females often spawn in the jar, releasing large amounts of eggs and mucus. This material becomes entangled with the fecal matter and regurgitated food, making it extremely difficult to collect all of the ingested food items as the time between capture and preservation increases. The contents of each jar must be carefully examined to be sure that no food items are overlooked.

Large fragments of tintinnid loricae and copepod exoskeletons often occurred in fecal pellets, whereas no *Limacina* spp. shell fragments were found. Copepod fragments measuring ca 800 µm (Fig. 5e) were present in several fecal pellets, indicating that larger crustaceans than those we sampled can be eaten. It is also possible that these larger fragments were simply detrital material that had become stuck on the web. We have found 5 intact copepods (3.1 mm thorax length) in the gut of a single *L. helicoides* collected discretely at 800 m with the Johnson Sea-Link submersible, how-

ever. This specimen had a shell diameter of ca 15 mm (only slightly larger than specimens of *L. helicina* examined in this study). Thus, *L. helicina* may ingest much larger copepods than we sampled, and large zooplankton probably constitute a sizeable fraction of the diet of other limacinids as well.

The apparently rapid disappearance of intact copepods in the residence-time experiments (Fig. 6) poses a problem in interpretation. It should be noted that pieces of copepod exoskeletons were present in the gut contents, which suggests that these crustaceans were rapidly digested. Alternatively, the copepods could have been regurgitated during the experiments, although there is no reason to expect that this group would be preferentially regurgitated. Since we used different specimens in this series of experiments, variability in the results could be due in large part to differences in previous feeding history. Further, since *L. helicina* does not feed in the laboratory, these experiments were done on starved specimens, which could have affected the results.

Although the percent contribution of intact *Limacina* spp. juveniles to total volume was essentially unchanged during the course of the residence-time experiments (Fig. 6), the absolute amount of material was greatly reduced, indicating that these animals were being digested as well. The absence of intact shells and large shell fragments from the fecal material of freshly collected specimens (Fig. 4, Table 2) suggests that the shells are ultimately broken apart after a period of dissolution in the gut. This, together with the rapid disappearance of intact copepods, suggests that the gizzard may be able to triturate material that has already passed through it into the stomach. However, since the residence-time experiments could have been biased by previous feeding history and the unnatural conditions under which the pteropods were held in the laboratory, this suggestion should be regarded as speculative.

There are considerable difficulties with our identification and measurements of the smallest size fraction. The walls of the gizzard sac and esophagus of *Limacina helicina* often broke apart during dissection and became mixed with the gut contents, undoubtedly accounting for many of the unidentified cells in the 10 to 20 µm range. Also, many of the tintinnids were separated from their loricae (Fig. 5a, d) so we only counted intact loricae in the water and gut content samples (Fig. 4). The soft parts could sometimes be identified in the guts, but were never identifiable in the fecal matter. Aloricate ciliates, including a plastidic oligotrich *Strombidium* sp. (70 × 40 µm), were numerous in the upper water column at most stations, including our study sites (Putt 1990), but were never found in the gut contents or fecal pellets.

We have probably overestimated the contribution of small particles to the diet of *Limacina helicina*. We assigned greater-than-average volumes to the small size classes (Table 1), and did not subtract those cells that appeared to pass through the gut intact. Determining the importance of the smaller cells as food was made more difficult since it was not possible to assess their condition with light microscopy, as we could do with the larger food items. Further, the contribution of the larger size fraction was probably underestimated, since we used mean values for volume calculations, which do not reflect the great size variation within the metazoan fraction. Taking all these factors into account, we regard our results as conservative estimates.

The taxonomic ratios (Table 2) indicate that *Limacina helicina* traps motile unicellular and metazoan organisms at levels above their concentrations in the water. Since limacinids have no mechanism for moving water through the web (Gilmer & Harbison 1986), all evidence suggests that they are trappers, rather than true filter feeders. One method of trapping motile prey might be the attraction of these organisms into the feeding web, a hypothesis we have suggested previously (Gilmer & Harbison 1986). Such an attraction must be chemical in this case, since limacinids lack the brightly colored mantle appendages of other pteropods, and it must at this juncture be considered as speculative. Another more likely possibility is that limacinids are employing a strategy similar to that of spiders, and deploy mucous webs to capture the more motile organisms that blunder into them. An indirect piece of evidence for this is the reaction of limacinids and other euthecosomes to slight turbulence (Gilmer & Harbison 1986). Slight turbulence, such as might be caused by a struggling organism, will cause rapid ingestion of the web. In fact, at least one gymnosome pteropod, *Pneumodermopsis canephora,* captures its thecosome prey by attaching to the mucous web and allowing itself to be drawn onto its prey as the web is rapidly ingested (Lalli & Gilmer 1989). In addition, *L. helicina* may be able to sense the presence of elevated prey abundance, since the vertical distributions of this species and of prey-sized copepods within the upper 30 m are similar (Fig. 2).

Limacina helicina often occurs in shallow zones of high abundance throughout much of the Arctic and subarctic regions (Hansen & Dunbar 1970, Kobayashi 1974). Hansen & Dunbar (1970) found *Limacina* spp. present at densities of up to 24 ind. m^{-3}, resulting in pronounced acoustic scattering layers between 35 and 55 m. Their specimens were much smaller (maximum shell diameter ca 1 mm) than the ones we studied, and it is doubtful that larger zooplankton could play much of a role in their diet. Nevertheless, motile phytoplankton and protozoans could be captured preferentially even by these smaller specimens. Hopkins (1987) found that

the Antarctic variety of *L. helicina* accounted for 23 % of the total biomass in the upper 800 m of the Ross Sea. He concluded from examination of the gut contents of 30 specimens that they fed only on phytoplankton. His specimens were also small, averaging 2.6 mm in shell diameter. Thus, it is possible that smaller specimens are herbivores, and switch to omnivory only at larger sizes.

Nevertheless, our study shows that *Limacina helicina* is an opportunistic feeder at larger sizes. Its ability to switch from herbivory to omnivory would be of obvious advantage in protecting it from the precipitous declines in phytoplanktonic food levels that occur after blooms in the subarctic and temperate regions. We have recently made Antarctic collections of *L. helicina* in McMurdo Sound. Our collections included many specimens up to 7 mm in shell diameter. Ultimately it may be possible to determine at what size *L. helicina* can effectively feed as a carnivore and what other factors, such as time of year and prey abundance, can influence its dietary switch.

Acknowledgements. We thank the captain and crew of the RV 'Endeavor' for their help; G. R. Dietzmann, J. Lindsey, G. Matsumoto, C. Mann, D. Backus, T Falkenhaug, R. Larson and N. Wu for diving assistance; P. Hernandez for laboratory help at sea; and M. Putt for providing station data on ciliates and chlorophyll. Research supported by N.S.F. Grants OCE 85-16083, OCE 87-46136 and DPP 86-13388 to G. R. H. Harbor Branch Oceanographic Institution Contribution No. 792.

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This article was presented by R. S. Scheltema, Woods Hole, Massachusetts, USA

Manuscript first received: May 15, 1990
Revised version accepted: September 18, 1991