ARCTIC
VOL. 42, NO. 4 (DECEMBER 1989) P. 339-346

Source and Fate of Lipids in Polar Gelatinous Zooplankton

R.J. LARSON[1] and G.R. HARBISON[1]

(Received 6 December 1988; accepted in revised form 30 March 1989)

ABSTRACT. The presence or absence of accumulated lipids in arctic and Antarctic medusae and ctenophores was determined by visual examination of living specimens with a dissecting microscope. Lipid accumulations were obvious because of their high refractive indices. Lipids were seen in many of the 200+ gelatinous zooplankton specimens collected. They always consisted of various-sized droplets and larger masses within the lumen of the gastrovascular system. No true depot lipids or adipose tissue were present. The accumulation of lipids was observed in feeding animals, suggesting that the prey-derived lipids were unmodified. Disappearance of lipids in starved animals suggested that lipids are taken up and assimilated. In medusae, they occurred in the stomach, ring and/or radial canals. In most ctenophores, lipids were found in the meridional canals below the comb rows. However, in one ctenophore species, *Mertensia ovum*, lipids are stored in special sacs associated with the tentacle bulbs. Lipids were more frequently observed in arctic than in Antarctic gelatinous zooplankton. A review of the literature suggests that in the Antarctic, the average lipid content of gelatinous predators is about 3% DW (range = 0.4-6%), whereas in the Arctic it is nearly three times higher, about 8% DW (range = 1.5-22%). These differences are probably related to the amounts of lipids in their prey. The abundance of lipid-rich *Calanus* spp. copepods in the Arctic may be responsible for the high levels of lipids in gelatinous predators.

Key words: lipids, gelatinous zooplankton, ctenophores, medusae, Arctic, Antarctic, polar, feeding, starvation

RÉSUMÉ. On a déterminé la présence ou l'absence d'une accumulation de lipides chez les méduses et les cténaires de l'Arctique et de l'Antarctique en examinant des spécimens vivants avec un microscope de dissection. On remarquait très nettement les accumulations de lipides à cause de leurs indices de réfraction élevés. On a observé des lipides chez beaucoup des plus de 200 spécimens de zooplancton gélatineux recueillis. Ces accumulations consistaient toujours en gouttelettes de différentes tailles et en amas plus volumineux dans la lumière du système gastrovasculaire. On n'a pas observé de véritables dépôts de lipides ou de tissus adipeux. On a observé une accumulation de lipides chez des animaux en train de se nourrir, ce qui suggère que les lipides dérivés des proies n'étaient pas modifiés. La disparition des lipides chez les animaux à jeun suggère que les lipides sont ingérés et assimilés. Chez les méduses, on a trouvé des lipides dans l'estomac, l'anneau et/ou les canaux radiaires. Chez la plupart des cténaires, on a trouvé des lipides dans les canaux méridionaux sous les couronnes de peignes, mais chez une espèce de cténaire, la *Mertensia ovum*, les lipides sont emmagasinés dans des sacs spéciaux associés aux bulbes tentaculaires. On a plus souvent observé la présence de lipides dans le zooplancton gélatineux de l'Arctique que dans celui de l'Antarctique. Un examen de la documentation publiée donne à penser que dans l'Antarctique, le contenu lipoïdique moyen des prédateurs gélatineux est environ 3 % du poids sec (gamme de 0,4 à 6 %), alors que dans l'Arctique, il est environ trois fois plus élevé, soit près de 8 % (gamme de 1,5 à 22%). Ces différences sont probablement reliées à la quantité de lipides contenue dans les proies. Dans l'Arctique, l'abondance de copépodes de l'espèce *Calanus* riche en lipides, est sans doute responsable des niveaux élevés de lipides chez les prédateurs gélatineux.

Mots clés: lipides, zooplancton gélatineux, cténaires, méduses, Arctique, Antarctique, polaire, alimentation, état de jeûne

Traduit pour le journal par Nésida Loyer.

INTRODUCTION

Polar zooplankton can be rich in lipids. At high latitudes, herbivorous copepods rapidly synthesize wax esters when phytoplankton are seasonally abundant. These lipids are stored and later used for egg production and energy when microalgae are in lower concentrations (Clarke, 1983). Other lipid classes are also synthesized and stored by high-latitude zooplankton. Planktonic predators, whose food supplies are more constant, mainly store triacylglycerols. This suggests that wax esters are stored for long terms whereas triacylglycerols are used as short-term energy reserves (Lee *et al.*, 1971; Lee and Hirota, 1973; Bensen and Lee, 1975; Sargent, 1976; Clarke, 1980; Reinhardt and Van Vleet, 1986; Eastman, 1988).

Some arctic medusae and ctenophores are known to have higher lipid levels than those from lower latitudes (Table 1). Species from tropical and temperate waters contain $\leq 5\%$ lipid on a dry weight basis (Aarèm *et al.*, 1964; Ikeda, 1972; Yasuda, 1974; Hoeger, 1983), whereas boreal and arctic species can have lipid levels of 10-20% of dry weight (Lee, 1974; Percy and Fife, 1981; Clarke *et al.*, 1987). Yet, in some Antarctic species, lipids equal only about 1-6% of dry weight (Clarke, 1983, 1984; Reinhardt and Van Vleet, 1986; Hagen, 1988). In fact, lipid levels in Antarctic gelatinous zooplankton resemble those of species from lower latitudes, with the exception of Clarke's (1984) value for *Beroe* sp. (Table 1).

The dominant type of lipid in gelatinous zooplankton varies. Wax esters are often the major class in polar species (Clarke *et al.*, 1987; Hagen, 1988). But triacylglycerols predominate in some polar and non-polar species (Clarke, 1984; Reinhardt and Van Vleet, 1986). Membrane-bound phospholipids are usually present at low concentrations regardless of latitude (Sipos and Ackman, 1968; Hooper and Ackman, 1972; Lee, 1974; Joseph, 1979; Hagen, 1988). Morris and McCartney (1983) reported unusually high phospholipid values for *Bolinopsis*.

In copepods, lipids are stored in oil sacs, whereas in fishes they are stored in subcutaneous and intramuscular deposits (Clarke, 1980; Reinhardt and Van Vleet, 1986; Eastman, 1988). Little is known about where lipids are stored in gelatinous zooplankton. In certain calycophoran siphonophores, e.g., *Muggiaea* and *Lensia*, a small oil droplet occurs in the somatocyst, an interior extension of the gastrovascular system within the nectophore (Hyman, 1940; Mackie, 1974). In another species, *Nanomia cara*, oil has been seen to accumulate in the palpon diverticulum (Mackie, 1974). Joseph (1979) noted that medusae lacked visible lipid deposits except in their gonads. In these cases the amount of lipid (a few mg) appears too small to serve as a substantial

---

[1] Harbor Branch Oceanographic Institution, 5600 Old Dixie Highway, Fort Pierce, Florida 34946, U.S.A.

TABLE 1. Lipids as percent dry weight in gelatinous predators from different geographic areas

Taxon	Lipid % dry wt*	Geographic** area	Reference
Medusae			
Aglantha digitale	3	B	Ikeda, 1972
Aglantha digitale	6-7	AR	Percy and Fife, 1981
Atolla wyvillei	1.1	AN	Reinhardt and Van Vleet, 1984
Aurelia aurita	0.4	B	Hooper and Ackman, 1972
Aurelia aurita	0.3*	B	Yasuda, 1974
Bougainvillia superciliaris	7-10	AR	Percy and Fife, 1981
Calycopsis borchgrevinki	0.4-3	AN	Hagen, 1988
Chrysaora quinquecirrha	5*	T	Joseph, 1979
Cyanea capillata	0.3-0.8*	B	Sipos and Ackman, 1968
Halitholus cirratus	5-8	AR	Percy and Fife, 1981
Hybocodon prolifer	13-22	AR	Percy and Fife, 1981
Rhizostoma pulmo	3.5	T	Ceccaldi *et al.*, 1978
Rhizostoma sp.	1	B	Aarem *et al.*, 1964
Sarsia princeps	8-9	AR	Percy and Fife, 1981
Sibogita borchgrevinki	1.2*	AN	Clarke, 1983, 1984
Spirocodon saltatrix	0.3*	B	Yasuda, 1974
Stomolophus sp.	0.5*	B	Yasuda, 1974
Siphonophores			
Diphyes antarctica	2.5*	AN	Clarke, 1983, 1984
Diphyes antarctica	0.5	AN	Reinhardt and Van Vleet, 1984
Diphyes antarctica	0.4-3	AN	Hagen, 1988
Pyrostephos vanhoeffeni	1	AN	Hagen, 1988
Ctenophores			
Beroe cucumis	13	B	Lee, 1974
Beroe cucumis	4-6	AR	Percy and Fife, 1981
Beroe cucumis	1.5*	AR	Clarke *et al.*, 1987
Beroe gracilis	4	AR	Hoeger, 1983
Beroe ovata	2.8	T	Ceccaldi *et al.*, 1978
Beroe sp.	72*(?)	AN	Clarke, 1984
Bolinopsis infundibulum	0.5	B	Hoeger, 1983
Bolinopsis infundibulum	16(?)	B	Morris and McCartney, 1983
Bolinopsis infundibulum	12*	AR	Clarke *et al.*, 1987
Cestum veneris	1.7	T	Ceccaldi *et al.*, 1978
Leucothea multicornis	2.5	T	Ceccaldi *et al.*, 1978
Mertensia ovum	5-14	AR	Percy and Fife, 1981
Pleurobrachia pileus	9	B	Lee, 1974
Pleurobrachia pileus	1.7	B	Hoeger, 1983
?*Pleurobrachia* sp.	2.5	AN	Clarke, 1984
ctenophore	4.5-6.3	AN	Hagen, 1988

*Converting by assuming dry weight = 4% of wet weight.
**AN = Antarctic; AR = Arctic; B = Boreal; T = Tropical-subtropical.

energy reserve, although it could add positive buoyancy for maintaining a particular fishing posture.

For only one species of gelatinous zooplankton are there data that suggest that amassed lipid could later be utilized for energy. In the arctic ctenophore *Mertensia ovum*, Percy (1988) found a seasonal change in the oxygen-uptake/ammonium-excreted ratio, suggesting winter utilization of lipids.

In this study we report observations on the storage sites of lipids in arctic and Antarctic medusae and ctenophores. Observations were made both *in situ* and in the laboratory to document the dietary origin of lipid accumulations and to determine their role during starvation.

MATERIAL AND METHODS

In the Arctic, gelatinous zooplankton were collected during a cruise in July and August 1988. The ship went from Iceland to Svalbard, and then to the northwest, west, and south-southeast of Svalbard, ending in Norway. Specimens were hand collected in jars using scuba at depths of 0-25 m. Surface water temperatures ranged from −1 to 11°C (averaging 2–4°C), with a strong thermocline. In the Antarctic, studies were done at McMurdo Sound, Ross Sea (77°38′S, 166°25′E) in November 1987 and December 1988. Specimens were collected using scuba and with a 1 m plankton net fished through holes in the ice. Water temperatures in the upper 20 m were nearly isothermal, ranging from −1.6 to −0.6°C.

For experiments on the origin and fate of lipids, specimens were individually maintained for up to three weeks in jars in an incubator at *in situ* temperatures. The water was changed every 2-3 days.

The presence or absence of accumulated lipids was determined by examination of living specimens with a dissecting microscope. Lipid accumulations were readily visible because of their high refractive indices. Dissections were necessary for observation of lipids in the guts of some medusae — e.g., *Euphysa* and *Sarsia* — because pigment over the stomach prevented visual analysis. The relative abundance of lipids was qualitatively compared on a scale of 1-4. If no lipids were visible they were listed as absent. When present only as a few small droplets they were listed as present and when slightly more numerous as low abundance. When lipids were mainly present as large accumulations, rather than as small droplets (although droplets could also be present), they were categorized as abundant or very abundant depending on their quantity. Amounts of lipids were quantitatively estimated from size measurements of deposits using a dissecting microscope and an ocular micrometer and multiplying the volume by the specific gravity for wax esters (0.85 g·cm^{-3}).

RESULTS

Observations of Freshly Collected Live Animals

Lipids were seen in most of the 200+ gelatinous zooplankton specimens collected (Table 2). They always consisted of various-sized droplets and larger masses within the lumen of the gastrovascular system. Lipids were not seen in tissues. In medusae, they occurred in the stomach, ring and/or radial canals. In ctenophores, lipids were found in the meridional canals below the comb rows, or in one species (*Mertensia ovum*) in special sacs extending from the tentacular canals.

TABLE 2. List of gelatinous zooplankton collected and examined for lipid accumulations

Taxon	Visible lipids*	N
Arctic Hydromedusae		
Aegina citrea	+ to + +	19
Aglantha digitale	+	7
Bougainvillia superciliaris	–	18
Catablema sp.	– to + + +	13
Euphysa japonica	+ + + +	15
Halitholus pauper	– to + + +	12
Halopsis ocellata	–	1
Hybocodon prolifer	+ + + to + + + +	7
Phialidium hemisphaericum	–	2
Phialidium islandicum	–	5
Sarsia princeps	+ to + + + +	50+
Staurophora mertensi	– to + +	6
Arctic Scyphomedusae		
Aurelia aurita	–	5
Cyanea capillata	+	6
Arctic Ctenophores		
Beroe cucumis	– to + +	50+
Bolinopsis infundibulum	– to +	8
Mertensia ovum	+ + to + + + +	50+
Antarctic Hydromedusae		
Kollikerina maasi	–	1
Mitrocomella frigida	–	4
Leuckartiara sp.	–	5
Solmundella bitentaculata	– to +	9
Antarctic Scyphomedusae		
Diplulmaris antarctica	– to +	15
Antarctic Ctenophores		
Beroe cucumis	– to +	27
Callianira antarctica	– to + + +	12

*Lipids: – = absent; + = present; + + = low abundance; + + + = abundant; + + + + = very abundant.

Lipids were seen in most arctic medusae. In *Aegina citrea*, lipid droplets of varying sizes were seen only within the stomach. In *Aglantha digitale*, a single droplet was seen at the base of the stomach adjacent to the gelatinous peduncle (Fig. 1). In *Catablema* sp., lipid droplets of varying sizes and colors occurred within the stomach and in the radial canals. Most droplets were clear, but reddish ones were also present, suggesting that they came from several sources. All specimens of *Euphysa japonica* and *Hybocodon prolifer* contained lipids. They were present as yellowish droplets in the radial canals and as large yellowish masses in their stomachs (Fig. 1). Both species were neutrally buoyant, possibly due to the large accumulations of lipids. In *Halitholus pauper*, both colorless and red droplets were seen in the stomach and in the radial canals. Lipid droplets were seen in all *Sarsia princeps* examined. They were mostly within the stomach but some smaller amounts were seen in the radial canals.

In Antarctic medusae, lipids were seen in only one of the four species examined. A few small droplets were present in the stomachs of *Solmundella bitentaculata.*

The ctenophore *Beroe cucumis* was one of the dominant species of gelatinous zooplankton in both the Arctic and Antarctic. Most arctic specimens contained some small reddish-colored oil droplets (0.05-0.3 mm) within the meridional canals (Fig. 1). These lipids contained red pigment granules that apparently came from its prey, *Mertensia ovum.* This was later verified by feeding experiments. In specimens with small deposits, lipids mostly consisted of medium-sized droplets (0.4-0.6 mm) in the aboral portion of the meridional canals. Antarctic specimens of *B. cucumis* contained only a few small droplets in the meridional canals.

The arctic ctenophore *Bolinopsis infundibulum* contained small oil droplets (0.1-0.3 mm) in the meridional canals (Fig. 1).

Mertensia ovum was the most abundant species of gelatinous zooplankton in the Arctic. It was unique in that large amounts of lipids occurred in specialized storage structures: paired, bicornate "oil sacs" extending orally along the tentacle bulbs (Fig. 2). In small specimens (<15 mm TL), the sacs appeared as discrete organs on either side of the tentacle bulbs (Fig. 2E). In larger individuals, the sacs obscured the tentacle bulbs. In all the bicornate sacs that we observed, one branch was longer than the other. When empty, the sacs are nearly invisible (Fig. 2F), but when full they are conspicuous (Figs. 2A-E). In relationship to the length of the specimen, a full sac had a diameter of about 2-4% and a length of about 40-55%. Based on these measurements, a 40 mm long specimen could contain about 10-20 mg of lipid. The amount of lipid in the sacs varied. They appeared fullest in ctenophores collected where *Calanus* spp. were most abundant.

In the Antarctic ctenophore *Callianira antarctica,* juvenile specimens (1-2 mm in length) contained an abundance of lipid droplets both in the stomodeum and in the meridional canals. In larger specimens (12-45 mm) lipids were confined to the stomodeum. Although this species resembles *M. ovum* in general appearance, it lacks oil sacs.

In Situ *Observations of Feeding*

Because visible lipid accumulations were confined to the digestive tract of the gelatinous zooplankton, they probably came from ingested prey. In the Arctic we saw many of these

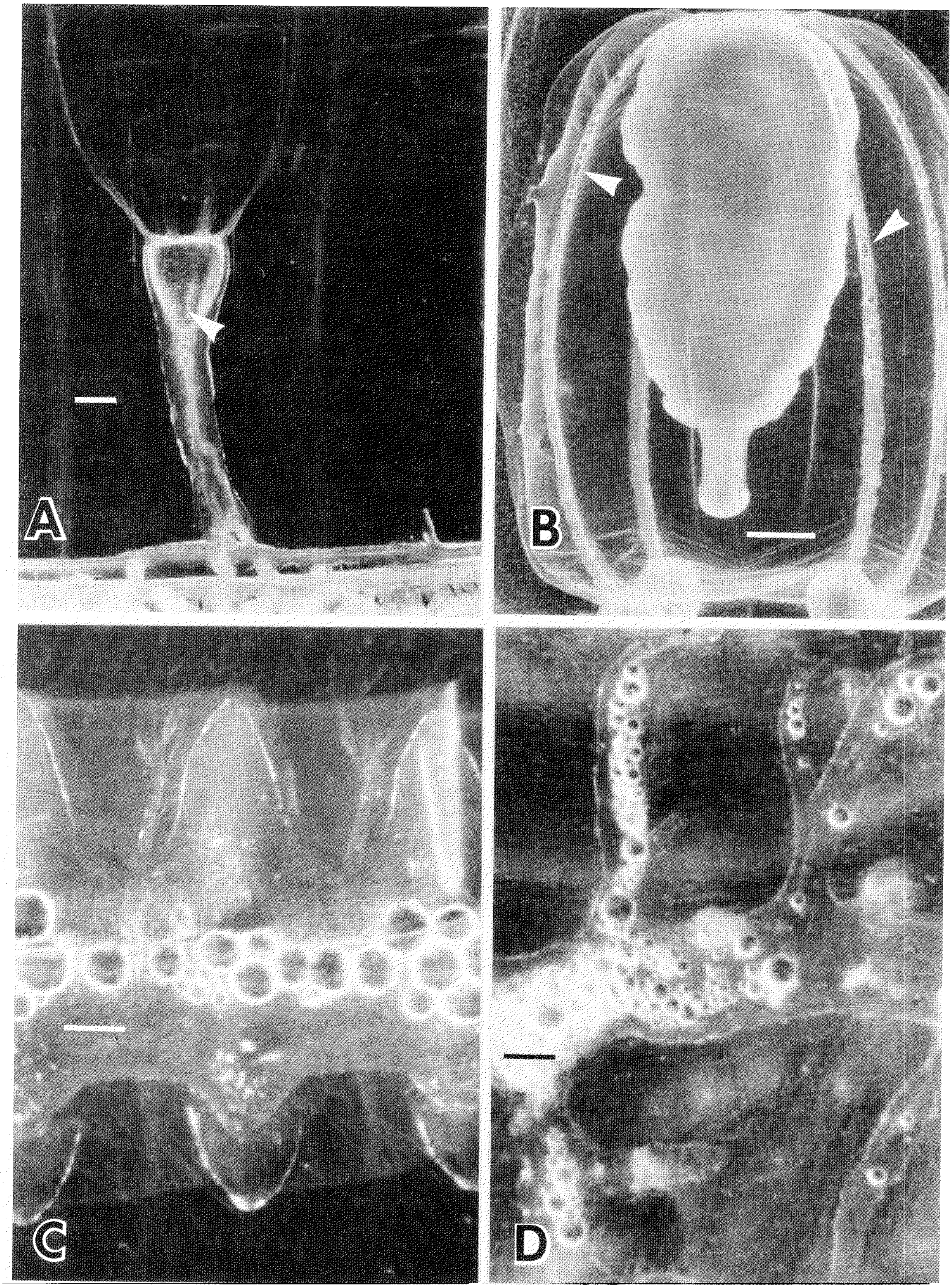

FIG. 1. Photographs of *in situ* collected gelatinous predators with lipids. A. *Aglantha digitale* manubrium with lipid droplet (arrow) at base of stomach; bar = 0.5 mm. B. *Euphysa japonica* manubrium and radial canals showing lipids in radial canals (arrow); not visible are extensive lipid accumulations in the opaque stomach; bar = 1 mm. C. *Bolinopsis infundibulum* meridional canal below comb row with lipids; bar = 0.25 mm. D. *Beroe cucumis* branching meridional canal with lipids; bar = 0.5 mm.

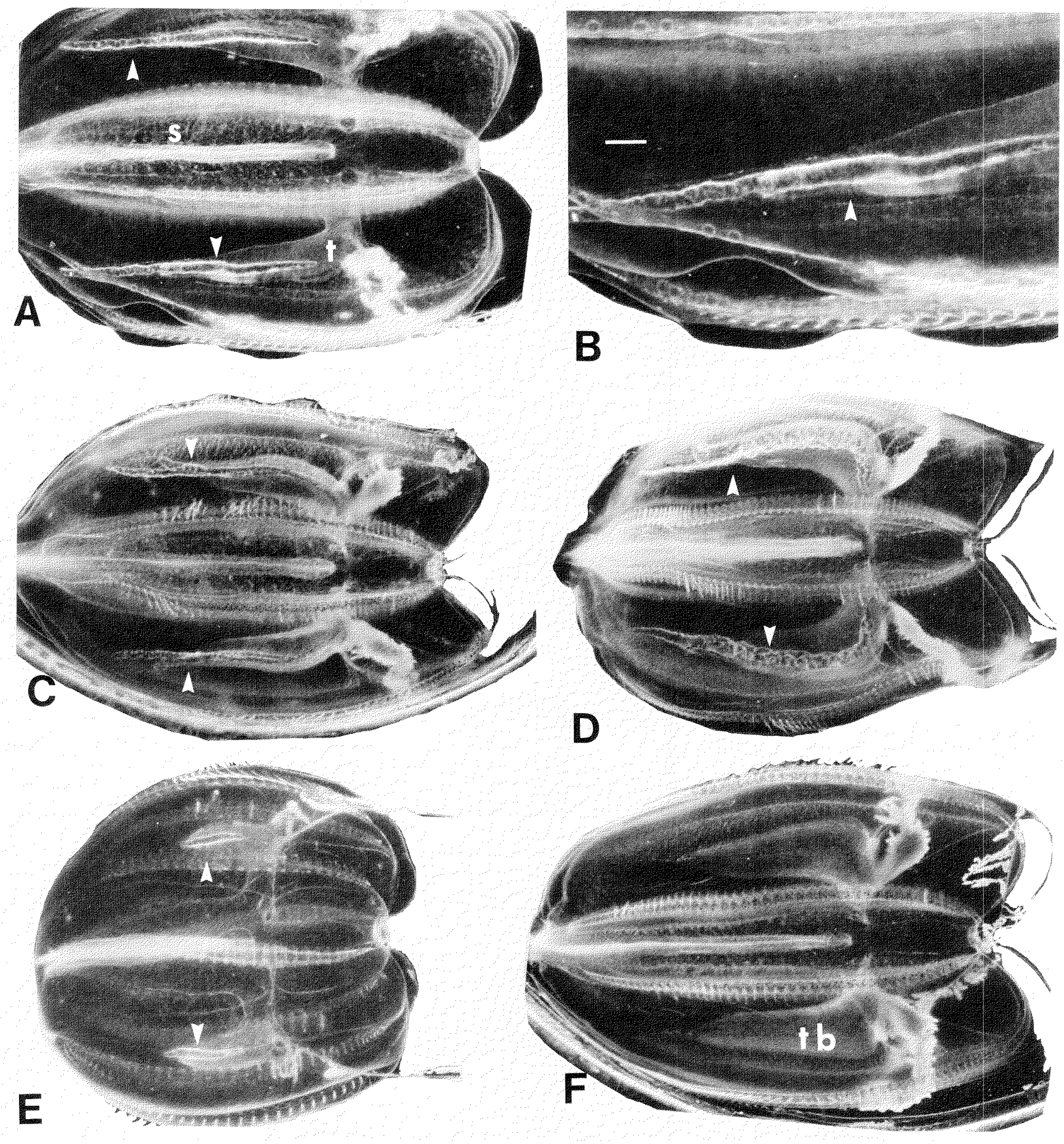

FIG. 2. Photographs of *Mertensia ovum* with and without lipids. A. Specimen (24 mm total length, TL) showing one-half of animal with mostly filled oil sac; o = oil sac, s = stomodeum, t = tentacle in tentacle sheath. B. Enlargement of one oil sac (arrow) of specimen in 2A; bar = 1 mm. C. Specimen (20 mm TL) with paired, bifurcated oil sacs (arrows). D. Specimen (27 mm TL) with very large rope-like oil sacs (arrows). E. Specimen (9 mm TL) with small oil sacs (arrows). F. Specimen (17 mm TL) starved for 3 weeks with no lipids in oil sacs; tb = tentacle bulb.

predators feeding on the oil-rich copepods *Calanus hyperboreus* and *C. glacialis.* We found *Calanus* ssp. in the guts of hand-collected *Euphysa*, *Catablema*, *Halitholus* and *Sarsia* medusae. *Mertensia ovum*, the most abundant gelatinous predator in surface waters of the Arctic, was observed feeding on copepods and was often collected with many *Calanus* spp. in its guts.

Mertensia ovum appears to be the major prey of both *Beroe cucumis* and *Aegina citrea*, and hence lipids in these animals probably originated from this source. The guts of both of these predators contained the distinctive red pigment of *M. ovum*, as well as copious amounts of lipid.

In the Antarctic, some *Callianira antarctica* were collected with ingested *Calanoides acutus*, a copepod that has large oil sacs. However, other specimens had fed on *Limacina helicina*, a pteropod that contained little or no visible lipids.

In Vitro Feeding Experiments

Calanus spp. copepods with large oil sacs were fed to starved medusae and ctenophores that contained no visible lipid or to animals where the amount of lipid was previously categorized. Within 6 h after feeding, large amounts of lipids were seen at the base of the stomachs of *Catablema* sp. and *Halitholus pauper.* After 12 h, the lipids appeared as small droplets in the radial canals and after 1-3 d no lipids were seen.

Similar results were obtained by feeding *Calanus* spp. to the ctenophore *Bolinopsis.* After feeding, lipids were concentrated in the aboral portion of the gut. Later they were seen in the meridional canals as small droplets. Even after 4-5 d a significant amount of lipids remained in the canals. Lipids in the canals of the preoral lobes were the last to disappear, after about 6 d.

When *Calanus* spp. were fed to *M. ovum*, lipids were seen in the canals within 12-18 h and subsequently began to accumulate in the paired oil sacs.

When *Calanoides acutus* were fed to *C. antarctica*, lipids accumulated in the gut as the prey were digested and remained there for more than two weeks. No lipids were seen in the meridional canals.

Fate of Lipids in Starved Animals

The amount of lipid present in the gastrovascular system of gelatinous predators depends on the amount of lipid consumed and the length of time since ingestion. In the medusae *Catablema* sp. and *H. pauper* that were fed *Calanus* spp., lipids disappeared after a few days of starvation. However, in *Beroe cucumis*, residual lipids were still seen in the canals after 12 d of starvation. In *Bolinopsis*, lipids remained in the canals for up to 5 d after feeding. In small *Mertensia* (15-20 mm TL) with full oil sacs, lipids decreased during starvation to about one-half their original amount after 20-25 d and the body length decreased by about 25%.

DISCUSSION

The majority of medusae and ctenophores collected in the Arctic contained visible lipids. This supports studies on their biochemical composition by Percy and Fife (1981), Clarke (1983) and others, who found that the lipid content could equal up to 20% of dry weight (Table 1). Visible lipids were much less abundant in Antarctic medusae and ctenophores in our study, corresponding with previous reports (Table 1). This apparent difference may be due to two factors. First, the frequency of Antarctic gelatinous zooplankton that contained ingested prey was low relative to the arctic. Thus prey-derived lipids in Antarctic predators may have been assimilated prior to collection. Second, most of the Antarctic medusae and some ctenophores may have fed primarily on *Limacina helicina*, a pteropod that contains little lipids (Hagen, 1988). However, the scyphomedusa *Diplulmaris antarctica* did ingest small numbers of the lipid-rich pteropod *Clione antarctica*. Only *Callianira antarctica* had ingested oil-rich copepods, but these prey are small relative to *Calanus* spp. and were always present in low numbers. It should be noted, however, that *L. helicina* is also extremely abundant in the Arctic (Kobayashi, 1974; unpubl. observations).

Differences in the amounts of lipids in polar gelatinous predators are probably related to amounts in their prey. In the Antarctic, the average lipid content of gelatinous predators is about 3% DW (range = 0.4-6%), if the 72% DW value for *Beroe* sp. is excluded, whereas in the Arctic, the mean is nearly three times higher, about 8% DW (range = 1.5-22%) (Table 1). In the Arctic, the abundance of lipid-rich *Calanus* spp. copepods may be responsible for the high levels of lipids in gelatinous predators.

No adipose tissues were seen in polar gelatinous predators. Lipids were always confined to the lumen of the digestive system. This contrasts with other zooplankton, where lipids are stored in specialized sites outside the lumen of the gut (Clarke, 1983; Reinhardt and Van Vleet, 1986). The only gelatinous species known with distinct lipid deposition sites is the ctenophore *Mertensia ovum*, which apparently amasses undigested lipid, until absorbed, in morphologically specialized areas of the gastrovascular system, i.e., oil sacs. These sacs probably serve as storage depots and thus are analogous to specialized storage sites in other taxa in that they probably serve as energy reserves.

Others have previously illustrated the oil sacs of *Mertensia ovum* without knowing their function (e.g., Martens, 1675: Fig. g; Scoresby, 1820: Fig. 4; Mertens, 1833: Plate 9). Mertens (1833), for example, thought that they were ovaries. Indeed, some of the smaller droplets do look like eggs.

During extracellular digestion, depot lipids from prey are released into the digestive tracts of gelatinous predators. The site of lipid absorption is uknown but it probably is in areas of the gastrovascular system where small oil droplets occur. Because visible lipids were confined to the coelenteron, they probably remain unmodified until slowly taken up by the gastrodermis as small oil droplets.

The role of lipids in regulating buoyancy has not been examined for gelatinous zooplankton but has been studied in other polar organisms, especially fishes (De Vries and Eastman, 1978; Neighbors and Nafpaktitis, 1982). Buoyancy regulation in gelatinous zooplankton is mostly achieved by elimination of sulfate ions (Denton and Shaw, 1962; Bidigare and Biggs, 1980; Mills and Vogt, 1984). Gelatinous species with large amounts of lipids may achieve some lift (about 150 mg per gram of wax esters). However, because lipid deposits vary with time, any resultant buoyancy would also vary.

Wax esters are an important lipid class in some boreal and polar gelatinous zooplankton (Lee, 1974; Clarke *et al.*, 1987; Hagen, 1988). Morris and McCartney (1983) suggested that the wax esters found in ctenophores were from prey still in the gut at the time of analysis, and Clarke (1984) mentions finding wax esters near the gut of a ctenophore that probably originated from prey. However, Clarke *et al.* (1987) found that the fatty acid composition of wax esters of two arctic ctenophores, *Bolinopsis infundibulum* and *Beroe cucumis*, was significantly different from that of their presumed prey. We agree with Morris and McCartney (1983), but would add that exogenic lipids could be outside the stomach in the gastrovascular canals. Unfortunately, Clarke *et al.* (1987) did not actually determine the diets of *B. cucumis* and *B. infundibulum* in their study. Instead, they surmised on the basis of other studies that the food web was invariable, i.e., *Calanus-Bolinopsis-Beroe*. On the contrary, *Mertensia ovum* is much more abundant (we collected it at 60 of 71 stations) than *B. infundibulum* (collected at only 24 stations) in the Arctic and probably is a more important predator of *Calanus* spp. (Percy and Fife, 1985; unpubl. observations). Because of this, *M. ovum* is probably the major prey of *B. cucumis* in the Arctic, although *B. cucumis* does eat other prey, such as the pteropod *L. helicina* (unpubl. observations). Furthermore, in the shallow waters near Svalbard, where Clarke *et al.* (1987) worked, prey other than *Calanus* spp. could be eaten by both *B. infundibulum* and *M. ovum*, thus possibly affecting the fatty acid composition.

Percy (1988) gives evidence for seasonal utilization of lipids in *Mertensia ovum* during the winter. He found that the O/N ratio (oxygen consumed to nitrogen excreted) in winter was about double that in the summer. This shift toward a more lipid-based metabolism in winter could be from catabolism of lipids, as Percy (1988) suggests, or to greater amounts of lipid in the diet. Dietary lipids could come from *Calanus* spp. that have large lipid reserves during the winter (Lee, 1975; Båmstedt, 1984).

The lipid deposits that we observed in *M. ovum* could provide a significant energy reserve. For example, an 8 g *M. ovum* with a 10 mg lipid deposit could fast for about one month without a change in size (using respiration data in Percy, 1988).

The presence of lipids in the gastrovascular systems of gelatinous predators could be a useful indicator of food availability, since during starvation lipids are slowly assimilated. However, low lipid levels may not necessarily mean a lack of prey, since some prey could be lipid-poor and digestion rates may vary.

ACKNOWLEDGEMENTS

We would like to thank the captain (Adrian Lonsdale) and crew of the R/V *Endeavor* for making our cruise in the Arctic both productive and enjoyable. We also wish to thank our fellow divers in both the Arctic and Antarctic. This research was supported by NSF grants OCE-8516083, OCE-8746136 and DPP-8613388 to G.R. Harbison and grant DPP-8716337 to R.J. Larson. This is contribution No. 700 of Harbor Branch Oceanographic Institution.

REFERENCES

AAREM, H.E., VONK, H.J., and ZANDEE, D.I. 1964. Lipid metabolism in *Rhizostoma*. Archives Internationales de Physiologie et de Biochemie 72:607-614.

BÅMSTEDT, U. 1984. Diet variations in the nutritional physiology of *Calanus glacialis* from Lat. 78°N in the summer. Marine Biology 79:257-267.

BENSEN, A.A., and LEE, R.F. 1975. The role of wax in oceanic food chains. Scientific American 232:77-86.

BIDIGARE, R.R., and BIGGS, D.C. 1980. The role of sulfate exclusion in buoyancy maintenance by siphonophores and other gelatinous zooplankton. Comparative Biochemistry and Physiology 66(A):467-471.

CECCALDI, H.J., KANAZAWA, A., and TESHIMA, S. 1978. Chemical composition of some Mediterranean macroplanktonic organisms. 1 — Proximate analysis. Tethys 8:295-298.

CLARKE, A. 1980. The biochemical composition of krill, *Euphausia superba* Dana, from South Georgia. Journal of Experimental Marine Biology and Ecology 43:221-236.

______. 1983. Life in cold water: the physiological ecology of polar marine ectotherms. Oceanography and Marine Biology Annual Review 21:341-453.

______. 1984. The lipid content and composition of some Antarctic macrozooplankton. British Antarctic Survey 63:57-60.

______, HOLMES, L.J., and HOPKINS, C.C.E. 1987. Lipid in an arctic food chain: *Calanus*, *Bolinopsis*, *Beroe*. Sarsia 72:41-48.

DENTON, E.J., and SHAW, T.I. 1962. The buoyancy of gelatinous marine animals. Journal of Physiology 161:14-15.

DE VRIES, A.L., and EASTMAN, J.T. 1978. Lipid sacs as a buoyancy adaptation in an Antarctic fish. Nature [London] 271:352-353.

EASTMAN, J.T. 1988. Lipid storage systems and the biology of two neutrally buoyant Antarctic notothenioid fishes. Comparative Biochemistry and Physiology 90(B):529-537.

HAGEN, W. 1988. On the significance of lipids in Antarctic zooplankton. Reports on Polar Research 49:1-129.

HOEGER, U. 1983. Biochemical composition of ctenophores. Journal of Experimental Marine Biology and Ecology 72:251-261.

HOOPER, S.N., and ACKMAN, R.G. 1972. Presence of trans-6-hexadecenoic acid in the white jellyfish *Aurelia aurita* Lamarck and in a Caribbean gorgonian. Lipids 7:624-626.

HYMAN, L.H. 1940. Observations and experiments on the physiology of medusae. Biological Bulletin 79:282-296.

IKEDA, T. 1972. Chemical composition and nutrition of zooplankton in the Bering Sea. In: Takenouti, A.Y., ed. Biological Oceanography of the Northern North Pacific Ocean. Tokyo: Idemitsu Shoten. 433-442.

JOSEPH, J.D. 1979. Lipid composition of marine and estuarine invertebrates. Porifera and Cnidaria. Progress in Lipid Research 18:1-30.

KOBAYASHI, H.A. 1974. Growth cycle and related vertical distribution of the thecostomus pteropod *Spiratella* (*"Limacina"*) *helicina* in the central Arctic Ocean. Marine Biology 26:295-301.

LEE, R.F. 1974. Lipids of zooplankton from Bute Inlet, British Columbia. Journal of the Fisheries Research Board of Canada 31:1577-1582.

______. 1975. Lipids of arctic zooplankton. Comparative Biochemistry and Physiology 51(3B):263-266.

______ and HIROTA, J.A. 1973. Wax esters in tropical zooplankton and nekton and the geographical distribution of wax esters in marine copepods. Limnology and Oceanography 18:227-239.

______ and BARNETT, A.M. 1971. Distribution and importance of wax esters in marine copepods and other zooplankton. Deep-Sea Research 18:1147-1165.

MACKIE, G.O. 1974. Locomotion, flotation and dispersal. In: Muscatine, L., and Lenhoff, H.M., eds. Coelenterate biology: reviews and perspectives. New York: Academic Press. 313-357.

MARTENS, F. 1675. Spitzbergische oder Groenländische Reise beschreibung gethan in Jahr 1671. Hamburg: Gottfried Schultzen Kosten.

MERTENS, H. 1833. Beobachtungen und Untersuchungen über die Beroeartigen Akalephen. Mémoires de L'Académie Impériales des Sciences de St. Pétersbourg. 6th Series. 2:479-543.

MILLS, C.E., and VOGT, R.G. 1984. Evidence that ion regulation in hydromedusae and ctenophores does not facilitate vertical migration. Biological Bulletin 166:216-227.

MORRIS, R.J., and McCARTNEY, M.J. 1983. *Bolinopsis infundibulum* (O.F. Müller): Biochemical composition in relation to diet. Journal of Experimental Marine Biology and Ecology 67:149-157.

NEIGHBORS, M.A., and NAFPAKTITIS, B.G. 1982. Lipid compositions, water contents, swimbladder morphologies and buoyancies of nineteen species of midwater fishes (18 myctophids and 1 neoscopelid). Marine Biology 66:207-215.

PERCY, J.A. 1988. Influence of season, size, and temperature on the metabolism of an arctic cydippid ctenophore, *Mertensia ovum* (Fabricius). Sarsia 73:61-70.

______ and FIFE, F.J. 1981. The biochemical composition and energy content of arctic marine macrozooplankton. Arctic 34:307-313.

______. 1985. Energy distribution in an arctic coastal macrozooplankton community. Arctic 38:39-42.

REINHARDT, S.B., and VAN VLEET, E.S. 1984. Lipid composition of Antarctic midwater invertebrates. Antarctic Journal 19(5):139-141.

______. 1986. Lipid composition of twenty-two species of Antarctic midwater zooplankton and fishes. Marine Biology 91:149-159.

SARGENT, J.R. 1976. The structure, metabolism and function of lipids in marine organisms. In: Malins, D.C., and Sargent, J.R., eds. Biochemical and biophysical perspectives in marine biology. Vol. 3. New York: Academic Press. 149-212.

SCORESBY, W. 1820. An account of the arctic regions, with a history and description of the northern whale-fishery. 2 vols. Edinburgh: Archibald Constable and Co.

SIPOS, J.C., and ACKMAN, R.G. 1968. Jellyfish (*Cyanea capillata*) lipids: fatty acid composition. Journal of the Fisheries Research Board of Canada 25:1561-1569.

YASUDA, S. 1974. Sterol composition of jelly fish (medusae). Comparative Biochemistry and Physiology 48B:225-230.