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NOTE

Lipid and lipid class content of the pelagic tunicate *Oikopleura vanhoeffeni*

Don Deibel[1], Joann F. Cavaletto[2], Mike Riehl[1], Wayne S. Gardner[2]

[1] Ocean Sciences Centre and Department of Biology, Memorial University, St. John's, Newfoundland, Canada A1C 5S7
[2] Great Lakes Environmental Research Laboratory, National Oceanic and Atmospheric Administration, 2205 Commonwealth Blvd., Ann Arbor, Michigan 48105, USA

ABSTRACT: Lipid biochemistry of pelagic tunicates is poorly known, despite the fact that the larvae of several flatfish species depend exclusively on oikopleurid appendicularians at time of first feeding. Microgravimetric analysis and thin-layer chromatography with flame ionization detection (TLC-FID) were used to determine the total lipid content and lipid class composition of the pelagic tunicate *Oikopleura vanhoeffeni*. Our goal was to determine the dominant storage form of lipid in *O. vanhoeffeni* before and after the spring diatom bloom. Lipid levels and lipid class composition were measured for all 5 ontogenetic stages of *O. vanhoeffeni*, plus eggs. Levels ranged from 23 to 525 µg ind.$^{-1}$, over the entire life cycle, increasing exponentially with increasing body size and ontogenetic (i.e. maturity) stage. Regression analyses showed that 84 % of the variation in the logarithm of total lipid content was explained by the logarithm of ontogenetic stage. Per unit dry weight, the mean (± SE) lipid concentration was 5 ± 0.3 % before the bloom and 7.5 ± 1.2 % after the bloom. Lipid class composition provided scant evidence for energy storage by *O. vanhoeffeni*, with no wax esters before or after the spring bloom and moderate levels of triacylglycerols present in pre-bloom animals only. Individuals collected after the spring bloom were significantly smaller than those from before the bloom, suggesting that a spawning event had occurred sometime during the bloom. Predominant lipid classes before and after the bloom were phospholipids (65 to 90 % of total lipid) and acetone-mobile polar lipids (4 to 24 %). Thus, although this appendicularian is a suspension feeder inhabiting very cold water, it does not store wax esters as do high-latitude copepods. Rather, *O. vanhoeffeni* has the lipid characteristics of a gelatinous, opportunistic colonist, i.e. that of an omnivore with the ability to direct ingested food energy into rapid somatic growth or gamete production.

Planktonic copepods living at high latitudes store energy seasonally in the form of deposit lipids, primarily triacylglycerols (TAG) and wax esters (WE) (Lee 1975, Falk-Petersen et al. 1987, Larson & Harbison 1989, and references therein). These compounds provide energy for overwintering metabolism and spring egg production (Lee et al. 1972, Lee 1975, Gatten et al. 1980, Larson & Harbison 1989, Smith 1990). In comparison, energy storage by gelatinous zooplankton is poorly known and studies have been limited to carnivorous species (Joseph 1979, Clarke et al. 1987, Larson & Harbison 1989). We have found no information on lipid levels in gelatinous suspension feeders such as the pelagic tunicates.

Oikopleura vanhoeffeni is a large, common, cold ocean pelagic tunicate with a pronounced seasonal cycle of abundance and spawning (Mahoney & Buggeln 1983, Deibel 1988). It reproduces at least once each year, during the decline of the spring diatom bloom in April and May (Davis 1982, 1986). Individuals are hermaphroditic, producing several hundred eggs and copious sperm prior to spawning by rupture of the body wall. Large, pre-spawning tunicates are common in surface waters during mid-winter, when the concentration of particulate organic carbon (POC) and chlorophyll *a* are at their annual minima (Deibel 1988).

Oikopleura vanhoeffeni is a generalist grazer, using a fine, mucous filter for feeding, ingesting particles from a wide size range including diatom chains (Deibel & Turner 1985) and colloids (Flood et al. 1992). *O. vanhoeffeni* populations have a grazing impact in Newfoundland (Canada) waters equivalent to that of all the copepods combined (Knoechel & Steel-Flynn 1989), and are a favored prey of larval and juvenile cod and flatfish (Shelbourne 1962, Gadomski & Boehlert 1984, Keats et al. 1987, K. Frank pers. comm.). Thus, this link in the food chain may represent a means by which energy flux from diatoms to fish is mediated.

Our goal was to determine the dominant storage form of lipid in *Oikopleura vanhoeffeni* collected before and after the spring diatom bloom. We have been able to document the lipid content of all 5 ontogenetic stages of *O. vanhoeffeni*, including eggs. These results may clarify the mechanism whereby

O. vanhoeffeni is able to overwinter despite low food particle concentrations and may help to define its role in lipid and energy flux from phytoplankton to fish.

Methods. *Oikopleura vanhoeffeni* was collected individually into 500 ml glass jars by SCUBA divers working in Logy Bay (47° 37′ N, 52° 40′ W), insular Newfoundland, in February and May 1990 (water temperature −1.5 and 3.0 °C respectively). Within 30 min of collection the individuals were transferred into filtered seawater (GF/C) for at least 60 min to permit gut evacuation. When the guts were colorless, each individual was prodded from its mucous 'house', then rinsed briefly in distilled water. The gonad was removed, and the remaining trunk measured to the nearest 10 μm using a dissecting microscope with ocular micrometer. Each tunicate was assigned to 1 of 5 ontogenetic stages, after the categories introduced for *O. labradoriensis* by Shiga (1976). These are, (1) gonad absent, (2) small, undifferentiated testis present, (3) testis greater in height than in stage 2, and divided into right and left halves, but both still less than the width of the trunk, (4) increase in height of gonad and first appearance of the ovary, and (5) gonad (testis + ovary) very large, wider and higher than the trunk.

Individuals were then placed in small, 2 ml glass test tubes and dried under N_2 at 55 °C for at least 48 h. This protocol was designed to destroy lipases while causing little or no oxidation of lipids. Small individuals were pooled (Table 1) to provide sufficient material for subsequent lipid analyses. It is not possible to determine accurately the dry weight of pelagic tunicates because of confounding problems with salt and chemically 'bound' water (Madin et al. 1981). The method of choice is to express weight as the mass of a particular element, such as nitrogen or carbon, determined by high-temperature combustion. In the present case, body length (mm) was converted to carbon content (μg) using the following power curve developed previously for *O. vanhoeffeni* (Deibel 1986).

$$\text{Carbon} = 4.59\ \text{Trunk}^{3.2} \quad (n = 25,\ r^2 = 0.90,\ p < 0.001) \qquad (1)$$

Carbon content was then converted to an estimate of dry weight by multiplying by 12, a factor derived for salps by Schneider (1989). After drying, the samples were shipped to the Great Lakes Environmental Research Laboratory, where they were stored frozen in a desiccator under vacuum and N_2 to prevent lipid oxidation.

Total lipids were extracted with chloroform : methanol (2 : 1 v/v), washed with an aqueous salt solution (0.9 % NaCl), and quantified gravimetrically using a micro-version (Gardner et al. 1985) of the method of Folch et al. (1957). A subsample (ca 5 to 10 μl) of each lipid extract was sealed under nitrogen in a capillary tube and stored at < 0 °C for later determination of lipid classes by thin-layer chromatography with flame ionization detection (TLC-FID), (Parrish 1986, 1987, Parrish et al. 1988). The lipid extract was spotted directly onto silica-coated Chromarods-SIII (RSS Inc.).

Table 1. *Oikopleura vanhoeffeni*. Lipid content before and after the spring diatom bloom. Data is arranged both before and after the bloom in ascending order of ontogenetic stage. No. tunicates: number of individuals of similar body size pooled for the analysis; stage: a relative ranking (1 to 5) of the ontogenetic state of the specimens after the system of Shiga (1976; see 'Methods' for explanation)

No. tunicates	Stage	Trunk length (mm)	Total lipid (μg)	Lipid (% of dry wt)
February (pre-bloom)				
5	3	2.93	91	5.3
1	4	4.38	278	4.5
1	4	5.00	492	5.2
1	4–5	4.88	376	4.3
1	4–5	4.50	395	5.8
1	5	3.00	525	28
May (post-bloom)				
5	1	1.44	26	15
3	2	2.38	23	2.6
3	2	2.40	53	5.8
3	2	2.25	41	5.5
3	2	2.38	57	6.5
3	2	2.53	77	7.1
3	3	2.58	88	7.7
1	4	2.90	191	11
1	4	3.10	269	13

Lipid classes were separated by sequentially developing the rods in increasingly polar solvent systems (Parrish 1986, 1987). After solvent development, rods were scanned with an Iatroscan Mark IV (Iatron Labs, Tokyo, Japan) connected to a Hewlett-Packard 3392A integrator A mixed lipid standard, containing 1 compound from each of the following lipid classes: hydrocarbon, sterol ester, triacylglycerol, free fatty acid, alcohol (aliphatic), sterol (alicyclic alcohol), and phospholipid, was used for TLC-FID calibration and quantification. Calibration curves were determined over a range of 0.15 to 30 μg for each standard compound.

All mean values reported in the text are ± 1 SE unless indicated otherwise. All statistical tests of differences between mean values are *t*-tests unless indicated otherwise. All proportions were transformed using the arcsin before hypothesis testing.

Results. The individuals analyzed in this study ranged in trunk length from 1.44 to 6.25 mm ($\bar{x}$ ± SD = 3.38 ± 1.26 mm, n = 18). Mean body size was significantly greater ($p < 0.01$) before the spring bloom ($\bar{x}$ = 4.45 ± 0.38 mm, n = 8) than after the bloom ($\bar{x}$ = 2.53 ± 0.16 mm, n = 10). This result is consistent with the occurrence of a spawning event sometime during the bloom, in April or early May. This difference in body size was reflected in the total lipid content, with a mean of 359 ± 65 μg ind.$^{-1}$ before the bloom (n = 6), and a significantly lower mean ($p < 0.001$) of 92 ± 28 μg ind.$^{-1}$ after the bloom (n = 9, Table 1; 3 samples lost during analysis). Considering all data from before and after the bloom, total lipid content increased exponentially with increasing body size (Fig. 1a) and ontogenetic stage (Fig. 1b). Regression analyses indicated that ontogenetic stage was a better predictor of lipid content than was body size, accounting for 84 % of the total variability (Fig. 1b). The slight overlap in body size of individuals collected before vs after the bloom prohibited meaningful statistical comparison of slopes and intercepts for the 2 sampling dates shown in Fig. 1a, b. After converting body length to an estimate of dry weight (see 'Methods'), lipid content of ontogenetic stages 2 to 4 ranged from 4.3 to 5.8 % of dry weight before the bloom ($\bar{x}$ = 5.0 ± 0.3 %, n = 5) and 2.6 to 13 % after the bloom ($\bar{x}$ = 7.5 ± 1.2 %, n = 8; Table 1).

The lipid class data provided scant evidence of energy storage in *Oikopleura vanhoeffeni* (Fig. 2). Sterol and wax esters (WE), methyl esters (ME) and diglycerides (DIG) were not detectable before or after the bloom. The predominant classes were acetone-mobile polar lipids (AMPL, which may include chlorophylls, glycolipids and monoacylglycerols; range 4 to 24 % of total lipid) and phospholipids (PL, range 65 to 90 % of total lipids). There were no triacylglycerols (TAG) found in individuals collected after the bloom, and no hydrocarbons (HC) or alcohols (ALC) in those collected before the bloom. Free fatty acids (FFA) and sterols (ST) were found in limited quantities in individuals collected before and after the bloom.

Combining lipid class data from before and after the bloom revealed little trend in % composition with increasing body size (Fig. 3a to c). This result indicates that although lipid levels increased with increasing body size (Fig. 1a), lipid class composition was relatively independent of body size. Simple linear regression analyses showed that only TAG had a significant relationship with body size (the slope was significantly different from 0 at $p < 0.05$). However, between indi-

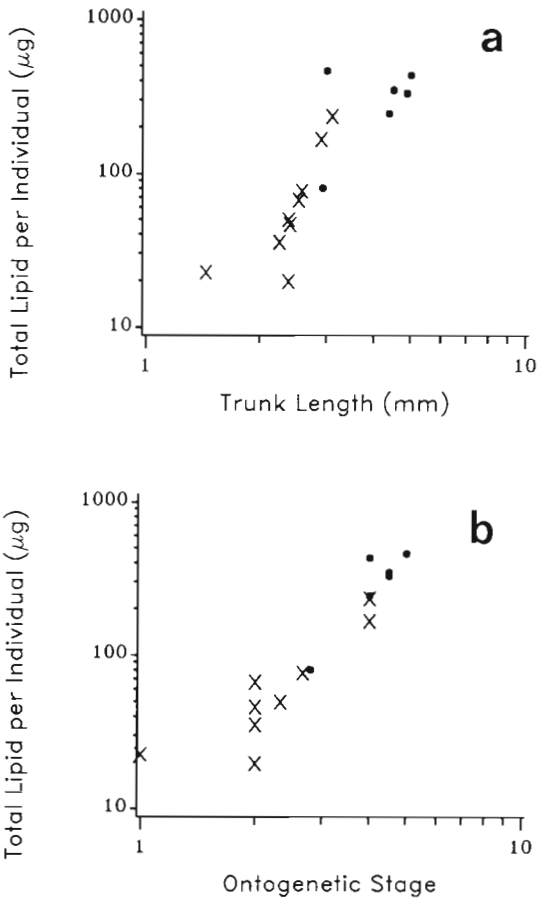

Fig. 1 *Oikopleura vanhoeffeni*. Log-log plot of total lipid content (μg ind.$^{-1}$) vs (a) body size (i.e. trunk length in mm) and (b) ontogenic stage, (•) before (n = 6) and (×) after (n = 9) the spring diatom bloom. Ontogenetic stage ranking (1 to 5) is after the system developed by Shiga (1976; see 'Methods'). A stage of 4.5 represents 2 individuals that were judged to be intermediate between stages 4 and 5. All other fractional values of maturity stage represent the mean stage of a pool of individuals of similar length (see Table 1 for the number of individuals pooled in each case). The equation for the power curve relationships are: (a) lipid content = 6.7 × trunk length$^{2.69 \pm 0.46}$ (n = 15, adjusted r^2 = 0.70), with slope significantly different from zero (F = 34.4, $p < 0.001$); and (b) lipid content = 12.0 × stage$^{2.22 \pm 0.26}$ (n = 15, adjusted r^2 = 0.84), with slope significantly different from zero (F = 75.2, $p < 0.001$)

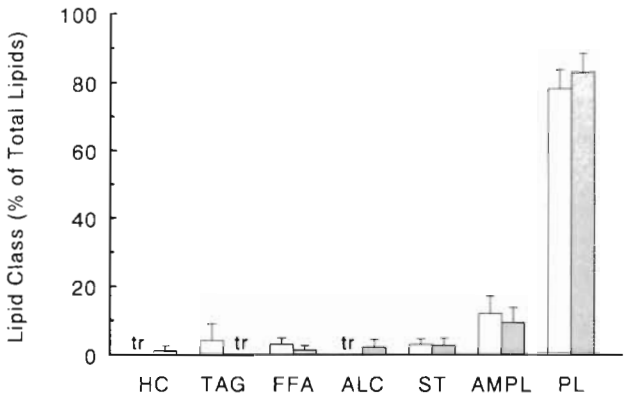

Fig. 2. *Oikopleura vanhoeffeni*. Lipid class composition (% of total lipid + 2 SE) (open bars) before and (shaded bars) after the spring diatom increase. (n = 6 for all before bloom samples, and n = 8 for all samples taken after the bloom.) HC: hydrocarbons; TAG: triacylglycerols; FFA: free fatty acids; ALC: alcohols; ST: sterols; AMPL: acetone-mobile polar lipids; PL: phospholipids; tr: levels not quantifiable. Sterol esters, wax esters, methyl esters and diglycerides were never found in any of our samples

vidual variability was high, since TAG's were found in only 4 of the 6 specimens collected before the bloom (Fig. 3c). In addition, there were no statistically significant relationships between the proportion of any of the lipid classes and ontogenetic stage (data not shown, slopes not different from 0 at $p > 0.15$). A single sample of *Oikopleura vanhoeffeni* eggs that was examined presented a lipid class signature similar to the above pattern, containing predominantly PL (85 %), with lesser content of ST (7 %) and AMPL (6 %).

Discussion. The exponential increase in total lipid content with increasing body size and ontogenetic stage (Fig. 1a, b) and the predominance of PL (Fig. 2), both suggest that the lipid biochemistry of *Oikopleura vanhoeffeni* is dominated by the accretion of somatic tissue during growth. The presence of a high proportion of PL indicates investment in cell membranes, and is similar to the lipid class composition of deep-living sea anemones (PL is 70 to 75 % of total lipids; Joseph 1979), ctenophores (PL is 67 to 70 %; Lee 1974, Morris et al. 1983) and chaetognaths (PL is 63 to 78 %; Lee 1975, Falk-Petersen et al. 1987). Although not examined here, it is possible that polyunsaturated fatty acids (PUFA's) within the PL of oikopleurid cell membranes may help to maintain membrane fluidity at sub-zero water temperatures, as is true for the giant scallop *Placopecten magellanicus* living in the same waters as *O. vanhoeffeni* (Napolitano et al. 1992).

Because *Oikopleura vanhoeffeni* is large, it may serve as a significant source of dietary lipid and other nutrients for predators, including larval and juvenile fish (Shelbourne 1962, Gadomski & Boehlert 1984,

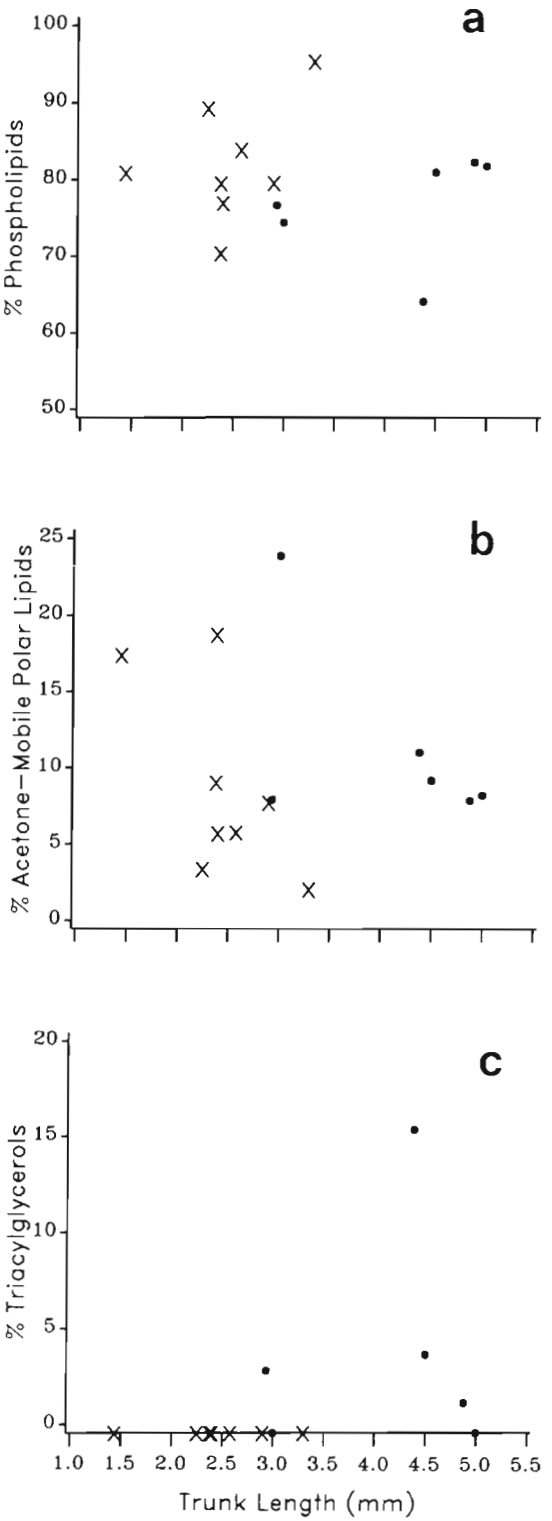

Fig. 3. *Oikopleura vanhoeffeni*. Lipid class composition (% of total lipid) vs body size (i.e. trunk length in mm) (•) before and (×) after the spring diatom bloom. Only % TAG shows a significant positive relationship with trunk length (n = 14, adjusted $r^2 = 0.23$). The slope is significantly different from 0 ($F = 4.8$, $p < 0.05$). All other slopes are not different from 0 ($p > 0.15$). Note the different scaling of the *y*-axes

Keats et al. 1987). *O. vanhoeffeni* has a lipid content ($\bar{x}$ ± SD = 199 ± 177 µg, range 23 to 525 µg; Table 1) equivalent to ca 6, stage 5 copepodites of *Calanus finmarchicus* (ca 30 µg ind.$^{-1}$, Kattner & Krause 1987), the predominant, large copepod in Newfoundland waters. Data from Conception Bay, Newfoundland (K. Frank pers. comm.), indicate that the guts of juvenile Atlantic cod *Gadus morhua*, ca 90 mm long, at times may contain the remains of 170 oikopleurids. This is equivalent to a minimum of 3.9 mg of lipid larva^{-1} if only the smallest oikopleurids are being eaten, or 34 mg of lipid larva^{-1} if oikopleurids of average size are being eaten.

Most of the existing information on lipids in gelatinous zooplankton concerns 'carnivorous' species. Arctic medusae and ctenophores have a mean lipid content of 8% of dry weight (range of 1.5 to 22%, Clarke et al. 1987, Larson & Harbison 1989). These values are much lower than the lipid content of suspension-feeding copepods in these waters (8 to 64%, Lee 1975, Kattner & Krause 1987, Tande & Henderson 1988, Hargrave et al. 1989, Smith 1990). Thus, the metabolism of oikopleurid tunicates appears to be more similar to that of gelatinous predators than to copepods. Possible reasons for this difference are that oikopleurids may not depend on a seasonally-pulsed food supply as do copepods, or that these tunicates may store energy in other more useable forms, e.g. glycogen. As far as we know, no one has examined the carbohydrate metabolism of a pelagic tunicate. Alternatively, pelagic tunicates may simply grow or produce gametes in response to pulses in food supply (Lee 1974) and shrink when food is scarce (Morris et al. 1983). This strategy is typical of opportunistic or 'colonist' species.

The lipid class composition of *Oikopleura vanhoeffeni* provides scant evidence for energy storage by overwintering populations or by populations responding to the spring diatom bloom. The absence of WE in specimens collected before or after the bloom is consistent with published information on sponges, ctenophores and chaetognaths (Joseph 1979, Morris et al. 1983), and shows that oikopleurid tunicates do not store neutral lipid as a long-term, overwintering energy reserve or in response to the bloom. Some pre-bloom specimens contained moderate levels of TAG (2 to 16% of total lipids; Fig. 3c), although between-individual variability was high. This low occurrence of storage lipids may indicate a population under nutritional stress (Clarke et al. 1987), or a rapidly growing population (Norrbin et al. 1990). The latter strategy would be consistent with our observations of active feeding of *O. vanhoeffeni* throughout the year (Urban et al. 1992), and somatic growth in the late spring and summer (Deibel 1988).

In summary, *Oikopleura vanhoeffeni* has a relatively low lipid content, on average ca 6.5% of dry weight. This is similar to the mean lipid content of a number of arctic, gelatinous 'carnivorous' zooplankton (Larson & Harbison 1989). Triacylglycerol, the only storage lipid observed, occurred in only a few tunicates collected before the spring diatom bloom had begun. The predominant lipid class was phospholipids, indicating investment in cell membranes. Thus, although *O. vanhoeffeni* is a cold ocean, suspension-feeding zooplankter, it does not show the usual adaptation to pulsed food supplies shown by high-latitude copepods, i.e. storage of large quantities of wax esters and triacylglycerols. Rather, *O. vanhoeffeni* has the lipid characteristics of a gelatinous, opportunistic colonist, i.e. that of an omnivore, with the ability to direct ingested food energy into rapid somatic growth or gamete production.

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