UC San Diego
UC San Diego Previously Published Works

Title

Sustained fecundity when phytoplankton resources are in short supply: Omnivory by Calanus finmarchicus in the Gulf of St. Lawrence

Permalink

https://escholarship.org/uc/item/59c8g9rp

Journal

Limnology and Oceanography, 39(1)

ISSN

0024-3590

Authors

Ohman, Mark D
Runge, Jefrey A

Publication Date

1994

DOI

10.4319/lo.1994.39.1.0021

Peer reviewed

eScholarship.org Powered by the California Digital Library
University of California

Limnol. Oceanogr., 39(1), 1994, 21-36
© 1994, by the American Society of Limnology and Oceanography, Inc.

Sustained fecundity when phytoplankton resources are in short supply: Omnivory by *Calanus finmarchicus* in the Gulf of St. Lawrence

Mark D. Ohman
Scripps Institution of Oceanography, UCSD, La Jolla, California 92093-0227

Jeffrey A. Runge
Department of Fisheries and Oceans, Institut Maurice Lamontagne, 850 Route de la Mer, P.O. Box 1000, Mont-Joli, Québec G5H 3Z4

Abstract

Despite low ambient concentrations of phytoplankton, *Calanus finmarchicus* sustained relatively high rates of egg production (11–45 eggs female^{-1} d^{-1}) in the open waters of the Gulf of St. Lawrence in late June–early July. These rates were comparable to egg production rates observed in high-chlorophyll waters of the lower St. Lawrence estuary. Contrary to classical, linear food-chain models, variations in egg production of *C. finmarchicus* were therefore not predictable from variations in standing stocks of autotrophic cells. Egg production rates were independent of the concentration of chlorophyll in situ, the abundance of autotrophic microplankton cells, in situ gut fluorescence, and the rate of ingestion of autotrophic particles. Heterotrophic microplankton—including ciliates and dinoflagellates presumed to be heterotrophic—constituted a disproportionate fraction of the ration of *C. finmarchicus* in the open Gulf of St. Lawrence, despite their relatively low cell densities. Evidence suggests that heterotrophic microplankton frequently provided a prey resource sufficient for net lipid synthesis as well as for egg production.

For several decades the dominant view in marine zooplankton ecology has been that population growth of suspension-feeding copepods is governed by fluctuations in the availability of phytoplankton, principally larger autotrophic diatoms and dinoflagellates. Variability in the abundance and composition of autotrophic cells has been translated into variability in ingestion, growth, and fecundity of planktonic metazoans in models of simple linear food chains. Even recent models (Marra and Ho 1993) have taken this perspective. The development of predictive indices for population growth of planktonic copepods, thus, has focused narrowly on the role of phytoplankton and assumed a nearly instantaneous translation of ingested cells into somatic growth and fecundity.

More recently, as the structure and dynamics of pelagic microbial food webs have become better understood, the suggestion has been repeatedly made that heterotrophic protists could be a significant prey resource for larger metazoans (*see* Stoecker and Capuzzo 1990; Gifford 1991). However, despite evidence from laboratory investigations for the ingestion of cells such as aloricate ciliates and tintinnids in simplified prey suspensions, there is limited evidence for the significance of this food-web link in nature (*see* Tiselius 1989; Gifford and Dagg 1991; White and Roman 1992). Part of this scarcity stems from methodological difficulties in conducting incubation experiments with fragile, soft-bodied taxa such as choreotrich and oligotrich ciliates. For example, Tiselius (1989) observed up to 80% mortality of aloricate ciliates in control containers. Moreover, population growth of metazoans cannot be inferred from ingestion alone; variability in rates of assimilation, respiration, and lipid synthesis confounds simple translation of feeding rates into rates of growth and reproduction. Thus, evidence that heterotrophic microorganisms are a significant prey resource for planktonic copepods in situ and that they contribute not only to ingestion but also to the growth of natural populations (measured, e.g. by fecundity) is limited indeed (*but see* White and Roman 1992).

Acknowledgments

Supported by NSF OCE 90-19639, by the Department of Fisheries and Oceans, and by the Natural Sciences and Engineering Research Council, Canada.

We thank L. Berard-Therriault for microscopic analysis of microplankton samples; P. Joly, J.-F. St. Pierre, and other participants in the maiden research voyage of the RV *Fogo Isle*, as well as T. Bender, for their assistance. We also thank the anonymous referees for comments.

Much of the foundation for the development of simple, linear food-chain models came from early experimental work conducted with the planktonic marine copepod *Calanus finmarchicus*) (Gunnerus). Here, in contrast, we illustrate that *C. finmarchicus,* the predominant macrozooplankton species in the Gulf of St. Lawrence (de Lafontaine et al. 1991), sustains relatively high rates of egg production in its low-chlorophyll waters. Egg production by *C. finmarchicus* is not predictable from the ingestion of autotrophic cells alone. We present four lines of evidence in support of this finding. Egg production was found to be independent of ambient Chl *a* concentrations, ingestion of phytoplankton cells in situ as inferred from copepod gut fluorescence, ingestion of chlorophyll-bearing cells in simulated in situ incubations, and ingestion of autotrophic microplankton taxa based on floristic analysis in simulated in situ incubations. We find that egg production in the low-chlorophyll waters of the gulf is explainable by predation on microzooplankton, especially aloricate ciliates, supplemented by dinoflagellates and other microflagellate taxa.

Understanding the factors controlling the fecundity of *C. finmarchicus* in the Gulf of St. Lawrence takes on added significance because of the remarkable dependence of larval redfish (*Sebastes* spp.) on a diet of *Calanus* eggs. Typically, 90–100% of the prey of larval redfish in the gulf is comprised of *Calanus* eggs (Runge and de Lafontaine unpubl. obs.). The association between larval redfish and *C. finmarchicus* may extend over a broad sector of the North Atlantic (Bainbridge and McKay 1968). Reproductive responses of *C. finmarchicus* in the Gulf of St. Lawrence are of further interest because the gulf may provide a source of *C. finmarchicus* for the Nova Scotia Shelf via outflow through Cabot Strait in the Nova Scotia Current (Sameoto and Herman 1992). Hence, variations in population growth rate in the gulf, together with variations in flow through Cabot Strait, may influence the abundance of *C. finmarchicus* on the Scotian Shelf and perhaps other regions of the Northwest Atlantic.

Methods

Vertical profiling—Sampling and experimental work was conducted aboard the RV *Fogo Isle* from 21 June to 3 July 1991. Vertical profiles were obtained with a CTD-Rosette, using an Applied Microsystems STD-12 and 5-liter Go-Flo water bottles. In vivo fluorescence was recorded at stations 0 and 1 with a Sea-Tech fluorometer but was not recorded at subsequent experimental stations because of a battery failure. In vivo fluorescence was calibrated against extracted chlorophyll. Extracted Chl *a* was determined on 90% acetone extracts of material retained on Whatman GF/F filters (150–1,000-ml subsamples, depending on the depth), extracted for 24–36 h at 4°C, then analyzed before and after acidification on a Sequoia-Turner model 112 fluorometer. The fluorometer was calibrated with pure Chl *a* from Sigma Chemical Co. Chlorophyll in the >5-μm size fraction was determined at some depths by passing a separate seawater subsample through a 5-μm polycarbonate filter. Water samples were also filtered onto precombusted GF/F filters for particulate N (PN) and particulate C (PC) analysis (200–1,000 ml). PN and PC contents were analyzed by a Perkin-Elmer 2400 elemental analyzer corrected for dissolved N and C blanks.

Simulated in situ incubations: omnivory experiments—*C. finmarchicus* females were incubated in a natural seawater suspension collected at or near the depth of the chlorophyll maximum layer. The chlorophyll maximum layer was selected from continuous profiles of in vivo fluorescence when available, otherwise from inspection of filtered samples. To reduce the abundance of mesozooplankton, we screened seawater gently through 202-μm mesh (505 μm in the case of Sta. 0) before incubations. Incubations were performed with 10–21 *C. finmarchicus* females in 2.2-liter polycarbonate bottles that were carefully topped off to minimize formation of air bubbles. Incubations (5–7 replicates per treatment plus 2–3 controls lacking copepods) began in the evening and lasted 8–10 h; bottles were kept in incubators in the dark and rotated intermittently through the night.

Initial and final samples of three kinds were taken: 150-ml subsamples were filtered for Chl *a* analysis by fluorometry, 250-ml seawater samples were fixed in 2% acid Lugol's solution for enumeration of microplankton, and 250-ml seawater samples were fixed in 1% glutaraldehyde for epifluorescence microscopy. Regrettably, our inability to refrigerate the glu-

taraldehyde samples until the end of the cruise resulted in loss of autofluorescence. Also, preliminary cell counts showed that the average abundance of ciliates (choreotrichs plus oligotrichs) preserved in glutaraldehyde was 33.2% their abundance when preserved in acid Lugol's solution. Therefore, glutaraldehyde samples were not processed further. For measurements by fluorometry and in Lugol's iodine, clearance and ingestion rates were calculated from the equations of Frost (1972).

Measurements of Chl *a* alone, excluding pheopigments, were used for calculating chlorophyll ingestion rates. We thus minimized the inclusion of pigments from copepod fecal pellets collected at the end of the experiments. We observed no consistent directional change in chlorophyll concentration in control containers. Out of seven experiments, Chl *a* in control incubations did not change in four, increased in one, and decreased in two.

Microscopic enumeration of samples was done by the Utermöhl technique. Samples were counted at 400× (smaller and more abundant diatoms, dinoflagellates, chlorophytes, cryptophytes, chrysophytes, prymnesiophytes, choanoflagellates, and other microflagellates) and at 200× (larger and less abundant diatoms, dinoflagellates, oligotrich, and other ciliates). Cells smaller than ~2 μm were not resolved at these magnifications. Four or five replicate fields were enumerated at each magnification, for a total of 200–3,000 cells. Cells were identified to species wherever possible, resulting in 132 species or cell categories. Resources permitted this level of analysis for five of the seven omnivory experiments. To calculate ingestion and clearance rates, we pooled cells into the following categories: dinoflagellates, microflagellates, diatoms, aloricate ciliates, and other ciliates (including gymnostomes—primarily *Mesodinium* spp.—and tintinnids). At Sta. 18 the final control samples were not properly preserved, so the conservative assumption was made that k (the growth rate in controls) was 0, which was equal to or slightly less than the average value of controls from other stations. Occasionally, small negative clearance rates were obtained due to sampling error; these values were eliminated from statistical analyses. In controls, recovery of aloricate ciliates—the most fragile taxon enumerated—averaged 102%.

Ingestion rates were computed in terms of organic C. We did not have sufficient data on the N content of prey to make calculations on a N-specific basis. Microscopic measurements of preserved cells were made by ocular micrometer or, in a few instances, obtained from literature sources or from unpublished measurements of F. M. H. Reid. Cell volume was computed from linear measurements after assignment of cells to one of six basic shapes (rhombiform solid, cylinder with elliptical cross-section, ellipsoid, right cylinder, spherical, or the ice-cream-cone approximation of Ohman and Snyder 1991). Tintinnid biovolume was estimated as the lorica volume/2 for cylindrical species or the lorica volume/3 for tapered species. Cell biovolume was converted to organic C content with the appropriate equations of Strathmann (1967) for diatoms, dinoflagellates, and microflagellates and the relation 0.21 pg C μm^{-3} for preserved ciliates (Ohman and Snyder 1991). No attempt was made to correct for shrinkage of naked flagellates in acid Lugol's solution because the Strathmann equations appear to be reasonable for these preserved cells (e.g. our 4-μm Lugol's-preserved flagellates were estimated to contain 0.22 pg C μm^{-3}). For each omnivory experiment, the mean cell C content for each cell category was obtained by weighting the C content for each species by the relative abundance of that species. C ingestion was then obtained from the product of the number of cells ingested and the weighted mean C content for that cell category.

Egg production rates—The method described by Runge (1985) was used to measure egg production rates of *C. finmarchicus*. Copepods for egg production and omnivory experiments were collected with a 1-m-diameter, 560-μm-mesh ring net towed at 0.5 m s^{-1} from ~150 m to the surface. The net was fitted with an 8-liter capacity cod end. The catch was immediately diluted into jars containing seawater from 20 m at a temperature of 4–10°C. Females were sorted into 1-μm filtered seawater at 7°C (±2°C). Each container (N = 6 replicates) held 10–12 females in a 1.5-liter Plexiglas cylinder covered with a mesh screen bottom and suspended in a 2-liter glass beaker. The containers were placed in the dark in incubators at 7°C (±2°C). The time between capture and start of incubations was usually <1.5

h. Separate containers were supplied with a superabundant suspension of the diatom *Thalassiosira weissflogii* cultured in f/2 medium aboard ship. After 24 h, females were removed from containers and the number of eggs laid was counted.

An unknown but potential bias in this method is egg cannibalism. Preliminary experiments (Runge pers. obs.) suggest that in some conditions rates of egg production may be higher when copepods are kept individually rather than grouped in containers. Work in progress will resolve this methodological issue, but does not affect our conclusions here.

Copepod C, N, gut fluorescence, and lipid analyses—Copepods were collected by a Tucker trawl (333-μm mesh) retrieved from 50 m to the surface at 55 m min^{-1} and were promptly frozen in liquid nitrogen. (Nearly all *C. finmarchicus* females occur in the upper 30 m of the water column both day and night in the gulf in summer, Runge and de Lafontaine unpubl. obs.). Animals were kept in liquid N_2 until thawed for gut fluorescence, lipid, and elemental analysis. Thawed *C. finmarchicus* females were carefully distinguished from *Calanus glacialis,* dipped twice in Milli-Q water, and their prosome lengths were recorded. Pairs of *C. finmarchicus* females were added to tared tin boats, dried 24 h at 55°C, weighed on a Cahn 25 electrobalance, and combusted in an elemental analyzer for analysis of N and C content.

For gut fluorescence measurements, a pair of *C. finmarchicus* females was homogenized in 90% acetone, extracted for 1–2 h at 4°C in the dark, centrifuged for 10 min at 16,000 × *g* in a refrigerated chamber, and analyzed on a Turner Designs model 10 fluorometer calibrated with pure Chl *a* (Sigma Chemical). From 7 to 21 replicate extractions were done per field station. Calculations of total gut pigment were made with no correction for possible degradation of pigments. It should be noted that the gut pigment values reported by Ohman (1988) should be divided by 2 because of an incorrect algorithm, but are otherwise correct. Gut pigments were corrected for the background fluorescence of animals starved for 24 h in filtered seawater.

For lipid analysis, animals were collected from 15 stations in the gyres to the west and east of Anticosti Island. Lots of 4–8 *C. finmarchicus* females were extracted in 2:1 chloroform:methanol (vol/vol) at 4°C under N_2 for at least 40 h (*see* Ohman 1988). Animals were then removed to tared boats, dried 24 h at 55°C, and weighed to determine lipid-free dry mass. Lipid class composition was determined by TLC-FID (thin-layer chromatography–flame ionization detection) with an Iatroscan Mark V with SIII chromarods. The analytical procedure was modified slightly from Ohman (1988). A single development was carried out in a mixture of hexane: diethyl ether: formic acid (82:18:0.1, vol/vol/vol) for 26 min, then each chromarod was scanned twice at 30 s $scan^{-1}$. The peak areas from the two scans were then summed and converted to lipid mass from calibration relations ($0.973 < r^2 < 0.998$). The compounds used for calibration were phosphatidylcholine, cholesterol, palmitic acid, tripalmitin, and palmitic acid arachidyl ester. Each extraction was analyzed 2–3 × by TLC-FID. From 1 to 6 copepod samples were extracted per field station. Chromarods were cleaned nightly in 50% nitric acid.

Egg lipid composition was determined from a batch of 406 eggs released by unfed *C. finmarchicus* females aboard ship. Eggs were frozen on a glass-fiber filter in liquid N_2, then later extracted for 46 h in chloroform: methanol as above. No lipids were obtained from blank filters treated and extracted in the same manner. To contrast the lipid content of late winter, prereproductive *C. finmarchicus* with reproductively active copepods collected in summer, we collected copepods in the lower estuary on 18 March 1992, kept them in filtered seawater for 4–7 d, then froze them in liquid N_2 and subsequently analyzed them as above.

The variance of replicate analyses of total lipid by TLC-FID was partitioned as follows: the C.V. of triplicate analyses of a single extraction averaged 7.5% ($N = 42$ comparisons), the C.V. of replicate subsamples from a single station was 7.8% ($N = 6$ subsamples), and the C.V. of total lipid content of animals from 15 stations in the central and northern Gulf of St. Lawrence was 15.9%. Hence, there is greater among-station variance than within-station variance, reflecting spatial variability in nutritional conditions.

Enrichment/starvation experiments analyzed the change in lipid composition of fresh-

ly collected *C. finmarchicus* females upon exposure to extremes of food supply. Females collected on 27 June were kept in several lots of 10 animals per 2-liter beaker for 3.5 d. Animals were incubated either in filtered seawater (FSW) or in saturating concentrations of *T. weissflogii*. The rate of depletion of lipid in the FSW treatment was used to estimate respiration rate.

Results

Physical characteristics of the lower St. Lawrence estuary and the Gulf of St. Lawrence—We studied zooplankton-microplankton interactions in three distinct regions of the estuary and Gulf of St. Lawrence system (Fig. 1). Stations 0 and 1 (station depth, 350 m) were located in the central region of the lower estuary, north of the buoyant coastal jet that moves discharge from the St. Lawrence and Saguenay Rivers out of the estuary along the south shore. These stations were characterized by a shallow mixed layer and low surface salinity (Fig. 2). Stations 7, 13, and 18 (station depths, 100–375 m) were located in the northern Gulf of St. Lawrence east of Anticosti Island. A large cyclonic eddy is a synoptic feature in summer in this region (Koutitonsky and Bugden 1991). Here the mixed layer was deeper and near-surface salinities were higher. Stations 27 and 35 (station depths, 350 m) were in the region of another large cyclonic eddy in the northwestern gulf between the Gaspé Peninsula and Québec's north shore (Koutitonsky and Bugden 1991). The thermal structure and near-surface salinities were intermediate at this location.

The cycles of phytoplankton biomass and composition differ markedly between the central lower estuary and the two gyres on either side of Anticosti Island. Upwelling resulting from tidal forcing at the head of the Laurentian Channel periodically supplies surface waters of the central lower estuary with nutrients that sustain high diatom and dinoflagellate concentrations throughout summer (Demers et al. 1988). In the northern gulf gyres, on the other hand, prevailing evidence indicates that a characteristic, highly stratified water column sets up after the start of the phytoplankton bloom (thought to occur in April–May in this region, de Lafontaine et al. 1991). Surface nutrient concentrations typically fall to low levels

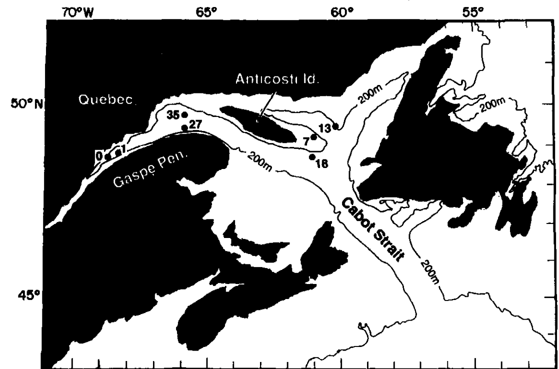

Fig. 1. Study site in the lower St. Lawrence River estuary (Sta. 0, 1) and the Gulf of St. Lawrence (Sta. 7, 13, 18, 27, 35).

by June, and the phytoplankton composition is dominated by dinoflagellates and flagellates <15 μm (de Lafontaine et al. 1991; Runge pers. obs.). Hereafter we will contrast the two stations (0 and 1) in the lower estuary with the remaining five stations referred to collectively as the "gulf" stations.

Characteristics of microplankton—Figure 3 contrasts characteristics of the planktonic particles available to *C. finmarchicus* in the lower estuary and the gulf at those stations where joint omnivory and fecundity experiments were performed. The lower estuary was characterized by a shallow chlorophyll maximum layer at 5–10-m depth, with peak concentrations of 10–14 μg Chl *a* liter^{-1}, all of which was >5 μm (Table 1). The gulf region had weakly developed chlorophyll maxima, usually between 20- and 30-m depth, with peak concentrations 10–38× lower than in the estuary. Relatively little (8–25%) of the Chl *a* collected at the depth of the chlorophyll maximum was retained on a 5-μm filter.

Particulate N showed a similar contrast, though the difference between maxima in the two regions was only 2–8×, and the maxima tended to be shallower in the water column than the chlorophyll maxima. The N : Chl *a* ratio differed between the two regions, illustrating that the organic composition of the microplankton is markedly different in the open gulf. In the estuary the N : Chl *a* ratio averaged 11.0, while it averaged 71.8 and showed greater variability with depth in the gulf. Comparable comparisons for C : Chl *a* are 121 and 528, and for the ratio of C to N (by mass) 10.9

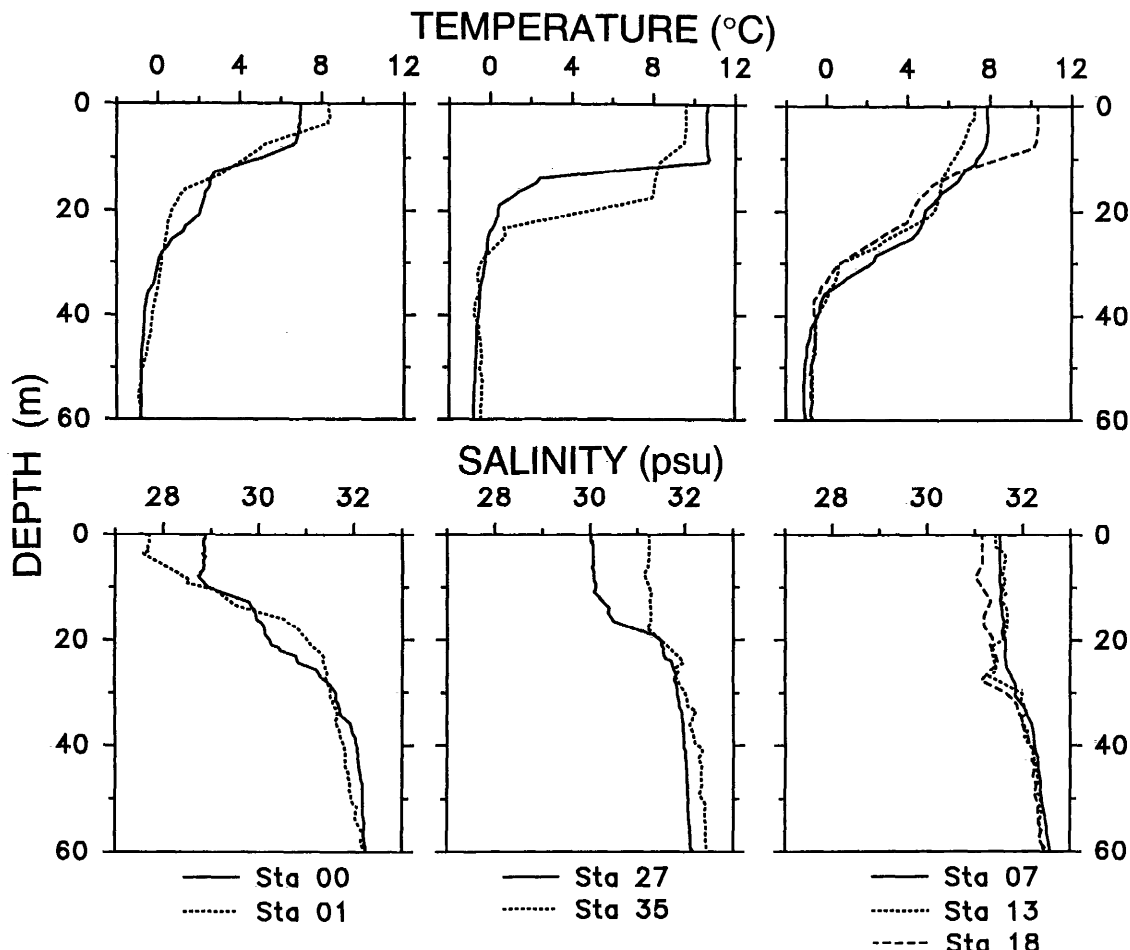

Fig. 2. Vertical profiles of temperature and salinity at the stations where experimental work was performed.

in the estuary and 7.3 in the gulf. The total biomass was appreciably greater in the lower estuary, but the seston biomass per unit chlorophyll was higher in the open gulf. Little of this difference is attributable to physiological changes in pigment content, which suggests that unpigmented microheterotrophs are of increased importance in the gulf.

The microplankton assemblages differed in several respects. The lower estuary was dominated by relatively large diatoms (Table 2; principally two species of *Thalassiosira, Chaetoceros debilis,* and a 3.5- × 12-μm pennate) and microflagellates (2–6 μm). The gulf stations had much lower concentrations of smaller diatoms (Table 2; primarily a 2.6- × 6-μm centric, *Chaetoceros simplex,* 2.8- × 13-μm pennate, and *Chaetoceros gracilis*). The abundance of aloricate ciliates was 2–4 times higher in the gulf than in the lower estuary, although the dominant taxa (primarily *Strombidium* spp. and *Lohmaniella oviformis*) were the same in the two regions. There were no consistent differences in the abundance or cell sizes of dinoflagellates between the lower estuary [primarily small (8 × 11 μm) and medium-sized (26 × 31 μm) *Gymnodinium/Gyrodinium,* and *Katodinium rotundatum*] and the gulf (small and medium-sized *Gymnodinium/Gyrodinium, Protoperidinium* sp., and *Cachonina nei*). We assume that most of these taxa were heterotrophic (Larsen and Sournia 1991), although this could not be confirmed by epifluorescence microscopy.

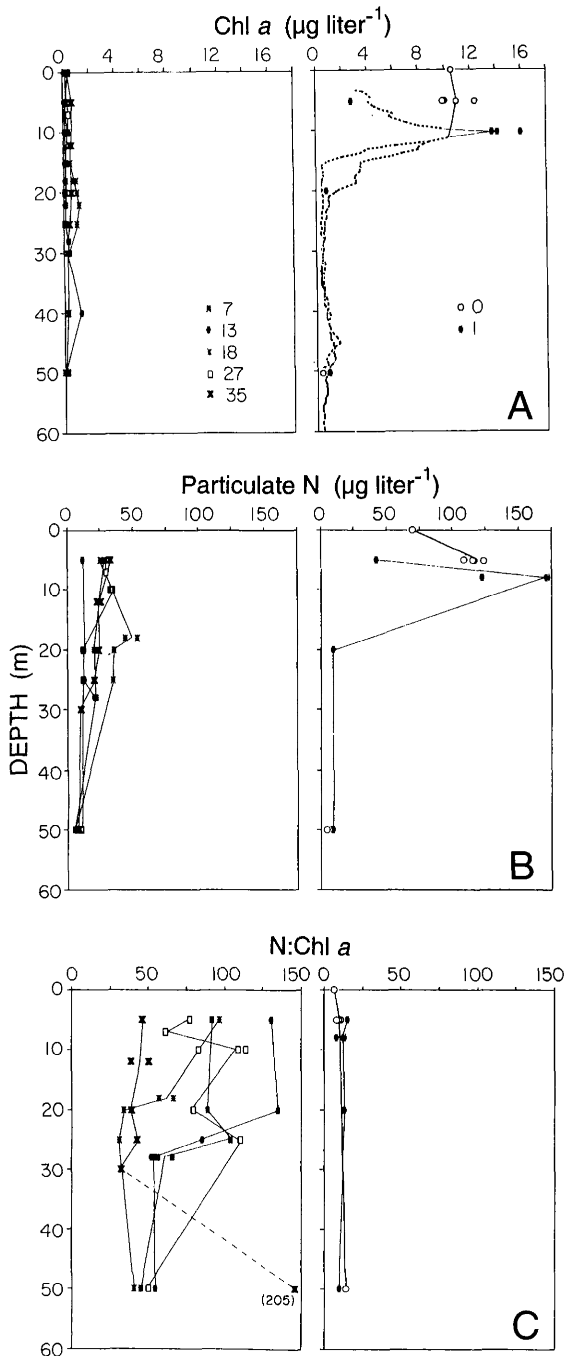

Fig. 3. Vertical profiles of Chl *a*, particulate nitrogen, and the ratio of particulate N to Chl *a* at stations in the St. Lawrence estuary (right panels) and the Gulf of St. Lawrence (left panels). Chl *a* at Sta. 0 and 1 was determined from continuous in vivo fluorescence measurements (dotted line; sensor saturated at 10 μg Chl *a* liter^{-1}) as well as from extracted in vitro measurements (points). Pigments at other stations were determined only from extracted in vitro measurements.

Table 1. Experimental conditions for omnivory experiments and time of collection of copepods for gut fluorescence assays. The fraction of Chl *a* > 5 μm was determined at or near (within 0–8 m) the collection depth for omnivory experiments.

Sta.	Time of collection (hours)	Seawater collection depth (m)	Avg incubation temp. (°C)	Initial Chl *a* (μg liter^{-1})	% Chl *a* >5 μm	Initial PN (μg N liter^{-1})	Initial PC (μg C liter^{-1})
0	2040	5	7.6	10.48	100.0	116.3	816
1	2220	8	7.5	14.01	100.0	173.0	1,132
7	0020	28	4.2	0.35	9.7	21.5	183
13	0115	28	4.4	0.40	8.4	21.3	164
18	1845	18	7.4	0.79	14.0	48.9	402
27	2044	10	8.9	0.34	25.0	33.8	241
35	2135	12	6.4	0.52	10.0	24.5	163

Ingestion of microplankton and production of eggs—Gut fluorescence of *C. finmarchicus,* reflecting recent in situ ingestion of phytoplankton, was appreciably higher in the estuary than in the gulf (Fig. 4), as might be expected from Fig. 3. The relatively low gut pigment content at Sta. 0 appears to be a consequence of the time of day of collection (near local sunset); because of diel variability in feeding, we expect that this value would have been higher had we collected copepods in full darkness a short time later. Pigment degradation within copepod guts remains a possibility (Penry and Frost 1991) but would not affect our overall conclusion. Indeed, if degradation is higher during bloom conditions (Penry and Frost 1991), then the true contrast between gut pigment content in the estuary and gulf is even greater than we measured.

Unlike the gut fluorescence determinations, the chlorophyll ingestion rate is determined from the disappearance of Chl *a* from incubations of copepods in natural seawater aboard ship. That is, it is a simulated in situ measurement. Like the static measure of gut pigment content, chlorophyll ingestion rates of *C. finmarchicus* showed the expected relationship with ambient chlorophyll concentrations, with appreciably higher rates of ingestion in the lower estuary (Fig. 5A).

Table 2. Mean cell density (±SD) and weighted mean organic C content for the major cell categories at the beginning of each omnivory experiment.

	Flagellates		Diatoms		Dinoflagellates		Ciliates	
Sta.	(cells ml^{-1})	(pg C cell^{-1})	(cells ml^{-1})	(pg C cell^{-1})	(cells ml^{-1})	(pg C cell^{-1})	(cells ml^{-1})	(pg C cell^{-1})
0	3,822±1,857	12.0	4,619±655	248.2	80±11	129.0	2.4±1.8	2,152
1	2,700±338	14.2	5,364±1,320	272.9	72±41	553.5	3.3±0.8	937
7	452±82	17.2	347±59	14.6	162±57	60.7	6.5±1.4	1,082
13	524±36	11.6	357±79	17.2	39±8	186.2	9.3±0.1	1,099
18	3,901±199	14.1	209±101	7.2	339±76	119.9	11.0±2.1	1,634

Rates of egg production by *C. finmarchicus* (Fig. 5B) contrasted markedly with expectations from the ambient chlorophyll concentrations (Fig. 3A), from in situ gut pigment content (Fig. 4), and from chlorophyll ingestion rates (Fig. 5A). Egg production rates did not decline in the low-chlorophyll waters of the open gulf. Rather, females sustained rates of 26±6 ($\bar{x}$±95%) eggs female^{-1} d^{-1} in the open gulf (Sta. 7, 13, 18, 27, 35 combined). These rates are not significantly different ($P > 0.10$, Mann-Whitney U-test) from the rates of 21±8 eggs female^{-1} d^{-1} in the lower estuary (Sta. 0 and 1 combined). Egg production rates were determined aboard ship in filtered seawater in the first 24 h after collection and thus are representative of in situ rates from recent feeding conditions. There was no relationship between rates of egg production and chlorophyll ingestion (Fig. 6). In the open gulf, *C. finmarchicus* did not obtain the substrates necessary for egg production from autotrophic particles bearing Chl *a*.

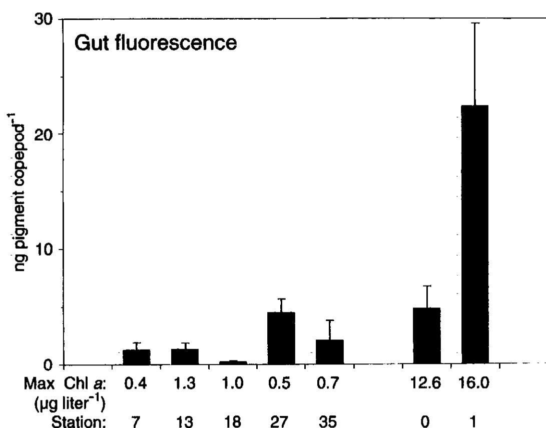

Fig. 4. Gut fluorescence of *Calanus finmarchicus* females collected at each of the experimental stations, reflecting ingestion of pigments in situ ($\bar{x}$±95%). Numerals beneath each bar report the maximum Chl *a* concentration measured in vertical profiles at each station.

In parallel egg production treatments in which *C. finmarchicus* was fed diatoms, egg production in the first 24 h after collection was higher than in FSW treatments but not appreciably so. At gulf stations, the rates in FSW averaged 59% (range, 38–78%, $N = 5$ experiments) of the rates in enriched food and 62% (one comparison, Sta. 1 only) at the lower estuary. In only one of these experiments, however, was fecundity in the enriched treatment significantly greater ($P < 0.05$) than in the FSW treatment.

The taxa of autotrophic and heterotrophic microplankton ingested by *C. finmarchicus* differed substantially in the lower estuary and the open gulf. Clearance rates of *C. finmarchicus* differed somewhat on four cell types (microflagellates, diatoms, dinoflagellates, and aloricate ciliates) in the lower estuary (Sta. 0 and 1; $P \leq 0.05$, Kruskal-Wallis ANOVA; Fig. 7). At each of the stations in the open gulf, clearance rates differed markedly among taxa ($P < 0.005$, Kruskal-Wallis). Clearance rates on aloricate ciliates were 3–23 times higher than the clearance rates on diatoms, dinoflagellates, or microflagellates at the gulf stations. The maximum clearance rates measured on ciliates were 24.6 ml copepod^{-1} h^{-1}.

Ingestion rates of *C. finmarchicus* in the chlorophyll-rich waters of the lower estuary were markedly higher on diatoms than on any other cell category (Sta. 0 and 1; right-hand panels in Fig. 7). For females of 222 µg C (Table 3), these ingestions rates corresponded to 42–48% body C d^{-1}. The contribution of other cell types to the daily ration of *C. finmarchicus* females was insignificant there. Because we could not reliably distinguish autotrophic from heterotrophic dinoflagellates and microflagellates, we made the cautious assumption that

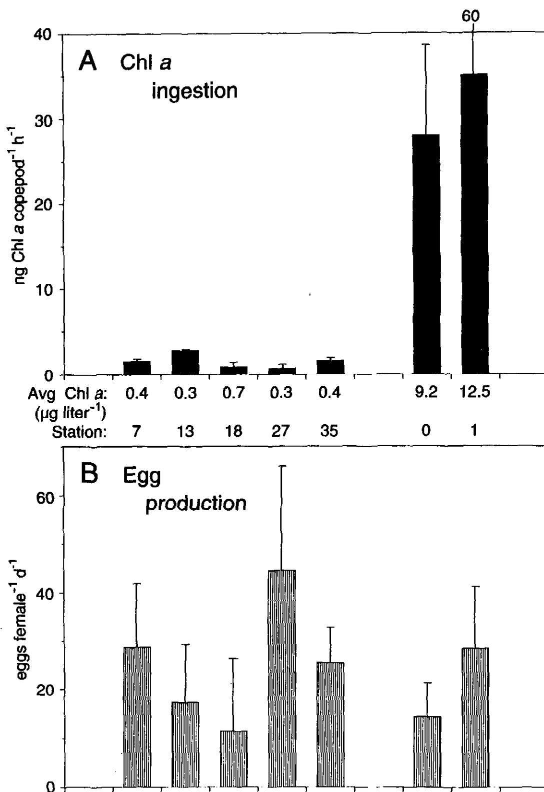

Fig. 5. *Calanus finmarchicus.* A. Rate of ingestion of Chl *a* in simulated in situ experiments performed aboard ship with a natural microplankton suspension. B. Rate of egg production in filtered seawater in the first 24 h of incubation. ($\bar{x}\pm95\%$) Numerals beneath each bar in panel A report the average Chl *a* concentration in the ingestion rate incubations.

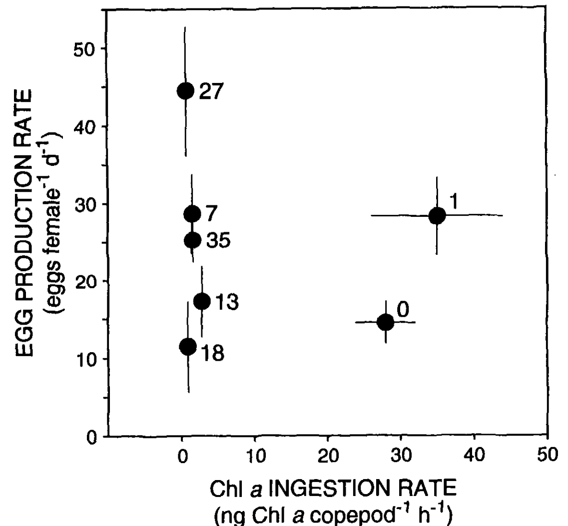

Fig. 6. Plot illustrating the independence of mean egg production rate and mean chlorophyll ingestion rate. Numerals indicate station numbers. Note the sustained egg production when Chl *a* ingestion is low. ($\bar{x}$ ± SE, where this exceeds symbol size.)

half of the ingested C from both of these taxa was heterotrophic. Accordingly, heterotrophic prey constituted 3.2–5.1% of the diet of *C. finmarchicus* in the lower estuary.

The diet of *C. finmarchicus* was appreciably different in the open gulf. Diatoms were a minor constituent of the ration, and aloricate ciliates constituted the most important prey category in all three experiments. Despite their relatively low cell density (Table 2), high clearance rates on ciliates combined with their organic content led them to be disproportionately significant in the diet of *Calanus.* Dinoflagellates were the second most important prey in the diet of *C. finmarchicus* in the open gulf at Sta. 13 and 18, but not at Sta. 7. Microflagellates provided a small supplement to the diet. The total daily ingestion by *C. finmarchicus* in the open gulf averaged 5.2 μg C female^{-1} d^{-1} (range, 2.4–9.3) or 2.3% body C d^{-1}. If we make the same assumptions as above, heterotrophic prey constituted at least 70.4–78.5% of the diet of *C. finmarchicus* in the gulf.

The average C content of an egg was 0.231 μg C (*see below*), so daily egg production in the open gulf was equivalent to 6.7, 3.9, and 2.5 μg C at Sta. 7, 13, and 18. The measured daily C ingestion was 2.4, 4.0, and 9.3 μg C in the corresponding omnivory experiments. At Sta. 7, the rate of carbon ingestion is insufficient to account for the measured rate of egg production. The two are equivalent at Sta. 13. At Sta. 18, the rate of ingestion exceeds the rate of egg production.

Calanus *lipid content and starvation experiments*—The lipid content of *C. finmarchicus* eggs averaged 68 ng. Egg lipids were predominantly phospholipids (Table 4), differing from the composition of reproductive females (Table 5) from which they were derived. The organic composition of *C. finmarchicus* eggs was 231±74 ng C and 43.5±13 ng N ($N = 5$; 700–800 eggs per replicate; Runge unpubl.). If the C content of eggs is 50% of dry mass, then total lipids averaged 15% of egg dry mass.

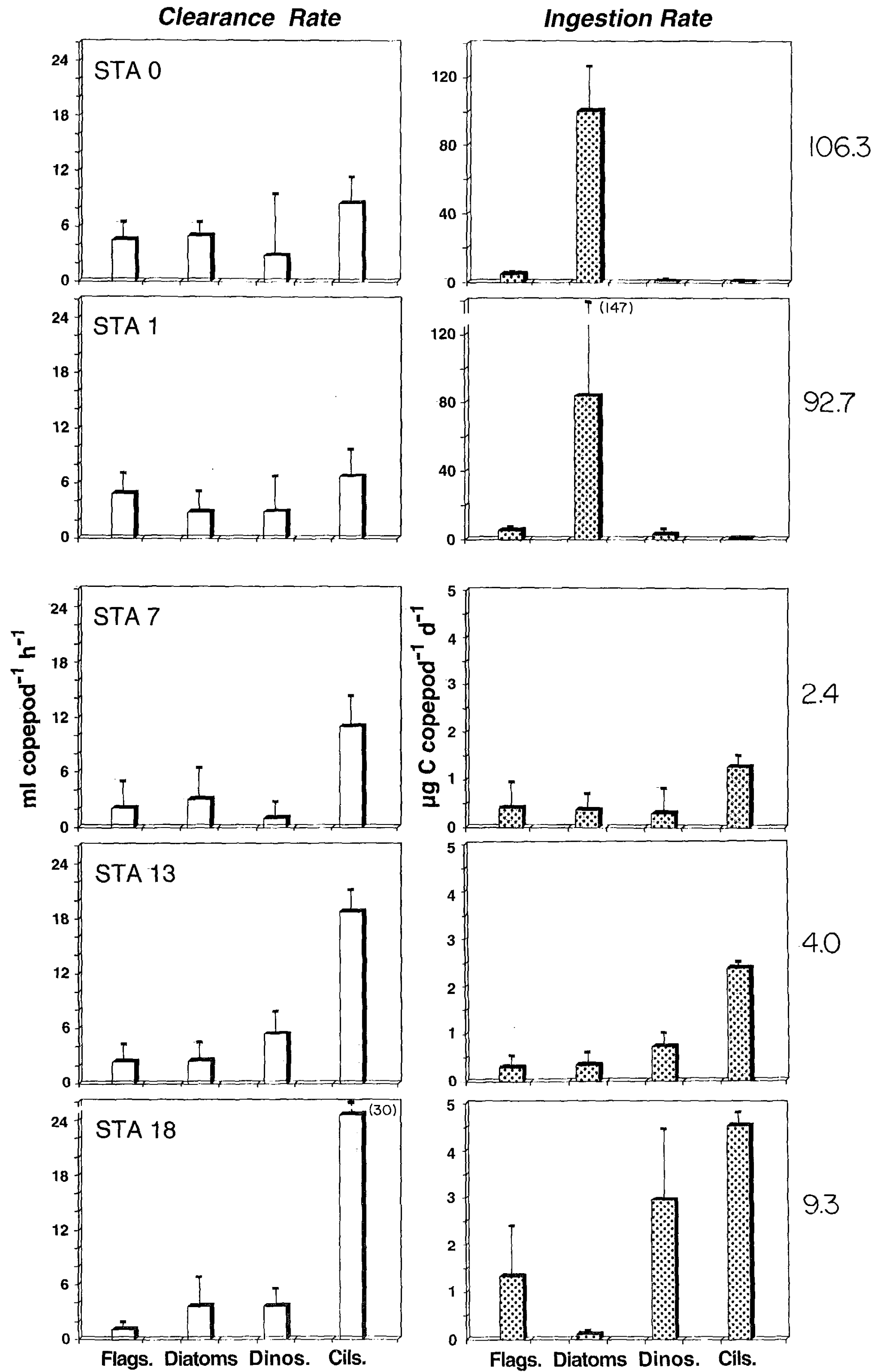
Clearance Rate
Ingestion Rate
STA 0
STA 1
STA 7
STA 13
STA 18
ml copepod^{-1} h^{-1}
µg C copepod^{-1} d^{-1}
(147)
(30)
106.3
92.7
2.4
4.0
9.3
Flags. Diatoms Dinos. Cils.
Flags. Diatoms Dinos. Cils.

Table 3. Composition of *Calanus finmarchicus* females from the central Gulf of St. Lawrence, June 1991.

	$\bar{x}\pm95\%$	N
Prosome length (mm)	2.97±0.01	553
Dry mass (μg)	409*±19	24
C (μg C copepod^{-1})	222.1±11.7	24
N (μg N copepod^{-1})	43.3±2.0	24
C:N	5.16±0.28	24
C (% dry mass)	54.2±1.2%	24
N (% dry mass)	10.6±0.4%	24

* Only those animals analyzed for C, N content; dry mass of a larger sample was 393±15 (N = 56).

Table 4. Composition of *Calanus finmarchicus* egg lipids, Gulf of St. Lawrence in June 1991. Lipid content averaged 68±22 ng egg^{-1} ($\bar{x}\pm95\%$, N = 7).

Lipid class	Percentage of lipids
Wax ester	16.7±3.3
Triacylglycerol	14.5±3.8
Free fatty acid	*
Sterol	trace
Phospholipid	68.8±6.1

* Not detectable.

The lipid content and lipid class composition of *C. finmarchicus* varied across the study site (Table 5). Triacylglycerols were the most variable lipid class, ranging ~4-fold at 15 different stations in the gulf, while other lipid classes tended to vary 2-fold. This is consistent with the interpretation that triacylglycerols vary in relation to recent nutritional conditions. The difference in total dry mass between Table 3 and 5 may reflect a difference between lots of animals analyzed, since those from Table 5 reflect sampling from a greater number of field stations.

The total lipid content of *C. finmarchicus* females averaged 30.5% of dry mass in June, but in late winter (March), the average was 46.1% of dry mass (Table 5). The higher wax ester and lower phospholipid content of late-winter females (also expressed by the ratio of WE+TAG to PL) suggests that they had molted recently from copepodid stage V and were not yet feeding to a great extent or producing eggs. The summer females that are the primary focus of this study retained a surprisingly high wax ester content, indicating that they had not been subjected to long-term starvation. Furthermore, the average female had an ample supply of triacylglycerols, suggesting relatively recent feeding and net assimilation of organic material.

Short-term enrichment of ambient seawater with saturating concentrations of diatoms resulted in increased triacylglycerol content but no change in wax ester content (Table 6). However, concurrent starvation of females resulted in depletion of both triacylglycerols and wax esters. The change in total lipid content over 3.5 d was a decrease of 19.6 μg, or 5.6 μg lipid d^{-1}. Converted to a respiration rate using a respiratory quotient of 0.7, this rate of lipid oxidation is equivalent to 14.9 μl O_2 consumed copepod^{-1} d^{-1}.

Discussion

The dietary shift of *C. finmarchicus* from abundant, large diatoms in the lower estuary to microzooplankton in the Gulf of St. Lawrence was not accompanied by a measurable diminution in fecundity during these experiments conducted in early summer. *C. finmarchicus* females sustained relatively high rates of egg production, comparable to those attained in the eutrophic, diatom-rich waters of the lower estuary (but note, as discussed later, that egg production rates in the lower estuary at the time of our measurements may not have been in equilibrium with the food supply). Contrary to expectations from linear food-chain models (and contrary to expectations from Runge 1988), autotrophic cells were not the exclusive or necessarily the dominant prey of *Calanus*. In the relatively oligotrophic waters of the gulf, microzooplankton increased in both relative and absolute dietary importance. The dominant prey in the gulf were oligotrich ciliates, supplemented by dinoflagellate and other microflagellate taxa.

←

Fig. 7. Clearance rate and C ingestion rate of *Calanus finmarchicus* females in omnivory experiments ($\bar{x}\pm95\%$). Note scale change for lower three ingestion rate panels. The microplankton categories are flagellates, diatoms, dinoflagellates, and aloricate ciliates. Numerals to the right indicate the total C ingestion (μg C copepod^{-1} d^{-1}) from all prey categories combined.

Table 5. Lipid class composition of *Calanus finmarchicus* females from the central Gulf of St. Lawrence in June 1991 ($N = 15$) and from the lower St. Lawrence estuary in March 1992 ($N = 3$). Units for lipids and dry mass are μg copepod^{-1}. Final column is the ratio of storage lipids (WE + TAG) to phospholipids (PL).

	PL	Sterol	Free fatty acid	TAG	WE	Total lipid	Dry mass		Lipid % dry mass	$\frac{WE+TAG}{PL}$
							Lipid-free	Total		
June 1991										
$\bar{x}\pm SD$	25.6±4.6	0.91±0.16	1.06±0.29	2.12±1.18	74.8±15.2	104.5±16.6	238±33	343±39	30.5±4.3	3.00
(min–max)	(19.5–33.4)	(0.69–1.37)	(0.58–1.56)	(1.07–4.55)	(41.2–98.5)	(65.5–124.0)	(174–297)	(257–400)	(22.7–37.8)	
March 1992										
$\bar{x}\pm SD$	10.6±1.4	0.63±0.09	0.10±0.17	0.35±0.14	91.2±10.8	102.9±11.2	120±3	223±9	46.1±3.2	8.60
(min–max)	(9.0–11.5)	(0.53–0.68)	(0.0–0.3)	(0.19–0.45)	(84.2–103.6)	(96.2–115.8)	(117–123)	(215–233)	(43.9–48.7)	

The significance of aloricate ciliates as prey may be surprising given the ciliate densities (~2–11 cells ml^{-1}) measured. However, their importance stems from the high clearance rates attained by *C. finmarchicus* on this prey type combined with their relatively high organic content. Consider, for example, that a common ciliate in these experiments (provisionally identified as *Strombidium delicatissimum*) has 4 times the organic C content of a diatom and 1.8 times that of a dinoflagellate of the same biovolume (from the relations of Ohman and Snyder 1991 and Strathmann 1967). If we had had sufficient information to compute rations in terms of N rather than C, the relative importance of ciliate prey might have been still greater. Furthermore, microzooplankton may be more readily assimilated than other prey (Corner et al. 1976), and ciliates may contain essential micronutrients lacking in autotrophic cells (Stoecker and Capuzzo 1990), increasing their nutritional value. It is noteworthy that the increase in dietary significance of ciliates was disproportionate to their increased abundance in the water column. Though ciliates increased in both relative and absolute abundance in the gulf in comparison with the lower estuary, their increase in dietary significance was greater still. Such a nonlinear increase is suggestive of the kind of "switching" response documented by Landry (1981) for *Calanus pacificus* feeding on nauplii.

The true rate of ingestion of ciliates and other microzooplankton taxa has probably been underestimated in these experiments. Some aloricate ciliates are known to perish when screened through meshes such as those used at the beginning of these experiments (Gifford 1985). However, we saw no feasible alternative to this treatment for the purpose of these experiments. Work in progress will compare our present results with those obtained by immunochemical methods. Also, there were remarkably few tintinnids, nauplii, radiolaria, and other large microzooplankters in these experiments because of exclusion by the prescreening treatment; each of these taxa would provide an additional increment to the daily ration. In addition, we have no assurance that the maximum ciliate concentration in the water column was sampled for the omnivory experiments. Vertical profiles of ciliate abundance measured in 1989 showed that ciliate

Table 6. Lipid content of *Calanus finmarchicus* females at the time of collection (initial) and after 3.5 d in a suspension of filtered seawater (starved) or diatoms (fed). ($\bar{x}$ ± SD, *N* usually = 3.)

Lipid class	Initial lipid (μg)	Starved		Fed	
		Lipid (μg)	% change	Lipid (μg)	% change
Triacylglycerol	2.63±0.67	1.21±0.10	−54.0	4.87±0.40	85.2
Wax ester	89.9±14.2	69.6±1.1	−22.6	87.5±3.9	−2.7
Total lipids	116.8±18.0	97.2±4.1	−16.8	117.8±4.8	+0.8

concentration was maximal at 20–30 m (*N* = 7 profiles; Runge unpubl.), which may have been missed in our efforts targeted at the chlorophyll maximum. Indeed, since we did not always incubate copepods in the maximum concentration of phytoplankton either, we suspect that we have not measured the maximum rate of ingestion at any station in the gulf.

Gifford and Dagg (1991) documented a seasonal shift from a diet dominated by phytoplankton in January to one dominated by microheterotrophs in August for *Acartia tonsa* in the Gulf of Mexico. In experiments in Chesapeake Bay, White and Roman (1992) observed that egg production of *A. tonsa* was uncorrelated with ambient chlorophyll concentrations or with rates of phytoplankton ingestion but was correlated with the biomass of microzooplankton (ciliates plus flagellates). In the low-chlorophyll waters of the open Gulf of Alaska, Gifford and Dagg (1991) estimated that heterotrophic prey were 1.6–3.7 times as important as autotrophic prey for the large calanoid *Neocalanus plumchrus.* These experimental results are consistent with Frost's (1987) model of subarctic Pacific plankton dynamics in which microzooplankton comprised ~75% of the diet of *N. plumchrus.* The total ingestion rates calculated by Gifford and Dagg (1991) were not sufficient to meet the metabolic requirements of *N. plumchrus,* though, and additional assimilation is required for lipid synthesis at the time of year of their experiments. Ingestion of microzooplankton prey may also account for some of the relatively high rates of egg production of *C. pacificus* that Mullin (1991) documented in low-chlorophyll waters of the Southern California Bight (*see* his figure 15, especially 8901, 8907, 9004).

Other methods have been used to distinguish herbivory and carnivory, including high performance liquid chromatography on pigment extracts from whole zooplankton (Kleppel et al. 1988). However, it is not clear why the composition of copepod and cladoceran pigments assumed to originate from predator guts is dominated overwhelmingly by the pigment astaxanthin (Kleppel et al. 1988), since astaxanthin is virtually absent from two dominant microzooplankton taxa that are likely prey (*Strombidium* sp. and *Gymnodinium* sp.; Kleppel and Lessard 1992). Canthaxanthin, which appeared to be of negligible significance in the field study of Kleppel et al. (1988), was the most important animal pigment in three of six taxa in the laboratory cultures of Kleppel and Lessard (1992). Also unresolved is the possibility that differential digestion of pigments (Head and Harris 1992) may influence the pigment ratios used to infer carnivory.

The difficulty of using gut or fecal pellet content analysis to infer copepod diets is exemplified by the study of Urban et al. (1992). Their study was qualitative and based on microscopically recognizable hard fragments of cells, and they concluded that *C. finmarchicus* did not ingest ciliates in spring or summer. Because aloricate oligotrich ciliates leave no remains recognizable by conventional means, we suspect that analysis of fecal pellet contents in our study would have led to a similar conclusion.

Clearly the growth efficiency of copepods is not 100%. In addition to the nutritional requirements for egg synthesis there is, of course, a C requirement for respiration as well as smaller loss terms. The C requirement of respiration appears to be met by the oxidation of depot lipids (triacylglycerols and wax esters) and perhaps supplemented with assimilated microplankton. The typical *C. finmarchicus* female collected in the gulf in summer has a relatively high depot lipid content, which implies that *C. finmarchicus* is relatively well nourished by ambient microplankton. *C. finmarchicus* must rarely experience periods lon-

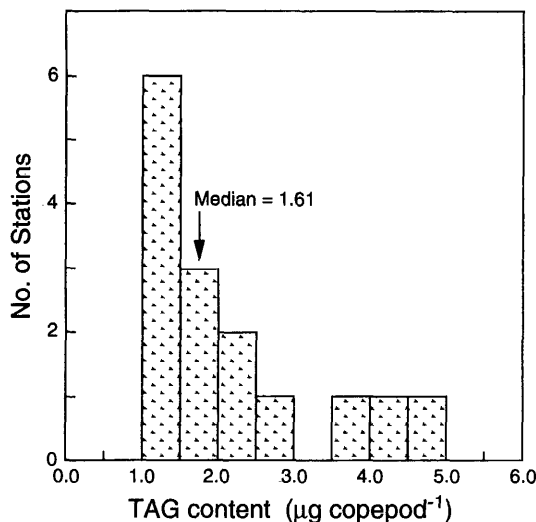

Fig. 8. Frequency distribution of triacylglycerol content of *Calanus finmarchicus* females at 15 stations in the Gulf of St. Lawrence.

ger than a few days without ingesting a ration from the water column sufficient to support respiration, some egg production, and synthesis of lipids. If it were not the case, and if there were consistent net catabolism of lipids on a daily basis, then their triacylglycerol (TAG) content should be vanishingly small and wax esters should be markedly lower than observed (cf. Hakanson 1984).

The frequency distribution of TAG content from stations in the gulf provides some insights here. In planktonic copepods, TAGs are metabolized relatively quickly upon short-term starvation (e.g. Hakanson 1984). If the TAG content of *C. finmarchicus* in situ generally exceeds that of animals starved for 3.5 d, then it is reasonable to infer that animals obtain a substantial ration no less often than every 3–4 d. Figure 8 illustrates that the median TAG content at 15 stations in the gulf was 1.61 μg TAG copepod^{-1}, exceeding the TAG content of starved animals. On the basis of the distribution in Fig. 8, females at >60% of the field stations obtained a surfeit of assimilated food so that net lipid synthesis was possible.

Our estimate of respiration rate was obtained from respiratory lipid oxidation and did not require enclosure of animals in small respiration chambers. The respiration rate inferred by this method was 14.9 μl O_2 copepod^{-1} d^{-1}, which compares with 18.1 obtained from Conover and Corner's (1968) maximal rates for reproductive *C. finmarchicus* in May (computed for animals of 393 μg of dry mass). Ikeda's (1985) regressions yield respiration rates ranging from 12.0 to 16.6 μl O_2 copepod^{-1} d^{-1}, assuming 6°C average temperature and the body dry mass (393 μg), C (222 μg), or N (43.3 μg) content measured here. Our method for estimating respiration may prove useful for other zooplankton species whose primary energy storage is in the form of lipids.

The predominance of phospholipids (69%) in eggs of *C. finmarchicus* recalls the results observed with *Neocalanus tonsus* eggs (66% phospholipids; Ohman et al. 1989). Phospholipids may be of particular significance in developing ova since cell division will be accompanied by a substantial requirement for membrane synthesis.

In terms of numbers of eggs, the rates we observed (11–45 eggs female^{-1} d^{-1}) are of the same magnitude as the daily egg production of other populations of *C. finmarchicus*. Runge (1985) observed egg production rates of 13–29 eggs female^{-1} d^{-1} in the sea off Nova Scotia. Hirche (1990) found that *Calanus* from the Norwegian and Greenland Seas in April and June, respectively, were producing 12–14 eggs female^{-1} d^{-1}. Diel and Tande (1992) reported a maximum daily production of 33 eggs for *C. finmarchicus* in spring in a subarctic Norwegian fjord. For comparison of actual with potential fecundity, the body size and ambient temperature of each population must be taken into account, as both factors strongly influence maximum rates of egg production (Runge 1985).

The C-specific rates of egg production measured at the lower estuary stations (1–3% body C d^{-1}) were less than maximal, which we estimate to be 5–8% for ambient temperatures in the surface layer of these stations (cf. Runge 1985; Plourde and Runge 1993). However, ingestion rates of *C. finmarchicus* females measured at the location (42–48% body C d^{-1}) were probably maximal for this species (*see* Båmstedt et al. 1992). We believe that this difference is attributable to a time lag between the onset of maximum ingestion and the response in fecundity. In an independent study conducted 10 km from the location of Sta. 0 and 1 by Plourde and Runge (1993), fecundity

of *C. finmarchicus* reached 45–60 eggs female^{-1} d^{-1} several days after the experiments reported here. That study also showed that the "spring" bloom occurred abruptly on 11–15 June, ~1 week before our first two experiments and that the start of reproduction lags the start of the bloom by ~1 week. This interval represents the time required for immature oocytes to proceed through secondary vitellogenesis and be ready for release. Thus, in our first two omnivory experiments at Sta. 0 and 1 we probably captured females that were feeding optimally but were still developing oocytes to maturity. However, this phase lag does not affect our overall conclusions regarding the increased importance of microzooplankton prey in waters of the gulf.

The conditions in the Gulf of St. Lawrence during our June–July study are postbloom, reflecting a food web that appears to be shifted to greater preponderance of heterotrophic ciliates and perhaps heterotrophic dinoflagellates. Under such conditions, which may prevail for considerable periods of time for *C. finmarchicus* across much of the North Atlantic Ocean, the conventional autotrophic pathway will be a poor predictor of fecundity and rates of population growth.

References

BÅMSTEDT, U., H. C. EILERTSEN, K. S. TANDE, D. SLAGSTAD, AND H. R. SKJOLDAL. 1992. Copepod grazing and its potential impact on the phytoplankton development in the Barents Sea. Polar Res. **10:** 339–353.

BAINBRIDGE, V., AND B. J. MCKAY. 1968. The feeding of cod and redfish larvae. ICNAF Spec. Publ. 7, p. 187–217.

CONOVER, R. J., AND E. D. S. CORNER. 1968. Respiration and nitrogen excretion by some marine zooplankton in relation to their life cycles. J. Mar. Biol. Assoc. U. K. **48:** 49–75.

CORNER, E. D. S., R. N. HEAD, C. C. KILVINGTON, AND L. PENNYCUICK. 1976. On the nutrition and metabolism of zooplankton. 10. Quantitative aspects of *Calanus helgolandicus* feeding as a carnivore. J. Mar. Biol. Assoc. U.K. **56:** 345–358.

DE LAFONTAINE, Y., S. DEMERS, AND J. RUNGE. 1991. Pelagic food web interactions and productivity in the Gulf of St. Lawrence: A perspective, p. 99–123. *In* J.-C. Therriault [ed.], The Gulf of St. Lawrence: Small ocean or big estuary? Can. Spec. Publ. Fish. Aquat. Sci. 113.

DEMERS, S., L. LEGENDRE, AND J.-C. THERRIAULT. 1988. Phytoplankton responses to vertical tidal mixing, p. 1–40. *In* J. Bowman et al. [eds.], Tidal mixing and plankton dynamics. Springer.

DIEL, S., AND K. TANDE. 1992. Does the spawning of *Calanus finmarchicus* in high latitudes follow a reproducible pattern? Mar. Biol. **113:** 21–31.

FROST, B. W. 1972. Effects of size and concentration of food particles on the feeding behavior of the marine planktonic copepod *Calanus pacificus*. Limnol. Oceanogr. **17:** 805–815.

———. 1987. Grazing control of phytoplankton standing stock in the open subarctic Pacific Ocean: A model assessing the role of mesozooplankton, particularly the large calanoid copepods *Neocalanus* spp. Mar. Ecol. Prog. Ser. **39:** 49–68.

GIFFORD, D. J. 1985. Laboratory culture of marine planktonic oligotrichs (Ciliophora, Oligotrichida). Mar. Ecol. Prog. Ser. **23:** 257–267.

———. 1991. The protozoan-metazoan trophic link in pelagic ecosystems. J. Protozool. **38:** 81–86.

———, AND M. J. DAGG. 1991. The microzooplankton-mesozooplankton link: Consumption of planktonic protozoa by the calanoid copepods *Acartia tonsa* Dana and *Neocalanus plumchrus* Murukawa. Mar. Microb. Food Webs **5:** 161–177.

HAKANSON, J. L. 1984. The long and short term feeding condition in field-caught *Calanus pacificus*, as determined from the lipid content. Limnol. Oceanogr. **29:** 794–804.

HEAD, E. J. H., AND L. R. HARRIS. 1992. Chlorophyll and carotenoid transformation and destruction by *Calanus* spp. grazing on diatoms. Mar. Ecol. Prog. Ser. **86:** 229–238.

HIRCHE, H.-J. 1990. Egg production of *Calanus finmarchicus* at low temperature. Mar. Biol. **106:** 53–58.

IKEDA, T. 1985. Metabolic rates of epipelagic marine zooplankton as a function of body mass and temperature. Mar. Biol. **85:** 1–11.

KLEPPEL, G. S., D. FRAZEL, R. E. PIEPER, AND D. V. HOLLIDAY. 1988. Natural diets of zooplankton off southern California. Mar. Ecol. Prog. Ser. **49:** 231–241.

———, AND E. J. LESSARD. 1992. Carotenoid pigments in microzooplankton. Mar. Ecol. Prog. Ser. **84:** 211–218.

KOUTITONSKY, V. G., AND G. L. BUGDEN. 1991. The physical oceanography of the Gulf of St. Lawrence: A review with emphasis on the synoptic variability of the motion, p. 57–90. *In* J.-C. Therriault [ed.], The Gulf of St. Lawrence: Small ocean or big estuary? Can. Spec. Publ. Fish. Aquat. Sci. 113.

LANDRY, M. R. 1981. Switching between herbivory and carnivory by the planktonic marine copepod *Calanus pacificus*. Mar. Biol. **65:** 77–82.

LARSEN, J., AND A. SOURNIA. 1991. The diversity of heterotrophic dinoflagellates, p. 313–332. *In* D. J. Patterson and J. Larsen [eds.], The biology of free-living heterotrophic dinoflagellates. Clarendon.

MARRA, J., AND C. HO. 1993. Initiation of the spring bloom in the northeast Atlantic (47°N, 20°W): A numerical simulation. Deep-Sea Res. **40:** 55–73.

MULLIN, M. M. 1991. Production of eggs by the copepod *Calanus pacificus* in the southern California sector of the California Current system. Calif. Coop. Fish. Invest. Rep. **32:** 65–90.

OHMAN, M. D. 1988. Sources of variability in measurements of copepod lipids and gut fluorescence in the

California Current coastal zone. Mar. Ecol. Prog. Ser. **42:** 143–153.

———, J. M. Bradford, and J. B. Jillett. 1989. Seasonal growth and lipid storage of the circumglobal, subantarctic copepod, *Neocalanus tonsus* (Brady). Deep-Sea Res. **36:** 1309–1326.

———, and R. A. Snyder. 1991. Growth kinetics of the omnivorous oligotrich ciliate *Strombidium* sp. Limnol. Oceanogr. **36:** 922–935.

Penry, D. L., and B. W. Frost. 1991. Chlorophyll *a* degradation by *Calanus pacificus*: Dependence on ingestion rate and digestive acclimation to food resources. Limnol. Oceanogr. **36:** 147–159.

Plourde, S., and J. A. Runge. 1993. Reproduction of the planktonic copepod, *Calanus finmarchicus*, in the lower St. Lawrence estuary: Relation to the cycle of phytoplankton and evidence for a *Calanus* pump. Mar. Ecol. Prog. Ser. **102:** 217–227.

Runge, J. A. 1985. Egg production rates of *Calanus finmarchicus* in the sea off Nova Scotia. Ergeb. Limnol. **21:** 33–40.

———. 1988. Should we expect a relationship between primary production and fisheries? The role of copepod dynamics as a filter of trophic variability. Hydrobiologia **167/168:** 61–71.

Sameoto, D. D., and A. W. Herman. 1992. Effect of the outflow from the Gulf of St. Lawrence on Nova Scotia shelf zooplankton. Can. J. Fish. Aquat. Sci. **49:** 857–869.

Stoecker, D. K., and J. M. Capuzzo. 1990. Predation on Protozoa: Its importance to zooplankton. J. Plankton Res. **12:** 891–908.

Strathmann, R. R. 1967. Estimating the organic carbon content of phytoplankton from cell volume or plasma volume. Limnol. Oceanogr. **12:** 411–418.

Tiselius, P. 1989. Contribution of aloricate ciliates to the diet of *Acartia clausi* and *Centropages hamatus* in coastal waters. Mar. Ecol. Prog. Ser. **56:** 49–56.

Urban, J. L., C. H. McKenzie, and D. Deibel. 1992. Seasonal differences in the content of *Oikopleura vanhoeffeni* and *Calanus finmarchicus* faecal pellets: Illustrations of zooplankton food web shifts in coastal Newfoundland waters. Mar. Ecol. Prog. Ser. **84:** 255–264.

White, J. R., and M. R. Roman. 1992. Egg production by the calanoid copepod *Acartia tonsa* in the mesohaline Chesapeake Bay: The importance of food resources and temperature. Mar. Ecol. Prog. Ser. **86:** 239–249.

Submitted: 11 March 1993
Accepted: 5 May 1993
Amended: 7 July 1993