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Energy sources for recruitment of the subantarctic copepod *Neocalanus tonsus*[1]

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Abstract

Neocalanus tonsus Brady was collected in subantarctic waters off southeastern New Zealand to test experimentally the importance of storage lipids and particulate matter as energy sources for recruitment. Reproductive copepods occur in mesopelagic depths (1,000–500 m) in austral winter and in epipelagic depths (150–0 m) in spring. Winter copepods released up to 19 eggs female^{-1} d^{-1} in filtered seawater; spring copepods required a particulate food source to release eggs. Winter females ingested diatoms at half the rate of spring females. Winter CVs did not ingest diatoms, in contrast to spring and summer CVs. Winter females had 24 times the wax ester content, half the phospholipid, and half the nitrogen content of spring females. In contrast, the two groups did not differ in dry mass or carbon content. Application of a proposed method for estimating reproductive potential, combined with experimental results, suggests that stored lipids are the energy source for recruitment of mesopelagic winter animals but not epipelagic spring animals.

Subantarctic *N. tonsus* is distinguished from subarctic Pacific *Neocalanus plumchrus* and *Neocalanus cristatus* by residence of adult females in surface waters, active suspension feeding, and the dependence of egg production on particulate food in spring. Divergent life history traits may be observed for copepod species occupying parallel subpolar habitats in the southern and northern hemispheres.

Subpolar zooplankton assemblages in the southern hemisphere, subantarctic ocean and the northern hemisphere, subarctic Pacific are dominated by copepods currently referred to the genus *Neocalanus*. *Neocalanus tonsus* Brady is endemic to the oceanic subantarctic, bounded approximately by the polar front to the south and the subtropical convergence to the north (Vervoort 1957; De Decker and Mombeck 1965; Brodskii 1964; Jillett 1968; Kawamura 1974). *Neocalanus plumchrus* Marukawa and *Neocalanus cristatus* Krøyer are endemic to the subarctic North Pacific, occurring principally in the open ocean (Brodskii 1950; Miller et al. 1984), some neighboring seas (Marukawa 1921; Vidal and Smith 1986), and deep fjords (Fulton 1973; Mackie 1985). It is now recognized that two species are subsumed under the designation *N. plumchrus* (C. B. Miller pers. comm.).

A singular feature of recruitment of the North Pacific species is that mating and reproduction occur exclusively in mesopelagic depths (Beklemishev 1954; Heinrich 1962; Miller et al. 1984). Adult males and females do not occur in surface waters at any time of year (Vinogradov 1968; Minoda 1971; Miller et al. 1984). Adult females have reduced, nonfunctional mouthparts (Campbell 1934; Beklemishev 1954; Vyshkvartzeva 1977) and do not feed before releasing eggs at depth (Heinrich 1962; Fulton 1973). In the laboratory *N. plumchrus* females maintained in filtered seawater release several hundred eggs (Fulton 1973). Recruitment is therefore decoupled from primary production in the euphotic zone. Rather, it depends on high concentrations of wax esters deposited by copepodid stage V, retained in females after the molt (cf. Gatten et al. 1980) and subsequently used in egg production (Lee et al. 1972). Although lipids are commonly stored by copepod species from higher latitudes (Lee et al. 1971; Sar-

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gent and Henderson 1986), the lack of viable feeding appendages in adult females and *obligate* dependence on stored lipids are unique characteristics of the subarctic Pacific calanids.

The distinctive life history characteristics of the subarctic species suggested comparison with the subantarctic *N. tonsus*. Jillett's (1968) study off the South Island of New Zealand indicated that males appeared first and then females in deep water in austral winter. Production of a first generation apparently occurred at depth, followed by ascent of developing nauplii and copepodids into surface waters. The occurrence of *N. tonsus* eggs in mesopelagic depths in August–September (pers. obs.) confirms that deep reproduction occurs in situ. Unlike *N. plumchrus* and *N. cristatus*, however, once the developing copepodids of *N. tonsus* attained the CV stage in surface waters they did not descend to deeper waters. Instead development continued in surface waters to the adult stage followed by production of a second generation (Jillett 1968). Lipid-rich CVs arising from this second, surface generation were then thought to descend into mesopelagic depths. Occurrence of adult females in surface waters in spring–summer elsewhere in the subantarctic province (Vervoort 1957; Bradford 1970; Kawamura 1974; Voronina 1975; Taw and Ritz 1979) supports Jillett's interpretation of spring surface recruitment and suggests a significant departure from the life history of the subarctic Pacific species.

Because of the parallel subpolar habitats occupied, yet suggested differences in life history between *N. tonsus* and its congeners, the present study was designed to determine the processes controlling recruitment of *N. tonsus*. This investigation compares the feeding behavior, fecundity, and organic composition of deep winter and shallow spring *N. tonsus*. The objective was to evaluate the importance of particulate matter in the water column as contrasted with storage lipids as energy sources for recruitment of the two apparent generations. One of the approaches is to estimate the reproductive potential of *N. tonsus* females under the assumption that only storage products provide the energy source for egg production. This method makes use of the observation that storage lipids are the proximate energy sources for egg production of nonfeeding adult copepods (Heinrich 1962; Conover 1967; Fulton 1973). This method, an extension of the approach of Gatten et al. (1980), requires knowledge of adult lipid content, egg lipid content, and daily respiratory lipid oxidation. In addition, for comparison of *N. tonsus* with a species known to feed actively, parallel feeding experiments were performed with *Calanus australis* Brodskii (cf. Drits 1985).

The generic assignment *Neocalanus* is used herein, following Bradford and Jillett (1974), although the evolutionary relationships among calanid lineages are currently under review (Fleminger 1985).

J. B. Jillett and J. M. Bradford shared ideas and expertise and were instrumental in facilitating all aspects of this research. Numerous individuals at the Portobello Marine Laboratory and the D.S.I.R. Division of Marine and Freshwater Science and Chemistry Division contributed to this effort. Space for experimental work was made available at the University of Otago, Department of Microbiology. I thank M. R. Grigor, B. W. Frost, M. F. Barker, C. W. Burns, P. Jones, B. Chapman, and R. Baldwin for their help. J. M. Bradford, C. B. Miller, and an anonymous referee provided comments and criticisms of the manuscript.

Methods

Collection—Live collections were made at a continental slope station (45°55′S, 171°06′E) 32 km southeast of Taiaroa Head, Otago Peninsula, New Zealand, or at a shelf station 15 km offshore. Copepods were collected in the upper 150 m in austral spring–summer (October 1984–January 1985) and between 1,000–500 m in winter (August 1985). A 1-m-diameter, 333-μm-mesh ring net or a 0.7-m, 202-μm-mesh closing net (Brown and Honegger 1978) was used; cod ends were nonfiltering. Live animals were transported to a shore laboratory in thermally insulated containers. Copepods intended for lipid, dry mass, carbon, and nitrogen analysis were quickly frozen in liquid nitrogen aboard ship and transferred to a −70°C freezer ashore.

C, N, and lipid analysis—Dry mass was determined with a Cahn G-2 electrobalance after briefly rinsing in distilled water and desiccating at 55°C. Nitrogen and carbon were determined by combustion in a CN elemental analyzer (courtesy of M. Downes). Lipids of adults were extracted twice by homogenization (Bligh and Dyer 1959). Eggs released by *N. tonsus* females in the laboratory were extracted by sonication, followed by the Bligh and Dyer phase separation. Lipids were analyzed by thin-layer chromatography-flame ionization detection with an Iatroscan TH-10 Mark III (Parrish and Ackman 1985). Chromarods were developed for 20 min in hexane : diethyl ether (95 : 5, vol/vol) followed by 20 min in hexane : diethyl ether : formic acid (82 : 18 : 0.1, vol/vol/vol). Cetyl alcohol was the internal standard, since copepod free alcohols were below the limits of detection.

Feeding experiments—Feeding and egg production experiments were performed at 9°C to approximate the mixed-layer temperature in subantarctic water during the spring–early summer growing season (Jillett 1969). Incubations were done in the dark, on a roller mixing device which rotated jars at 1.5 rpm. Seasonal and stage-specific rates of phytoplankton uptake by *N. tonsus* were determined with gut fluorescence (Dagg 1983). All gut fluorescence experiments were conducted with the same clone of *Thalassiosira weissflogii,* cultured in standardized conditions, at similar cell concentrations (5,469±439 cells ml^{-1}, $\bar{x}$±95% C.L.), with consistent preconditioning of experimental animals. After at least 12 h of starvation in filtered seawater (AP1 filter bags, Strainrite), copepods were transferred to a series of replicate jars containing *T. weissflogii.* (For one treatment with *N. tonsus* CIV, a 3 : 1 mixture of the diatoms *Cyclotella cryptica* and *T. weissflogii* was used.) Seven to 15 *N. tonsus* CVs or adult females or 20 *Calanus australis* adult females were added to a series of 1,000-ml jars; 4–16 CIVs were added to 500-ml jars. At intervals following the onset of incubation in the diatom suspension, the contents of a jar were passed through a 202-μm Nitex screen to recover copepods. Animals were rinsed quickly in distilled water, then 1–4 pooled animals were macerated in 90% acetone. Chlorophyll *a* and pheopigments were assayed on a Turner model 111 fluorometer with a high-sensitivity door, and pigment content was computed based on the equations of Strickland and Parsons (1972). Total pigment per copepod is the sum of Chl *a* and pheopigments resulting from these equations, without further correction (cf. Conover et al. 1986). No correction was made for apparent loss of Chl *a,* since Dagg and Walser (1987) reported that pigment losses averaged 11%. Background fluorescence was determined for each developmental stage by starving animals in filtered seawater. Animals were collected for experiments as follows: *N. tonsus* CIV (November and December), CV (November, December, January, August), males (August), females (November and August); *C. australis* females (January).

Gut residence time was determined as follows. A group of *N. tonsus* CVs was fed *T. weissflogii* at a concentration of 6,010 cells ml^{-1} for 6.5 h; they were then transferred to filtered seawater and the decline in gut fluorescence with time was measured. Or CVs were starved for 1–2 d in AP1-filtered seawater, transferred to individual vials containing 12 ml of *T. weissflogii* at about 5,000 cells ml^{-1}, and then observed every 2–4 min under dim red light with a dissecting microscope until a fecal pellet was detected.

Prey disappearance experiments were used to define the critical concentration for egg production experiments and to compare ingestion rates on different prey items. *Neocalanus tonsus* CVs were acclimated to prey for at least 16 h. Ten to 20 *N. tonsus* CVs were placed in 1-liter jars containing prey with 4–8 replicate jars per treatment. All incubations lasted 4 h. Algal prey were the diatoms *T. weissflogii, Thalassiosira pseudonana,* and the flagellate *Isochrysis galbana,* cultured in f/2 medium at 15°C in constant illumination and used in exponential growth phase. Microzooplankton prey were simulated by 1.5-d-old nauplii of *Artemia salina.* Three controls were run for each experiment to correct for phytoplankton growth or for efficiency of recovery of *Artemia* nauplii (recovery = 99.4±1.6%, $\bar{x}$±95% C.L.). Changes in cell concentration

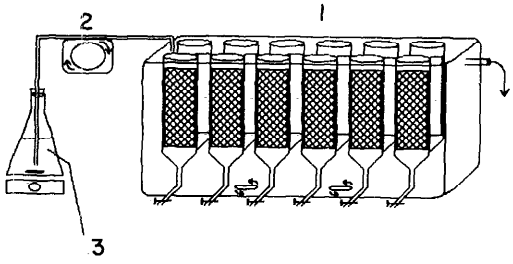

Fig. 1. Schematic illustration of egg production chamber. Copepods were retained within Perspex cylinders with walls and floors of Nitex screen. Eggs were collected from ports beneath each cylinder. Phytoplankton cells circulated throughout the chamber, providing uniform cell concentrations for all copepods. The pumping rate was adjusted to maintain steady state cell concentrations (*see methods*). Egg production chamber—1; peristaltic pump—2; diatom suspension or filtered seawater control—3.

were determined with a model Z_{BI} Coulter counter and ingestion rates calculated with the equations of Frost (1972). Application of these equations assumes constant clearance rates during a 4-h experiment. Calculations with the equation suggested by Marin et al. (1986; equation 14, corrected) altered clearance rates by an average of 3.0%, indicating only minor deviations from this assumption. Ingestion of nauplii was calculated analogously by assuming constant exponential decline of prey. The functional response curve was fitted with the Levenberg-Marquardt algorithm (More et al. 1980).

Egg release—Incubations were started within 24 h of capture of the animals in the field. Continuous-flow egg production chambers were designed to reduce daily oscillations in food concentration. Individual *N. tonsus* females were added to Perspex cylinders housed in 9-liter reservoirs (Fig. 1). Each cylinder (105-ml volume) had Nitex mesh walls, permitting algal cells to circulate but retaining the copepods. The floor of each cylinder was Nitex, allowing eggs and fecal pellets—but not females—to sink into collecting funnels (cf. Runge 1984). A peristaltic pump delivered algal cells to one egg production chamber and filtered seawater to a separate control chamber, totaling 12 cylinders in each treatment. Magnetic stirring bars maintained cells in suspension. On a daily basis, eggs and fecal pellets were collected from each sampling port and the algal culture and filtered seawater reservoirs replenished. The pumping rate was adjusted to maintain approximately uniform cell concentrations by solving

$$P = \frac{FNC_{res}}{C_{cul} - C_{res}} \quad (1)$$

where P is the pumping rate, C_{res} the reservoir cell concentration, C_{cul} the culture cell concentration, F the clearance rate per copepod, and N the number of copepods.

Table 1. Regression equations for ingestion and gut residence time experiments. Copepods were incubated at 9°C in the dark with the diatom *Thalassiosira weissflogii* at 5,500 cells ml^{-1}. The units of Y are ng pigment copepod^{-1} and of x min.

Species/developmental stage	Date collected	N	Equation	r^2	P
			Ingestion		
Neocalanus tonsus					
Female	Nov 84	20	$Y = 2.308X + 2.372$	0.888	<0.001
	Aug 85	9	$Y = 0.819X - 6.013$	0.583	<0.020
Copepodid V	Nov 84	16	$Y = 1.323X - 0.724$	0.829	<0.001
	Jan 85	18	$Y = 0.533X - 2.789$	0.898	<0.001
	Aug 85	14	No uptake detected		
Copepodid IV	Nov 84 and Dec 84	21	$Y = 0.122X + 0.716$	0.692	<0.001
Calanus australis					
Female	Jan 85	23	$Y = 0.649X - 3.950$	0.871	<0.001
			Gut residence time		
Neocalanus tonsus					
Copepodid V	Jan 85	25	$Y = 45.879 \exp(-0.046X)$	0.562	<0.001

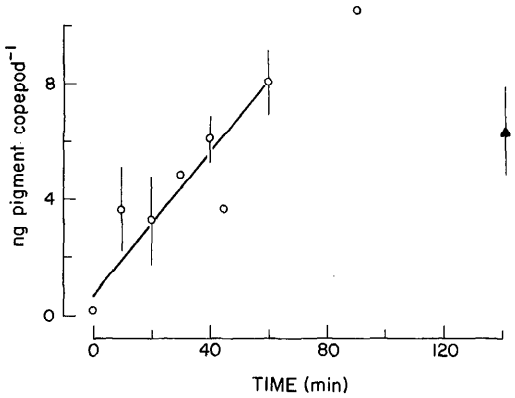

Fig. 2. Time-course of increase of gut pigments of *Neocalanus tonsus* CIVs incubated with the diatom *Thalassiosira weissflogii* (○) or a 3 : 1 mixture of *Cyclotella cryptica* and *T. weissflogii* (▲). Experiment conducted in November–December with animals collected in the upper 150 m ($\bar{x}\pm$SE).

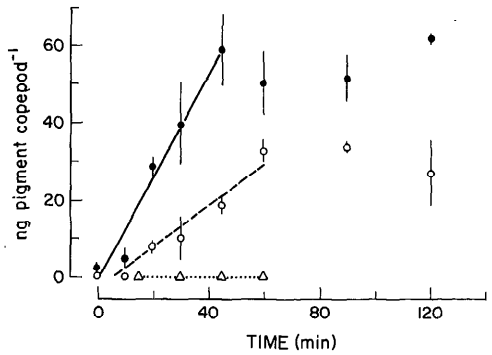

Fig. 3. Time-course of increase of gut pigments of *Neocalanus tonsus* CVs incubated with the diatom *Thalassiosira weissflogii* in November (●; animals collected between 150 and 0 m), December (○; 150 and 0 m), and August (△; 1,000 and 500 m).

The clearance rate was determined in independent grazing experiments and C_{cul} and C_{res} were monitored by cell counts. After solving for P and adjusting pumping rates accordingly, between 8 and 15% of the reservoir volume turned over each day. The cell concentration, monitored once or twice per day, averaged 5,707±285 cells ml^{-1} ($\bar{x}\pm$95% C.L.; C.V. = 13.4%) in November experiments and 5,480±413 cells ml^{-1} (C.V. = 19.0%) in August.

Results

Feeding behavior—Uptake experiments revealed an initial 45–60-min period of linear increase followed by a plateau of approximately constant gut fluorescence (*see Figs. 2–4, 6*). Only those data from the initial linear response region were included in regression analyses (Table 1). Preliminary experiments showed gut pigment levels decreasing 2–4 h after ingestion began. Consequently incubations were ended after 2 h (*see also* Mackas and Burns 1986). *Neocalanus tonsus* CIVs were collected for experiments only in spring–early summer (November–December; Fig. 2).

Ingestion rate of *N. tonsus* CVs varied significantly by season (Fig. 3). The initial slope of the ingestion curve was greater in spring than in summer ($F_{1,30} = 29.29$, $P < 0.001$, ANCOVA). This difference was more pronounced ($F_{1,30} = 47.01$, $P < 0.001$) when slopes were expressed on a mass-specific basis. The mean dry mass of a *N. tonsus* CV in spring was 350±73 μg ($\bar{x}\pm$95%) and in summer was 513±48 μg. In contrast to results with surface-collected CVs in spring and summer, no uptake of diatoms was detected with CVs collected between 1,000 and 500 m in winter (Fig. 3). Winter CVs were viable, robust in appearance, and showed excellent survivorship but exhibited minimal swimming activity.

Incubations with adult *N. tonsus* females established that their mouthparts are fully functional. Between-season differences existed in behavior however, since females collected in spring near the surface showed

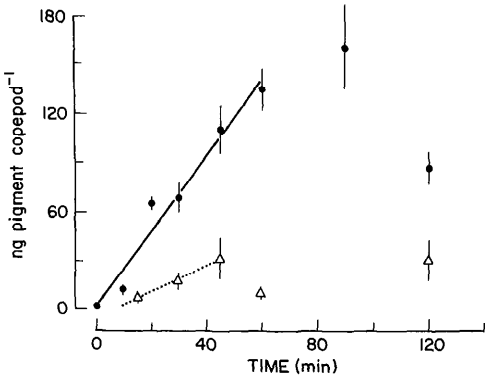

Fig. 4. Time-course of increase of gut pigments of *Neocalanus tonsus* females incubated with the diatom *Thalassiosira weissflogii* in November (●; animals collected between 150 and 0 m) and August (△; 1,000 and 500 m).

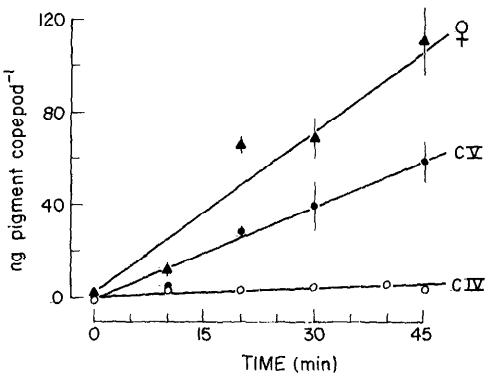

Fig. 5. Comparative initial rate of increase in gut fluorescence of *Neocalanus tonsus* CIVs, CVs, and females. All copepods collected between 150 and 0 m in November–December.

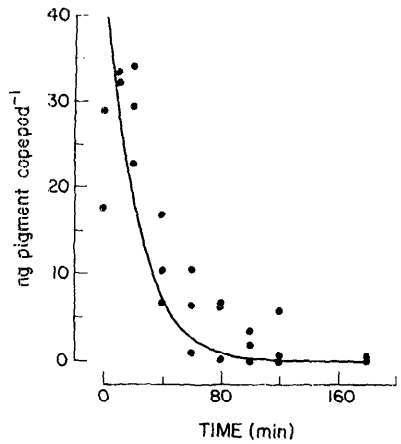

Fig. 7. Time-course of decrease of gut pigments of *Neocalanus tonsus* CVs transferred to filtered seawater after ingesting *Thalassiosira weissflogii* (animals collected between 150 and 0 m in January).

higher rates of cell uptake than females collected in winter at depth ($F_{1,25} = 8.61$, $P < 0.01$, Fig. 4). Expressed as mass-specific rates of uptake (dry mass: *see Table 4*), this difference remained significant ($F_{1,25} = 8.41$, $P < 0.01$). Visual inspection of gut pigments of females frozen in the field corroborated this result. Among females collected near-surface on three dates in October–November, most individuals had conspicuous greenish-brown guts; none of the females collected in deep water on three dates in July–August had visible gut pigments. A limited number of males were collected in August for experimental purposes. After 60 min of incubation, adult males collected at depth in late winter had 2.6±6.0 ng of pigment per animal ($\bar{x}$±95%, $N = 5$)—a twelfth the pigment content of winter females. Male mouthparts are only partially reduced in *N. tonsus* (Jillett 1968; Bradford and Jillett 1974), but, like other amphascandrid calanoid copepods, they exhibit little feeding activity.

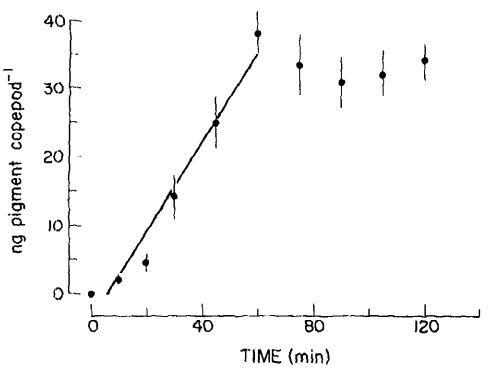

Fig. 6. Time-course of increase of gut pigments of *Calanus australis* females incubated with the diatom *Thalassiosira weissflogii* in January (collected between 150 and 0 m).

Comparative diatom uptake by CIVs, CVs, and adult females is shown in Fig. 5—all for animals collected in late spring–early summer. There is significant heterogeneity among slopes ($F_{2,51} = 81.91$, $P < 0.001$). The Tukey pairwise comparisons test established that all slopes differed ($P < 0.001$: Zar 1984), confirming that females ingest diatoms at higher rates than CVs and CIVs.

In addition to assessments of ingestion rates of *N. tonsus* females relative to those of younger developmental stages, incubations were performed with *C. australis* females for comparison with a species for which feeding is necessary before egg production. In comparable experimental conditions, active summer females of *C. australis* showed lower rates of uptake (Fig. 6) than active spring females of *N. tonsus* when expressed as pigment per copepod (Table 1, $F_{1,39} = 74.04$, $P < 0.001$). Body mass of *C. australis* females was estimated as 200 μg, by extension of determinations of mass of *C. australis* CVs (175±23 μg, $\bar{x}$±95%, $N = 20$). Expressing slopes of curves of gut fluorescence on a mass-specific basis, there remained a significantly higher rate of uptake

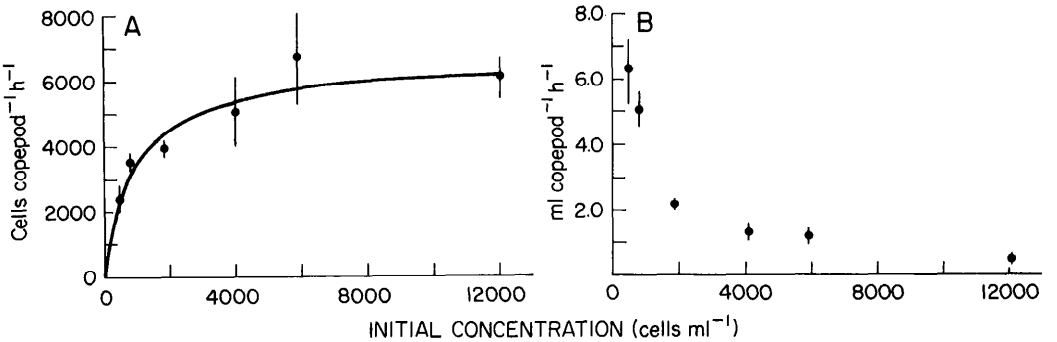

Fig. 8. Variations in ingestion rate (A) and clearance rate (B) of *Neocalanus tonsus* CVs as a function of concentration of the diatom *Thalassiosira weissflogii*. Animals were collected in the upper 150 m in December–January.

by *N. tonsus* females ($F_{1,39} = 9.94, P < 0.01$). Hence, spring *N. tonsus* females exhibit ingestion rates consistent with those of actively feeding copepods.

Gut residence time experiments were conducted only with *N. tonsus* CVs in summer. Decline in gut fluorescence with time after transfer to filtered seawater was described by an exponential decay (Fig. 7, Table 1) with a slope of -0.046 min^{-1}. In separate experiments, visual observations were made of the time to produce a first fecal pellet after transfer from filtered seawater to a diatom suspension. The median time to first pellet was 68 min (47–85 min, 95% C.L., $N = 29$). This value is in accord with the 60-min period of continuous increase of gut fluorescence in summer CVs, followed by a platcau, observed for previously starved individuals (Fig. 3).

Ingestion rate of *N. tonsus* CVs varied with cell concentration in prey depletion experiments with *T. weissflogii* as prey (Fig. 8A, $P < 0.001$, Jonckhere's test). Ingestion was described by the curve $I = (7.0726\ C)/(1 + 0.00106\ C)$, where I is cells ingested copepod^{-1} h^{-1} and C is cells ml^{-1}. The critical concentration for 90% satiated ingestion was ~4,800 cells ml^{-1}. Egg production experiments with CVI females were therefore conducted at 5,500 cells ml^{-1}, on the assumption that the critical concentration for CVIs was somewhat higher than that for CVs (Mullin and Brooks 1976; Vidal 1980). Over the range of prey concentrations tested, the clearance rate declined monotonically (Fig. 8B).

The relative ability of *N. tonsus* CVs to ingest different prey types is shown in Table 2. Experiments were performed at similar prey concentrations (as nitrogen or carbon), selected to represent food-limited feeding conditions that probably typify conditions in situ. Although suspension-feeding *N. tonsus* can utilize a variety of prey, estimated daily rations were highest on the diatom *T.*

Table 2. Daily carbon- and nitrogen-specific rations of *Neocalanus tonsus* CVs feeding on three species of phytoplankton and on nauplii of *Artemia salina* at 9°C. Prey concentration averaged 210–288 μg C liter^{-1} and 32–48 μg N liter^{-1}. Experiments conducted in January with 5–8 replicates per treatment. Phytoplankton carbon content estimated from Strathmann (1967). C : N ratio approximated as 6.50 from Heinbokel (1978) and Harris et al. (1986). *Artemia* nauplii carbon content estimated from Mullin and Brooks (1967) and C : N ratio obtained from Oppenheimer and Moreira (1980). *Neocalanus tonsus* CVs contained 336±22 μg C and 37±2 μg N ($\bar{x}$±95%).

Prey	Prey dimensions (μm)	Prey C, N content (pg C)	(pg N)	*N. tonsus* CV daily specific ration (% C d^{-1}) ($\bar{x}$±95%)	(% N d^{-1}) ($\bar{x}$±95%)
Thalassiosira pseudonana	4.6 × 6.2	12.7	1.9	1.4±0.6	1.9±0.9
Isochrysis galbana	4.8 × 7.1	22.9	3.5	1.1±0.4	1.5±0.5
Thalassiosira weissflogii	12.7 × 16.1	122.1	18.8	3.4±0.5	4.8±0.7
Artemia salina nauplii	140 × 467	500,000	83,000	3.8±0.9	5.7±1.3

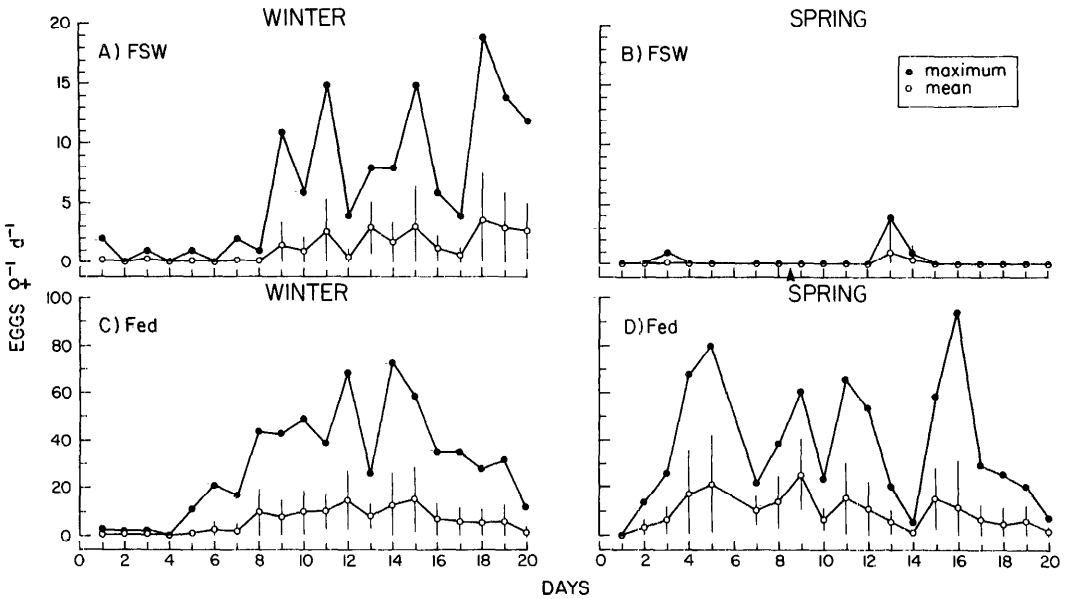

Fig. 9. Egg release by *Neocalanus tonsus* females starved in filtered seawater (A, B) and fed a suspension of *Thalassiosira weissflogii* (C, D). Winter animals were collected in August between 1,000 and 500 m and spring animals were collected in November between 150 and 0 m. Arrow in panel B indicates time at which cells were added to the starved treatment. Vertical line denotes 95% C.L.

weissflogii and on *Artemia salina* nauplii, differing on a C-specific and a N-specific basis because of the high lipid content of summer CVs (Ohman et al. in prep.). Animals were collected for these experiments in late December–January when feeding rates were below seasonal maxima (*see above*); hence the absolute rates should not be considered typical of *N. tonsus*.

Egg production—Individual *N. tonsus* females usually released eggs for 3–5 d, followed by a 1–4-d hiatus. This contributed to relatively high variance associated with mean egg production rates on a single date, because individuals did not release eggs synchronously. Hence, the daily mean value considerably underestimates the maximum short-term capabilities of individuals (Fig. 9).

Egg production by *N. tonsus* females collected in mesopelagic depths in winter differed from that of females collected near the surface in spring. Some females collected in winter released eggs at the beginning of the experiment, and as many as 19 eggs were subsequently released per day by unfed females (Fig. 9A). In contrast, with a single exception, females collected in spring and maintained in filtered seawater did not produce eggs (Fig. 9B). After 8 d of starvation, subsequently feeding spring females for 12 d resulted in only a nominal increase in egg release (Fig. 9B). Feeding diatoms to females in both winter and spring resulted in higher rates of egg release than in filtered seawater, apparently with a longer lag time for the response in winter than in spring (Fig. 9C, D). Egg viability was not systematically evaluated, but nauplii were produced from eggs released by both starved

Table 3. *Neocalanus tonsus* female and egg dimensions in winter (16 August 1985) and spring (2 November 1984). Eggs were released in the laboratory. Egg lipids were not analyzed in spring. Values are $\bar{x}\pm$95% (*N*).

Season (depth, m)	♀ prosome length (μm)	Egg diameter (μm)	Egg lipid (ng)
Winter (1,000–500)	3,050±28 (120)	139±1 (55)	144±120 (3)
Spring (150–0)	3,203±42 (43)	143±1 (30)	–

Table 4. Comparative composition of *Neocalanus tonsus* females collected at depth in winter (16 August 1985) and near-surface in spring (2 and 27 November 1984). Sample sizes for lipids were 10 extractions in winter, 12 in spring, and for other constituents were 19 in winter and 17 in spring. *P* value for Mann-Whitney *U*-test of winter–spring differences indicated in final column.

	Winter (1,000–500 m)	Spring (150–0 m)	
	μg ($\bar{x}$±95%)		*P* value
Dry mass	478±44	487±45	>0.10
Carbon	250±29	219±22	>0.10
Nitrogen	30.8±2.5	60.1±5.5	<0.001
C:N	8.09±0.58	3.64±0.15	<0.001
Total lipid	162±30	47±10	<0.001
Wax ester	145±30	6±4	<0.001
Phospholipid	14±2	27±4	<0.001

and fed females and development to CV was obtained in independent experiments where animals were fed (Bradford et al. in prep.).

Egg diameters were significantly smaller in winter than in spring ($P < 0.001$, Mann-Whitney *U*, two-tailed; Table 3). Eggs in both seasons were spherical with no surface ornamentation. The lipid content of ova released in the laboratory, determined only for August females, averaged 144 ng of total lipid. Egg dry mass was not determined, but assuming the specific gravity of the eggs was 1.027 and egg dry mass is 0.15 × wet mass, lipids constituted 66% of egg dry mass.

Winter and spring females did not differ in dry mass or in body carbon content (Table 4). In contrast, winter females had half the nitrogen content of spring females and thus twice the C:N ratio. Lipid content and lipid class composition were significantly different between groups of females (Table 4). Winter females had 3.4 times the total lipid content, 24 times the wax ester content, and half the phospholipid content of spring females.

Estimated reproductive potential—Nonfeeding copepods that release eggs must do so at the expense of storage products. Hence the mass of storage products, combined with consumption rates, can provide an estimate of total reproductive potential. Here it is proposed that the information required to estimate reproductive potential of nonfeeding females includes female lipid content, egg lipid content, daily respiratory losses, and the time-course of egg release. Respiration rate as a function of lipid-free dry mass was estimated from the regression of Vidal and Whitledge (1982) for *N. plumchrus* and *N. cristatus* and converted to equivalent lipid oxidation rate (Table 5). For simplicity eggs were assumed to be released at their maximal daily rate, thereby providing an upper estimate. Spring eggs were assumed for this calculation to have the same lipid content as winter eggs. The conclusions are shown below to be insensitive to this assumption. Because female phospholipids or their constituent fatty acids may be transferred to eggs as well as storage lipid classes (Clarke et al. 1985), total lipid content of females was considered in estimating reproductive potential.

Winter mesopelagic females have a predicted reproductive potential of 285 eggs, in contrast to the 4-egg potential of the epipelagic spring females (Table 5). If nonfeeding, overwintering copepods have

Table 5. Comparative reproductive potential of *Neocalanus tonsus* in winter and spring under the assumption that females utilize lipids as an energy source for egg production. All values except egg lipid content are expressed per female.

	Winter (1,000–500 m)	Spring (150–0 m)	Comments
Lipid content (μg)	162	47	Table 4
Lipid-free dry mass (μg)	315	440	Table 4
Respiration rate			
Oxygen consumption (μl O_2 d^{-1})	17.4	22.9	Vidal and Whitledge 1982
Equivalent lipid oxidation (μg lipid d^{-1})	8.1	10.8	Assuming respiratory quotient = 0.7 and lipid = 1.25 carbon
Max egg release rate (eggs d^{-1})	19	1	Fig. 9
Egg lipid content (μg lipid egg^{-1})	0.144	0.144	Table 3; assume spring = winter
Total lipid consumption rate (μg lipid d^{-1})	10.8	10.9	Σ (respiration + egg release)
Potential fecundity (eggs)	285	4	

metabolic rates half those of actively metabolizing animals, as suggested by the experiments of Conover (1962) and Conover and Corner (1968), then respiratory lipid oxidation would consume a smaller fraction of lipids each day. The potential fecundity of deep-dwelling *N. tonsus* females would increase from 285 to 453 eggs under this assumption. Reproduction by mesopelagic females can be fueled by lipid reserves, while spring females have virtually no reproductive potential in the absence of an exogenous food source.

Discussion

Feeding experiments, egg production experiments, and estimated reproductive potential demonstrate that the energy sources for recruitment of *N. tonsus* differ between winter and spring. The lipid content of deep-dwelling winter animals is sufficient for release of about 300 eggs in the absence of feeding, but spring females must use an exogenous energy source to produce offspring. Although reproduction at depth in winter from lipids is analogous to the recruitment mechanism of the subarctic species *N. plumchrus* and *N. cristatus,* the subsequent appearance of *N. tonsus* females in the surface layer in spring and their active ingestion of particulate matter in the water column represents a marked departure from the northern species.

This facultative feeding response of *N. tonsus* is similar to that reported for *Calanus hyperboreus* by Conover (1967). *Calanus hyperboreus* females release eggs in the absence of particulate food, but the highest egg viability is observed when females are fed (Conover 1967). Indeed, the life history of *N. tonsus* resembles that of *C. hyperboreus* more than that of either *N. plumchrus* or *N. cristatus.* Eggs of *C. hyperboreus* are released at depth in later winter, apparently from lipid reserves, before emergence of females into the surface layer (Sømme 1934; Conover 1962, 1967). Some species of serially spawning clupeoid fishes also use storage lipids as an energy source for early broods and planktonic prey for production of later broods (Lasker and Smith 1977; Hunter and Leong 1981; Blaxter and Hunter 1982).

The quiescent behavior of *N. tonsus* CVs collected at depth in winter, their lack of feeding response, and high lipid content (Ohman et al. in prep.) suggest reduced metabolic activity and diapause. Both *N. plumchrus* and *N. cristatus* enter diapause as CVs (Fulton 1973; Miller et al. 1984), as is typical of temperate and higher latitude calanoid copepods (Voronina 1972; Corkett and McLaren 1978; Grigg and Bardwell 1982; Hirche 1983). The depressed feeding rates of CVs of *N. tonsus* collected in summer, which cannot be explained by changes in body size alone (cf. Runge 1980), suggest that they were in transition to diapause. This result confirms that care should be taken when making cross-seasonal comparisons of ingestion rates and other physiological parameters of high-latitude zooplankton species.

At present it is not certain that the winter and spring females of *N. tonsus* represent two discrete, nonoverlapping generations. The alternative cannot yet be ruled out that emergence from CV diapause occurs over a broad time interval with early-maturing females remaining at depth and late-maturing females ascending to the surface. Work in progress may resolve this issue. However, the 3-month interval between predominance of the two modes of female behavior suggests that they are unlikely to be the same individual copepods.

Suspension feeding—Adult *N. tonsus* females from the subantarctic ocean are active suspension feeders, in marked contrast to *N. plumchrus* and *N. cristatus.* These results are consistent with interspecific differences in morphology of feeding appendages. Upon molting to the CVI female the mandibular palp, first maxillae, second maxillae, and maxilliped of *N. tonsus* all enlarge, and the associated setae elongate for both winter and spring females (pers. obs., light and scanning electron microscope). The mandibular gnathobase of *N. tonsus* females also enlarges and retains crisp dentition (Tanaka 1956; Vervoort 1957). In contrast, the terminal molt to adult female by *N. plumchrus* and *N. cristatus* is accompanied by reduction in size and setation of the first maxillae, second maxillae, and maxilliped and complete loss of the cutting edge of the mandibular gnathobase (Campbell 1934; Tanaka 1956; Omori 1970; Bradford and Jillett 1974; Vyshkvartzeva 1976, 1977).

Adult females of the latter two species do not feed (Beklemishev 1954). *Neocalanus plumchrus* and *N. cristatus* differ not only from *N. tonsus,* but from all other members of the Calanidae in this atrophy of female mouthparts (Vyshkvartzeva 1976).

Differences between CVs of *N. tonsus* and *N. plumchrus* in maximum ingestion (Dagg et al. 1982; Dagg and Wyman 1983; Dagg and Walser 1986) and maximum clearance rates (Frost et al. 1983; Dagg and Walser 1987) are probably attributable to the larger body size of *N. plumchrus.* No reduction in clearance rate by *N. tonsus* CVs was observed at lower cell concentrations (Fig. 8B) as reported for *N. plumchrus* and *N. cristatus* (Frost et al. 1983). However, conversion of food concentrations to common units reveals that I conducted experiments with *N. tonsus* at concentrations above the region of prey concentrations where the reduction in clearance rate by the subarctic species was observed.

The exponent for gut evacuation of *N. tonsus* CVs at 9°C, -0.046 min^{-1}, compares with -0.039 min^{-1} for *N. plumchrus* CVs at 9.2°C (Dagg and Wyman 1983). The reciprocal of this exponent, 22 min, estimates gut residence time for animals with a previous feeding history. For *N. tonsus* CVs fed continuously above the critical concentration (Fig. 8) the average interval between pellets was 30 min. Arashkevich and Tseytlin (1978) estimated the average interval between pellets as 16–19 min for *N. tonsus* CVs feeding continuously at an unspecified temperature. These estimates for previously fed copepods differ considerably from the average gut residence time determined above for previously starved animals (68 min). This disparity probably reflects a true behavioral alteration of gut residence time. Dagg and Walser (1987) document a strong negative relationship between gut residence time and food concentration. Increased gut residence time for starved animals is also consistent with increased gut residence time of mysid shrimp fed at low food concentrations (Murtaugh 1984) and with higher assimilation efficiency of copepods fed at low food concentrations (Gaudy 1974).

Reproductive potential—Gatten et al. (1980) projected total egg production of female *Calanus helgolandicus* from the lipid content of copepodid V. They did not take into account respiratory oxidation of lipids—the magnitude of which is shown here to be a major loss term. Reproductive rates of *C. helgolandicus* and most of its congeners have been observed to depend on particulate food substrates ingested by females (Marshall and Orr 1955; Heinrich 1962; Runge 1984, 1985; Hirche and Bohrer 1987).

Long-term egg production experiments could not be carried out to compare total fecundity of *N. tonsus* with the reproductive potential estimated from lipid content. One comparison can be made with Fulton's (1973) study in which the total fecundity of *N. plumchrus* is described as a function of prosome length. For this comparison, the egg number predicted from his regression must be corrected to account for the difference in egg volumes between the two species [a factor of 2.17 by volume for eggs of diameter 139 μm (*N. tonsus*) and 180 μm (*N. plumchrus*)]. The regression must also be extrapolated beyond the domain of prosome lengths observed for *N. plumchrus.* Accordingly, for *N. tonsus* winter females Fulton's regression predicts total fecundity of 320 eggs, comparing favorably with the estimate from lipid content (285–453 eggs). Conover (1967) reported that another boreal species, *C. hyperboreus,* released about 400 eggs in the absence of food. Future studies will be required to verify this method for other high latitude and mesopelagic species that do not feed at the time of reproduction. However, considerable ability to predict recruitment variations in natural populations may be obtained from the relatively simple lipid method proposed.

Estimates of lipid-derived reproductive potential are sensitive to daily respiratory demand, since a larger fraction of each day's lipid consumption is used in respiration than in egg production. One source of error in estimating metabolic rates is use of the relation of Vidal and Whitledge (1982) determined at 4°C—a temperature substantially lower than that experienced by epipelagic spring *N. tonsus* (Jillett 1969). However, upward adjustment of respiration rates of spring females by warmer surface temperatures would further accentuate their de-

pendence on exogenous food to control spring recruitment. Copepods in Vidal and Whitledge's experiments were feeding, hence the metabolic rate of nonfeeding, winter mesopelagic animals may be overestimated. Metabolic rate of females also varies with reproductive condition (Conover 1962). Oxidation of nonlipid substrates could also alter reproductive potential. The time-course of egg release is another factor important to this calculation, since it is unrealistic to assume that egg release is continuously sustained at its maximum daily rate (Fulton 1973; Runge 1984). However, another source of error, overestimation of spring egg lipid content, would not significantly alter this analysis. Even if the lipid content of spring eggs were twofold to threefold lower than that of winter eggs, respiration would consume maternal lipids quickly enough that few eggs would be released in the absence of a supplemental source of nutrition. Because of the sensitivity of the estimate of reproductive potential to respiratory lipid oxidation, future applications of this method should include careful determinations of female metabolic rates in conditions simulating those in situ, for animals in an appropriate state of metabolic activity.

This estimate is overly simplistic in that for egg synthesis, nitrogen, other elements, and trace metabolites will be required in addition to lipids. Nevertheless, the ability of females of *N. tonsus* and other species (Conover 1967; Fulton 1973) to release eggs in the absence of particulate food sources suggests that these other constituents are available. Maternal protein or nitrogen-containing phospholipids may provide a nitrogen source. Furthermore the predominance of lipids as a component of the organic matter of *N. tonsus* eggs suggests they are a reasonable currency for such estimates.

In conclusion, the oceanic subantarctic copepod *N. tonsus* exhibits seasonal changes in feeding behavior, egg production response, and organic composition. Winter females dwelling in mesopelagic depths can release eggs in the absence of particulate food and have substantial lipid reserves that make possible recruitment decoupled from primary production in surface waters. In contrast, spring females dwelling epipelagically have limited lipid reserves and must obtain an exogenous source of nutrition to fuel egg production. The spring individuals are therefore directly coupled to the primary production cycle for recruitment. This alternation between reproduction decoupled from the primary production cycle and that directly coupled to it is unusual by comparison with most other suspension-feeding copepods. It differs markedly from the feeding behavior and recruitment mechanisms of the nonfeeding, deep-reproducing Pacific species dwelling in a parallel subpolar habitat in the northern hemisphere.

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