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Importance of food quantity to structural growth rate and neutral lipid reserves accumulated in *Calanus finmarchicus*

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**Abstract** Growth and developmental rates were determined for copepods of *Calanus finmarchicus* (Gunnerrus) from experimental seawater mesocosms in a western Norwegian fjord. The instantaneous growth rates (g) from copepodid stage I (CI) to adult ranged from 0.08 to 0.10 d\(^{-1}\). Daily per capita mortality rate of the cohorts was as low as 0.012 d\(^{-1}\) (1.2% d\(^{-1}\)). At local increasing temperatures (5.1 to 8.3 °C), development was equi-proportional, and the cumulative median development time from egg to CV was approximately 65 d. CV molted to males and females, and egg production was initiated. Enhancement of food resources by nutrient addition caused a 23.4% increase in growth rates from CI to adult. Additionally, copepodid stages showed a generally larger body size, carbon and nitrogen content and total storage lipid content (wax esters + triacyl-glycerols) in response to enhanced resources. Our data support an elsewhere proposed exponential-growth hypothesis; growth of the structural compartments and store lipids (mostly wax esters) was exponential during the copepodid stages. However, a sigmoidal pattern of growth best described growth of adult stages if reared at high resources, and depot lipid accumulation in late CVs and adults at high resources. Body nitrogen growth increased exponentially, however, no significant changes in nitrogen specific growth rates were found between individuals from low and high resources. CV and adults seem to have reached near-maximal weights at high resources, whereas structural weight continued to increase at low resources. Despite the differences in structural growth dynamics, cohort development was similar until the end of CV. During the onset of sexual differentiation, the male:female ratio and the adult:CV ratio were highest at high food resources, suggesting that the time used for the final moult depends on the feeding history of the copepods in relation to food quality and quantity. It appears that relatively small changes in food availability strongly influence the biochemical composition of *C. finmarchicus* copepods.

**Introduction**

The calanoid copepods occupy a key position in the food chain in boral North Atlantic and North Sea waters, dominated by the herbivorous species *Calanus finmarchicus* and *C. helgolandicus* (Marshall and Orr 1955; Conover 1988). The dominant copepod in the North Sea and in the Norwegian fjord areas is *C. finmarchicus* (Williams and Lindley 1980; Tande 1982; Aksnes and Magnesen 1983; Backhaus et al. 1994) *C. finmarchicus* populations have an important impact on higher trophic levels in northern ecosystems in that eggs and nauplii are the principal food for the first-feeding larval stages of fish stocks (Marshall and Orr 1955; Runge 1988; Cushing 1990).

In order to understand the life cycle and production of *Calanus* spp. in the oceanic food web, a description of the quantitative relationship between phytoplankton and copepod production is of importance. In general, the growth rates of zooplankton are likely to be limited by the availability of food in open ocean environments, but not in coastal regions (Huntley and Boyd 1984). Food availability may fall below the critical concentration induced by marked seasonality of phytoplankton...
community composition or senescent blooms reflecting diets of different size and nutritional quality (Sargent and Falk-Peterson 1988). *Calanus* spp. have developed the capability to accumulate extensive lipid stores in the form of wax esters (WE) and triacylglycerols (TAG) as a consequence of the strongly seasonal food availability in their habitat (e.g. Lee et al. 1970; Kattner and Krause 1987; Sargent and Falk-Peterson 1988; Miller et al. 1998; Hygum et al. 2000b). The amount of lipid deposited seems to be linearly related to the available food concentration (e.g. Lee et al. 1970, 1971b) and quality of food (Håkanson 1984). The lipid stores have several important metabolic functions in *Calanus* spp., e.g. fuelling their metabolism during food-limitation in the growth season and especially during winter when the copepods are diapausing at great depth (reviewed by Hirche 1996b). Further, the depot lipids have a central role during the energy-demanding processes of gonadogenesis and oogenesis (reviewed by Hirche 1996a).

The functional relationship between growth of *Calanus* spp. and the supply of food has been investigated by laboratory studies (e.g. Paffenhofer 1971; Vidal 1980; Thompson 1982; Peterson 1986; Pedersen and Tande 1992). It is relatively easy to measure the response by copepods to different conditions of food in the laboratory, but the relevance of these observations for describing conditions at sea is doubtful (Håkanson 1987). The quality of food and the feeding history of the copepod are important for the nutritional status of the copepods (Huntley 1988; Harris 1996), however, in nature, food is often patchily distributed, which makes it difficult to describe both in quantitative and qualitative terms. A complete understanding of the reasons underlying changes in biochemical composition of *Calanus* spp. requires knowledge about the time of recruitment of a particular developmental stage and how long it persists in the population (Hopkins et al. 1984). This requires frequent sampling of a particular population with a long generation time which is almost impossible to accomplish in the ocean. However, Hygum et al. (2000b) demonstrated that aspects of the development and the nutritional status of nauplii and copepodid stages of *C. finmarchicus* could be followed in mesocosms at excess food concentrations.

It has been suggested that when the development rate is at a maximum in *Calanus finmarchicus*, the "structural" growth rate is exponential (McLaren 1986). We here address this hypothesis by comparing and contrasting patterns of "structural" growth with the production of lipid for storage by *C. finmarchicus* copepods reared in mesocosms at different natural plankton concentrations in a Norwegian fjord. Two separate papers describe the growth and development rate of nauplii (Hygum et al. 2000a), and the fecundity of the females reared in mesocosms (Rey et al. 1999). In the present study we examine how different levels of food availability influence the cohorts in relation to: (i) mortality rate, (ii) growth, development and sex ratios and (iii) biochemical changes in terms of carbon, nitrogen, and storage lipid (WE and TAG) deposited within each stage.

### Materials and methods

#### Mesocosm set-up

Large scale incubations were conducted with artificial cohorts of *Calanus finmarchicus* at the Marine Biological Field Station, Espedregd, University of Bergen, Norway, 11 March to 12 May 1997. The experiment included four mesocosms made of polyethylene (90% penetration for PAR), with an enclosed volume of approximately 18 m$^3$ (diameter: 2 m, depth: 7 m). Further details of the design of the mesocosm experiments have been presented in Hygum et al. (2000b). The mesocosm water was screened while being filled using 50 µm Nitex, to remove potential predators and mesozooplankton competitors of the cultured cohorts. The mesocosms were manipulated by addition of inorganic nutrients simulating near-natural food concentrations for the fjord (termed L1, L2 for low resources) and enhanced food concentrations (termed H1, H2 for high resources). Growth dynamics of the copepods in terms of stage specific body carbon, nitrogen and lipid storage, and information on the diet (phytoplankton and microplankton) will be presented with a focus on mesocosms L1 and H1. To compare the biochemical composition of the copepods from the replicate mesocosms, L2 and H2 and in situ, Copepodid Stage V (CV) males and females were measured at the end of the experimental period.

#### Female collection and egg production

*C. finmarchicus* females were collected in Raunefjord (60°17’N; 05°10’E) using a pelagic fish larval trawl, 4 m$^2$ opening and 600 µm mesh size, fitted with a non-filtering 40-litre plastic cod end. Hauls covered the depth strata from 0 to 100 m. The net was retrieved at low speed, and the contents of the cod end were gently emptied into a darkened container with 30 litre seawater. The copepods were transported to the laboratory within 2 to 3 h of collection and brought to a walk-in cold room at 4 to 5 °C. Large-scale egg production for the build-up of the artificial *C. finmarchicus* cohorts was conducted in the cold room with females kept in 100-litre cylinders with 400 µm mesh false bottoms suspended in 120-litre containers. The females were fed cultures of *Rhodomonas baltica* in excess concentrations. Every 24 h the produced eggs were decanted from the 120-litre containers. The eggs were then suspended in 10-litre glass cylinders containing filtered, aerated seawater. Numbers of nauplii were recorded every 24 h allowing an estimate of total numbers. Approximately 80000 nauplii, 1 to 2 d old, were added to mesocosms L1 and L2 on 10 March, and H1 and H2 on 12 March.

#### Abiotic and biotic analyses

Temperature (°C) was measured continuously with a temperature data-logger, and salinity and oxygen were measured at regular time intervals with a Sea Cat Profiler (Sea Bird Instruments). Water sampling was conducted with a 3-litre heart-valve water-sampler every second day, representing the depth strata 0, 1, 2, 3, 4 and 5 m. Samples were pooled in a container, and subsamples were taken for chemical and biological analysis.

The concentrations of particulate organic carbon and nitrogen (POC, PON) were measured on precombusted GF/C (47 mm) filters and analysed with an EA 1110 CE Instruments CHNS analyser. Samples for chlorophyll $a$ and phaeopigment were extracted with methanol and measured fluorometrically using a Turner fluorometer (methods of Holm-Hansen et al. 1965). On the first three sampling days in March, total plant pigment was spectrophotometrically determined in ethanol extract according to Jespersen and