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Seasonal changes in feeding, gonad development and lipid stores in *Calanus finmarchicus* and *C. hyperboreus* from Malangen, northern Norway

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**Abstract** Seasonal dynamics of feeding activity, oil sac volume, gonad development, sex ratio and spawning periods in the two sibling species *Calanus finmarchicus* and *C. hyperboreus*, the key zooplankton copepod organisms throughout the northern Atlantic waters, were studied simultaneously in Malangen, northern Norway, during 1992. We were also tracing differences in surface- and deep-dwelling components of these populations in terms of oil sac volume and gonad development during the time period when the G1 is preparing for a subsequent generation (G2) or hibernation. The main difference in the life cycle strategies of these species is the earlier maturation and spawning of *C. hyperboreus*. No feeding activity in either of the two species was found in February, but both commenced feeding in March, prior to the spring phytoplankton peak. The larger copepod, *C. hyperboreus*, had a more intensive energy deposition than *C. finmarchicus*. The period of active feeding was much shorter for the former species, only from March through July in copepodite stages CV and CV, and even less in females – March and April. Basically, a similar pattern of seasonal changes in gonad length and lipids was observed in the two species. In June, oil sacs in the surface- and deep-dwelling specimens were about equal, during the rest of the year, lipids in the deep CVs exceeded those in the surface. We propose that as copepods accumulated sufficient lipid reserves, they started to descend, while others, containing less fat, stayed in the upper layers feeding. The mean length of the gonads in the surface-dwelling copepods was consistently less than in their deep counterparts from October to February, so that gonad development at the expense of accumulated reserves during resting stage was confirmed. *C. finmarchicus* males were found in considerable numbers only in February and March, and were only occasionally found in the upper layers (0–100 m), while adult male *C. hyperboreus* were present from October to March, but were never found in the surface layers. The differences in life cycle timing among the two species are discussed in relation to tradeoffs with regard to foraging strategies, generation numbers, bioenergetics and predator avoidance.

**Introduction**

In the high-latitude pelagic systems, adaptations to overwintering are a pivotal part of the life cycle strategies of planktonic copepod species. The *Calanus* species, which often dominate biomass of the high-latitude plankton communities, adjust the timing of their reproduction to phytoplankton bloom. Basically, their life cycle strategies are believed to be similar: after a period of active feeding and accumulating of lipid reserves, older copepodite stages cease feeding and descend into the deep water layer, where they reduce their metabolic rates and enter a resting state. During this resting period, gonad growth and development are sustained by internal energy deposits (Hirche 1996), processes which are extremely important for the *Calanus* populations, because they determine not only a successful overwintering, but also a subsequent successful reproduction.

The two sibling species *C. finmarchicus* and *C. hyperboreus* are the key copepod species throughout North Atlantic waters, and the former is one of the most studied marine copepod species. Besides the fundamental study on the biology of *C. finmarchicus* by Marshall and Orr (1955), a number of studies dedicated to the gonad development and reproduction of both species have been carried out more recently (i.e. Conover 1965,
1967; Tande and Hopkins 1981; Grigg and Bardwell 1982; Tande et al. 1985; Smith 1990; Hirche 1996; Hirche and Niehoff 1996; Niehoff and Hirche 1996). Previously it has been claimed that stored lipid was used mainly to sustain basic metabolism during starvation. It has recently been advocated that lipid reserves fuelled primarily gonad development, molting and reproduction, and only a smaller part of stored energy is used to support basic metabolic requirements (Tande 1982; Sargent and Falk-Petersen 1988; Hirche and Kattner 1993; Hagen and Schnack-Schiel 1996; Hirche 1996).

The reproductive event within a generation cycle could be suggested to fit into the following scheme: during high phytoplankton concentration, copepods of the recruiting generation feed and grow actively with a subsequent increase in oil sac volume. Gonads are very small in newly molted CIV and CV, and show no pronounced tendency to enlarge until autumn, when fat, older copepodes cease feeding and descend. Then, their gonads begin to grow and differentiate. As both gonad development and molting occur at the expense of stored lipids, towards the end of the winter, oil sacs decrease in volume.

In high latitudes this reproductive scheme is expressed at different time scales for the two species, although the environmental conditions determining the number of generations are not well understood. *C. hyperboreus* in most regions needs more than a year to complete its life cycle (Conover 1967, 1988; Hirche 1998). For *C. finmarchicus*, the prevailing pattern is on an annual basis (as a G1), but there are regions which have been found to enable the species to produce another generation (G2) as well. In northern Norwegian

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**Fig. 1** Map of the region of investigation with a detailed map of Målen with depth contours and the location of the two sampling stations, Målsfjord (M) and Spildernes (S).

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**Table 1** Classification system of gonad maturity applied in the present study in comparison with that of Niehoff and Hirche (1996)

<table>
<thead>
<tr>
<th>Present paper</th>
<th>Niehoff and Hirche (1996)</th>
<th>Diverticula and oviducts</th>
<th>Oocytes</th>
</tr>
</thead>
<tbody>
<tr>
<td>Immature</td>
<td>GS 1 and GS 2</td>
<td>Single rows of small dark red stained oocytes</td>
<td>Oogonia and oocytes in ovary, only small oocytes</td>
</tr>
<tr>
<td>Mature</td>
<td>GS 3 and GS 4</td>
<td>Several rows of oocytes increasing in size ventrally, large pink oocytes visible in one or more rows</td>
<td>Oogonia and oocytes in ovary, oocytes of every size</td>
</tr>
<tr>
<td>Spent</td>
<td>Senescent</td>
<td>Oviducts not filled, few oocytes there</td>
<td>Abnormal degenerated oocytes present, no smallest oocytes</td>
</tr>
</tbody>
</table>