

Distribution of *Calanus finmarchicus* in the northern North Atlantic and Arctic Ocean—Expatriation and potential colonization

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Abstract

The distribution of *Calanus finmarchicus* was studied on a transect across the central Greenland Sea, and on five transects from the Eurasian shelves across the Atlantic Inflow in the Arctic Ocean. Stage composition was used as an indicator for successful growth; gonad maturity and egg production were taken as indicators for reproductive activity. On the Arctic Ocean transects, these parameters were measured simultaneously from the sibling species *Calanus glacialis*. Response of egg production rate to different temperatures at optimal food conditions was very similar between both species in the laboratory. *C. finmarchicus* was present at all stations studied, but young developmental stages were only present close to the regions of submergence of Atlantic water under the Polar water. This together with a decreasing abundance and biomass from west to east along the Atlantic Inflow in the Arctic Ocean and reproductive failure indicates that *C. finmarchicus* is expatriated in the Arctic Ocean. We hypothesize that the late availability of food in the Arctic Ocean, rather than low temperature per se, limits reproductive success. Better reproductive success in the very low temperature regions of the Return Atlantic Current and the marginal ice zone in the Greenland Sea supports this hypothesis. The possibility for a replacement of *C. glacialis* by *C. finmarchicus* and consequences for the ecosystem after increasing warming of the Arctic are discussed.

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1. Introduction

Calanus finmarchicus is a key species in the zooplankton of the North Atlantic, where it is prey for many species of fish. Due to its biomass, its role in carbon flux is also important. *C. finmarchicus* is found all over the North Atlantic (Jaschnov, 1970;

Conover, 1988). Its centre of activity is confined to ice-free water, while its congeners, *Calanus hyperboreus* and *Calanus glacialis*, inhabit the seasonal ice-covered seas and the Arctic Ocean (Conover, 1988). Due to the circulation system in the North Atlantic, high numbers of *C. finmarchicus* are transported by the North Atlantic Current (NAC) into subarctic and arctic seas. The main northward transport of Atlantic water is through the NAC and its northern continuation, the West Spitsbergen

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Current (WSC), which, after its passage through the Greenland Sea, finally drains into the Arctic Ocean in Fram Strait. In the Greenland Sea, part of the Atlantic water recirculates and flows southwards as the Return Atlantic Current (RAC) along the East Greenland Shelf (EGS) underneath the Polar waters of the East Greenland Current (EGC) (Gascard et al., 1988). Via troughs, Atlantic water also reaches far onto the EGS (Budéus and Schneider, 1995). The large frontal systems of the Arctic Front (AF) in the east and the East Greenland Polar Front (EGPF) in the west are interfaces between Atlantic, Arctic and Polar water masses and allow exchange of faunistic elements. Atlantic water is advected onto the Barents Shelf from the Lofoten Basin through the Barents Sea Opening into the Barents Sea (Loeng, 1991). Portions of Atlantic water submerge under the lighter Arctic water at the Polar Front and flow north following troughs on the shelf (Schauer et al., 2002). From the north, branches of Atlantic water enter the Barents Sea between Nordaustlandet and Franz-Josef-Land as a near-bottom water mass (Pfirman et al., 1994).

In the Arctic Ocean, water of Atlantic origin forms a layer several 100 m thick between 200 and 1000 m depth. Atlantic water enters mainly via the Fram Strait (Rudels et al., 1994) and forms a boundary current running counter-clockwise along the perimeter of the Arctic Ocean. Recirculating branches of Atlantic water are deflected seaward where mid-ocean ridges, like the Nansen-Gakkell Ridge, the Lomonosov Ridge (Anderson et al., 1989), and the Alpha-Mendeleev Ridge, meet the Eurasian Shelf (Rudels et al., 1994).

While in many of these regions *C. finmarchicus* constitutes a large part of the biomass (Hirche and Mumm, 1992; Kosobokova and Hirche, 2000), we suggest that it is not actively growing and reproducing there, but is expatriated. The low temperatures in Polar water have been suggested as the cause for low growth and reproduction of *C. finmarchicus* in the Arctic Ocean (Jaschnov, 1970). Corkett et al. (1986) observed embryonic development at 0 °C, development to CI at 2 °C, and older stages at 5 °C, but do not comment why they did not conduct all measurements at 0 °C. Campbell et al. (2001) for *C. finmarchicus* and Thompson (1982) for *Calanus* spp. studied the development at 4, 8, and 12 °C and found successful growth at all temperatures. Tande et al. (1985) and Hansen et al. (1996) assumed from field observations in the Barents Sea that temperature hindered gonad development of CV and ovary

maturation in adult females. On the other hand, females collected in the EGC in June at –1.6 °C continued to spawn at 0 °C for 22 days (end of experiment), and females collected in the WSC in April spawned continuously for 77 days at 0 °C (Hirche, 1990).

Recent climate models forecast large environmental changes, especially in the subarctic and arctic regions (Polyakov et al., 2002). These changes include increase of water temperatures, thinning of sea ice, and reduction of the duration of ice coverage (Johannessen et al., 2002). Increased inflow of Atlantic water into the Arctic Ocean has been observed, which caused a shift in the balance between Pacific and Atlantic waters there (Carmack et al., 1995; McLaughlin et al., 1996, 2002; Swift et al., 1997). Although we do not know yet which physiological or other barriers prevent *C. finmarchicus* from inhabiting these regions, it is possible that the environmental changes associated with the climate changes will allow future colonization and replacement of the autochthonous congeners *C. glacialis* and *C. hyperboreus*. This would dramatically affect the ecosystems, as *C. finmarchicus* is smaller and has a different life cycle strategy than the other species.

Here we describe the distribution of *C. finmarchicus* on transects across the central Greenland Sea and the Atlantic Inflow in the Arctic Ocean combining observations from several expeditions. By comparing total abundance with stage composition (as an indicator for active growth), and with gonad stage and egg production rate (as indicators of reproductive activity) on transects across different water masses, we try to distinguish expatriated populations from actively growing and reproducing ones. As reduced growth and reproduction of *C. finmarchicus* could instead be caused by food limitation, we used the sibling species *C. glacialis* as an indicator for feeding conditions, assuming that food requirements and preferences are similar. Finally, we compared egg production rates of the two species at different temperatures in the laboratory and in the field.

2. Material and methods

2.1. Zooplankton collection

Calanus spp. were collected during several expeditions of the RV 'Polarstern' to the Greenland Sea and the Arctic Ocean. Cruise dates and station

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