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Structure and resilience of overwintering habitats of *Calanus finmarchicus* in the Eastern Norwegian Sea

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Abstract

Very high concentrations of overwintering *Calanus finmarchicus* were found in the eastern Lofoten Basin of the Norwegian Sea close to the shelf break in January 2001–2002. A coupled 3D hydrodynamic and ecological model was used to study the formation of this deep overwintering aggregation and its stability. The ecological model includes nutrients, phytoplankton and microzooplankton in addition to a stage-structured model of *C. finmarchicus*. Using a Eulerian approach, the model was initiated with an overwintering stock evenly distributed in the oceanic regions of the Norwegian Sea, i.e. where depths > 600 m. Spawning and development of the new generation take place in response to vertical mixing and phytoplankton development. Animals are assumed to begin their descent to overwintering depths of 700–1000 m as late stage Vs. Model results show that, in late summer, high concentrations of animals were found at overwintering depths near the shelf break north of the North Sea, off the northeastern Vøring Plateau and in the eastern Lofoten Basin along the slope of the Barents Sea shelf. They remained there for months due to deep eddies and southward, deep currents along the Norwegian shelf. The simulation experiments indicate that the combined effect of deep anticyclonic circulation and vertical migration behavior of the animals may explain the high concentrations of overwintering *C. finmarchicus* found in field surveys in the Eastern Lofoten Basin, close to the shelf break.

Keywords: *Calanus finmarchicus*; Norwegian Sea; Modeling overwintering populations; Circulation

1. Introduction

During the last three decades, much research has been devoted to various aspects of copepod overwintering strategies in high latitudes. A detailed study of the population dynamics of *Calanus finmarchicus* during an annual cycle (Tande and Hopkins, 1981) prompted many papers on diapause, utilization of lipids, vertical migration, timing of reproduction, and spawning. Studies of all these aspects have provided valuable insights about how overwintering strategies are affected by physical and biological characteristics of their various winter habitats.

More quantitative investigations have emerged. For instance, Colebrook (1985) demonstrated a positive relation between the size of the overwintering population and the subsequent recruiting

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generation in early summer in waters around the British Isles. Regional studies via large coherent programmes such as the "Investigation of *C. finmarchicus* migrations between oceanic and shelf seas off north-west Europe (ICOS; Fisheries Oceanography, 8 (1), 1999)" and "Population dynamics of *Calanus* in the North Atlantic (TASC; ICES Journal of Marine Science, 57 (6), 2000)" have improved our knowledge of how vertical migration behavior of *C. finmarchicus* coupled with deep currents combine into an effective seeding mechanism. Several examples are available (see Skjoldal et al., 2004), but a strong case has been made for southward deep-water flow in the central Norwegian Sea bringing overwintering *C. finmarchicus* from there to the Faroes, and then transported, as a recruiting generation, by westerly wind-forced currents towards the North Sea the following spring and early summer (Heath et al., 2000).

In addition, *C. finmarchicus* in the Norwegian Sea migrate onto the Norwegian shelf and are transported downstream into the Barents Sea by the Norwegian Coastal Current (NCC) (Skjoldal and Rey, 1989). Studies to investigate the magnitude of advection across the western boundary of the Barents Sea have estimated the advection of *C. finmarchicus* to that Barents Sea from March to October to be of the same order of magnitude as the annual endemic production in the Atlantic part of the Barents Sea (Edvardsen et al., 2003). Also, winter surveys to generate long-term data (i.e. >5 years) on area distribution and population size of overwintering *C. finmarchicus* in the northeastern Norwegian Sea have been conducted. High overwintering biomass of *C. finmarchicus* was found in the eastern Lofoten Basin in 2001–2002 (Halvorsen et al., 2003), patterns that have been confirmed by more recent data (Edvardsen et al., 2006). A particularly high biomass of overwintering stage CVs was found in deep water close to the shelf break off Troms, with a horizontal diameter of several 10's of kilometers. The current model indicated the existence of a semi-permanent anticyclonic eddy in the cold Norwegian Intermediate Water below the Norwegian Atlantic Current (NAC) in this region.

The aim of the present paper is to determine if we can model the observed high concentration areas of overwintering *Calanus* in the northeastern Norwegian Sea, including off Troms county, and if so, to identify and explain their likely origins. We also investigate the importance of the downstream source areas for the spring advection of *Calanus* to the Barents Sea. This is accomplished using a coupled hydrodynamic and ecosystem Eulerian-based model including different stages of *Calanus*, combined with a particle-tracking Lagrangian model where the particles mirror the ontogenetic migration behavior of copepodite stage Vs.

2. Model description

2.1. Hydrodynamic model

The hydrodynamic model is based on the primitive Navier–Stokes equations solved by a finite difference scheme. The model uses the *z*-coordinates in the vertical direction (i.e. each model level has a fixed thickness except for the surface and bottom levels). A detailed model description is found in Slagstad and McClimans (2005) and Støle-Hansen and Slagstad (1991). The model domain covers the Norwegian Sea, Lofoten Basin and most of the Barents Sea (Fig. 1). The horizontal grid point distance is 6.7 km and there are 21 vertical levels. The open boundaries for this (nested) model are generated by a regional model covering the Norwegian Sea, Barents Sea, and the Greenland Sea. The coupling between the models is performed by a flow relaxation scheme (Martinsen and Engedahl, 1987). The horizontal grid point distance for the regional model is 20 km and the vertical resolution is the same as for the nested model. On the open boundaries in the North Atlantic and the Arctic Ocean, the current velocities are specified (Slagstad and Wassmann, 1996). The Arctic boundaries were specified based on the climatology taken from a 20-km model encompassing the whole Arctic Ocean. Four tidal components (M_2, S_2, K_1 and N_2) were imposed by specifying the various components at the open boundaries of the large-scale model. Tidal data were taken from Schwiderski (1980).

Atmospheric forcing is the same for both models. Wind and air pressures (6 h) were taken from met.no's hindcast data archive (Reiestad and Iden, 1998). The heat flux is calculated from air temperature, humidity, cloud cover estimated by interpolation from available meteorological stations within the model domain and the theoretical height of the sun. Initial and boundary values of temperature and salinity were taken from NODC (Levitus) World Ocean Atlas 1998 data provided by the NOAA-CIRES Climate Diagnostics Center, Boulder, CO, USA, from their Web site at: http://www.cdc.noaa.gov/. Freshwater input is