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Overwintering habitat of *Calanus finmarchicus* in the North Atlantic inferred from autonomous profiling floats

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Abstract

Autonomous instrumented floats deployed by the international Argo programme and its predecessors were used to produce inferred temperature–salinity–depth records for overwintering plankton in the North Atlantic, with special reference to *Calanus finmarchicus* (the biomass-dominant mesozooplankton in the region). In addition, a model for the density of a plankter was used to estimate changes in vertical position over time. Results from 456 individual winter float records show that environmental conditions were most stable in the Nordic Seas, less so in the subarctic basins of the Labrador Sea, Irminger Sea, and Iceland Basin, and most variable in regions to the south. Model results show that neutral buoyancy at the beginning of the overwintering period is insufficient to guarantee that individuals will stay at depth for the entire overwintering period, which suggests some kind of active buoyancy control mechanism is at work.

Keywords: *Calanus finmarchicus*; Diapause; Overwintering; North Atlantic; Phenology; Float; Model; Buoyancy

1. Introduction

The free-living calanoid copepod *Calanus finmarchicus* is found throughout the North Atlantic (reviewed by Jaschnov, 1970) and dominates the mesozooplankton biomass in spring (Mauchline, 1998); as such it is an important component of ecosystems in the area. A large proportion of the life span of *C. finmarchicus* is spent at depth (~300 to 1300 m), in a dormant state, which may be characterised as a diapause phase (Hirche, 1996). This behaviour is generally considered to be an overwintering adaptation, in order to deal with the strong seasonality in food availability characteristic of subarctic ecosystems, as well as to reduce predation during the dormant phase (Kaartvedt, 1996).

The distribution of overwintering *C. finmarchicus* in the open ocean is not well described in the horizontal or the vertical: the sole large-scale description is that given by Heath et al. (2004), using combined net and optical particle counter observations. Information on overwintering descriptions is unlikely to improve in the near future, given the scale of sampling required, and the difficulties one encounters while sampling the North Atlantic during the overwintering time (October–March). The physiology of overwintering in *C. finmarchicus* (and indeed other free-living calanoids)

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is described primarily from nearshore populations, in enclosed fjords and embayments (e.g. Tande, 1982; Hirche, 1983). It has been observed that overwintering *C. finmarchicus* are motionless (and in a characteristic "overwintering posture": Hirche, 1983), and have low metabolic rates (Hirche, 1996; Ingvarsdóttir et al., 1999).

Calanoid copepods store large amounts of lipids prior to their descent to depth, and lipids are a very large proportion of the dry mass (50–76%: Jónasdóttir, 1999). Lipids are more compressible than seawater (Yayanos et al., 1978), as are most other biochemicals, which results in a situation where neutral buoyancy is not stable (Campbell and Dower, 2003). A plankter thus cannot be expected to stay at a constant depth over time: it will tend to float or sink away from its depth of neutral buoyancy. Active buoyancy control has not been observed in the Copepoda, and it is uncertain how a motionless overwintering copepod is able to maintain depth for the long overwintering period. Campbell and Dower (2003) noted that if an individual were able to diagnose its depth of neutral buoyancy, it could stay at depth for considerable periods, though that work was specific to the Faero-Shetland channel, and assumed no change in water mass properties.

Autonomous instrumented floats have been deployed regularly for approximately one decade. The largest operational programme, Argo (http://www.argo.ucsd.edu; http://argo.jcommops.org), is a pilot programme of the Global Ocean Observing System. Argo has deployed floats worldwide since 2000, and also archives float data from prior programmes. Profiling floats are typically programmed to "park" at a given depth for a certain amount of time (usually 1000 m and 10 days), then descend to 2000 m and take measurements (pressure, temperature, and salinity) during an upward profile. At the surface, the profile data, as well as geographical position, is broadcast via satellite to a data acquisition centre for processing, quality control, and archiving.

Profiling floats are therefore much like overwintering copepods: their drift patterns will be similar, and the temperature and salinity data they collect is a record of the temperature and salinity changes that will occur at different depths during the overwintering period, taken at much higher temporal and spatial resolution than could be measured with ship-based measurements. In this study, changes in how the physical environment experienced by free-living plankton changes during the winter is inferred from Argo float records, and the model of Campbell and Dower (2003) is extended in a time-explicit manner to infer how hydrographic changes during the overwintering period may affect the depth distributions of overwintering copepods.

2. Methods

2.1. Float data and processing steps

Float data were downloaded from the Coriolis Argo Data Assembly Centre operated by the Institut français de recherche pour l'exploitation de la mer (IFREMER; ftp.ifremer.fr/ifremer/argo/) in April 2005. Several float types were used (PROVOR, APEX and SOLO), and delayed mode (i.e. post-processed and error-checked) data were used when available, but if not realtime mode (i.e. raw data, with some automated error checking) was used. All position, temperature, and salinity data were first checked for bad values with automated methods: quality control flags were examined, and unreasonable data points removed ($-2<$temperature>30; $0<$salinity>40; positions indicating drift rates $>5\,\mathrm{m\,s^{-1}}$). Every cast was also examined visually, and obviously bad pressure ($\geqslant 2000$ m), temperature (departures of $>5\,^{\circ}$C, below 500 m) and salinity (departures of >5, below 500 m) values removed. Of 424 float records in the area of interest (30°N–80°N and 80°W–20°E, excluding the Mediterranean Sea), 181 were discarded for data quality issues, because salinity was not measured, or because the cast depth was too shallow (<2000 m).

For the purposes of this study, "winter" was considered to be the period between October 1 and March 1 of a given year, and only float records that had at least one profile bracketing those dates for each winter were included; some floats yielded data for more than 1 year. Given that most floats cycle on a ~10-day period, one could expect approximately 15 float cycles during the winter period of this study. On average there were 16 cycles (i.e. profiles) for each winter float record, a maximum of 34 cycles, and float records with <11 profiles were not used. After all the quality control steps, the data set used here comprised 243 floats and a total of 456 separate winter float records, with a total of 7471 individual profiles.

The choice of dates for "winter" used here is somewhat arbitrary since phenology in *C. finmarchicus*