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Inter-annual variability in spring abundance of adult *Calanus finmarchicus* from the overwintering population in the southeastern Norwegian Sea

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ABSTRACT

Calanus finmarchicus is the dominant copepod species in the Norwegian Sea, where it plays a key role in the ecosystem by transferring energy from primary producers to higher trophic levels. This paper analyses a 17-year time series, 1996–2012, on *C. finmarchicus* collected within the Atlantic Water mass along the Svinøy transect in the southeastern Norwegian Sea. We use the spring abundance of adult as a proxy for the size of *C. finmarchicus*' overwintered population. The inter-annual trend in spring abundance of adult *C. finmarchicus* in the 200–0 m depth-stratum is assessed while accounting for spring population development to the adult stage represented by day of year for sampling, inter-annual changes in timing of population development, and spatial differences. For the most oceanic stations, a significant inter-annual trend in spring abundance of adult *C. finmarchicus* was revealed using generalized additive models (GAM). This trend primarily consists in an increase prior to year 2000 and a decrease between years 2000 and ca. 2011. For the stations closer to the coast, the identified inter-annual trend is a decrease during a longer period from the late 90s until ca. 2011. From 2000 to 2011, our estimates suggest a 50% decrease for the most oceanic stations, and as much as an 81% decrease for the stations closer to the coast. In addition the results suggest a consistent change in phenology over the years and the stations. The predicted spring peak of overwintered adult population abundance is suggested to become shorter by 3 days, and the predicted maximum of abundance to take place 4 days earlier over the 17 years of the time-series. The results highlight significant changes in intensity and timing of the overwintered population of a key zooplankton species in the Norwegian Sea that may have important implications on the scale of an entire ecosystem.

1. Introduction

The large and lipid-rich calanoid copepod species, *Calanus finmarchicus*, is a key component in the North Atlantic ecosystems and can be found from the Gulf of St. Lawrence and coast of Newfoundland in the west (Ringuette et al., 2002; Heath and Lough, 2007; Dalpadado and Mowbray, 2013) to the shores of Norway in the east (Propochuk and Sentyabov, 2006; Langøy et al., 2012). In the Northeast Atlantic, the southern and northern gyres of the Norwegian Sea together represent one of the main centers of distribution of the species (Wiborg, 1955; Halvorsen et al., 2003; Broms et al., 2009; Head et al., 2013; Melle et al., 2014), where *C. finmarchicus* represents the main food source and is essential to life processes of both juveniles and adults of important commercial fish stocks such as Norwegian spring spawning herring, Northeast Atlantic mackerel and blue whiting (Dalpadado et al., 2000; Skjoldal et al., 2004; Olsen et al., 2007; Huse et al., 2012; Langøy et al., 2012; Utne et al., 2012).

Concern has been expressed regarding recent years with low zooplankton biomasses and the consequences this may have for the large stocks of commercial fish in the Norwegian Sea (e.g. Huse et al., 2012). Furthermore, *Calanus finmarchicus* also impacts the lower trophic levels, and has been suggested to be a significant regulator of the spring phytoplankton bloom in the oceanic parts of the Norwegian Sea (Rey, 2004). Hence in this area, there is a strong interest in the population size and inter-annual variability of this species. A long-term effort of collecting and analyzing *C. finmarchicus* samples was started in 1949 by means of the Continuous Plankton Recorder (CPR) in the Southern Norwegian Sea (Aßmus et al., 2009). However, in 1982, the CPR-line sampling

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the Norwegian Sea from the North Sea and up to Weather station Mike (64.26°N, 2°E) was terminated. Since then, knowledge on the inter-annual variation of *C. finmarchicus* population size is lacking for this area. For the period between 1981 and 1993, there was no regular zooplankton sampling in the southern Norwegian Sea, but in 1993 routine monitoring was initiated by the Institute of Marine Research (IMR, Norway), using plankton nets at stations along the Svinøy and Gimsøy sections.

The Norwegian Sea upper layers are divided into three different main water masses based on hydrography (Nilsen and Falck, 2006). The cold and comparatively fresh Artic Water flows southward in the western part. It is delimited by the warmer and more saline Atlantic Water, which prevails in the central area. The Coastal Water is located east of the Atlantic Water, and has a lower salinity and a strong seasonal temperature signal. The core distribution of *Calanus finmarchicus* with the highest abundance is located in the Atlantic Water domain (Melle et al., 2004). In this water mass, *C. finmarchicus* has been described to have predominantly a one-year life cycle producing one generation (G_1) which develops from early spring to late summer (Melle et al., 2004; Bagøien et al., 2012). Thereafter, the *C. finmarchicus* belonging to G_1 enters an overwintering phase (Østvedt, 1955; Niehoff et al., 1999; Melle et al., 2004, 2014), relying on fat reserves accumulated during summer as nutritional source (e.g. Jonasdottir, 1999). In late winter and the following spring the overwintering individuals exit diapause and ascend into the surface-near layers (Sømme, 1934; Østvedt, 1955; Hirche, 1996; Melle et al., 2004). The emerging overwintered individuals (G_0) mainly consist of the copepodite developmental stage 5 (CV) (Hirche, 1996; Heath et al., 2004), although some copepodites of stage 4 (CIV) and adult females occur (Østvedt, 1955; Broms and Melle, 2007; Melle et al., 2014). Following metamorphosis to the adult stage and further maturation, spawning can take place, producing the new G_1, and thereby completing the life cycle.

In order to elucidate the knowledge-gap regarding the fate of the *Calanus finmarchicus* population in the Norwegian Sea in recent years, the present paper addresses inter-annual trend in abundance of overwintered *C. finmarchicus*. Here, we consider the spring abundance of adult *C. finmarchicus* as a proxy for the size of the overwintered population. Our purpose is to extract the "truest" inter-annual trend from a time-series observations during spring. However in our dataset, the temporal irregularity of the sampling represented a challenge. Our approach is to develop state-of-the-art statistical models to extract the inter-annual trend for spring abundance of adult *C. finmarchicus* while accounting for other sources of variation in our observations such as (1) intra-annual changes due to the progression of the population development to the adult stage depending on the time of sampling, (2) the timing of the spring peak of adult *C. finmarchicus*, and (3) the location along the transect where the observations were made. Finally, we select the model which best describes our data, and analyze its results. On this basis, we present the estimated inter-annual trend for overwintered *C. finmarchicus* in the Norwegian Sea, and discuss the relevant sources for the observed variability in our dataset. The present paper focuses primarily on assessing the inter-annual trend in the time series for the spring population of adult *C. finmarchicus*. Relating this trend to climatic, physical, and biological conditions (lower and higher trophic levels) will be addressed in a subsequent study.

2. Material and methods

2.1. Description of the data set

The total Svinøy transect forming the basis of the present dataset stretches from 62.37°N and 5.2°E to 64.67°N and 0°E (Fig. 1) off the western coast of Norway. The observational data were distinguished by date of sampling (year, and day of year, Fig. 2), fixed geographic positions (station numbers 1–17), geographical distance (km) from station 1, and by water masses (Artic, Atlantic and Coastal), the latter defined according to Broms and Melle (2007), and Bagøien et al. (2012). Initially we considered including samples from stations 3 to 17, where Atlantic Water, the water mass associated with overwintering *Calanus finmarchicus*, is found. Thereafter we decided to exclude stations 3–8, because they either were most of the time identified as Coastal Water, or were close to an area influenced by it, or again were relatively shallow. In addition, we only included samples collected in spring (day of year 56–147). Thus, the original dataset of 1363 samples was reduced to 290, the latter which had been collected at stations 9–17 in spring, between 1996 and 2012, by vertical net hauls between 200 m and the surface (WP2, 0.25 m^2 mouth area, 180 μm mesh, see Melle et al., 2004 for details). It took about 3 days to sample the stations along the section, and the first sampling date of a given section coverage, expressed as "day of year" (cf. Fig. 2), was used as the sampling date for all stations sampled on that occupancy. The observations were made at irregular intervals and at different frequencies during the years (Fig. 2).

The samples were preserved in formalin (4%) at sea and subsequently analyzed in the laboratory. In our samples, *Calanus* spp. individuals were classified into three different species groups: *C. finmarchicus/helgolandicus* (pooled), *C. glacialis*, or *C. hyperboreus*. They were thereafter separated further according to developmental stage, and in the case of adults also to sex. *C. finmarchicus/helgolandicus* of all copepodite stages have been distinguished from *C. glacialis* on the basis of prosome-length using fixed cut-off points and *C. hyperboreus* by morphology (see Broms et al., 2009 for details). Distinguishing *C. glacialis* from *C. finmarchicus/helgolandicus* by prosome length is not a fool-proof method as recent analyses based on genetics have suggested that the species can overlap regarding prosome length (Gabrielsen et al., 2012; Nielsen et al., 2014). In our samples, adult *C. glacialis* were identified together with adult *C. finmarchicus/helgolandicus* in 9% of our observations. When present, the adult *C. glacialis* represented a median percentage of 0.6% of the abundance of adult *C. finmarchicus/helgolandicus*

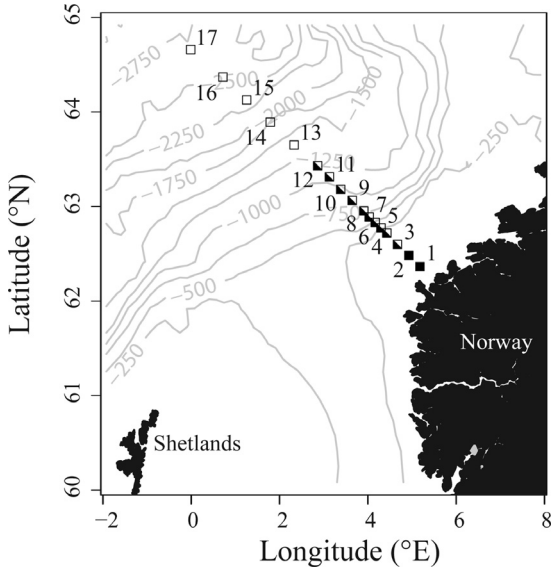

Fig. 1. Map showing the Svinøy transect. Squares indicate fixed positions for stations. Empty squares indicate stations classified as Atlantic Water. Half-filled squares indicate stations that can be classified either as Atlantic Water or Coastal Water. Full squares indicate stations classified as Coastal Water. Bathymetry isolines in meters are shown in gray.