Journal of Marine Systems 165 (2017) 69–76

Contents lists available at ScienceDirect

Journal of Marine Systems

journal homepage: www.elsevier.com/locate/jmarsys

Coupling survey data with drift model results suggests that local spawning is important for *Calanus finmarchicus* production in the Barents Sea

Kristina Øie Kvile [a,*], Øyvind Fiksen [b], Irina Prokopchuk [c], Anders Frugård Opdal [b,d]

[a] *Centre for Ecological and Evolutionary Synthesis (CEES), Department of Biosciences, University of Oslo, PO Box 1066 Blindern, 0316 Oslo, Norway*
[b] *Department of Biology and Hjort Centre for Marine Ecosystem Dynamics, University of Bergen, PO Box 7803, 5020 Bergen, Norway*
[c] *Knipovich Polar Research Institute of Marine Fisheries and Oceanography (PINRO), 6 Academician Knipovich Street, 183038 Murmansk, Russia*
[d] *Uni Research and Hjort Centre for Marine Ecosystem Dynamics, PO Box 7810, 5020 Bergen, Norway*

ARTICLE INFO

Article history:
Received 25 May 2016
Received in revised form 9 September 2016
Accepted 25 September 2016
Available online 28 September 2016

Keywords:
Copepod
Spawning grounds
Zooplankton
Advection
Norwegian Sea
Barents Sea

ABSTRACT

The copepod *Calanus finmarchicus* is an important part of the diet for several large fish stocks feeding in the Atlantic waters of the Barents Sea. Determining the origin of the new generation copepodites present on the Barents Sea shelf in spring can shed light on the importance of local versus imported production of *C. finmarchicus* biomass in this region. In this study, we couple large-scale spatiotemporal survey data (>30 years in both Norwegian Sea and Barents Sea areas) with drift trajectories from a hydrodynamic model to back-calculate and map the spatial distribution of *C. finmarchicus* from copepod to egg, allowing us to identify potential adult spawning areas. Assuming the adult stage emerges from overwintering in the Norwegian Sea, our results suggest that copepodites sampled at the Barents Sea entrance are a mix of locally spawned individuals and long-distance-travellers advected northwards along the Norwegian shelf edge. However, copepodites sampled farther east in the Barents Sea (33°30′E) are most likely spawned on the Barents Sea shelf, potentially from females that have overwintered locally. Our results support that *C. finmarchicus* dynamics in the Barents Sea are not, at least in the short-term, solely driven by advection from the Norwegian Sea, but that local production may be more important than commonly believed.

1. Introduction

The southwestern Barents Sea is a highly productive area, hosting the world's currently largest stocks of cod (*Gadus morhua*) and capelin (*Mallotus villosus*) (Gjøsæter, 2009). The largest herring stock in world, the Norwegian spring spawning herring (*Clupea harengus*), has its main nursery areas in the Barents Sea (Stenevik et al., 2015). The copepod *Calanus finmarchicus* dominates mesozooplankton biomass in the area (Orlova et al., 2010), and constitutes an important part of the diet of these fish stocks; nauplii and younger copepodite stages for various larval and juvenile fish (e.g. cod, herring) and older copepodite stages and adults for adult pelagic fish (e.g. herring, capelin) (Loeng and Drinkwater, 2007; Melle et al., 2004).

It has been suggested that advection from the Norwegian Sea is the dominant source of *C. finmarchicus* biomass in the Barents Sea (Edvardsen et al., 2003b; Helle, 2000; Skjoldal and Rey, 1989; Torgersen and Huse, 2005). The deep basins of the Norwegian Sea are the main overwintering areas of the species in the Northeast Atlantic, and spawning takes place in the upper water masses when adults emerge in early spring (Melle et al., 2014). Depending on ambient ocean current dynamics, the new generation might be transported out of the Norwegian Sea gyres and into the Barents Sea (Edvardsen et al., 2003a; Samuelsen et al., 2009; Torgersen and Huse, 2005). The dominant surface currents in the area are the North Atlantic Current (NAC), which brings relatively warm and saline Atlantic water northward with branches into the Barents Sea, and the cooler and fresher Norwegian Coastal Current (NCC), which follows the Norwegian coastline into the Barents Sea (Loeng, 1991; Blindheim, 2004).

Several studies have used oceanographic particle tracking to investigate the degree of retention or export of *C. finmarchicus* in the Norwegian Sea. Bryant et al. (1998) found that *C. finmarchicus* populations could be retained for several years within the Norwegian Sea gyres, but individuals present north of these gyres were rapidly flushed out, potentially into the Barents Sea. Torgersen and Huse (2005) found on the other hand that zooplankton advection into the Barents Sea was almost exclusively from the Norwegian continental shelf, but hypothesised that the coarse resolution of the oceanographic model (20 × 20 km) could cause an underestimation of transport from the Norwegian Sea onto the Norwegian shelf. This was supported by

---

[*] Corresponding author.
E-mail address: k.o.kvile@ibv.uio.no (K.Ø. Kvile).

http://dx.doi.org/10.1016/j.jmarsys.2016.09.010

Samuelsen et al. (2009), who observed an overall increase in cross-shelf transport when applying an embedded model with finer grid resolution (4.5 × 4.5 km).

Contrary to the idea of the Barents Sea as a sink of zooplankton advected from the Norwegian Sea, it has recently been estimated that 67–77% of zooplankton production in the Barents Sea is local (Dalpadado et al., 2012; Skaret et al., 2014). In this study, we couple output from a hydrodynamic model with large-scale biological survey data (>30 years in both Norwegian Sea and Barents Sea areas) to find the origin of *C. finmarchicus* individuals observed in the Barents Sea.

2. Materials and methods

2.1. Overview of the approach

To estimate *C. finmarchicus* spawning areas, we use the following approach: (1) Drift particles representing the new generation of *C. finmarchicus* (G1) forward in time, (2) sample particles present at the time and location of observed *C. finmarchicus* copepodites representing endpoints of modelled drift trajectories, (3) estimate ages of observed copepodites and (4) estimate the spatial distribution of eggs, and thus potential adult spawning locations, from the particles' locations at the observed copepodites' estimated spawning days (Fig. 1). Below we describe in detail the biological data, the particle tracking procedure and the approach used to estimate spawning locations.

2.2. Survey data

Knipovich Polar Research Institute of Marine Fisheries and Oceanography (PINRO, Murmansk, Russia) collected stage-specific abundance data (ind. m^{-3}) of *C. finmarchicus* during bi-annual surveys between 1959 and 1992 (described in Kvile et al., 2014; Nesterova, 1990). Samples were collected with a Juday plankton net (37 cm diameter opening, 180 μm mesh size) with a closing mechanism. Since in the present study we were interested in observations of the new generation (G1), we focused on data of copepodite stages CI–CIV collected in spring (mid-April to late May). This period covers the mid–late peak period of stages CI–CIII and early accumulation of stage CIV for southwestern parts of the study area, and the early peak period of these stages for northeastern parts of the study area (Kvile et al., 2014). Since our focus was to estimate spawning areas for the new generation spawned in spring, we did not include information on the stages CV–CVI, which likely belong to the parental generation emerging from overwintering (G0). Naupliar stages, which due to their small size are under-sampled by the mesh size used (Hernroth, 1987; Nichols and Thompson, 1991), were also excluded from the analyses.

Further, we only used data collected in the upper water column (0–60 m depth), corresponding to the depth layer with highest abundances of young copepodites during the growth season (Dale and Kaartvedt, 2000; Kvile et al., 2014; Unstad and Tande, 1991). To avoid bias due to inter-annual variation in survey coverage, we only included data from repeatedly sampled transects, and within these transects, we only included survey stations sampled at least as many times as the average for that transect. This gave us three off-shelf transects and four on-shelf transects to work with (Fig. 2), and a minimum number of stations sampled per year ranging from 4 (NS·Open3) to 14 (Kola) per transect. The number of stations sampled varied between years, and the total number of stations per year ranged from a minimum of 6 (1959, only one transect included) to 66 (1975, all transects included).

The survey generally covered the transects in a southwest–northeast direction, starting in the southernmost Norwegian Sea transect in mid–late April, and ending with the easternmost Barents Sea transects in mid–late May (Fig. 2., see also Kvile et al., 2014). On average, both the total copepodite abundance (CI–CIV) and the contribution of the youngest copepodites (CI–CII) to the total abundance were higher at the Barents Sea transects compared to the Norwegian Sea transects (Fig. 2).

2.3. Particle-tracking procedure

To simulate past ocean current dynamics in the Norwegian Sea–Barents Sea area, we extracted flow fields from a numerical ocean model hindcast archive (Lien et al., 2013), coupled to a regional ocean model system (ROMS, Haidvogel et al., 2008) with atmospheric forcing from the NORA10 archive (Reistad et al., 2011). This archive provides hydrographic information for the Nordic Seas at daily intervals from 1959 to 2014, with 4 × 4 km horizontal resolution and 32-layer terrain following vertical resolution, and has been shown to realistically reproduce observed hydrographic conditions and circulation in these areas (Lien et

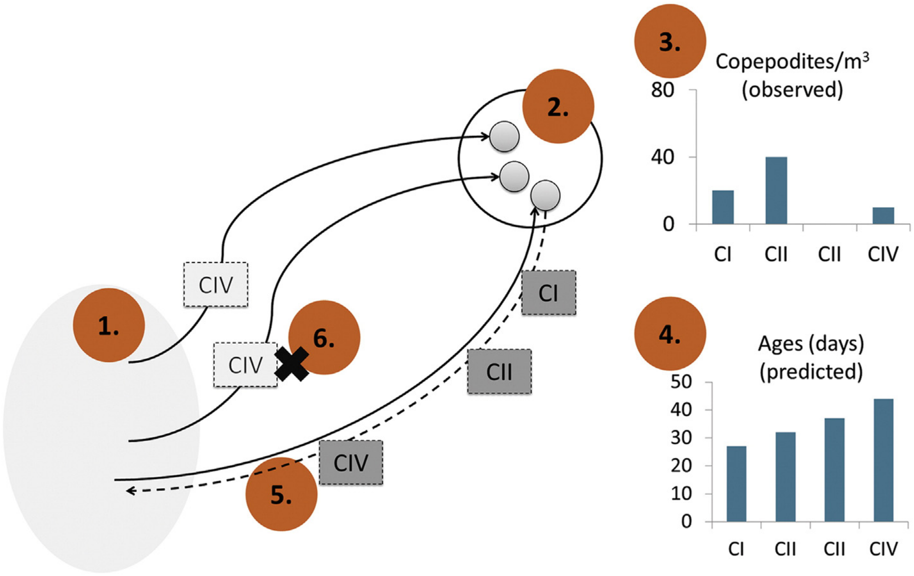

Fig. 1. The approach used to estimate spawning locations. Particles representing the new generation (G1) *C. finmarchicus* are released and advected from the Norwegian Sea in spring (1). Particles are sampled at the time and location of actual survey stations (2). Based on the observed distribution of G1 copepodites at the station (3) and their predicted ages from temperature-dependent development functions (4), we can estimate potential spawning locations as the sampled particles' positions at the estimated stage-specific spawning days (5). We calculate average spawning locations for each stage sampled in a station as the centre of gravity of the stage-specific spawning locations of all particles sampled (shown as a cross for stage CIV), (6).