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Modeling the interactions between the seasonal and diel migration behaviors of *Calanus finmarchicus* and the circulation in the Gulf of St. Lawrence (Canada)

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ABSTRACT

The Gulf of St.-Lawrence (GSL) is a dynamic region supporting a productive pelagic ecosystem. This environment presents unique opportunities to study the interactions between the population dynamics of planktonic species and the variability of physical processes. The copepod *Calanus finmarchicus* is a dominant component of zooplankton biomass and abundance in the GSL. We developed a 3-D coupled physical–biological numerical model in order to study the population dynamics of *C. finmarchicus* in the GSL for the year 1999. We coupled a life cycle model of *C. finmarchicus* representing the average properties of the population in terms of egg production, development, migration behavior and mortality to a regional circulation model driven by realistic atmospheric, hydrological and oceanic forcing. The distribution and abundance patterns of *C. finmarchicus* were sensitive to the migration behavior owing to the strong vertical and horizontal shears in the circulation. Both the timing of seasonal ontogenetic vertical migrations and the diel vertical migrations appeared to be essential to produce simulation results similar to the observations and to ensure the perennial presence of a local population in the GSL.

1. Introduction

One goal of modern oceanographic research is to gain a better understanding of the complex interactions between the ocean's dynamic physical environment and the distribution, abundance and productivity of the pelagic species (*e.g.*Eckman, 1994). From this perspective, copepods represent a keystone of pelagic ecosystems, by filtering the environmental variability through trophic transfer from primary production to higher trophic levels (Williams et al., 1994; Smith, 1995; Kobari et al., 2003; Wassmann et al., 2006; Olli et al., 2007). Significant links between the variability of physical properties of the ocean, population dynamics of copepods and fisheries productivity have already been observed (Runge, 1988; Anderson, 1994; Skreslet, 1997; Runge et al., 1999; Lehodey et al., 2006; Loeng and Drinkwater, 2007). Copepods undergo important physiological and behavioral changes during their development from the egg stage to the adult (Mauchline, 1998). Their physiologic and demographic responses to the variability of the environment are not linear (*e.g.* Campbell et al., 2001). Moreover, the swimming velocities developed by copepodite stages are several orders of magnitude greater than the typical vertical velocities in the ocean (Yamazaki and Squires 1996; Incze et al., 2001). Several species perform extensive vertical migrations in the water column. Ontogenetic migration associated with the winter-time dormancy process has basin-scale implications on the population dynamics of calanoid copepods (Backhaus et al., 1994; Heath et al., 1999, 2008; Falk-Petersen et al., 2008), while the diel vertical migrations (DVM) performed by copepodite stages during the productive season complicates the way they interact at meso- to regional scales with the vertical gradients in the physical and biological environments and the sheared circulation (Hannah et al., 1997; Zakardjian et al., 1999; Batchelder et al., 2002; Genin et al., 2005; Carr et al., 2008).

The Gulf of St. Lawrence (GSL) is a semi-enclosed marginal sea, characterized by pronounced horizontal and vertical gradients in circulation, temperature and salinity, and the southern-most seasonal sea-ice covered sea in the North Atlantic. The GSL circulation is to a large extent controlled internally rather than remotely by large-scale oceanic processes. The general cyclonic circulation in the GSL is driven by both the seasonal freshwater discharge from the St. Lawrence River and the synoptic meteorological systems (Koutitonsky and Bugden, 1991; Saucier et al., 2003, 2009). This region sustains a productive pelagic ecosystem, within which the copepod *Calanus finmarchicus* represents a key component of the zooplankton community (de Lafontaine et al., 1991). A few studies provided some insights into the interactions

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between the hydrodynamics and the population dynamics of *C. finmarchicus* in the GSL. Plourde and Runge (1993) developed the concept of the "*Calanus* pump". While in summer females of *C. finmarchicus* sustain high egg production rates in the Lower St. Lawrence Estuary (LSLE), the residual surface circulation would supply surface-dwelling early development stages to downstream regions of the GSL through the Gaspé Current (GC). Plourde et al. (2001) also argued for the existence of a compensatory upstream advection at depth of overwintering *C. finmarchicus* from the GSL in order to maintain the population within the estuary. In the shallow southern GSL downstream of the GC, Runge et al. (1999) reported a negative correlation between an index of the St. Lawrence River freshet (RIVSUM index: Koutitonsky and Bugden, 1991) and the *Calanus* spp. biomass, but no causal relationship. Using a climatological coupled physical–biological model, Zakardjian et al. (2003) found that advection of *C. finmarchicus* by horizontal currents indeed plays an important role in its population dynamics at the regional scale, between different subareas of the GSL/Scotian Shelf system. Only ontogenetic migrations were considered however, and the relatively coarse time and space resolutions of this first modeling study did not allow exploration of the interactions between the DVM behavior and the natural variability of the oceanographic conditions. DVM is however a potentially efficient way to retain a zooplankton population into an advective environment such as the LSLE–GSL system, whenever a vertically (Wroblewski, 1982; Zakardjian et al., 1999) and/or horizontally sheared circulation exists (Sourisseau et al., 2006). Hence DVM should be considered with ontogenetic migrations as an element of a life cycle strategy adapted to this environment (Eiane et al., 1998).

In order to achieve a thorough understanding of the population dynamics of *C. finmarchicus* in the GSL system, we coupled a stage-based biological model of *C. finmarchicus* to a regional circulation model of the GSL, driven by realistic atmospheric, hydrologic and oceanic forcing (Saucier et al., 2003). The model was applied for 1999, the second year of data acquisition of the Atlantic Zonal Monitoring Program (AZMP) of the Department of Fisheries and Ocean Canada, which covers the Canadian Atlantic continental shelf with several fixed stations (Therriault et al., 1998). The high spatio-temporal resolution of the model allowed the characterization of (1) the predominant features of the spatio-temporal patterns of distribution and abundance of *C. finmarchicus* in the GSL, (2) the role of both the ontogenetic and DVM of late copepodite stages in shaping these patterns and (3) the relative contributions of advection, temperature and food as environmental forcing.

2. Material and methods

2.1. Circulation and ecological models

Saucier et al. (2003, 2004) and Smith et al. (2006) presented the details and the validation of the 3-D sea ice-ocean model driving the *C. finmarchicus* life cycle model. This circulation model was used in several coupled biological–physical modeling studies in the GSL (Le Fouest et al., 2005, 2006, 2010; Sourisseau et al., 2006).The physical model is the current sea-ice and ocean components of the Canadian Operational Weather Forecast model Global Environmental Multiscale (GEM; Pellerin et al., 2003) and the Canadian Regional Climate Model (Faucher et al., 2004). The physical model is based on shallow water and hydrostatic approximations. It includes a 3-D flux-corrected transport scheme and a level 2.5 turbulence closure model. The coastal ocean model is coupled to a multi-category dynamic sea ice model and a two-layer plus one snow layer thermodynamic model. The model domain covers the estuary and the Gulf of St. Lawrence, from the inland limits of the upper estuary near Québec City (Ile d'Orléans), to the open boundaries delimited by the Strait of Belle-Isle and Cabot Strait (Fig. 1). The grid resolution is 5 km in the horizontal (approximately half the local Rossby radius of deformation) and 5 m in the vertical, with the free surface and the bottom layers adjusted respectively to the sea level and the local topography. The model was forced by 3-hourly atmospheric fields provided by the Canadian Operational Weather Forecast Model, daily run-off data of 28 major tributaries and a monthly reanalysis of Bourgault and Koutitonsky (1999) for the St. Lawrence River run-off. Hourly water levels and monthly temperature and salinity profiles were prescribed at Cabot Strait and the Strait of Belle-Isle. The forcing fields were interpolated at the time resolution (5 min) of the model. The model computed fully prognostic solutions for water levels, currents, temperature, salinity, turbulent kinetic energy and sea-ice properties. Comparisons of the model output to recent and historical observations have shown that the model reproduced the high frequency to inter-annual variability in the circulation, water masses properties and sea-ice conditions of the GSL under the given realistic hydrological and atmospheric forcing (Saucier et al., 2003; Smith et al., 2006).

The 3-D Nutrient–Phytoplankton–Zooplankton–Detritus (NPZD) model developed by Le Fouest et al. (2005, 2006) provided food concentrations for the egg production of females (see Section 2.2 below). It comprised two classes of phytoplankton (small and large cells), two classes of zooplankton (micro- and meso-zooplankton), and two classes of detritus (dissolved and particulate organic matter). The NPZD model was coupled to the 3-D circulation model described above. Profiles of observed chlorophyll *a* and nitrate concentrations as well as SeaWIFS- and AVHRR-derived data were used to validate the ability of the model to simulate realistic seasonal and spatial patterns at meso- and regional scales in primary production and micro-plankton biomass (Le Fouest et al., 2005, 2006). Food fields were obtained by summing large and small phytoplanktonic cells owing to the diet of *C. finmarchicus* (*e.g.*Ohman and Runge, 1994). Units of the NPZD model were mmol N m^{-3}, which were converted to mg C m^{-3} according to a constant conversion factor of 79.5 mg C mmol N^{-1}(Le Fouest et al., 2006).

2.2. C. finmarchicus life history model

The life-history model of *C. finmarchicus* (Tables 1–3) was adapted from Zakardjian et al. (2003). The biological rates of development, reproduction and mortality depended on the local environmental conditions and neglected the individual histories. This approach was favored owing to our objective of reproducing a complete phenological cycle, as well as accurate abundances of the various development stages of the species. The model took into account the egg, five naupliar and six juvenile copepodite stages, along with a dormant copepodite stage (C5d) and the male and female adult stages (C6m and C6f respectively). The first two non-feeding nauplii stages were grouped together. The model used molting rates defined from stage-specific, temperature-dependent development times without any significant influence of food concentration (Campbell et al., 2001). A Monotonic Upstream Scheme for Conservation Laws (MUSCL, van Leer, 1979) was used to compute the transfer from one stage to the next (Record and Pershing, 2008). This numerical scheme significantly reduced the numerical dispersion along the stage axis compared to the forward Euler method routinely employed to resolve the partial differential equations system generated by the biological stage-based model. The final molt into adults was equally partitioned between C6m and C6f. A sexual maturation time of 10 days was assumed for C6f (Plourde and Runge, 1993). The spawning function for C6f varied according to food concentration only (mg C m^{-3}), as Runge and Plourde (1996) showed a weak temperature dependence of egg production rates in the GSL area. Spawning occurred only at night, when modeled C6f were close to the surface (see Section 2.3 below; Runge and Plourde, 1996).

The dynamics of dormancy is a key element in the population dynamics of *C. finmarchicus*. A considerable part of the life cycle is spent in dormancy (mainly as C5) deep in the water column (Plourde et al., 2001; Heath et al., 2004; Head and Pepin, 2007, Johnson et al.,