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A coupled ecological–hydrodynamic model for the spatial distribution of sessile aquatic species in thermally forced basins

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ABSTRACT

The life cycle of several sessile or highly sedentary aquatic species is characterized by a pelagic stage, during which propagules are dispersed by the water flow. As a consequence, hydrodynamics plays a crucial role in redistributing offspring. In this work, we describe an integrated modeling framework that couples a minimal – yet biologically well founded – ecological model for the population dynamics at the local scale to an efficient numerical model of three dimensional free surface flows in a thermally forced basin. The computed hydrodynamical fields are employed in a Lagrangian description of larval transport at the basin scale. The developed modeling framework has been applied to a realistic case study, namely the spread of an idealized aquatic sedentary population in Lake Garda, Italy. The analysis of this case study shows that the long-term interplay between demography and hydrodynamics can produce complex spatiotemporal dynamics. Our results also evidence that larvae can travel over relatively long distances even in a closed basin. A sensitivity analysis of the model outcomes shows that both biological traits and external forcings may remarkably influence the evolution of diffusion patterns in space and time.

1. Introduction

One of the most important and challenging problems in population ecology is the understanding of the spatial dynamics of animal populations. This represents indeed a very complex task, since it requires the study of processes occurring at different spatial scales, ranging from local ones, such as birth and death processes, to non-local ones, such as dispersal processes (Levin, 1992). A case of particular interest is represented by those aquatic species that are sessile or highly sedentary as adults, but have a pelagic stage at the beginning of their life cycle (e.g., mussels, corals, etc.; see Guichard et al., 2004; Cowen and Sponaugle, 2009). For these species, the redistribution of organisms between subsequent generations is almost exclusively operated by the water flow. The resulting patterns of larval dispersal can thus be extremely complex, since they reflect the effects of the underlying hydrodynamics (Becker et al., 2007; Cowen and Sponaugle, 2009; Siegel et al., 2008), and play a key role in determining long-term spatiotemporal population dynamics.

Both numerical simulations and measurements of dispersal abilities have contributed to better understanding of some features of larval transport in marine and freshwater ecosystems (Sammarco and Andrews, 1988; Cowen et al., 2000). The outcomes of numerical models have been sometimes profitably compared to those of genetic models (Galindo et al., 2006), elemental fingerprinting techniques (Shank and Halanych, 2007) or *in situ* larval culturing (Becker et al., 2007). Nevertheless, coupled ecological–hydrodynamic models are still needed in order to understand and forecast spatial population dynamics in a comprehensive way, as first clearly stated by Roughgarden et al. (1988). Such models may in fact contribute to answering the basic questions concerning larval dispersal, i.e., where do larvae go and where do larvae come from (Levin, 2006). Although questions of this kind could seem even too naive, they correspond *de facto* to some of the most debated topics in the literature on larval dispersal, such as the estimation of the spatial scale over which larval transport occurs (Cowen et al., 2006) and the relevance of self-recruitment (that is, the retention of larvae in their native site) on population dynamics at the basin scale (Cowen et al., 2000, 2006; Becker et al., 2007). A comprehensive understanding of spatiotemporal recruitment patterns is also required to face important applied issues, such as population management and the design of protected areas (Guichard et al., 2004; Werner et al., 2007; Cowen and Sponaugle, 2009).

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In this work, we propose an integrated modeling framework that combines a minimal (yet ecologically well-founded) population model for the local demographic dynamics of a spatially structured sessile population with a rigorous description of transport effects. In particular, we aim to describe long-term population dynamics. This actually represents a necessary condition to understand the interplay between hydrodynamic and demographic processes and the resulting spatiotemporal patterns of population abundance at the basin scale. Remarkably, very few works have reported the results of long-term analyses in the context of larval dispersal. In point of fact, a recent literature survey (Miller, 2007) has reported that just 5 on the 69 reviewed papers on fish recruitment in marine ecosystems were multigenerational (e.g., Rose et al., 2003; see also Bode et al., 2006). Moreover, most works devoted to the analysis of larval dispersal refer to marine ecosystems, while we specifically address the study of closed water bodies. Larval dispersal is described here by a Lagrangian approach. The velocity fields used to evaluate larval trajectories are computed using the volume-conservative finite element model described in Miglio et al. (1999) and Causin and Miglio (2002), subsequently extended in Biotto (2007) to include baroclinic effects due to thermal forcing induced by solar radiation. The resulting coupled model is applied to a case study concerning the spread of an ideal sessile organism in Lake Garda, Italy. Our analysis demonstrates that demography and hydrodynamics work together to produce complex spatiotemporal dynamics. We also show that the presented results are quite robust to changes in the modeling assumptions, while biological parameters and environmental forcing terms may sensibly affect the long-term evolution of spatiotemporal diffusion patterns.

The paper is organized as follows. In Section 2 we describe the hydrodynamic model and the numerical approach to its solution. The solar radiation model is described in Section 3, while the ecological model and its coupling to hydrodynamics are presented in Section 4. The main features of the case study are introduced in Section 5. The model is first validated with respect to its capability of reproducing realistic temperature fields. The results of several simulations of larval spread in Lake Garda are then presented and discussed. In Section 6 some conclusions are drawn on the applicability of the present approach to other similar problems and further developments of the present model are discussed.

2. The hydrodynamic model and its numerical discretization

The hydrodynamical model used in this work is based on the Reynolds averaged equations for 3D free-surface baroclinic flows, derived under hydrostatic and Boussinesq assumptions. Baroclinic terms allow the model to account for pressure variations due to fluid density variations, while a realistic definition of thermodynamic forcings enables the correct estimation of the heat budget of the water basin. The variations of fluid density responsible for the baroclinic component of fluid pressure are here assumed to be dependent on temperature only. Other factors (such as water salinity) have been disregarded, thus limiting the applicability of the model to freshwater ecosystems.

The equations of the hydrodynamic model read as follows:

$$\frac{Du}{Dt} = -g\frac{\partial \eta}{\partial x} - g\frac{\partial}{\partial x}\int_z^{\eta} \Delta\rho\, dz + \frac{\partial}{\partial z}\left(\nu_{Vv}\frac{\partial u}{\partial z}\right) + f_C v, \tag{1}$$

$$\frac{Dv}{Dt} = -g\frac{\partial \eta}{\partial y} - g\frac{\partial}{\partial y}\int_z^{\eta} \Delta\rho\, dz + \frac{\partial}{\partial z}\left(\nu_{Vv}\frac{\partial v}{\partial z}\right) - f_C u, \tag{2}$$

$$\frac{\partial \eta}{\partial t} = -\frac{\partial}{\partial x}\int_{-h}^{\eta} u\, dz - \frac{\partial}{\partial y}\int_{-h}^{\eta} v\, dz, \tag{3}$$

$$\frac{DT}{Dt} = \frac{\partial}{\partial z}\left(\nu_{Tv}\frac{\partial T}{\partial z}\right) + q, \tag{4}$$

$$\frac{\partial w}{\partial z} = -\left(\frac{\partial u}{\partial x} + \frac{\partial v}{\partial y}\right). \tag{5}$$

Flow velocities along x, y and z directions are denoted by u, v and w, respectively. Water temperature and free surface elevations are denoted by T and η, while h, f_C and q denote the bottom depth, Coriolis parameter and the sum of all heat sources and sinks (to be described later in greater detail). In the present formulation, density is computed by the state equation

$$\rho = \rho_0[1 - \alpha_T(T - T_R)^2],$$

where T is the temperature expressed in °C, $T_R = 4$ °C, $\alpha_T = 6.8 \times 10^{-6}\,\mathrm{K}^{-2}$ and $\rho_0 = 1000\,\mathrm{kg\,m}^{-3}$ is a reference density value, while the relative density variations are denoted by $\Delta\rho = (\rho - \rho_0)/\rho_0$. Atmospheric pressure gradients have been neglected, since only applications to relatively small basins will be considered. It is to be remarked that the horizontal viscosity terms in the momentum and temperature equations have been omitted, since in the applications considered in this paper we have employed only relatively coarse meshes, for which the intrinsic numerical diffusion of the horizontal advection scheme is significant. In a more complete implementation, higher order interpolation methods should be used in the semi-Lagrangian scheme (see, e.g., Baudisch et al., 2006), along with an appropriate horizontal viscosity model. On the other hand, the algebraic eddy viscosity model derived in Colombini and Stocchino (2005) has been employed for the vertical viscosity terms.

From a technical perspective, the system of hydrodynamic equations (1)–(4) has been discretized by an extension of the semi-implicit and semi-Lagrangian numerical method proposed in Miglio et al. (1999), as described in Biotto (2007) in full details. A Crank–Nicolson time discretization has been chosen for the semi-implicit scheme. This method has in fact been proven to be linearly unconditionally stable with respect to the celerity of external gravity waves (Casulli and Cattani, 1994). The Coriolis terms have been discretized explicitly, since they do not imply severe stability restrictions on the computational meshes used in the present application. As for the spatial discretization, the (x, y) plane has been covered with an unstructured triangular mesh, while the z direction has been discretized in a suitable number of horizontal layers. Along the lines of Miglio et al. (1999), Raviart–Thomas elements of order 0 are used for the momentum equations, while $\mathbf{P}_0$ finite elements have been employed for the free surface and the temperature equations.

The temperature equation (4) is solved first, uncoupled from the momentum and free surface equations. As shown in (4), temperature advection is treated in a semi-Lagrangian fashion, employing respectively cubic and linear interpolations in the vertical and horizontal directions for the reconstruction step. The vertical turbulent viscosity term is discretized by a finite volume approach in space and by the Crank–Nicolson method in time. The computation of the heat fluxes due to solar radiation is described in detail in Section 3. The solution of the temperature equation yields an updated density value that is used to compute baroclinic gradients. After this step, the algorithm follows exactly Miglio et al. (1999). The updated value of η^{n+1} is computed by solving a Helmholtz equation obtained by substitution of (1) and (2) into (3). Finally, the velocity field is updated and the vertical velocity is recovered from the incompressibility constraint (5). It is to be remarked that, due to the lack of full coupling between baroclinic gradients and the momentum equation, the resulting time discretization is only conditionally stable with respect to internal gravity waves. On the other hand, unconditional stability with respect to external gravity waves is guaranteed