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Modelling dispersal dynamics of the early life stages of a marine flatfish (*Solea solea* L.)

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ABSTRACT

Connectivity throughout the life cycle of flatfish remains an open question, especially during the early life stages. Their effective management requires understanding of how spawning grounds and nurseries are connected and what processes influence larval retention and dispersal. The case of sole (*Solea solea* L.) is of particular interest because it is one of the most valuable commercial species in the North Sea, although stocks are chronically overexploited and variability in interannual recruitment is high. The transport of sole larvae from the spawning grounds to the nurseries is driven by hydrodynamic processes, but the final dispersal pattern and larval survival/abundance might be influenced by both behavioral and environmental factors. Therefore it is important to understand the relative impact of hydrodynamics, environment, behavior and ecophysiology on sole larval dispersal. Here we use a particle-tracking transport model coupled to a 3D hydro-dynamic model of the North Sea to investigate interannual variability of the transport of sole larvae over a 12-year period (1995–2006). A sensitivity analysis is performed to assess the relative impact of hydrodynamics, temperature and behavior on the recruitment dynamics to the nurseries. Four scenarios have been tested: (i) constant forcing of sea surface temperature during all years but varying meteorological forcing and river runoff, (ii) constant meteorological forcing during the whole period but varying sea surface temperature and river runoff, (iii) no vertical migration and (iv) an extended drift period (max. 30 days) before settlement if the larvae are not close to a suitable sediment type. Results suggest that year-to-year variability of larval supply to the nurseries is high, both in terms of abundance and larval source (balance between retention and dispersal). Sensitivity analysis shows that larval abundance at the end of the larval stage increases considerably if a settling delay is included. The impact of vertical migration on larval transport and the variations in larval retention at the nurseries due to varying meteorological conditions and sea surface temperature forcing are not spatially consistent.

1. Introduction

Population connectivity, the demographic linking of populations through the dispersal of individuals as larvae, juveniles or adults, requires that individuals move between populations (dispersal), and settle successfully into the recipient population (Sale et al., 2005). Such migrations happen over both small and large distances and for various reasons (in search of foraging, mating or optimal larval habitat). Hence migrants connect different habitats resulting in processes at one location potentially influencing the dynamics at another location (Gaines et al., 2007). The life cycle of fishes is separated into various stages, each requiring specific habitat characteristics (Harden Jones, 1968) and hence requiring active movements between habitats. Once released in the water column, eggs and later on larvae are transported by advection and diffusion, although this is often constrained by hydrodynamic retention (Saenz-Agudela et al., 2011; Taylor and Hellberg, 2003). Advection is a deterministic component related to winds, tides and density gradients, while diffusion represents the random component related to turbulence. The final dispersal pattern of larvae might not only include hydrodynamic forces, but might be affected by biological and behavioral traits. Fish larvae may alter their tracks by swimming actively in response to environmental and prey conditions (Leis, 2007; Runge et al., 2005). For example, a settling delay of recently metamorphosed larvae has been reported for plaice (*Pleuronectes platessa*) (Bolle et al., 2009 and ref. therein). By increasing the duration of the larval phase the search period is extended for nursery grounds with a suitable food supply and reduced predation pressure. Larval abundance at the nurseries is determined by the survival of the early life stages, which on its turn is dependent on factors such as environmental constraints (temperature), the availability of food and the presence of predators. Subadults mature at the feeding grounds and return as adults to the spawning grounds at regular intervals, hence closing the migration triangle (Harden Jones, 1968).

The dispersal capacity of fish throughout the life-cycle is strongly affected by body size. Hence young planktonic fish with characteristic low Reynolds numbers were thought to be almost exclusively influenced by

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local hydrodynamics. This was for a long time the central dogma, until it was realized that various modes of behavior may affect the dispersal of larval fish (e.g. Fiksen et al., 2007; Gerlach et al., 2007; Sentchev and Korotenko, 2007). Evidence from modelling points to the exploitation of selective tidal stream transport (Fox et al., 2006), a combination of selective tidal stream transport and passive drift in the bottom layer (Bolle et al., 2009), or fully passive transport (Champalbert and Koutsikopoulos, 1995). The consensus that active (biological/behavioral) and passive (hydrodynamic) dispersal affect the early life-history stages does not provide an answer to the relative contribution of each component. Which active processes modulate the passive processes such that larvae grow, escape predators and reach suitable feeding grounds? Understanding larval dispersal is of utmost importance as temporal recruitment patterns are characterized by incidental very strong and very weak year-classes (cohorts) which cause strong fluctuations in stock size (Rijnsdorp et al., 1992). The period during which recruitment strength is generally accepted to be determined occurs during the planktonic and early demersal juvenile phases (type III 'survival curve'; Campbell and Reece, 2005). Hence large spawning biomasses do not necessarily correlate with strong recruitment (e.g. Ottersen, 2008; e.g. Able et al., 2011).

Individual-Based Coupled Physical–Biological Models are standard tools for studying fish recruitment (reviewed by Miller, 2007). A Lagrangian particle tracking model describes larval transport by using current velocities and diffusivities predicted from the hydrodynamic model to calculate the movement of individual particles in space and time. In addition, the individual life history may be taken into account. Such models of fish larval transport allow to understand ecosystem functioning and human impact, such as fishing, climate change (Van den Eynde et al., 2009) and land reclamation (Erftemeijer et al., 2009). Among the models of larval transport (e.g. Brochier et al., 2008; Daewel et al., 2011), some have addressed flatfish, the focal group of this paper (Bolle et al., 2009; Erftemeijer et al., 2009; Rochette et al., 2012; Savina et al., 2010). However, all models were constrained either in spatio-temporal coverage or the very specialized/narrow aims. For example Erftemeijer et al. (2009) evaluated the impact of land reclamation on transport patterns and therefore did not include mortality in the model. In Savina et al. (2010), the model (SOLEMOD v1) covered two contrasting years in terms of meteorological forcing (1995 and 1996), but was rather 'simplistic' in terms of processes included in the Individual Based Model (IBM): vertical migration, no mortality and fixed duration of the larval stages.

The target species of this study is common sole *Solea solea* L. (Soleidae, Teleostei), one of the most valuable commercial species in the southern North Sea. The North Sea sole stock is believed to be close to its precautionary reference points, indicating that the stock is at risk of unsustainable exploitation (ICES, 2011). Sole is a batch spawner (e.g. Houghton et al., 1985; Rijnsdorp and Witthames, 2005; Urban, 1991); in the North Sea it spawns in coastal waters of less than 30 m depth in spring (e.g. Borremans, 1987; van der Land, 1991). Sole has a clear preference for the southern part of the North Sea with a tidally mixed water column and bottom temperatures of up to 17 °C in summer and autumn (Rijnsdorp et al., 1992). Climate (and fishing) have resulted in a southwestward shift in range during the last decades (Engelhard et al., 2011). Larval development is temperature dependent (e.g. Fonds, 1979), while survival is linked to the access to prey and the avoidance of predators and infections. Supply to the nurseries may be affected by advection and diffusion processes acting on the planktonic eggs and larvae. In addition, annual variability in survival has been correlated with strong recruitment after cold winters (Rijnsdorp et al., 1992). Nurseries, which shield juveniles from predators and provide a good supply of benthic prey, are located in shallow muddy to sandy coastal areas of less than 20 m depth (Le Pape et al., 2003, 2007). Adult feeding grounds may have a strong link with local continental run-off (Darnaude et al., 2004; Philippart et al., 2007).

In this study, we evaluate the significance of the duration of dispersal and the (a)biotic characteristics affecting dispersal behavior in regards to the larval distribution and postlarval settlement of sole. We implement a particle-tracking model coupled with a 3D hydrodynamic model of the North Sea to investigate the interannual variability of larval transport over a 12-year period. We discuss the impact of interannual variability of hydrodynamics and temperature on larval dispersal and transport success to the nurseries. A sensitivity analysis assesses the relative impact of hydrodynamics, temperature and behavior on larval abundance at the end of the larval stage. Estimated abundances of sole larvae at the nurseries are correlated with virtual population analysis (VPA) estimates of recruitment (ICES, 2011).

2. Methods

2.1. The hydrodynamic model

The 3D hydrodynamic NOS (NOrth Sea) model is based on the COHERENS code (Luyten et al., 1999). It covers the region between 4°W and 9°E, and between 48.5°N and 57°N (Fig. 1) with a resolution of 5′ in longitude and 2.5′ in latitude, and 20 σ-coordinate vertical layers. It is forced by 6-hourly wind and atmospheric pressure fields from the analyzed data of the UK Meteorological Office and by weekly sea surface temperature (SST) data (Bundesamt für Seeschifffahrt und Hydrographie, Loewe, 2003) on a 20×20 km grid interpolated in space and time according to the model resolution. Daily river discharges were included for fourteen rivers (Fig. 1), which were selected from the main North Sea rivers (Lacroix et al., 2007; van Leeuwen, pers. comm.) on the basis of their long term average (1990–2006) discharge (data sources in Savina et al. (2010)). Details about the hydrodynamic model (equations, implementation, forcing, initial and boundary conditions) and its validation can be found in Savina et al. (2010). The model is run over 12 years (after a 2-year spin-up period) to cover a broad range of different meteorological conditions (1995–2006).

2.2. The particle-tracking model (transport model)

Larval trajectories were calculated online using the particle tracking model SEDLAG (Luyten et al., 1999), which was slightly modified by adding a non-random component which counteracts the erroneous particle accumulation in low-diffusivity areas (Visser, 1997) when only a 'naïve' random walk formulation is considered. Details on the implementation are presented in Savina et al. (2010). Explicit representation of horizontal diffusion was neglected because at this scale vertical turbulent diffusion is considered as the dominant horizontal dispersal mechanism in the North Sea (Christensen et al., 2007 and ref. in).

2.3. Individual Based Model (IBM)

Since the first version of the SOLEMOD model (Savina et al., 2010), the following improvements have been made: (i) the parameterization of spawning has been modified to increase realism, both the period of spawning (temperature dependent) and the design of spawning grounds (position and egg number) have been improved, (ii) the nurseries have been re-designed based on the sediment map (Kaskela et al., 2010), (iii) four stages (eggs, yolk-sac larvae, first-feeding larvae, metamorphosing larvae) of larval development are considered instead of three (eggs, early larvae, post-larvae), to allow refinement of stage-related parameterization, (iv) the duration of larval stages is temperature dependent instead of constant, (v) mortality is included and is temperature-dependant for eggs and yolk-sac larvae and constant for other stages. Amongst the different parameterizations of vertical migration tested in Savina et al. (2010) the set combining diel and tidal vertical migration has been kept (see Section 2.3.4.1). All the details about