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Growth and survival of larval and early juvenile Lesser Sandeel in patchy prey field in the North Sea: An examination using individual-based modeling

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ABSTRACT

Disentangling physical–biological interaction processes during early life-stages of fish is crucial for the understanding of fish stock recruitment. Among many individual and environmental aspects affecting mortality during the early life-stages of fish, encountering food at greater than average concentrations is regarded important for survival. Intense aggregations of zooplankton in near-surface waters provide these conditions for larval fish. Simulation studies by individual-based modeling can help understanding of the mechanisms for survival during early life-stages. In this study, we examined how growth and survival of larvae and early juveniles of Lesser Sandeel (*Ammodytes marinus*) in the North Sea are influenced by availability and patchiness of the planktonic prey by adapting and applying a generic bioenergetic individual-based model for larval fish. Input food conditions were generated by modeling copepod size spectra dynamics and patchiness based on particle count transects and Continuous Plankton Recorder time series data. The study analyzes the effects of larval hatching time, presence of zooplankton patchiness and within patch abundance on growth and survival of sandeel early life-stages in the North Sea. Simulations of patchiness related starvation mortality are able to explain observed patterns of variation in sandeel growth. Reduced prey densities within patches decrease growth and survival rate of larvae and match–mismatch affect growth and survival of larvae with different hatch time due to plankton seasonality. Of general scientific and environmental management interest, the results indicate a steep threshold concentration critical for survival at around 0.04–0.05 no. zooplankton/mL.

1. Introduction

Disentangling the physical–biological interaction processes during early life-stages of fish is suggested as a potentially useful approach for understanding recruitment mechanisms and providing scientific management advice for sustainable exploitation of the stocks (Letcher et al., 1996). It appears more rational to aim for a better mechanistic understanding of the processes and interactions underlying stock dynamics (Rose and Cowan, 1993; Fiksen and MacKenzie, 2002; Hinrichsen et al., 2002; Kristiansen et al., 2007) than to investigate correlations between fisheries data and the environment (Brander, 2000; Arnott and Ruxton, 2002; North and Houde, 2003). Simulation studies by individual-based modeling can be useful in facilitating this process-based approach (Letcher et al., 1996).

Patches can be described as regions of higher abundance of zooplankton as zooplankton is sparse in the water column with few high-density aggregations of up to 10^3 times the median abundance (Folt and Burns, 1999). Patchiness or the spatial heterogeneity in the distribution of plankton at different scales and the physical and biological processes that are drivers of these observations have been studied considerably (Krause and Martens, 1990; Steele and Henderson, 1992; Solow and Steele, 1995; Folt and Burns, 1999). Intense aggregations of zooplankton abundance are important for fish larval and juvenile stages in general, since patches with above average concentrations may provide opportunities for high food encounter rates necessary for survival (Mackas and Boyd, 1979). In a simulation study using the generic individual-based model by Letcher et al. (1996) and Letcher and Rice (1997) found that swimming behavior of fish affected prey encounter and feeding rate. They indicated that patch intensity might have a major effect on growth and survival rates of larval fish.

Lesser Sandeel, *Ammodytes marinus* (Raitt, 1934), is the most common of the five sandeel species in the North Sea making up more than 90% of the sandeel catch and is also the most important species for the industrial fishery in the area. Catches of sandeels constitute the largest harvest of any single-species in the North Sea fishery providing about 36% of the total catch in the area. Furthermore, it is one of the most abundant fish species in the North Sea and it is a key species in the functioning of the ecosystem due to its role in the trophodynamics (Pedersen et al., 1999; Gallego et al., 2004; Christensen et al., 2008a, 2008b). The sandeel stock

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is estimated to be 10–15% of the total fish biomass in the North Sea (Arnott et al., 2002). Sandeels are preyed upon primarily by fish, such as cod, haddock, whiting and mackerel, which are species important for the human consumption fishery. At the same time, they are consumed by marine mammals, such as seals and whales, and by sea birds, such as kittiwakes, gannets, puffins, razorbills and guillemots, although in comparison in minor proportions (Pedersen et al., 1999). They form a major part, about 40–60%, of the consumed fish biomass and about 15–25%, of the total consumed biomass in the North Sea (Arnott et al., 2002). Given its ecological and economic importance, it is crucial to understand the processes that affect recruitment in sandeel populations, such as prey dynamics, by developing a model based on disentangling the underlying essential physical–biological processes. The existing knowledge of the processes useful for the sandeel model is reviewed next.

The spawning season of Lesser Sandeel corresponds to midwinter between December and January in the North Sea and the spawned eggs remain attached to sand until they hatch from February to May at the sea bottom in the sand banks that are habitats of sandeels (Macer, 1966; Jensen et al., 2003; Christensen et al., 2008a). It is already suggested for the species that early life-stages determine the recruitment strength and it is important to identify what factors are influencing growth in order to understand survival and recruitment of sandeel (Jensen, 2001). Buckley et al. (1984) place sandeels among fast-growing planktivorous fish species. The growth mortality hypothesis summarizes the influence of feeding success and predation on mortality by stating that growth is increasing and probabilities of starvation and predation mortality are decreasing with increasing feeding success (Anderson, 1988; Shepherd and Cushing, 1980). Hence, fast-growing larvae are hypothesized as having higher survival probabilities than slow-growing larvae. Major factors influencing growth are temperature and prey, where the prey factor not only includes prey density (Kuhn et al., 2008) but also encounter rates with prey and foraging ability of larvae. Wright and Bailey (1996) present evidence for the importance of high growth rate attained by high food intake for early survival in *A. marinus* larvae. They show that growth rate differences occur when there is variation in food availability. They point to the importance of the temporal overlap between timing of hatching and occurrence of zooplankton peak abundances in the same area as proposed in match–mismatch hypothesis (Cushing, 1990).

Survival at the early stages of sandeel is also linked to zooplankton prey availability on a longer time frame. Frederiksen et al. (2006) suggest evidence for a bottom-up control of sandeel larvae in the western parts of the North Sea by zooplankton showing a positive correlation in abundance indices between the two trophic levels in the years 1973–2003. Furthermore, Frederiksen et al. (2007) summarizes the likely structure of trophic and climatic interactions in the pelagic ecosystem of the North Sea, e.g. indicating a possible bottom-up control by zooplankton availability and a top-down control by herring predation and human fisheries. They also suggest that these factors vary in space and time in their relative importance in controlling the sandeel abundance in the North Sea and may act directly, indirectly and interactively. Other studies specifically suggest that sandeel larval survival depends on the abundance of *Calanus* (Arnott and Ruxton, 2002) with a further corroborated and refined analysis showing the specific effect of *Calanus finmarchicus* winter abundance and not of *C. helgolandicus* (van Deurs et al., 2009). Links between recruitment/early survival of fish and abundance of zooplankton prey are also suggested for another species, namely Atlantic Cod (*Gadus morhua*) in the North Sea (Beaugrand et al., 2003; Heath and Lough, 2007). Moreover, Jensen et al. (2003) describe that Lesser Sandeel larvae in the North Sea congregate, where there is a peak abundance of zooplankton in the water column. They show that sandeel larvae may show a vertical behavior that is determined by prey availability and feeding potential over different patchiness and light regimes.

In this study, we examine the growth and survival of Lesser Sandeel larvae and early juveniles in the North Sea under patchy food conditions. We especially adopt a mechanistic modeling approach to disentangle the processes at the early life-stages of sandeel by adapting and applying a generic bioenergetic individual-based model (IBM) for larval fish (Letcher et al., 1996) to the Lesser Sandeel and the North Sea conditions. Employing an IBM as described in this study for examining the growth and survival of sandeel early life-stages linked with patchy prey conditions in the North Sea may provide insight for understanding the recruitment of the species in the area. We have chosen to use an IBM due to its ability to capture the effects of environmental variability on foraging and growth among individual fish, effects that lead to variability in size within and among cohorts and subsequent variation in survival probability among individuals. We model the patchy food conditions for sandeel larvae by generating patchy and size-structured prey fields as input to the IBM.

The aim of this study is to develop a model that enables us to understand some of the mechanisms involved in recruitment of sandeel based on the existing knowledge about interacting physical–biological processes during early life-stages. More specifically, the following questions are focused on: (1) Can the formulated IBM approach explain the observed patterns in larval and juvenile sandeel growth? (2) What are the implications of prey patchiness on the growth and survival of sandeel early life-stages in the North Sea? (3) Does a patchy prey environment create selective survival in accordance with the growth mortality hypothesis? (4) What is the effect of reduced zooplankton productivity on larval growth and survival? In order to investigate this, three patch states, where prey densities are reduced in relation to the base condition, are applied. (5) What is the influence of larval hatch date on growth and survival in relation to match–mismatch with seasonality in prey conditions?

2. Methods

Fig. 1 depicts the model approach developed and used here, including the prey field and the adapted IBM. Transect sampling data of zooplankton abundance in the North Sea (Mackas and Boyd, 1979; Steele and Henderson, 1992) are used to derive an average frequency distribution curve describing the patchiness conditions of the prey and this is used when constructing the prey field inputs to the IBM simulations. To derive prey size spectra and patch dynamics a simple zooplankton matrix model is scaled to time series data from the Continuous Plankton Recorder (CPR) survey obtained from the Sir Alister Hardy Foundation for Ocean Science (SAHFOS) for this study (Johns, 2009, 2010).

The prey dynamics and growth and survival of sandeel early life-stages are modeled with only temporal dimension. Our model state variables are length and survival chance of the individual sandeel. The probability of being in a patch density and the prey density are the forcing functions. The variation among individuals in the IBM is almost exclusively introduced by the described patchiness structure of the prey fields. Consequently, the variation in growth and survival among individuals in the IBM simulations is produced due to this variation in the prey conditions.

2.1. Prey field input to the IBM

The table and figures for this section are given in Appendix A.

2.1.1. Description of patchiness of the zooplankton concentration

Transect sampling in May 1976 in the North Sea shows the patchiness of zooplankton abundance at the near-surface waters