Progress in Oceanography 122 (2014) 131–152

Contents lists available at ScienceDirect

Progress in Oceanography

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

Floating along buoyancy levels: Dispersal and survival of western Baltic fish eggs

C. Petereit [a,*], H.-H. Hinrichsen [a], A. Franke [a], F.W. Köster [b]

[a] GEOMAR Helmholtz Centre for Ocean Research Kiel, Düsternbrooker Weg 20, 24105 Kiel, Germany
[b] Technical University of Denmark, National Institute of Aquatic Resources (DTU Aqua), Charlottenlund Castle, Jægersborg Allee 1, DK-2920 Charlottenlund, Denmark

ARTICLE INFO

Article history:
Received 24 January 2012
Received in revised form 25 November 2013
Accepted 6 January 2014
Available online 14 January 2014

ABSTRACT

Vertical distribution is an important feature of pelagic fish eggs and yolk sac larvae impacting their survival and dispersal, especially in heterogeneous and highly variable estuarine environments like the Baltic Sea. Egg densities determining the vertical distribution pattern were experimentally ascertained for cod (*Gadus morhua*), plaice (*Pleuronectes platessa*) and flounder (*Platichthys flesus*) from the western Baltic Sea. Plaice eggs floated at lower mean (±standard deviation) density range (1.0136 ± 0.0007 g cm^{-3}) compared to cod (1.0146 ± 0.0009 g cm^{-3}) and flounder eggs (1.0160 ± 0.0015 g cm^{-3}), which floated on the highest density level. In flounder egg diameter was significantly related to egg density and in cod a weak correlation could be found between egg dry weight and density. All other relationships between female size, egg size, egg dry weight and egg density were not significant for any of the species. Available egg density data for Baltic Sea cod, plaice and flounder are summarized considering ICES subdivisions and stock management units. A hydrodynamic drift modeling approach was applied releasing drifters in the Belt Sea continuously from December to May, covering the species' spawning seasons. The model implemented experimentally derived egg density ranges and included ontogenetic egg density modifications for cod eggs, increasing egg density from a late egg development stage to first hatch. A drifter was removed from the model, i.e. considered dead, when its initially prescribed density value exceeded the density range available at the temporally resolved geographical positions along the drift trajectories. Highest survival occurred during releases in April and May but no cohorts survived if they were drifted east into the central Arkona Basin or the central Baltic Sea, irrespective of whether a major Baltic Inflow (1992/1993) or a stagnation-year (1987/1988) was simulated. The dispersal characteristics of the surviving yolk sac larvae of all three species reflected retention within the Belt Sea or northwards transport through the Great Belt into the Kattegat and partly into the Skagerrak. There was no successful transport to more eastern Baltic areas past a hypothetical line from the island of Moen (Denmark) to Kap Arkona on Rügen Island (Germany).

1. Introduction

Fish eggs and larvae are important life stages to a large extend determining the recruitment strength in marine fish (Cowan and Shaw, 2002; Houde, 2002). The survival success of these stages can vary significantly both between years and within a spawning season due to a variety of factors (e.g. occurrence of unfavorable temperature and salinity conditions or hypoxia, Cushing, 1990; Bunn et al., 2000). Moreover, adequate neutral buoyancy of pelagic early life stages plays a major role in survival, distribution and dispersal, which can shape population structure (Ciannelli et al., 2010; Myksvoll et al., 2013). In addition, specific adaptations of egg buoyancy, fertilization and development of marine fish populations spawning in estuarine areas became evident in a meta-analysis of egg buoyancy data of 16 fish species (MacKenzie and Mariani, 2012).

A review on buoyancy patterns of eggs, yolk sac larvae and later larval stages of fish is given by Govoni and Forward (2008). They summarized the general assumptions and mechanisms on how egg density (buoyancy) is derived and controlled in marine fish eggs. It is achieved through passive physiological mechanisms due to the eggs' constituent compounds and through developmental events within the ovary of the female fish (Cerdà et al., 2007; Goarant et al., 2007; Govoni and Forward, 2008 and references therein). It is known that brackish water eggs have relatively higher water content (e.g. cod 97%) compared to marine cod eggs (93%), due to the increased water uptake during final oocyte maturation which is aquaporin-mediated (Thorsen et al., 1996; Craik and Harvey, 1987; Fabra et al., 2005). Recent studies on cod (Jung et al., 2012a,b; Guðmundsdóttir, 2013) and anchovy (Ospina-Álvarez et al., 2012) found egg buoyancy increasing and decreasing

* Corresponding author. Tel.: +49 431 600 4567; fax: +49 431 600 4553.
E-mail address: cpetereit@geomar.de (C. Petereit).

0079-6611/$ - see front matter © 2014 Elsevier Ltd. All rights reserved.
http://dx.doi.org/10.1016/j.pocean.2014.01.001

towards the end of the ontogenetic development, respectively. Changes in biochemical components are likely to be the main cause that accounts for decreased specific gravity towards hatching (Jung et al., 2012b). Several studies recommended incorporating such detailed density changes into the modeling of potential drift routes (Myksvoll et al., 2011; Jung et al., 2012a,b; Ospina-Álvarez et al., 2012). For Norwegian coastal cod, such density adjustment was applied using linear models considering development time and temperature (Myksvoll et al., 2013). For anchovy eggs a polynomial model estimating egg density as a function of temperature dependent time from fertilization was suggested (Ospina-Álvarez et al., 2012).

It is uncertain whether these models developed for full marine salinity conditions can be applied for the pelagic eggs of fish species adapted to the brackish water of the Baltic Sea. The western Baltic Sea is part of the world́s largest brackish sea with specific, highly variable hydrographic conditions in respect to time and space. All water flowing in and out of the Baltic Sea has to pass through the Belt Sea, the Sound or the Femern Belt (Matthäus and Franck, 1992). Through the Danish Straits (e.g. Belt Sea) on average, outflow is prevailing overlaid by highly fluctuating in- and outflow periods of a few days reaching occasionally volume changes of 100–200 km^3 (Lehmann and Hinrichsen, 2000a,b). Thus, volume changes during in and outflow situations are in the same order of magnitude as the river runoff and an averaged outflow rate of 1.24 km^3 day^{-1} (~453 km^3 $year^{-1}$) representing the mean Baltic Sea water discharge including river runoff and the net effect of precipitation minus evaporation (Lehmann and Hinrichsen, 2000a,b). Due to the strong current fluctuations in the Danish Straits the stability of the barotropic flow [0 = no stable current flow; 1 = high stable current flow] hardly reached values over 0.3 (Lehmann and Hinrichsen, 2000a,b). Characterized by an inhomogeneous bottom morphology and separated by small trenches and channels, the western Baltic acts as a shallow connection (<40 m) between the North Sea (high salinity) and the brackish central Baltic Sea which is characterized by deep basins with stratified water layers. The International Council for Exploration of the Sea (ICES) has partitioned the Baltic Sea into Subdivisions (SD's) according to prevailing hydrological and geographic conditions, wherein the Belt Sea (SD 22), the Sound (SD 23) and the Arkona Sea (SD 24) constitute the western Baltic Sea management unit for cod, *Gadus morhua* L. (Fig. 1).

The Belt Sea (SD 22, Fig. 1) is the main fishing area for plaice (*Pleuronectes platessa* L.) in the Baltic Sea and ~830 t were landed in 2009 (ICES, 2010). Slightly higher landings were reported for flounder (*Platichthys flesus* L.; ~1020 t) and cod (~3450 t) (ICES, 2010, 2011). To a high degree, these fish species form the basis for the local fisheries. They have their reproductive season during winter and early spring in the western Baltic Sea spawning pelagic eggs. The spawning season extends for cod from January to April (Bagge et al., 1994; Muus and Nielsen, 1999; ICES, 2011), for plaice from November to March (Muus and Nielsen, 1999) and for flounder from February to April (Saeger, 1974). To date, it is not well known at which depths, or corresponding density layers, the eggs from these three species are developing and where they get passively transported to. A first estimate has been given by Westernhagen von et al. (1988). They reported the highest proportions of eggs of all three species to occur in the salinity range from 17.5 to 21 psu [this calculates to densities of 1.0139–1.0168 g cm^{-3} at 1 °C (Fofonoff and Millard, 1983)].

The precise density layers for each species are of major interest since the existing transport mechanisms can be detrimental to the survival of the eggs. If the eggs are transported to areas with insufficient density levels, they sink to the bottom and die most probably. In addition, this information helps to disentangle small scale population structure of the species (Ciannelli et al., 2010; Myksvoll et al., 2013). For example, the degree and proportion of exchange between the two Baltic cod stocks (western Baltic versus eastern Baltic cod) are insufficiently understood (ICES, 2011; Hüssy, 2011). The existence of two separate cod stocks has been postulated and shown by various analytical methods such as different morphometric characteristics (for references see Aro, 1989 and Hüssy, 2011), otolith microchemistry (Heidemann et al., 2012), hemoglobin characteristics (Sick, 1961; Andersen et al., 2009) or population genetics (Nielsen et al., 2003, 2009). A hydrodynamic drift model study suggested that eggs or early larval stages of the western cod stock could have the potential to contribute under certain strong westerly wind conditions to the juvenile proportion of the eastern stock east of Bornholm Basin (Hinrichsen et al., 2001). However, at that time the authors had no neutral egg buoyancy data available which are mandatory to determine the initial depth of the released eggs in the water column.

In the present study, we measured neutral egg buoyancy of stage IA eggs obtained by strip spawning running ripe individuals of cod, plaice and flounder during participation in commercial fishing trips to the Northern Kiel Bight (SD 22), an area described historically as the main spawning ground for western Baltic cod (Kändler, 1944; Thurow, 1970; Westernhagen von et al., 1988). This study uses experimentally derived neutral egg densities (neutral buoyancies ranged from 1.011 to 1.018 g cm^{-3}) and ontogenetic egg density development (8–15 days duration) of three species in combination with literature-based temperature dependent development rates (7–31 days duration), to model survival rates and dispersal routes from newly fertilized egg stages until the start of mixed feeding larval stage, which was defined to start at the time of mouth gap opening (MGO).

The main focus of our experimental work was to answer the questions: (i) where (at which density layers) do the early egg stages of western Baltic cod, plaice and flounder float? (ii) do different salinity conditions during the fertilization process influence the final eggs' density? (iii) do ontogenetic (egg stage specific) differences exist?

In a subsequent step, we used hydrodynamic modeling approaches to evaluate possible consequences of different hydrographical and hydrodynamic conditions on egg survival and spatial horizontal distribution patterns within, and between spawning seasons. Two years with different hydrographical situations were selected. We used the same years as Hinrichsen et al. (2001) to achieve comparability of the improved model. Our major focus was on the transport potential of the passively drifting eggs and yolk sac larvae until these were able to start mixed feeding (MGO), and their possibility to contribute to recruitment in the central Arkona Basin (SD 24) or Bornholm Sea (SD 25).

2. Materials and methods

2.1. Gametes acquisition and processing

Starting early January, individuals of cod, plaice and flounder were acquired on 12 commercial fishing day-cruises every 7–10 days in the Northern Kiel Bight, western Baltic Sea (ICES SD 22; Fig. 1, Table 1). The sampling intervals covered largely the natural spawning seasons of the species in the western Baltic Sea and matched specifically well for cod and plaice as previously described (Strodtmann, 1906; Thurow, 1970; Westernhagen von et al., 1988). Trawling was performed but the specific gear type (shape, mesh size of the cod-end, haul duration) was changed during all trips depending on the captains' daily strategy and target fish species (flatfish/whiting/cod). Since the use of ship based oceanographic measurement systems (CTD) on commercial fishing boats was impossible, a small scale solution was applied instead.