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Potential transport of plaice eggs and larvae between two apparently self-contained populations in the Irish Sea

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ABSTRACT

A coupled physics particle-tracking model, driven by realistic meteorological forcing was used to examine the dispersal and transport of plaice eggs and larvae in the year 2000 from two spawning grounds in the Irish Sea. The model included passive transport of eggs and early stage larvae, diel vertical movements for larvae between 7 and 10.5 mm in body-length and tidally synchronised, vertical movements for larger larvae (>9 mm body-length). The year 2000 was chosen because of the availability of ichthyoplankton data with which to initialise the model. The majority of larvae originating from spawning in the eastern Irish Sea settled into nursery grounds along the Scottish, English and Welsh coasts, in agreement with previous findings. In contrast, a significant portion of larvae originating from spawning in the western Irish Sea was transported eastwards to these same nursery grounds. Transport across the Irish Sea resulted from the onset of tidally synchronised vertical behaviour encoded in the model for older larvae. Settlement of larvae into local nursery grounds along the Irish coast was limited. Because of the prevailing winds and currents in the region, plaice eggs and larvae are unlikely to be transported from east to west; in most years spawning in the western Irish Sea probably acts as an additional source of juveniles for nursery grounds along the Scottish, English and Welsh coasts.

1. Introduction

Plaice (*Pleuronectes platessa* L.) are an important commercial flatfish species occurring throughout the North-East Atlantic in waters down to 120 m (Wheeler, 1978; Millner et al., 2005). Their life cycle is characterised by offshore spawning, a period of egg and larval planktonic drift followed by metamorphosis and settlement into shallow, coastal nursery grounds (Gibson, 1999). Over the first few years of their settled life they gradually move into deeper water, eventually re-joining the adult populations. There are several recognised populations along the western seaboard of Great Britain (Fig. 1). For fisheries assessment purposes, these populations are grouped into larger management units (ICES Areas). To avoid confusion we refer to plaice within these management units as ‘stocks’ but each ‘stock’ may contain several ‘populations’. Furthermore, adult plaice have been shown to move between many of these populations and across management unit boundaries (Dunn and Pawson, 2002).

The most recent assessment suggests that the Irish Sea (Area VIIa) is the most important of these western stocks, both in terms of biomass and landings (Table 1). However, it is important to note that plaice off the west of Scotland are not formally assessed. Based on extensive plankton surveys over a number of years the spawning areas of plaice in the Irish Sea have been clearly defined (Simpson, 1959a; Fox et al., 2000; Bunn and Fox, 2004). In the eastern Irish Sea most plaice eggs are found off the North Wales coast but they occur as far north as the mouth of the Solway Estuary. In the western Irish Sea, the bulk of spawning occurs close to the Irish coast, with additional small amounts off Port Erin Bay, Isle of Man (Nash and Geffen, 1999). A deep-water channel, over which plaice eggs are only occasionally found, separates the main spawning grounds in the eastern and western Irish Sea. An additional minor spawning ground is located in Cardigan Bay (Fig. 1). Because the stock assessment is not spatially resolved below the management area scale, the only published estimate of the relative sizes of the plaice populations within the Irish Sea comes from an ichthyoplankton-based assessment in 1995 (Armstrong et al., 2001). This suggested that total biomass of mature fish would be distributed in approximate proportions of 61:31:8 (comparing the eastern spawning grounds, western spawning grounds and Cardigan Bay).

Spawning probably begins in December (as some eggs have been found on the first plankton surveys undertaken in early January) and peaks between mid-February and mid-March. Egg production has usually ceased by the end of April (Fox et al., 2007). At typical ambient temperatures, the duration of the egg stage is between 13 and 18 days (Fox et al., 2003). Following hatching,

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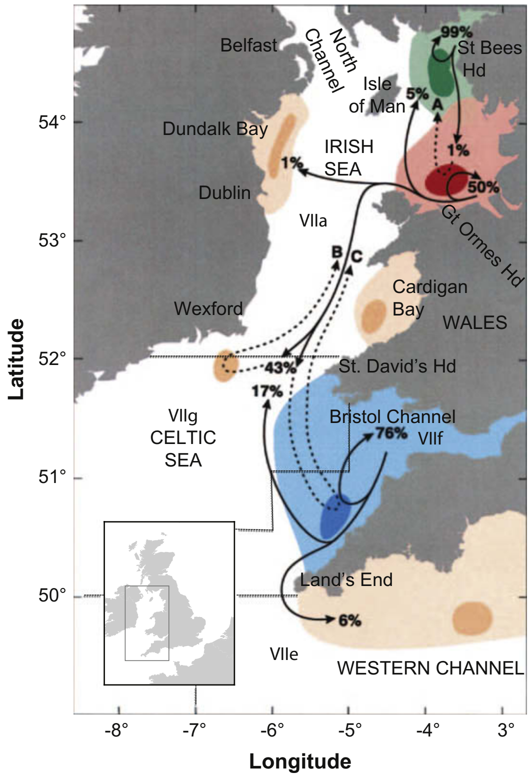

Fig. 1. A schematic diagram showing the principal population areas and movements of plaice on the west coast of England and Wales (Dunn and Pawson, 2002). For each population, the main feeding area (derived from tag recaptures during April–December; light shading), and the main spawning area (derived from tag recaptures during January–March, and published ichthyoplankton surveys; dark shading) are indicated. Dashed lines indicate boundaries of the ICES Fisheries Assessment Areas. Underlying map reproduced with permission from Blackwell Publishing.

plaice larvae in the Irish Sea drift in the plankton for up to 55 days before metamorphosing (Fox et al., 2007). Around this time, the juvenile plaice settle into inshore nursery grounds and spend the next few months in very shallow waters (Gibson, 1999; Nash and Geffen, 2000). The locations of the nursery grounds around the eastern Irish Sea are well known from inshore surveys and the relative distribution of the settled plaice population across different nursery sites has been estimated (Riley et al., 1981; Fox et al., 2007). In the North Sea, plaice eggs and larvae undergo an extensive drift from spawning to nursery grounds (Simpson, 1959b; van der Veer et al., 1998) but in the eastern Irish Sea, spawning and nursery grounds are in close proximity. Despite this, passive dispersal alone appears insufficient to transport the larvae to the nursery grounds. An individual-based particle-tracking model has previously been used to demonstrate that the inclusion of tidally synchronised behaviour (swimming vertically upwards on a rising tide and down on a falling tide) is necessary to concentrate the juveniles into the nursery grounds (Fox et al., 2006). Similar mechanisms are thought to operate during the final phase of plaice settlement in the North Sea (de Graaf et al., 2004).

Because of (1) the separation of the plaice spawning grounds, (2) the limited movement of adult plaice in an east to west direction and (3) the existence of different phenotypes (Nash et al., 2000), it has been hypothesised that two essentially independent populations of plaice might exist in the eastern and western Irish Sea. However, convincing genetic evidence to support this assertion is lacking. Apparent genetic homogeneity could, however, result from either recent re-colonisation of the Irish Sea following the last glacial maximum (Hoarau et al., 2002; Watts et al., 2004) or result from relatively small amounts of mixing between the populations. Although, movements of post-juvenile plaice in the Irish Sea and surrounding areas have been studied with tagging programs (Dunn and Pawson, 2002), relatively little is known about potential mixing at the egg and larval stages. To investigate this aspect, we conducted experiments using a coupled hydrodynamic-particle-tracking model. This model has already been used to explore how different larval behaviour affects the transport and settlement of plaice in the eastern Irish Sea (Fox et al., 2006).

Table 1
Status of the plaice stocks in 2007 according to ICES (2008a,b).

Assessment area	Spawning stock biomass (tonnes)	Landings (tonnes)
Irish Sea (Area VIIa)	7,675	804
Celtic Sea (Area VIIf & g)	999	406
Western Channel (Area VIIe)	1447	1012

2. Methods

2.1. Ichthyoplankton surveys

The plankton surveys used to generate starting positions for the particle-tracking model have been fully described by Bunn and Fox (2004). Briefly, five cruises covering the whole Irish Sea took place between 23 January and 10 April, 2000. Plankton samples were collected at around 100 locations per cruise using Gulf VII high-speed plankton samplers (Nash et al., 1998). The samplers were equipped with Valeport flowmeters (Valeport Ltd., Totnes, Devon, UK) to measure internal (in the nosecone) and external water flow and Guildline (Guildline Instruments, Lake Mary, FL, USA) or Seabird STDs for logging environmental parameters. The samplers were generally deployed from the sea surface to within 2 m of the seabed in double-oblique hauls but on shallow stations multiple-oblique hauls (saw-tooth pattern) were made to ensure a sufficient volume of water was filtered. Upon recovery, plankton samples were fixed in 4% buffered formalin (Tucker and Chester, 1984) and returned to participating laboratories for sorting. Plaice eggs were identified (Russell, 1976), assigned to one of five morphological stages (I, II, III, IV or V) following Simpson (1959b) and the total number of eggs of each stage caught at each plankton station determined. Numbers of eggs were converted to abundance (nos m^{-2} sea surface) by multiplying by the sampled depth (m) divided by the volume of water filtered (m^3) during collection of the sample. Egg abundance data were then converted to daily production (nos m^{-2} day^{-1}) by dividing abundance by stage duration calculated from the depth integrated sea temperature recorded at that station (Fox et al., 2003).

Initialisation matrices for the particle-tracking model were generated from Generalized Additive Models (GAMs) of the stage I daily egg production. Latitude, longitude and date were used as covariates and the degrees of freedom of the splines selected using the step.gam function (S-Plus 6, Insightful Corp., Seattle, USA). Prior to fitting, data were separated into western Irish Sea (west of longitude 4.5° W) and eastern Irish Sea (east of longitude 4.5° W) as this solves some of the problems encountered in Fox et al. (2000) of fitting a GAM to the whole region (Fig. 2 redrawn from Fox et al., 2007). Goodness of fit and predictions were assessed using standard residual plots and by visualising the timing and locations of modelled egg production against the raw data. Smoothed estimates of daily egg production were then generated from the GAMs at positions equivalent to the nodes of the hydrodynamic model grid.

2.2. Hydrodynamic model

The physical model has been fully described in Young et al. (2004) and Fox et al. (2006). Briefly, the model is a three-