



Review Article

The influence of oceanographic conditions and larval behaviour on settlement success—the European sea bass *Dicentrarchus labrax* (L.)

Claire Beraud^{1*}, Johan van der Molen^{1,2}, Mike Armstrong¹, Ewan Hunter¹, Leila Fonseca^{1,3}, and Kieran Hyder¹

¹Lowestoft Laboratory, Centre for Environment, Fisheries & Aquaculture Science, Pakefield Road, Lowestoft, Suffolk NR33 0HT, UK

²NIOZ Royal Netherlands Institute for Sea Research, Department of Coastal Systems and Utrecht University, Den Burg, 1797 SZ, The Netherlands

³Department for Environment, Food & Rural Affairs, Nobel House, 17 Smith Square, London SW1P 3JR, UK

*Corresponding author: tel: +44 (0)1502 521353; fax: +44 (0)1502 513865; e-mail: claire.beraud@cefas.co.uk

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The European Seabass (*Dicentrarchus labrax*) is a slow-growing late maturing fish. The northern stock has been declining since 2010 and is thought to be caused by a combination of fishing and weak year classes. Large inter-annual variation in settlement has been observed, so a better understanding of the mechanisms driving settlement success will aid interpretation of the variation between years, and help to improve the stock assessment models and management strategies. In this study, an individual-based model (IBM) was developed to investigate the factors affecting sea bass settlement on nursery grounds of the northern sea bass stock. The IBM was coupled with hydrodynamics to track particles, whereas egg and larval development, and vertical migration behaviour are fully incorporated. The IBM successfully predicted inter-annual differences in settlement regardless of larval behaviour. The highest settlement success was predicted with neutrally buoyant eggs, hatchlings, and larval stages, in combination with tidal migration at the final larval stage. Dispersal was driven mainly by the influence of wind on residual currents and water temperature, with warmer temperatures reducing the duration of the pelagic phase and stronger current increasing the potential to drift further. Eggs spawned in the central western English Channel settled in both England and France, with movement from the central to the eastern English Channel occurring only in warm years. Larval duration was driven by water temperature and showed an increase in duration from the southwest to northeast areas of the northern stock. The results are discussed in the context of sea bass management and conservation strategies.

Keywords: European sea bass, individual-based particle tracking model, larval migration behaviour, oceanographic conditions, pelagic stage modelling.

Introduction

Understanding the relationship between the adult stock and number of young fish recruiting to that stock (the stock–recruitment relationship) has been studied for many years (e.g. [Beverton and Holt, 1954](#)). Predicting this relationship remains one of the foremost challenges in fisheries science ([Houde, 2008](#); [Subbey et al., 2014](#)) as it underpins reference points for sustainable fishing, but is often obscured by large inter-annual variability and

autocorrelation between the environmental factors that drive recruitment. The pelagic egg and larval phases (hereafter termed pelagic phase) has been well studied in many marine systems including coral reefs ([Munday et al., 2009](#)), intertidal rocky shores (e.g. [Gaines and Roughgarden, 1985](#); [Caley et al., 1996](#)), and fully marine environments ([Bolle et al., 2009](#)). Marine systems described as “open” ([Roughgarden et al., 1985](#); [Hyder et al., 2001](#)) often have the potential for protracted larval dispersal ([Gaines](#)

et al., 2007; van der Molen et al., 2007). Consequently, the pelagic phase is important in determining the variability in year class strength of many fish (van der Veer et al., 2000), but the underlying influencing factors are poorly understood (Houde, 2008; Subbey et al., 2014).

To improve understanding of the pelagic larval phase of marine fish, mathematical models have been developed including simple statistical approaches (Subbey et al., 2014), non-spatial structured population models (Hyder and Nash, 1998), and spatially explicit particle tracking approaches combining both hydrodynamics and individual dynamics (van der Veer et al., 1998; van der Molen et al. 2007; Savina et al., 2010; Rochette et al., 2012; Lacroix et al., 2013; Tiessen et al. 2014). Individual-based models (IBMs) are popular tools to aid interpretation of ecological and evolutionary processes (DeAngelis and Grimm, 2014). IBMs have been used to model fish populations (DeAngelis and Mooij, 2005), and incorporate behaviours including shoaling (Jeon et al., 2013; Accolla et al., 2015) and migration (Okunishi et al., 2009). For example, the movement towards nursery areas has been modelled using IBMs that include vertical migration for European anchovy (Ospina-Alvarez et al., 2012) and sole (Savina et al., 2010; Lacroix et al., 2013), and consistent directional movement along a river towards nursery grounds (Baetens et al., 2013). IBMs coupled with hydrodynamic models have been used to assess the temporal distribution of larvae (van der Molen et al., 2007), the importance of passive drift for variation in year class strength (van der Veer et al., 1998; Tiessen et al., 2014), the supply of larvae to coastal nursery grounds (Rochette et al., 2012), and link larval supply and habitat models (Rochette et al., 2013).

The European sea bass, *Dicentrarchus labrax*, is distributed across the North-East Atlantic from northwest Africa to southern Scandinavia, with individuals present in the Mediterranean and Black Seas (Pickett and Pawson, 1994). Sea bass in the northern stock are relatively slow growing fish that can reach up to 30 years of age and take between 4 and 7 years to reach maturity (Pawson and Pickett, 1996). Mature sea bass aggregate to spawn between February and April from the Celtic Sea to the southern North Sea (Dando and Demir, 1985; Sabriye et al., 1988; Jennings, 1990). The geographic extent of spawning is thought to be bounded by the 9°C isotherm and can expand both as the season progresses and in warmer years (Pickett and Pawson, 1994).

Spawning involves the release of ripe ova in two to three batches over a two- to three-week period (Mayer et al., 1990). The pelagic phase of sea bass lasts between 50 and 70 days (Jennings and Ellis, 2015) and dispersal brings a proportion of the larvae to the vicinity of nursery grounds in estuaries, salt marshes, and other sheltered coastal sites. From around 4 years of age, the juveniles become widely distributed in coastal waters before joining the adult population once mature (Pawson et al., 2007). Settlement in the northern stock is highly correlated with temperature with poor settlement in cold years (ICES, 2012). Temperature may act as a direct stressor affecting survival of juveniles in nursery areas and could also be correlated with meteorological processes driving egg and larval drift patterns. Genetic studies show limited distinction between stocks (Fritsch et al., 2007), and tagging studies have shown large migrations of bass (Pawson et al., 2007; Quayle et al., 2009) with some evidence of philopatry, where adults return to the same coastal site after spawning each year (Pawson et al., 2008).

Sea bass is a high value fish that is exploited by commercial fisheries (ICES, 2012) and is an important species for recreational

anglers with removals constituting around 25% of the total harvest in 2012 for the northern stock (Armstrong et al., 2013). Bass are currently managed in four discrete regions: (i) Iberian Coast; (ii) Bay of Biscay; (iii) west of Scotland and south and west of Ireland; and (iv) North Sea, English Channel, Celtic Sea, and Irish Sea (ICES, 2012). Scientific assessments of the northern stock have shown a rapid decline in the spawning stock biomass (SSB) since 2010 attributed to a succession of weak year classes from 2008 to 2012 and increased fishing mortality (ICES, 2015). The stock exhibits very large inter-annual variability in settlement, most probably driven by environmental factors. To conserve the stock, significant reductions in the harvest of sea bass have been implemented by the European Commission through seasonal and area closures, increasing the Minimum Conservation Reference Size to 42 cm, monthly boat limits or bycatch limits for commercial fishers, and bag limits for recreational anglers (Council Regulation (EU) 2107/127). Similar patterns were observed in the late 1980s that led to a number of conservation measures including the designation of bass nursery areas (BNAs) around England and Wales to protect aggregations of fish below the minimum landing size (Pickett and Pawson, 1994).

In this study, factors affecting settlement of juvenile sea bass were investigated on nursery grounds in the North Sea, English Channel, Celtic Sea, and Irish Sea (the “northern stock”—ICES Areas IVb&c, VIIa, d–h). An IBM was developed that coupled hydrodynamics and particle tracking with a pelagic phase model that included egg and larval development and vertical migration behaviour. Potential effects of spawning stock and the spatial and temporal distributions of spawning were excluded to assess the effect of the physical environment on settlement levels, through adoption of a standardized method of particle release. Model predictions were assessed in terms of settlement density, spatial patterns, pelagic phase duration, and inter-annual variation, and were used to select the larval behaviour that maximized settlement in known nursery areas. The sensitivity of the settlement patterns to variation in the physical environment and the connectivity between spawning and nursery grounds were assessed. The implications of these findings are discussed in the context of management of sea bass.

Material and methods

The particle tracking model combines active and passive transport of a time-evolving “particle.” The aim was to simulate pelagic migration from spawning ground to nursery area, by defining growth and behaviour that was dependent on the physical environment. The selection of the most appropriate behavioural scenario was based on field observation in river estuaries and other coastal sites defined as BNAs [Bass (Specified Sea Areas) (Prohibition of Fishing) Order 1990: SI1990 No. 1156] that are now sampled in support of the Water Framework Directive (Coates et al., 2007).

The hydrodynamic and particle tracking models

A three-dimensional implementation of the Eulerian General Estuarine Transport Model (GETM—www.getm.eu, Burchard & Bolding, 2002) was used to derive current vectors and water temperatures for the particle tracking model [General Individuals Transport Model (GITM)] (Wolk, 2003; Tiessen et al., 2014; van der Molen et al., 2015). Here, a version of GITM was developed that simulated sea bass development depending on environmental

parameters (e.g. temperature) and drift using current fields mediated by position in the water column.

The north-west European shelf setup GETM was run using a time step of 10 s at a spatial resolution of $0.08 \times 0.05^\circ$, with 25 vertical sigma layers. The model was forced at open-boundaries by tidal elevations from Topex-Poseidon satellite altimetry (Le Provost *et al.*, 1998) and by winds, temperature, and humidity derived from the European Centre for Medium-Range Weather Forecast reanalyses (ECMWF, 2006a, b). The relative contributions of warm water pockets were not included (e.g. outflow pipes from industrial developments such as power stations). A full description of the model setup and forcing can be found in van der Molen *et al.* (2015).

The GITM model allows the pelagic phase to be split into different stages that are representative of a type of development and/or behaviour. For larval stages, a variety of vertical behaviours have been implemented including diurnal and tidal migration. Movement of particles related to buoyancy can also be incorporated, and settlement was simulated by freezing particle motion on reaching a certain size and/or appropriate physical conditions (e.g. water depth, temperature, salinity, and sea-bed composition) (see Tiessen *et al.*, 2014; van der Molen *et al.*, 2015 for a full description).

This study focused on the northern sea bass stock in the North Sea, English Channel, Celtic Sea, and Irish Sea (ICES Fishing Areas IVb-c and VIIa, d-h) (ICES, 2012). The domain of the particle tracking model was defined as the area from 48°N to 54.5°N and 8°W to 8.5°E (Figure 1). The domain was based on sea bass data from 28 sampled estuaries (Kelley, 1988) and 37 BNAs in England and Wales [The Bass (Specified Sea Areas) (Prohibition of Fishing) Order 1990: SI1990 No. 1156; The Bass (Specified Areas) (Prohibition of Fishing) (Variation) Order 1999: SI 1999 No. 75]. The model domain covers most sea BNAs as sampling of 64 UK waterbodies had not provided evidence of populations of juvenile sea bass above 54°N (see Coates *et al.*, 2007 for a description of sampling).

Spawning

A total of 46548 individual sea bass eggs (particles) were released at the surface over the whole model domain (Figure 2); with this number of particle dictated by available computational resource. One particle was released in every three longitudinal grid cells and every second latitudinal grid cell. A total of 1724 particles were released every 3 days between February and April, with the 3-day interval giving a reasonable representation of simulated environmental conditions. This release pattern covered the known offshore spawning grounds and time period of interest (Pickett and Pawson, 1994), and allowed for uncertainty in observed spawning areas and water temperature preferences. In addition, it provided a good balance between computation effort and numbers of particles. Although such a release scheme did not replicate the real spawning distribution, it allowed assessment of the effects of environmental conditions on connectivity between spawning locations and coastal nursery grounds. More realistic spatial egg production scenarios could be developed, but this was not done as it would make it difficult to assess the effects of environmental conditions on settlement, and there would be large uncertainties surrounding the spatial and temporal variation in spawning. To test the impact of different spawning parameters, post-processing scripts were used to select particles spawned within certain environmental conditions at particular locations. The 9°C isotherm has been postulated as the threshold above which bass spawning

occurs (Pickett and Pawson, 1994), and was used to define spawning areas in the model.

Nursery areas

In the United Kingdom, all non-polluted estuaries from the Ribble Estuary in the North-West to the Blackwater in the South-East England are likely to be nursery habitats (Kelley, 1988). In England and Wales, 37 rivers, estuaries, and other coastal sites have been defined as BNAs for juvenile bass, where additional restrictions on commercial and recreational fishing are imposed for all or part of the year [Bass (Specified Sea Areas) (Prohibition of Fishing) Order 1990: SI1990 No. 1156] (Figure 1). It is very likely that nursery areas occur in other countries within the northern stock area, with some identified (e.g. Wadden Sea—Cardoso *et al.*, 2015) and studies underway in some countries to map these areas (e.g. France).

Sea bass development and vertical behaviour

The pelagic phase of sea bass was split into egg and larval stages (see Jennings, 1990). One egg and three larval stages (hatchling, larva, and fry) were defined with distinct sizes, rates of development, and behavioural characteristics (Table 1). Sea bass eggs have been found at or near to the surface (Pickett and Pawson, 1994; van Damme *et al.*, 2011a, b), so were assumed positively buoyant in the model with an upward velocity of 0.002 m s^{-1} (Edwards *et al.*, 2008). The resulting vertical positions were driven by this buoyancy and physical mixing. The development of eggs was dependent on temperature using an existing relationship (Jennings and Pawson, 1991):

$$\ln(\text{age}) = a + bT, \quad (1)$$

where T was the temperature and a and b were defined for each of the 13 egg sub-stages (Jennings and Pawson, 1991). Jennings and Pawson (1991) also estimated the average hatching age, where half of the eggs have spawned, as 6.47 and -0.129 for a and b coefficient, respectively. Assuming a suitable temperatures range from 8 to 20°C , the average duration of the egg phase ranged from 3 to 7.5 days, which was consistent with reported duration in other studies (Olivier *et al.*, 2013). Once hatched, the hatchling carries a buoyant yolk sac and has limited swimming ability, so it was assumed that hatchlings were positively buoyant with an upward velocity of 0.003 m s^{-1} (Edwards *et al.*, 2008). Hatchlings were initially 1.5 mm in length and the duration of this stage (D) depended on temperature, using the following equation:

$$D = 10^a / 10^{(bT)} \quad (2)$$

with $a = 1.89$ and $b = 0.077$ (Jennings, 1990). The duration of the first larval stage was between 1 and 7 days and transition to the second larval stage occurred at a length of 5.5 mm that corresponded to absorption of the yolk sac (Jennings, 1990).

During the second larval stage, the “larva,” sea bass have a swim bladder, develop fins, and range from 5.5 to 10.5 mm in length (<http://www.fao.org/docrep/field/003/ac230e/AC230E02.htm#ch2.11>). Sea bass larvae have some swimming ability, but with few data on the swimming velocity or direction, the vertical swimming velocity measured for black sea bass of 0.01 m s^{-1} was used (Edwards *et al.*, 2008). No information about the impact of

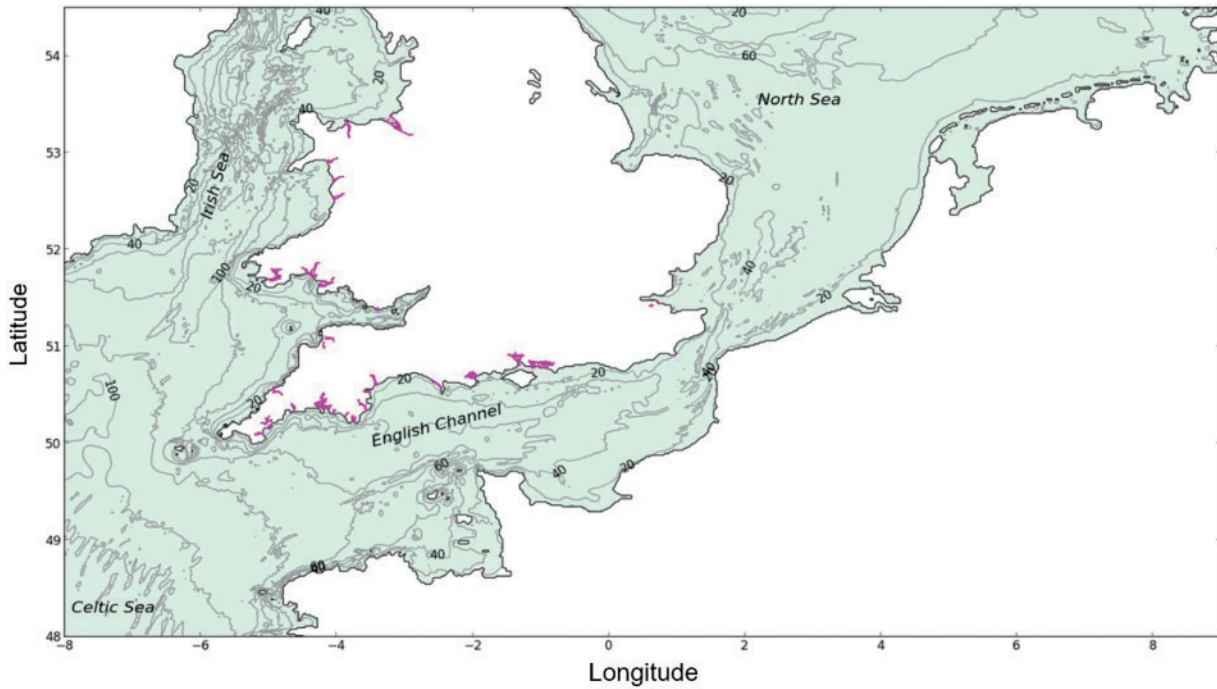


Figure 1. Known sea BNAs (purple/grey) in England and Wales (The Bass (Specified Areas) (Prohibition of Fishing) (Variation) Order 1999, SI 1999, No. 75). Contour lines indicate bathymetry (see online version for colours).

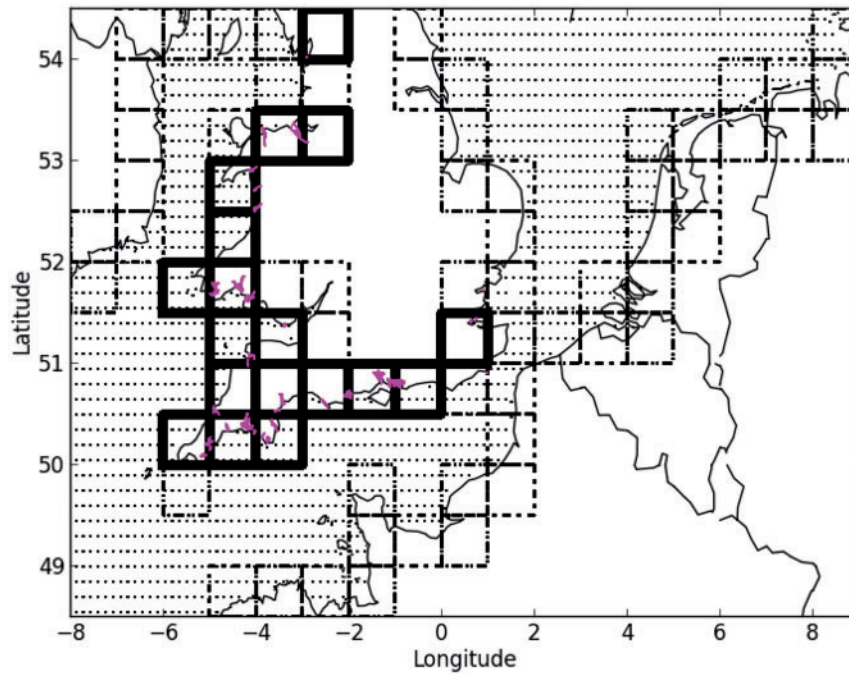


Figure 2. Coastal ICES rectangles ($1 \times 0.5^\circ$ subdivisions of ICES Area) (dashed line) containing known BNAs (bold solid line) for the model domain. Dots indicate potential spawning locations where eggs were released.

temperature on growth at this stage was available, so a constant larval growth rate of 0.2 mm day^{-1} was assumed (Jennings and Pawson, 1992). This gave a stage duration of 25 days that was consistent with other studies (<http://www.fao.org/docrep/field/003/ac230e/AC230E02.htm#ch2.10>).

The final larval stage, the “fry,” has good swimming ability and is ready to settle on a nursery ground, and was assumed to occur between lengths of 10.5 and 15 mm. A vertical swimming velocity based on black sea bass of 0.02 m s^{-1} was used (Edwards et al., 2008). A constant growth rate of 0.2 mm day^{-1} (Jennings and Pawson,

Table 1. Predicted duration and size of sea bass at different pelagic developmental stages, parameters used to model growth, and behaviours.

Phase Stage	Egg Egg	Larvae		
		Hatchling	Larva	Fry
Development	Egg	Yolk sac	Swim bladder and development of fins	Swim bladder and active swimming
Duration (days)	3–7.5	1–7	25	22.5
Size (mm)	1.3	1.5–5.5	5.5–10.5	10.5–18
Growth	Temperature dependent Exponential (base e) increase with temperature (Jennings and Pawson, 1991)	Temperature dependent Exponential (base 10) increase with temperature (Jennings, 1990b)	0.2 mm day ⁻¹ (Jennings and Pawson, 1992)	0.2 mm day ⁻¹ (Jennings and Pawson, 1992)
Behaviour	Drift + float (0.002 m s ⁻¹)	Drift + float (0.003 m s ⁻¹)	Vertical migration (0.01 m s ⁻¹)	Vertical migration at 0.02 m s ⁻¹ Settles in shallow coastal water (<20 m) if large enough (15–20 mm)
Behavioural regime				
• Scenario 1	Float	Float	Diurnal	Float when ready to settle
• Scenario 2	Float	Float	Diurnal	Tidal when ready to settle
• Scenario 3	Float	Float	Float	Float when ready to settle
• Scenario 4	Float	Float	Float	Tidal when ready to settle

1992) gave a duration of 22.5 days that was consistent with other studies (<http://www.fao.org/docrep/field/003/ac230e/AC230E02.htm#ch2.10>). When larvae are smaller than 15 mm, they are not able to swim sufficiently fast for long enough to influence dispersal (Leis *et al.*, 2012), so swimming was assumed not to influence settlement location significantly. Settlement was considered to have been successful when a fry of length of 15 mm or above (Jennings and Ellis, 2015) arrived in a coastal area at a depth of <20 m. The total pelagic phase duration based on this parameterization ranged between 49.5 and 61.5 days, and was consistent with the observed field settlement time of 50–70 days (Jennings and Ellis, 2015).

Mortality

Mortality studies generally focus on adult farmed fish (El-Shebly, 2009), but studies have provided constant daily instantaneous mortality rates for the larvae of some fish (Houde, 1989) or derived instantaneous mortality rates from other life history characteristics (McGurk, 1986). Daily instantaneous mortality has been implemented in some IBMs for egg and larval stages, but were generally not related to temperature or food availability (Rochette *et al.*, 2012). A variety of approaches have been used to model mortality including temperature-dependent mortality for egg and first larval stages (Lacroix *et al.*, 2013), partitioning instantaneous mortality into baseline and predation effects (Hyder and Nash, 1998), and exclusion of mortality (van der Molen *et al.*, 2007). However, as no mortality rates have been reported for sea bass eggs or larvae in field conditions (El-Shebly, 2009), the stage duration was used as a proxy for instantaneous mortality in the model, and was equivalent as assuming a constant daily instantaneous mortality rate. Considering the lack of information on sea bass mortality, this assumption was appropriate because only constant mortality rates could be applied, and was the most flexible approach to maximize the potential for use of post-processing.

Model behaviour selection

Behaviour was selected from simulated scenarios. First, the spatial distribution of larvae settling into coastal areas was compared with known nursery areas. Hence, when larvae did not reach a coastline encompassing reported nursery areas, larval behaviour

was not considered relevant. Second, relevant behaviour was selected when inter-annual differences in settlement rate between good and poor settlement years were properly reproduced, with the same method used to setup model forcing for the relevant period. Successful settlement was defined as larvae reaching coastal areas containing known nursery grounds (Figure 1).

Simulating the pelagic phase

Evaluating the effects of inter-annual variation and larval behaviour on settlement

Sea bass settlement has high inter-annual variation that is strongly associated with temperature (ICES, 2012). Hydrodynamics were simulated using a hindcast GETM model over the period 1995–2009, and predictions of monthly averaged salinity and temperature were assessed. In addition, a visual comparison between model outputs and yearly averaged SSB measurements from ICES was done over the same period. Environmental conditions were general similar between years, except for the two successive years, 1996 and 1997, which represented the minimum and maximum reported settlement for the modelled time period. Computational limitations meant that the number of years modelled was highly constrained, so two contrasting years were chosen based on a settlement index for year class strength derived from juvenile sea bass surveys conducted in the Solent since 1977 (Brown, 2013). These were 1996, a poor settlement year (hereafter PSY), and 1997, a good settlement year (hereafter GSY). The effects of the physical environment, life history characteristics, and vertical migration behaviours on settlement of sea bass were assessed for both years.

Eulerian GETM runs were used to force GITM simulations covering the pelagic phase period from February to September. Environmental parameters and current velocities were extracted hourly for both years and were used to drive the particle tracking model GITM. Hydrodynamics and temperature drove the particle passive motion, development, and growth over the pelagic phase. The number of particles released depended on the local temperature distribution. The number of particles settling in known nursery areas and the percentage of successful settlement were assessed and compared for both years.

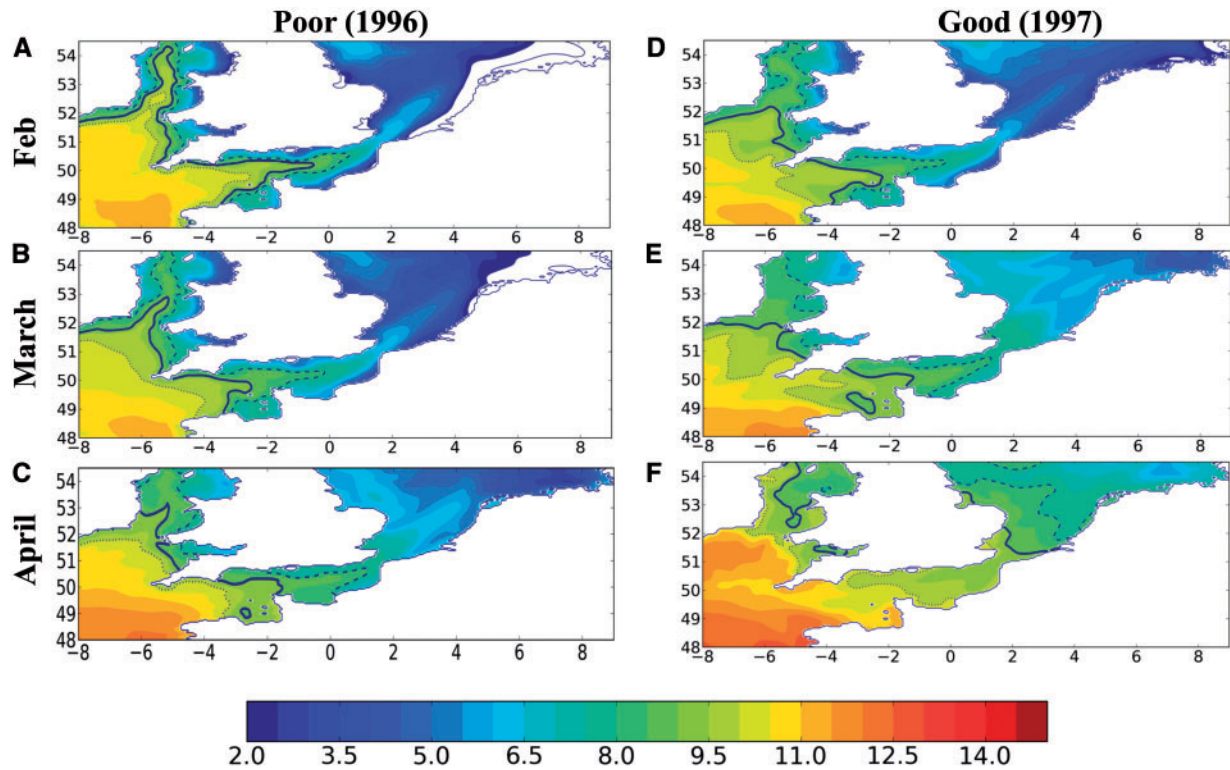


Figure 3. Monthly averaged temperature for February (a, d), March (b, e), and April (c, f) for poor (1996, a–c) and good (1997, d–f) settlement years. Contour lines represent the 8 °C (dashed), 9 °C (solid), and 10 °C (dotted) isotherms. Axes are longitude and latitude.

Sea bass eggs have been reported as buoyant, but little is known about larval behaviour. To establish vertical behaviour(s) leading to successful settlement, several biologically plausible combinations of vertical migration behaviours (floating, diurnal, and tidal vertical migration) were implemented for each larval stage (Table 1). Float was defined as a positively buoyant passive particle with a constant upward vertical velocity. Diel migration was defined as a vertical movement up to the surface during daylight hours and descent to depth at night, and is a commonly observed behaviour of planktonic organisms (Enright and Hamner, 1967). Tidal migration is a tactic used by many organisms to selectively achieve directional movement, where individuals move up into mid-water during transporting tides (Gibson, 2003). For both vertical diurnal and tidal migrations, movements occur at the vertical swimming velocity of the larvae and horizontal movement is passive (advection by ambient currents). Particles were assigned one of four possible behavioural regimes composed of combinations of behaviours at different larval stages, and successful settlement was assessed for each behavioural regime (Table 1), through the number of settlers reaching nursery areas, the associated number particles settling, and replicating the difference between the PSY and GSY. The behavioural regime that replicated these criteria most accurately was selected and used to assess the importance of physical parameters in successful settlement and connectivity between spawning and nursery areas.

Assessing the environmental drivers for success of settlement and pelagic duration

The main environmental drivers in the model are current velocities, air temperature and wind direction and strength, with air

temperature affecting water temperature and varying with wind. The differences in residual current velocities between years are also driven mainly by wind and will dominate the inter-annual variability in passive dispersal of particles. Wind velocity variability among the PSY and GSY was assessed by averaging the wind strength and direction over the pelagic phase. The differences between years were used to assess the importance of wind in driving settlement and pelagic phase duration (proxy for instantaneous constant mortality) in PSY (1996) and GSY (1997).

Water temperature defines the spawning area and affects growth, so will influence the location of release, settlement, and duration of the pelagic phase. Sea bass eggs are sensitive to water temperature and have been shown to develop at temperatures between 8.7 and 18.6 °C (Jennings and Pawson, 1991). As a result, the 9 °C isotherm has been postulated as the threshold at which bass spawning occurs (Pickett and Pawson, 1994). Post-processing scripts were used to assess the sensitivity of settlement to the spawning temperature threshold using the 8, 9, and 10 °C isotherms, with larger spawning areas at a lower than a higher temperature threshold. The impact on number of particles released, numbers settling, and percentage and duration of successful settlement was assessed for the PSY and GSY. As the spawning extent varies with temperature, only the ratio of the number settling to number released was compared for both years.

Connectivity between spawning areas and nursery ground

The connectivity between spawning and nursery areas was assessed using model outputs of the locations of spawned particles that settled successfully across the whole model domain. A more

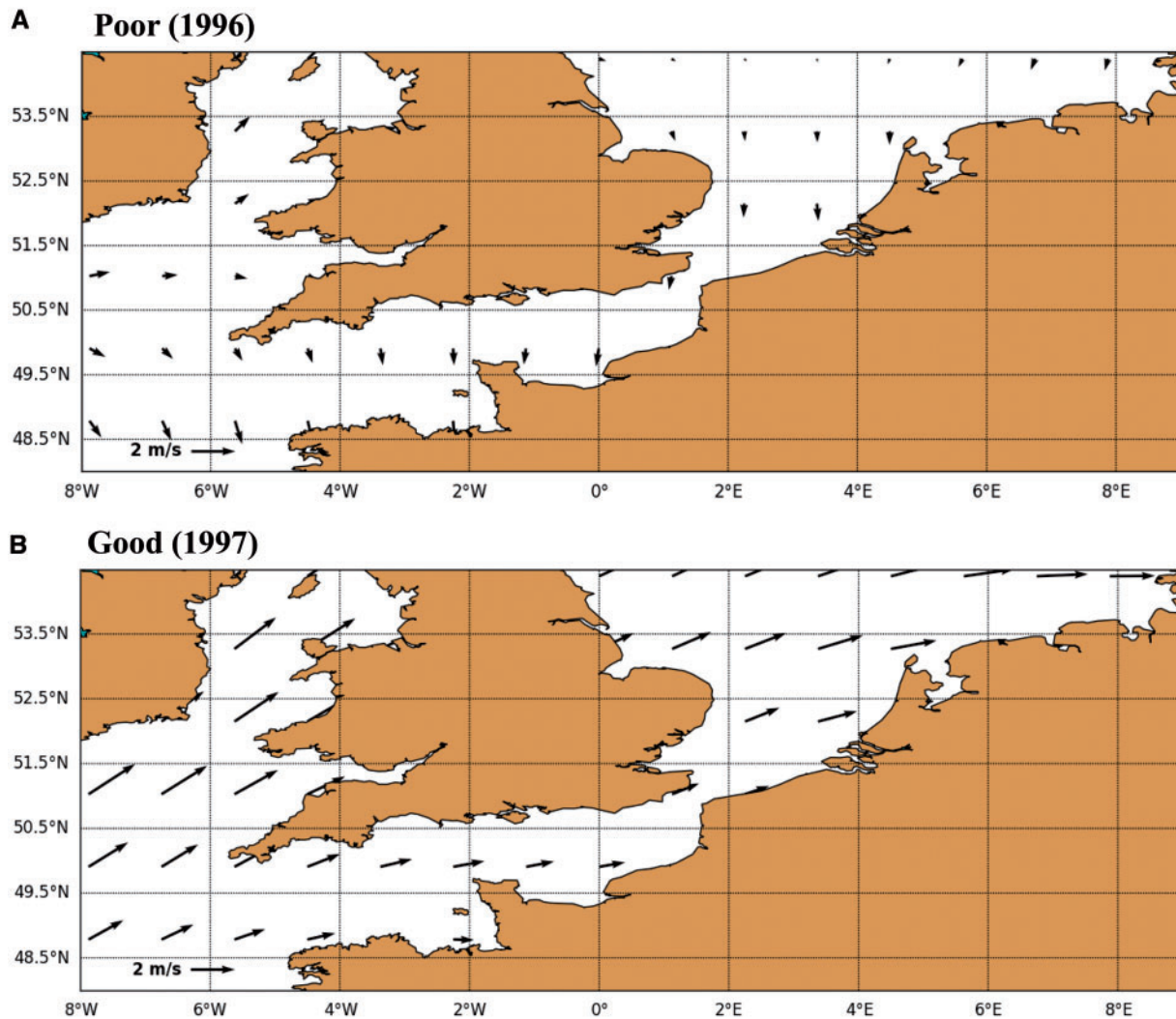


Figure 4. Wind velocity averaged over the sea bass pelagic phase duration (from February to September) for poor (1996—a) and good (1997—b) settlement years.

detailed spatial analysis was carried out for three regions representing differing environmental conditions: North Sea, English Channel, Celtic Sea and Bristol Channel, and Irish Sea. Analysis was performed to link the settlement of particles to spawning at an ICES area scale that included both transport (released in offshore water and settlement in coastal water) and self-seeding (particles released in a particular coastal area that settle in the same area) processes. The first of these processes linked different ICES areas and the second process implied local spawning population that supply nursery areas in the same ICES area.

Results

Environmental characteristics over 1996 and 1997

During the spawning period, the area delimited by 9 °C isotherm in the GSY (1997) gradually expanded with time, whereas in the PSY (1996), this area contracted slightly over the first two months and then expanded in April (Figure 3). Temperature gradients shown by distances among isotherms were much larger in the GSY (1997) than the PSY (1996) (Figure 3). The averaged wind field over the period simulated was markedly different in the PSY

(1996) and GSY (1997) (Figure 4). In the GSY (1997) winds were relatively strong and homogeneous westerlies, but in the PSY (1996) average winds were more variable with no particularly clear directionality or strength (Figure 4).

The effects of inter-annual variation

More eggs were spawned in the GSY (Table 2) as warmer sea temperatures increased the area available for spawning (Figure 5). Settlement in the known BNAs (indicated in Figures 1 and 2) was predicted to be higher in GSY than in PSY, the only exception was areas with very low settlement in North Wales (Rivers Conwy and Dee) and the Teifi Estuary (Table 3). However, the difference in predicted settlement between the two years was much smaller than estimated in the stock assessment (ICES 2016) (Table 2). Overall, more larvae and higher levels of settlement were observed in GSY than PSY irrespective of behaviour.

The effect of larval behaviour on settlement

Settlement in the Wadden Sea and Morecambe Bay only occurred in the model when tidal migration occurred (Scenarios 2 and 4),

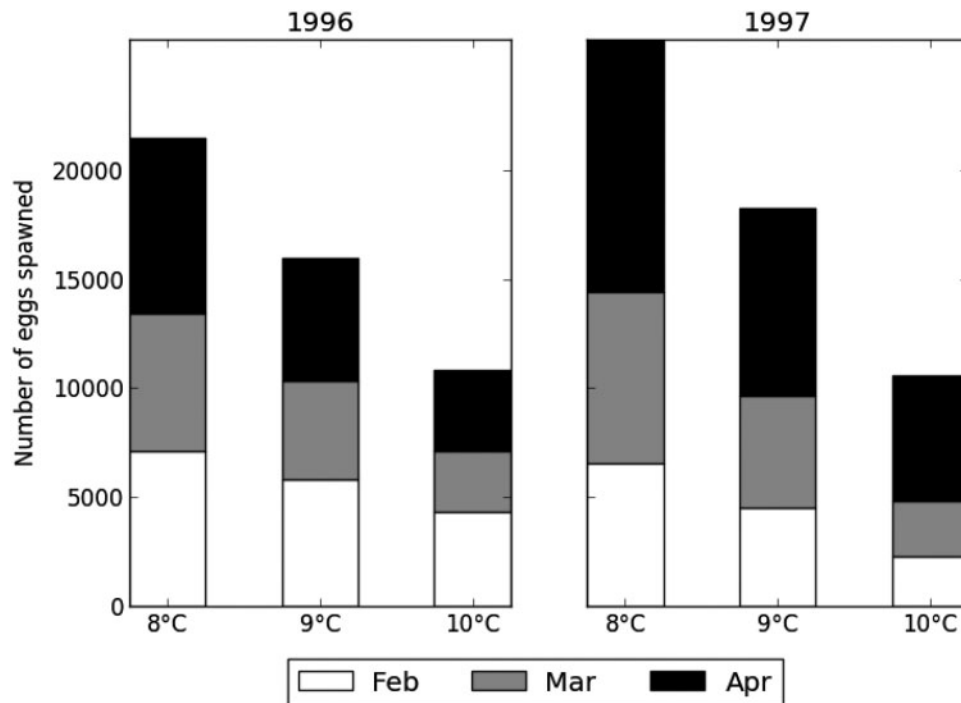


Figure 5. Number of eggs spawned between February and April for different temperature thresholds (8, 9, and 10 °C) in poor (1996—a) and good (1997—b) settlement years.

Table 2. ICES stock assessments estimated in 1997 and 1996 (ICES, 2016), number of particles released in poor (1996) and good (1997) settlement year, and the predicted numbers and percentage of released particles settling (reaching coastal areas) for spawning at water temperatures of above 9 °C and behavioural scenarios 1–4 (see Table 1).

Year	ICES stock assessments	Released particles	Number settling				Percentage settling			
			Scenario 1	Scenario 2	Scenario 3	Scenario 4	Scenario 1	Scenario 2	Scenario 3	Scenario 4
1996	1024	15 957	1919	3 105	2 112	3 882	12.0	19.5	13.2	24.3
1997	23 272	18 241	4 011	5 717	4 282	6 591	22.0	31.3	23.5	36.1
Ratio	22.7	1.14	2.09	1.84	2.03	1.70	1.83	1.61	1.77	1.49

Ratio represents the ratio between good (1997) and poor (1996) settlement years. Mortality is not included in those simulations and is investigated later as a post-process.

so Scenarios 1 and 3 were excluded from further analysis. Diurnal migration in the larva stage (Table 1) did not affect the number settling or nursery areas reached, but stronger larval dispersal was found with floating behaviour. Similar trends in connectivity were found for the scenarios including diurnal migration in Stage 3 (Figure 6). In this case, connectivity in the English Channel was split between the east and west, and was northward in the Irish Sea and the North Sea. However, connectivity depended on the behavioural scenario, with the maximum settlement obtained in Scenario 4 (float, float, float, and tidal) (Table 2). As a result, Scenario 4 was considered to be the most appropriate, as it produced the highest settlement and reproduced the PSY and GSY, so it was used for all subsequent model simulations. The spatial distribution of settlers in Scenario 4 showed that settlement occurred in most known bass nursery grounds and the highest levels were found in the southwest United Kingdom (Figure 7a and b). There was also settlement predicted in the more northerly regions of the Irish Sea and more broadly across the North Sea (Figure 7a and b).

Assessing the environmental drivers for success of settlement and pelagic duration

Lowering the spawning temperature threshold led to more eggs spawned, with larger numbers of settlers in the PSY than PSY (Figures 3 and 5). More particles were released in PSY than in GSY at a threshold of 10°C, but the opposite was observed at 8 and 9°C (Table 4). However, number settling was always larger in GSY than PSY, regardless of the spawning temperature threshold (Table 4). Settlement was lower and dispersal was over a smaller area in the PSY than GSY, because of weaker average wind speed in northerly or westerly directions (Figure 4a). However, in the warm year (1997), settlement was higher and extended further north in the Irish and North Seas, with prevailing westerly winds on average of 2 m s⁻¹ influenced dispersal (Figure 4b).

The average pelagic phase duration for successful settlement was only very slightly longer in the PSY (1996 ~ 75 ± 5.5 days) than in the GSY (1997 ~ 73 ± 5.5 days), but the spatial

Table 3. Locations of known BNAs by ICES rectangle, latitude and longitude, and percentage of released particles settling (reaching coastal areas) for spawning at water temperatures of above 9 °C and behavioural Scenario 4 (see Table 1).

BNAs	ICES rectangle	Latitude	Longitude	1996	1997	Ratio
Fal Estuary, Percuil River, Helford River	VIIIf10	50 to 50.5°	-6 to -5°	2.71	3.76	1.39
Milford Haven	VIIg05	51.5 to 52°	-6 to -5°	1.12	3.49	3.13
River Yealm, Plymouth Rivers—Plym, Tamar, Tavy and Lynher, River Fowey	VIIe03	50 to 50.5°	-5 to -4°	2.30	3.08	1.34
River Camel	VIIIf08	50.5 to 51°	-5 to -4°	0.76	1.14	1.50
River Torridge, River Taw	VIIIf04	51 to 51.5°	-5 to -4°	0.71	1.32	1.84
Burry Inlet, The Three Rivers—Taf, Tywi and Gwendraeth	VIIIf01	51.5 to 52°	-5 to -4°	1.47	2.04	1.39
Teifi estuary	VIIa22	52 to 52.5°	-5 to -4°	0.04	0.07	1.62
River Dyfi, River Mawddach, Dwyryd and Glaslyn Estuary	VIIa19	52.5 to 53°	-5 to -4°	0.32	0.29	0.89
River Dart, Salcombe Harbour, River Avon	VIIe04	50 to 50.5°	-4 to -3°	0.66	1.53	2.30
River Exe, River Teign	VIIe01	50.5 to 51°	-4 to -3°	0.11	0.30	2.67
Aberthaw Power Station Outfall	VIIIf05	51 to 51.5°	-4 to -3°	0.28	0.35	1.25
River Conwy, River Dee	VIIa16	53 to 53.5°	-4 to -3°	0.16	0.01	0.07
The Fleet	VIIe02	50.5 to 51°	-3 to -2°	0.13	0.40	3.19
Langstone Harbour, Portsmouth Harbour, Southampton water, Fawley Power Station Outfall—Stanwood Bay, Poole Harbour	VIIId01	50.5 to 51°	-2 to -1°	0.06	0.21	3.79
Chichester Harbour	VIIId02	50.5 to 51°	-1 to 0°	0.00	0.07	–
Dungeness Power Station	VIIId03	50.5 to 51°	0 to 1°	0.19	0.52	2.65
Grain Power Station Outfall, Kingsnorth Power Station Outfall	IVc25	51 to 51.5°	0 to 1°	0.00	0.01	–
Bradwell power station	IVc21	51.5 to 52°	0 to 1°	0.01	0.05	7.87

Ratio represents the ratio between good (1997) and poor (1996) settlement years. Map of ICES rectangle delimiting BNA is presented in Figure 1.

distribution varied between the years (Figure 8a and b). The longest pelagic stage durations in GSY were located at the extremities of the model domain (northern Celtic and North Seas), with shorter durations in southwest England (Figure 8b). In the PSY, longer pelagic duration was seen in coastal areas, notably on southern and western coasts in the PSY compared with GSY (Figure 8a and b). Limited larval dispersal in the PSY meant that only the southern North Sea was reached in the PSY, but settlement occurred in the northern North Sea nursery areas in GSY, even with moderate pelagic phase duration.

Connectivity between spawning areas and nursery grounds

The spawning location of particles that settled successfully showed a broader distribution in GSY than in PSY (Figure 9). Large numbers of particles were spawned in deep areas settled successfully, especially in the southern Irish Sea in the GSY and on the Cornwall promontory in both years (Figure 9). A detailed analysis of the mean connectivity patterns between spawning and nursery grounds was performed separately for the Irish Sea, North Sea, and English Channel. Self-seeding was more common in GSY than in PSY (Figure 6), with higher levels of self-seeding in the Irish Sea in GSY driven by sufficiently high sea temperatures for spawning close to nursery grounds (Figure 6e). Less self-seeding occurred in the central Irish sea in PSY (Figure 6b), yet successful migration towards the northern Irish Sea was driven by prevailing south-westerly winds (Figure 6a). The model also showed strong connections between north Cornwall, Devon, and Bristol Channel with the Irish nursery areas in both years, with spawning grounds extending westward in GSY (Figure 6b and e). Eggs spawned in the central western English Channel could settle both in England and France, with movement from the central to the eastern English Channel only found in GSY (Figure 6a and d).

Discussion

Model performance

Model performance in relation to the larval behaviour scenario had no effect on inter-annual settlement variability. The vertical behaviour strategy was selected to make larger numbers of particles reach nursery areas, and a combination of floating behaviour for the egg and early-larval stages in which no active vertical migration occurs, resulted in particles dispersion driven by wind. Coastward migration was only achieved in the model by implementing tidally synchronized vertical migration, with strong tidal currents occurring throughout the domain. The importance of active migration in the final larval stage has been reported for plaice (Fox *et al.*, 2006) and supports the patterns observed from our model.

The predicted areas of highest successful settlement showed good agreement with the main known spawning grounds located in the English Channel, Celtic Sea, Bristol Channel, and North Sea (Thompson and Harrop, 1987; Jennings and Pawson, 1992; Pickett and Pawson, 1994; Fritsch *et al.*, 2007); the annual variability between the GSY and the PSY was also reproduced. The model also predicted successful migration to known nursery grounds in the Wadden Sea (Cardoso *et al.*, 2015) and the Western Scheldt estuary although at lower abundance in other estuaries and lagoons surveyed (ICES, 2014). Sea BNAs occur in estuaries in France and southern Ireland, although at relatively low density in most years compared with similar habitats in England (Fahy *et al.*, 2000). No information on BNAs was available for the Belgian coast, although the short coastline has few potential habitats for young sea bass.

The observed differences in settlement between the GSY and the PSY could be driven by a combination of many factors including: spawning stock, spawning distribution and success, predation, food availability, disease, environmental conditions, and the larval dispersal patterns that we focus on here. The model

A Poor (1996)

		Settling							
		IVb	IVc	VIIa	VIIId	VIIe	VIIIf	VIIg	VIIh
Spawning	IVb	1	0	0	0	0	0	0	0
	IVc	0	12	0	0	0	0	0	0
	VIIa	0	0	489	0	0	0	8	0
	VIIId	0	27	0	202	17	0	0	0
	VIIe	0	0	1	145	1346	536	35	0
	VIIIf	0	0	15	0	3	180	35	0
	VIIg	0	0	241	0	0	81	98	0
	VIIh	0	0	41	0	12	149	25	0

B Good (1997)

		Settling							
		IVb	IVc	VIIa	VIIId	VIIe	VIIIf	VIIg	VIIh
Spawning	IVb	3	0	0	0	0	0	0	0
	IVc	0	115	9	0	0	0	0	0
	VIIa	0	50	449	12	0	0	2	0
	VIIId	0	176	0	674	26	6	0	0
	VIIe	0	0	82	215	1104	632	339	0
	VIIIf	0	0	200	0	20	320	128	0
	VIIg	0	0	534	1	0	200	85	0
	VIIh	0	0	7	0	32	148	201	0

Figure 6. Connectivity matrices between spawning and settlement by ICES areas for the whole model domain including Bristol Channel and Celtic Sea (VIIIf, g&h), English Channel (VIIId&e), Irish Sea (VIIa), and North Sea (IVb&c) for poor (1996—a) and good (1997—b) settlement years. Connectivity (number of particles) is coloured according to its strength, with white for no connectivity (0 particle), green for weak connectivity (1 to 100 particles), orange for medium connectivity (100 to 500 particles), and red for strong connectivity (more than 500 particles). ICES areas with self-seeding (the number of particles that are released in a particular coastal area that settle in the same area) have bold borders.

Table 4. Number of particles released, numbers and percentage of released particles settling (reaching coastal areas) for different spawning temperatures thresholds and behavioural Scenario 4 (see Table 1).

Year	Number released			Number settling			Percentage settling		
	8 °C	9 °C	10 °C	8 °C	9 °C	10 °C	8 °C	9 °C	10 °C
1996	21 458	15 957	10 810	6 282	3 105	1 069	29.3	19.5	9.9
1997	25 941	18 241	10 611	10 068	5 717	2 127	38.8	31.3	20.1
Ratio	1.21	1.14	0.98	1.60	1.84	1.99	1.33	1.61	2.03

Ratio represents the ratio between good (1997) and poor (1996) settlement years. Mortality is not included in those simulations and is investigated later as a post-process.

experiments were set up to focus on the effects of larval dispersal patterns in response to inter-annual differences in environmental forcing, so only included a subset of these factors and was likely to be the reason for differences in the magnitude of the ratio between PSY and GSY. The correspondence between model predictions and observations of higher settlement in the GSY was a strong indication that hydrodynamic conditions are an important factor in settlement success of sea bass.

Adult spawning in coastal waters led to higher settlement in the GSY than in the PSY, highlighting importance of appropriate

spawning conditions in the coastal water for settlement success. The spatial density of spawning was the same for both the PSY and the GSY, and only occurred where water temperature was above a threshold, leading to more particles being spawned in the GSY or warm year (1997) than for the PSY or cold year (1996). In reality, the spawning output of the stock will vary between years and also be a highest at the centre of spawning aggregations (Fahy et al., 2000), with this centre changing throughout the spawning season moving eastward in the English Channel as sea temperatures increase.

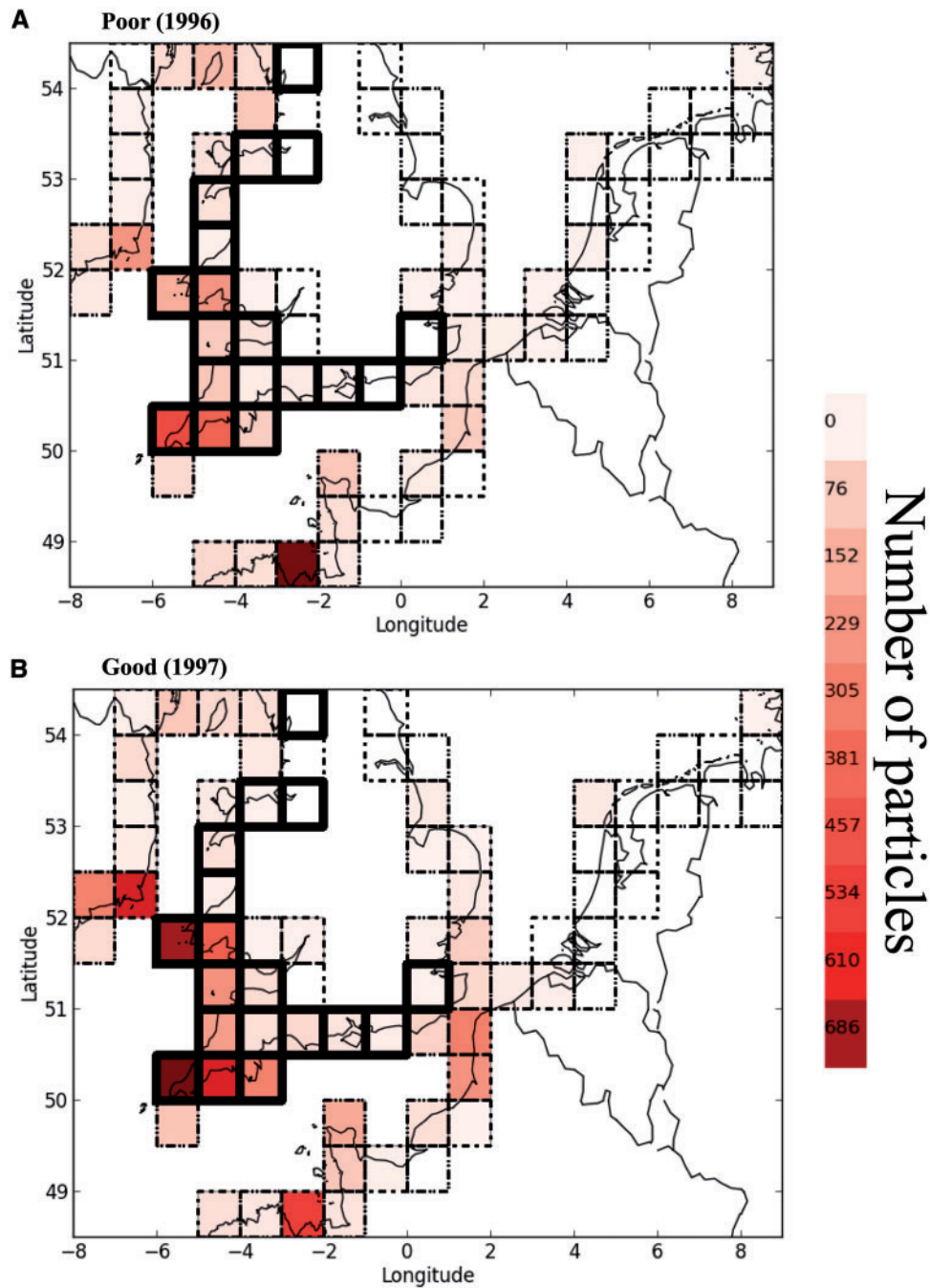


Figure 7. Number of particles settling in coastal areas in Scenario 4 for poor (1996—a) and good (1997—b) settlement years. Coastal ICES rectangles (dashed line) that contain known BNAs (bold solid line).

The present model can be used to predict the settlement pattern for larvae at nursery habitats [Kelley, 1988; Bass (Specified Sea Areas) (Prohibition of Fishing) Order 1999: SI1999 No. 75], based on any plausible time-dependent density distribution of eggs should such data be available for a given year. Currently, spawning distribution data for sea bass in the northern stock are limited to egg distribution maps from the early 1980s and one area in 1990 (Pickett and Pawson 1994). The IBM results presented here were based on uniform egg distribution, therefore provided a biased prediction of the numbers of sea bass larvae

reaching nursery habitats relative to numbers of eggs spawned. However, the model predicted the dispersal patterns from individual spawning locations, so indicates physically plausible connectivity between spawning locations and nursery areas and how this varied between years. Moreover, using the same spawning pattern for both years allows for closer identification of the contribution of environmental factors influencing larval dispersal on settlement (see later). For the years examined, the results showed that there was a greater incidence of shorter distance linkages between spawning location and nursery areas in the PSY than in the

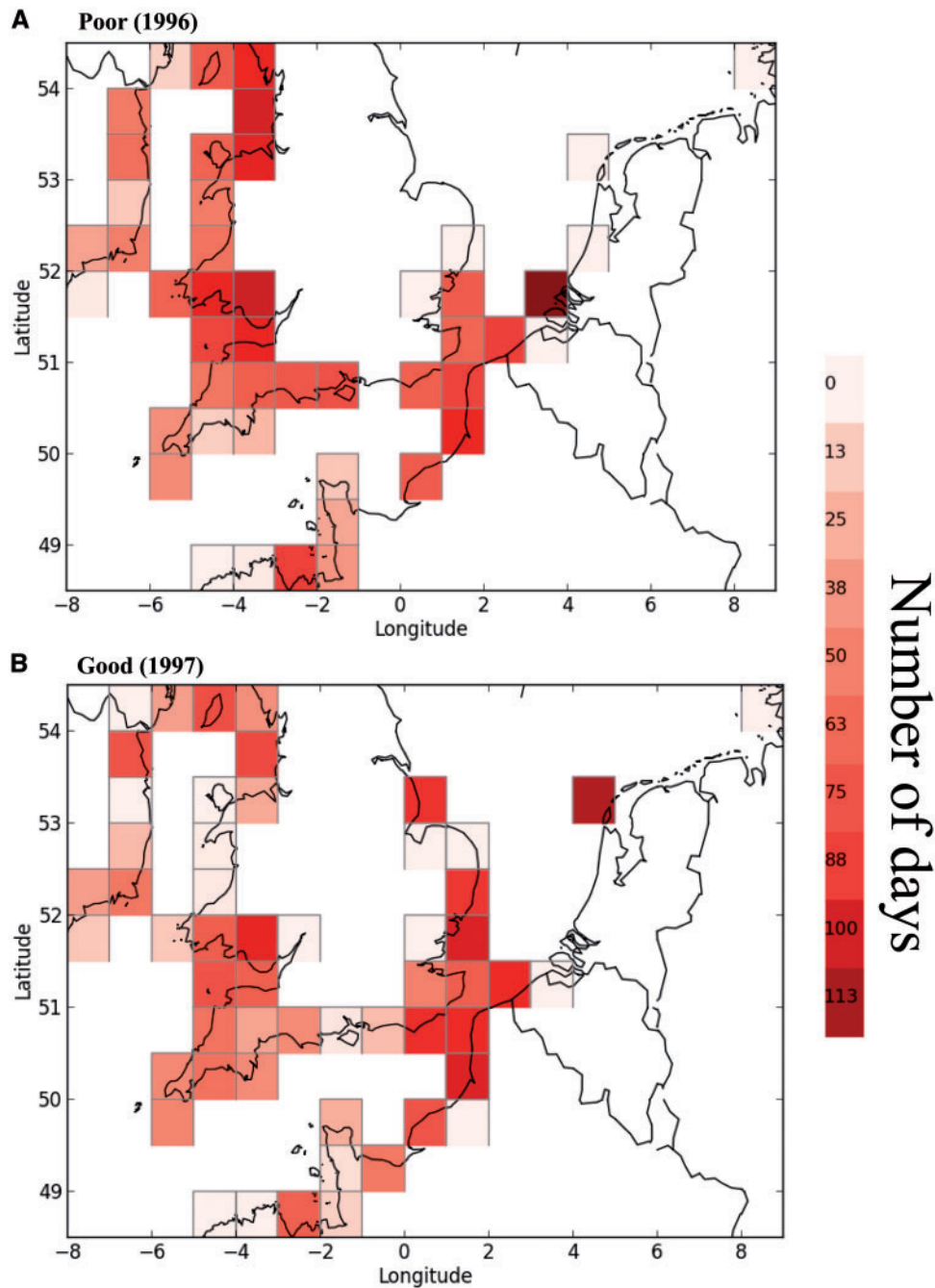


Figure 8. Average duration of pelagic phase for bass settling in different ICES rectangles for poor (1996—a) and good (1997—b) settlement years.

GSY. As similar trends in main connectivity directions and settlement success based on spawning locations were found for different migration strategies, a similar connectivity pattern would be found with a different spawning distributions despite differences in numbers of settlers.

Role of hydrodynamics in determining year class strength

The two environmental factors represented in the model forcing with potential to cause a difference in the results for the two years

were air temperature and wind stress, leading to differences in water temperature and residual circulation between the years. In this area, wind and temperature tend to be related. Westerly winds associated with Atlantic depressions bring temperate air from the Atlantic Ocean while enhancing the southwest to northeast residual circulation. In contrast, northerly and easterly winds, associated with high-pressure systems over the continent, bring arctic and/or continental air and stall the residual circulation (Furnes, 1980; Pingree and Griffiths, 1980). The differences in (surface) water temperature between the years affected the size of the spawning area through shifts in the position of the spawning

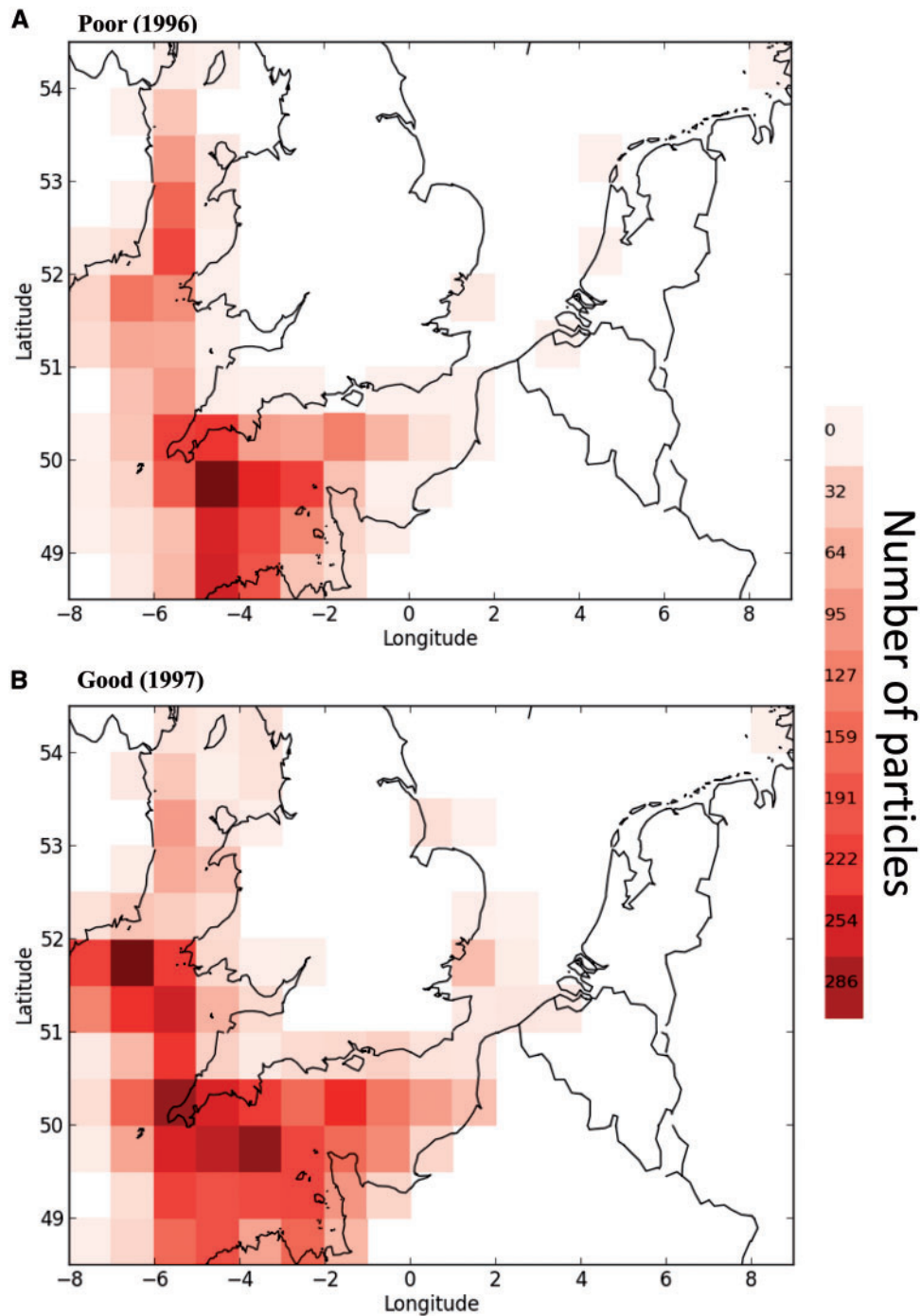


Figure 9. Number of particles originating from an ICES rectangle (spawning location) that settle in a nursery area for poor (1996—a) and good (1997—b) settlement years.

temperature threshold, and affected both development and growth rates. Hence, environmental changes related to increasing sea temperature could lead to earlier spawning and broader spawning area (Politikos *et al.*, 2015), but may also be mediated by latitudinal variations in day length (Vinagre *et al.*, 2009).

Hydrodynamics drive the variation of water temperature, so the spatial extent of an area with a temperature above a threshold varied. For example, in the GSY (1997), the 10 °C isotherm encompassed a smaller spawning area than in the PSY (1996). With

fewer eggs released at higher spawning temperatures threshold, lower settlement was observed, although the success rate was quite high in PSY compared with GSY. The effect of temperature on egg and larval stage duration, through growth and development rates, was probably under-estimated in the model. This was due to the assumption of constant growth rates for the last two larval stages, but a lack of information on temperature-dependant growth led to this approach. Nevertheless, slightly longer larval durations were simulated in the cold year (1996),

resulting in a longer time to reach the settlement size. Mortality was not included explicitly because of lack of data, with stage duration used instead as a proxy for mortality (equivalent to assuming a constant daily mortality). Hence, longer stage durations would also result in higher cumulative mortality. It is not possible to infer which of these effects would dominate, but it is likely that the effect was overshadowed in the model by the difference in wind-driven circulation. The effects of temperature and wind could be separated further with additional model runs using winds from one year and air temperatures from another, but was beyond the scope of the present study.

The difference in wind stress between the two years led to a reduction in north-eastward transport in the English Channel in the PSY (1996) that decreased the number transported successfully to UK nursery grounds. In the GSY (1997), westerly winds predominated, advecting warm oceanic water further eastwards into the English Channel. This caused more short-distance connections between spawning sites and nursery areas, and led to a higher proportion reaching nursery areas. At the local level of individual nursery areas, there were variations on this general theme, most likely related to the complex topography of the area, which could not be investigated within this study. The difference of settlement in the Morecambe Bay for both years was probably driven by the north-easterly wind, with a stronger wind for the GSY, even in the case where spawning in offshore waters was higher in the PSY because of local water temperature. Pelagic duration was negatively correlated with temperature and wind, and was proportional to the migration distance from the spawning ground to coastal areas. As a result, it may be possible to use averaged wind direction, influencing residual current and water temperature, as a proxy for successful settlement. This was not possible within the scope of the current study, but further investigation of the links between annual settlement variability and key drivers (i.e. wind and temperature) would enable a more thorough quantification of their effect, and help to develop a tool for forecasting sea bass settlement.

Implications of connectivity on sea bass management

The definition of biological stocks of sea bass in the NE Atlantic has proved elusive (ICES, 2012). Adult sea bass show strong site fidelity in the non-spawning period (Pawson *et al.*, 2008) and then undertake annual migrations of widely differing distances depending on their location to reach water of appropriate temperature for spawning. The IBM scenarios explored in this paper show that known nursery areas around southwest England, southwest Wales and coastal sites in northwest Brittany and southeast Ireland, are likely to have high settlement rates with relatively short larval transport connections with the main spawning sites in the western English Channel and Celtic Sea. As the spawning season progresses, and particularly in years with stronger westerly winds and warmer conditions, spawning is likely to penetrate farther east in the Channel and into the North Sea. The model shows that in years with stronger penetration of warmer water into the southern North Sea, spawning there can lead to advection of larvae into nursery areas such as in the Wadden Sea and estuaries in the Netherlands, or in the Thames.

From a fisheries management perspective, the results of this study suggest that there is considerable potential for genetic mixing because of larval dispersal leading to weak stock differentiation. Despite the wide and variable dispersal of larvae from spawning sites indicated by the model, spatial management

measures to reduce targeting of spawning aggregations in only some areas could have a disproportionate benefit on settlement of young sea bass in nursery areas, with the strongest transport connectivity with the spawning sites being protected. For example, protection of spawning aggregations in the northeast Celtic Sea and off the Bristol Channel might have greatest benefit for settlement to sea BNAs in the Bristol Channel, southwest Wales, parts of southeast Ireland, and in the Irish Sea. Conversely, protection of aggregations only in the Western Channel would mainly benefit nursery areas in both sides of the English Channel depending on the wind conditions and residual current patterns driving the larval transport. Finally, protection of spawning aggregations farther east in the English Channel and in the southern North Sea would have greatest benefits for nursery areas in the eastern Channel and North Sea. Ultimately, consideration of spatial management measures will need an understanding of where the fish spawning at any location have migrated from.

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