

Not to be cited without prior reference to the author

International Council for the
Exploration of the Sea
ICES / CIEM

ICES CM 2012/E:14

Connectivity patterns of anchovy larvae in the Bay of Biscay from a coupled transport-bioenergetic model forced by size-structured zooplankton.

M. Huret¹, P. Vandromme², P. Petitgas³, L. Pecquerie⁴

Abstract:

Connectivity during early life stages of pelagic fish, defined here by survival probability between spawning and early juvenile habitats, depends on a combination of sufficient food availability and low predator encounter along drift trajectories. For anchovy in the Bay of Biscay, larval transport experiments throughout the spawning season suggest accumulation of early juveniles in the offshore area of the southern Bay, as well as retention over the mid-shelf at mid-latitude. However, late summer-early autumn surveys suggest presence of juveniles only in the former region. From this observation, we set up a bioenergetic individual based model to test for the effect of food availability on survival patterns. The model couples a Lagrangian transport module to the hydrodynamic model MARS-3D, as well as a DEB (Dynamic Energy Budget) model for estimation of larval growth and mortality under starvation. Temperature is provided either from CTD casts or the hydrodynamic model, whereas food is provided by observation of size structured zooplankton biomass, from both in-situ LOPC (Laser Optical Plankton Counter) and Zooscan processing of net haul samples from the Pelgas survey in May. Results suggest that for early spawning season, most of the mortality from starvation occurs at early larval stage, mostly for eggs spawned in the deepest on-shelf and off-shelf areas. The southern bay of Biscay is more suitable for growth and survival than the north at that time of the year for both temperature and food limitations reasons. The offshore occurrence of late larvae in the south is consistent with observations in the area, but our model is not able to simulate a general drift of the whole distribution, that would be consistent with late larvae mostly found over the slope and off-shelf. Further simulations should investigate whether this comes from interannual and seasonal patterns explanations, or whether our model lacks an important process such as spatially explicit predation.

Keywords : Connectivity, Larval IBM, bioenergetics, zooplankton, Bay of Biscay, European anchovy

Contact author: Martin Huret.
Email : martin.huret@ifremer.fr

¹ IFREMER, Centre de Brest, STH, BP 70, 29280, Plouzané, France

² IFREMER, Centre de Brest, DYNECO, BP 70, 29280, Plouzané, France

³ IFREMER, Centre de Nantes, EMH, BP 21105, 44311 Cedex 03, Nantes, France

⁴ Univ. California, Santa Barbara, ERI, Santa Barbara CA, 93106-3060, USA

Introduction

Dispersal of early life stages is a key process in the life cycle of most marine populations. It has implications on the structure and dynamics of fish populations (Hjort, 1914; Sinclair, 1988), as well as the persistence, evolution and distribution of species through connectivity processes (Gaines et al., 2007; Cowen and Sponaugle, 2009).

Observed dispersal kernels or connectivity patterns of early life stages (ELS) of fish actually derive from both transport by currents but also from differential survival along these constrained trajectories. Potential trajectories going through low food or high predator concentrations areas may reveal unsuccessful and have no contribution to the resulting dispersal kernel. Therefore, if we are to assess correctly connectivity, we have to improve our understanding and prediction of survival, which variability strongly depends on growth and thus food availability (Gallego et al., 2012).

Coupled physical–biological models of early life stages received major attention during the past 20 years (Gallego et al., 2007; Werner et al., 2007). By tracking particles within a hydrodynamic 3D field, they have the ability of integrating all scales, from regional circulation to small scale physics, and processes, e.g. individual behavior, growth and survival, - involved in larval dispersal. However, for these latter aspects research is still largely to be developed (Peck and Hufnagl, 2012) in particular on the interaction between individuals and their feeding environment, for which information is often lacking.

For European anchovy (*Engraulis encrasicolus*) in the Bay of Biscay modelling studies have been used to assess transport of ELS (Allain et al., 2003; Huret et al., 2010), or survival but in this case mortality is based empirically on growth rate (Allain et al., 2007) lacking physiological basis, and growth rate itself is based only on physical variables (temperature) or proxy for food availability (turbulence or stratification). This can be successful in some cases, but lacks some mechanistic processes to really be generic and robust over large areas, whole season and many years, or to anticipate response to climate change.

For that reason IBMs including explicitly food were recently developed. They are either derived from in-situ data computed in a prey field (Lough et al., 2005; Kuhn et al., 2008; Kristiansen et al., 2009) and in this case scarcity of data often limits the model use to scenarios at relatively short spatio-temporal scales, and precludes its use for prediction, or food is derived from another plankton model, as in Daewel et al. (2008) who used the zooplankton outputs of a NPZD-type model. In the latter case data availability is no longer an issue, but the zooplankton output is not always representative of prey-type for larvae or not accurate enough in size. For that reason (Daewel et al., 2008a) proposed to combine the outputs from a NPZD model with available zooplankton size spectra available from in-situ data. This approach seems promising since prey selection is mostly based on size, and as the use of new automatic plankton counters providing abundance and size such as the in-situ LOPC (Laser Optical Plankton Counter) generalises.

We apply this approach in the present study to simulate Bay of Biscay anchovy larval growth and survival. Anchovy larvae are rather opportunistic feeders (Garcia and Palomera, 1996; Regner, 1996; Conway et al., 1998; Catalan et al., 2010; Morote et al., 2010) over a prey size range which depends on larval size (Tudela et al., 2002; Morote et al., 2010). Zooplankton size spectra could thus represent a well suited prey field to model anchovy larval growth. Such data on the distribution and size of the zooplankton are now available at the regional scale in the Bay of Biscay thanks to recent laboratory and in-situ OPC analysis (Nogueira et al., 2004; Sourisseau and Carlotti, 2006, Vandromme et al., in prep.).

Our objective in this study is to assess the importance of food distribution, in addition to transport on anchovy larval connectivity in the Bay of Biscay. We first describe the bioenergetic model that we use, the Dynamic Energy Model (DEB) developed by Pecquerie et al., (2009), then we describe how we derive the prey field use for larval growth in our IBM experiments. First experiment is conducted in 0-D, for each grid cell of the Bay of Biscay to assess the quality of the different habitats (coast to offshore, south to north) to support the growth at different sizes during the larval stage. A second

experiment is conducted in 3-D, to assess the interaction of these habitats with spawning and transport. We then discuss results and propose future requirements in terms of model development.

Methods

The bioenergetic model

We use the DEB model set up for the Bay of Biscay anchovy (Pecquerie et al., 2009). The model was developed as a full life cycle, here we only use it at larval stage. The DEB model is used from the mouth opening stage. Prior to that, we use the egg and yolk sac larvae development rate as function of temperature given by (Regner, 1996).

Model setup and parameters are the one described in (Pecquerie, 2008). The model simulates the acceleration of growth observed in the first days after mouth opening for fish (Kooijman et al., 2011) in agreement with a Gompertz growth function (e.g. Regner, 1996, for anchovy).

Larval growth rate depends on temperature and food availability. In the DEB model, food ingestion is expressed as a Holling type II scaled functional response :

$$f = \frac{X}{K + X} \quad \text{with } X \text{ food availability and } K \text{ the half-saturation constant. } 0 < f < 1.$$

Pecquerie (2008) used primary production as a proxy for food. Thus we also modified $K=7 \text{ mgC.m}^{-3}$ to account for the change in food to zooplankton biomass.

The anchovy DEB model proposes to support the lack of energy reserves to insure maintenance costs, a consequence of starvation, through body shrinking or atresia. At larval stage only shrinking is possible. Following Augustine et al., (2011) death then occurs when structure (size) reaches a fraction (0.75) of the structure at the onset of shrinking.

Forcing fields to the model

Prey field

Vandromme et al. (in prep.) have built a climatology of zooplankton biomass in spring over the Bay of Biscay from a LOPC database. This was built from casts available from the years 2005, 2007, and 2009 to 2011 from the PELACUS and PELGAS surveys of small pelagics. LOPC provides abundance of particles in size bins with good results in the size range 0.3-1.5 mm ESD (Equivalent Spheric Diameter). Size distribution of the mesozooplankton is then directly available under the form of the Normalized Biomass Size Spectra (NBSS, Platt and Denman, 1977) which has the theoretical characteristic of being linear:

$$\log\left(\frac{B_m}{\Delta_m}\right) = a \log w + b \quad \text{with } B_m \text{ the total biomass in carbon per size class } m, a \text{ (slope) and } b \text{ (intercept) are constants and } \Delta_m \text{ the size class interval.}$$

A major issue dealing with LOPC data is the 'pollution' of living particles signal by the large abundance of detritus (up to 90% of the signal in coastal areas). To correct for this effect, part of the samples (one third, 70 stations) from WP2 vertical net-hauls (200 μm , between 0 and 100m) collected in 2009, 2010 and 2011 were analysed with the Zooscan, providing size distribution of only living particles. From the comparison of both LOPC and Zooscan size spectra, we were able to build a multivariate regression model of the error in the LOPC database due to non-living particles. The model uses independent environmental variables (salinity, chlorophyll, bathymetry, ...) for the correction (Vandromme et al., in prep). To allow for this LOPC calibration procedure, biomass was integrated over the water column (0-100m) for similar vertical integration with the data from the WP2 net. Then the model was applied to all available LOPC casts to obtain annual spring maps of mesozooplankton size spectra (slope and intercept), from which a climatology was derived (Fig.1).

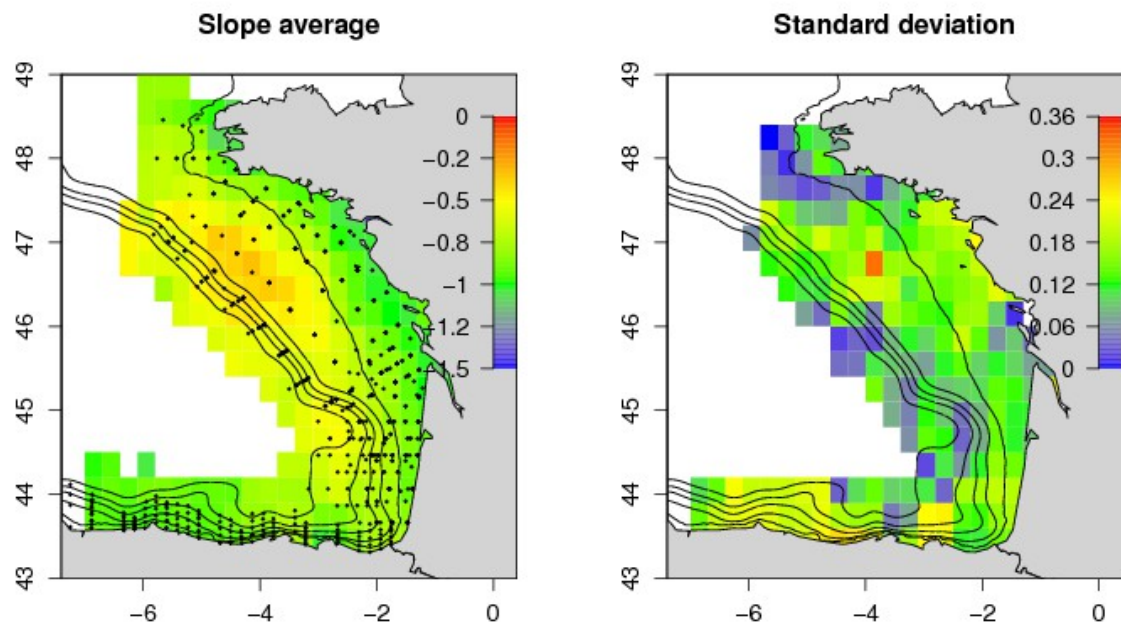


Fig. 1. Average (and standard deviation) of the slope of the NBSS during the PELGAS and PELACUS surveys (2005,2007,2009-2011). Dots are location of LOPC casts.

Anchovy larvae start feeding between 3.5 mm (Palomera et al., 1988) and 5 mm (Regner, 1996) on prey as small as 50 μm (Garcia and Palomera, 1996). However we are lacking the microzooplankton size range in the data from the LOPC. As the slope of the NBSS is expected to be continuous over a large size range (Platt and Denman, 1977), we extrapolated the NBSS from Vandromme et al. (in prep.) over the whole size range of prey (Fig.2).

Fig.2 shows the NBSS for extreme locations of the Bay of Biscay, in front of the Gironde estuary (45.5°N – 1.5°W), a productive region influenced by the river plume, and above 'la Grande Vasière' (46.5°N – 4°W), a low productive area of the Bay. We can see that depending on the prey size class the available biomass strongly varies, become similar for particles around 1mm ESD and large mesozooplankton biomass is potentially higher in the low productive area.

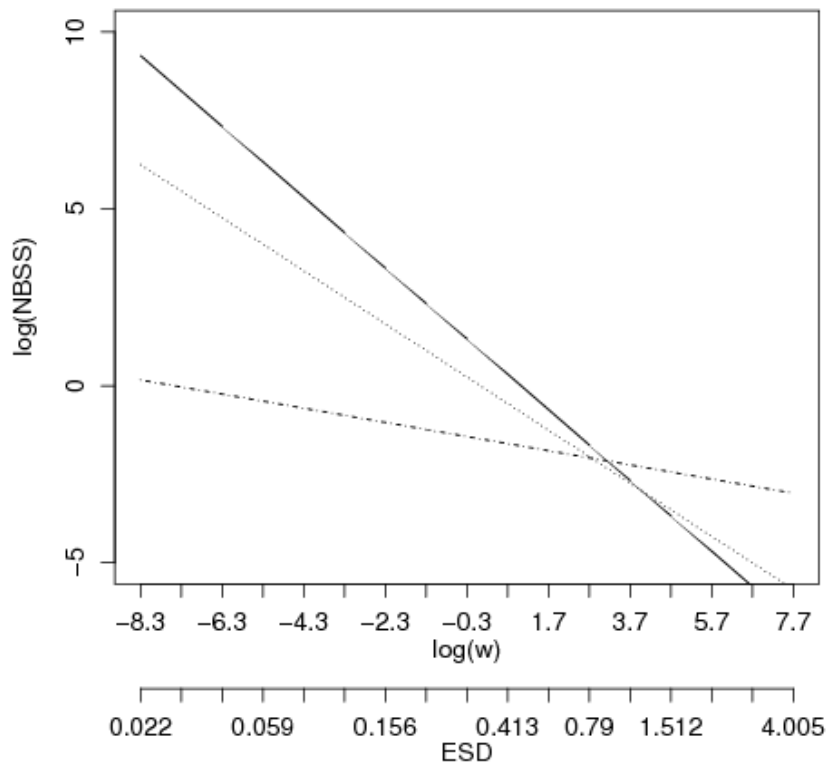


Fig. 2. Examples of size spectra ($\log \text{NBSS} = a \cdot \log(w) + b$) of the Bay of Biscay in spring (w in mgC, ESD in mm). Continuous line is for a slope $a = -1$ and intercept $b = 1$. Dotted line is for a coastal productive area in front of the gironde estuary, dashed line is for a mid-shelf (47°N, 'Grande Vasière') low food area. Note that for large preys ($\sim 0.8\text{mm}$), biomass can become higher in the low productive area.

Several authors propose maximum prey width or length depending on larval standard length (Garcia and Palomera, 1996; Conway et al., 1998; Tudela et al., 2002; Catalan et al., 2010; Morote et al., 2010). This data was compiled after conversion in ESD to propose a maximum prey size available for any larval size (Fig.3). The available size spectra widen as larva grow, but it also seems appropriate to constrain a minimum prey size to account for both its actual increase, even if less described in the literature, and the increase in optimal prey size in terms of foraging and bioenergetic efficiency, as our model does not include explicitly a foraging module.

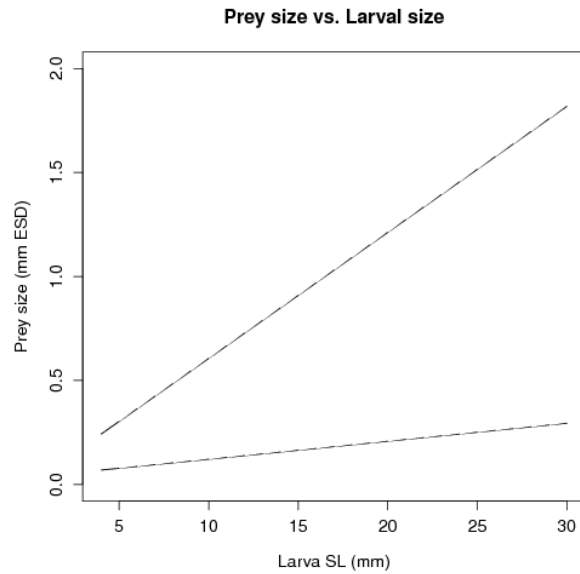


Fig. 3. Minimum and maximum prey size (ESD) for anchovy larvae between 5 and 30 mm

Given this prey size spectra for any larval size, the available zooplankton biomass is then calculated from the integration over the NBSS between the minimum and maximum prey size limits.

Temperature

A climatology was also built for surface temperature (Fig.4) from CTD casts from the same surveys, with surface temperature averaged over a 0-20 depth mixed layer, in which major part of the anchovy eggs and larvae are found (unpublished data).

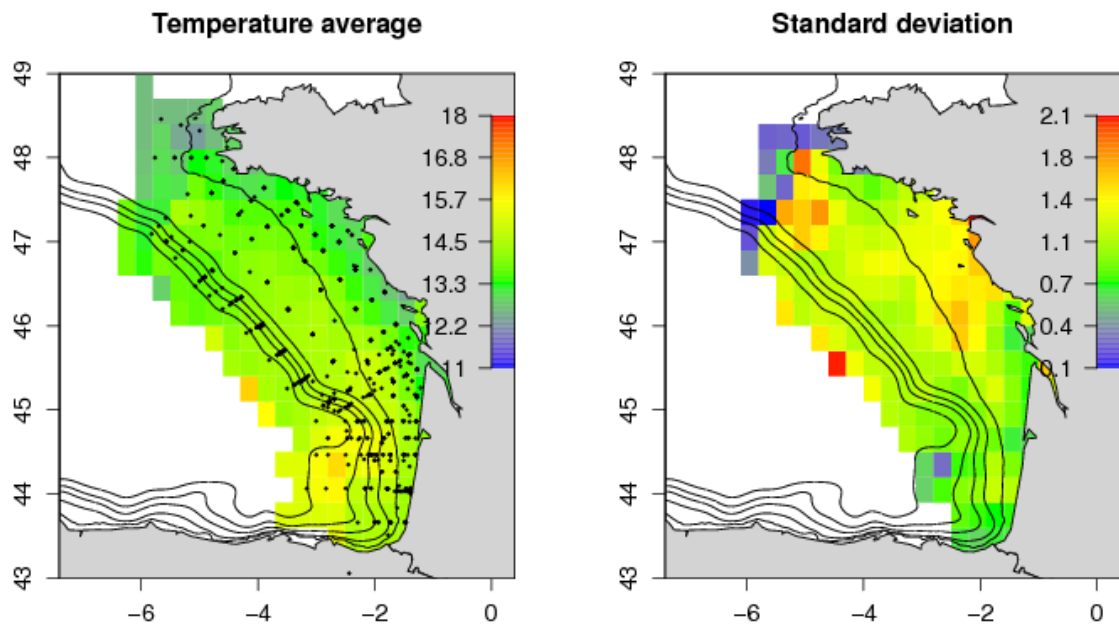


Fig. 4. Average (and standard deviation) of the surface temperature (0-20m) during the PELGAS surveys (2005,2007,2009-2011). Dots are location of CTD casts.

The modelling experiments

0D experiment

In this experiment simulated individuals are not transported. We have one individual per cell of a $0.3^\circ \times 0.3^\circ$ grid (as in Fig.1) and the growth model is run for these individuals with temperature and prey field of its position as defined previously. The model is run for 50 days, an approximate age for metamorphosis, and the larval size (if survived) is then given as an index of the quality of the habitat for growth.

To test the quality of the habitat at different larval stage independently of previous stages, we have also run the model without food limitation until the larva reach the size of 10mm or 15mm.

3D-IBM experiment

Here the simulated individuals grow and are transported. We use a Lagrangian module on-line coupled to the 3D hydrodynamic MARS model as in Huret et al., (2010). Particles are passive from egg (with buoyancy) to early larval stage (6mm) from when they start migrating vertically between surface at night and the thermocline during the day as observed in multinet data (unpublished data) with a swimming speed proportional to their body size.

For this experiment the temperature is directly derived from the hydrodynamic model, in time and place of the particle location. The prey field is derived from the LOPC database (climatology) as previously described.

The release locations for eggs is derived from the climatology of egg distribution during Pelgas survey in May (2000 to 2012), sampled with the CUFES (Continuous Underwater Fish Egg Sampler).

Simulated years are 2005 to 2007, with 2 releases per year from 1st and 15th of May, for consistency with the the observed spawning distribution and zooplankton size-spectra observation only available in spring from Pelgas survey.

Results

Prey availability

Fig.5 shows as example the available biomass of prey along larval stage for a given slope and intercept (the continuous NBSS of fig.2). We can see that from mouth opening, availability rapidly increases before reaching a sill from 20mm SL.

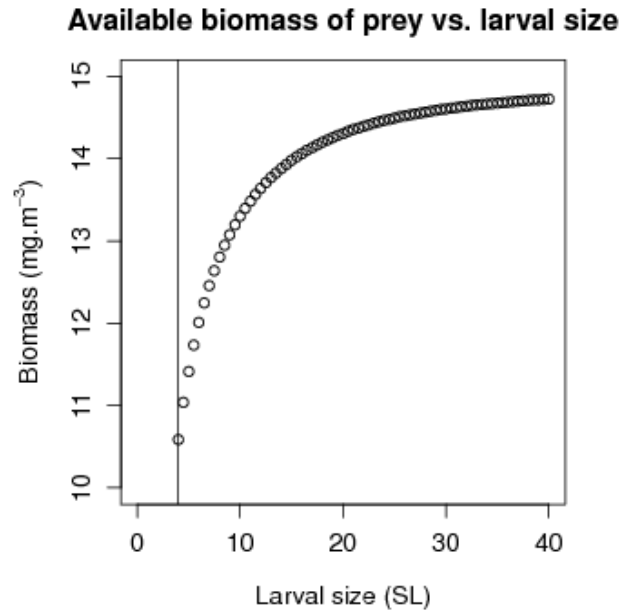


Fig. 5. Available biomass of prey (mgC.m⁻³) depending on larval size (SL). This example is given for a slope=-1 and an intercept=1 of the NBSS. The vertical line represents the larval size at first feeding (4 mm).

This available biomass then varies along larval stage but mostly spatially (Fig.6). For a first feeding larva (4mm) and over the french shelf, prey biomass is mostly available along the coast, decrease offshore and is very low between the isobath 100m and the shelf break. As larva grow, available biomass increases everywhere and spatial differences decrease. For a 30mm larva, the coastal-offshore gradient persists but prey biomass is almost homogeneous over the Bay of Biscay.

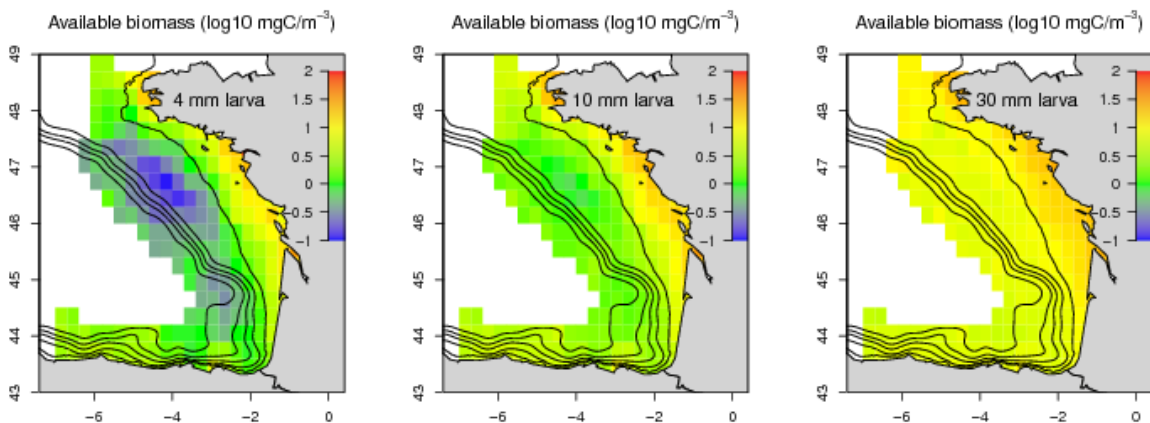


Fig. 6. Available biomass of prey for several larval sizes (SL): 4mm (left), 10mm (center) and 30mm (right)

0-D experiment

In the case of no food limitation, habitat quality for larval growth in spring is best in the south where biggest larvae at 50 days are simulated (Fig.7a) and decreases towards the north, with respect to the temperature gradient (Fig.4). There is also a small coast to offshore positive gradient, especially in the north of the Gironde estuary, due to lower temperature along the coast where mixing is stronger and stratification lower.

With food limitation (Fig.7b), only larvae along the coast can survive. Offshore the 100m isobath lack of food provoke starvation and death of early larvae. Along the coast, a positive north to south gradient is still present, mostly due to temperature.

When larvae grow without food limitation until 10mm, and then food limitation is applied, then all larvae survive. Biggest larvae at 50 days are found in the south just within the 100m isobath (Fig.7c). Same experiment with food limitation from 15mm (Fig.7d) shows a best habitat for growth shifted more offshore, still in the south.

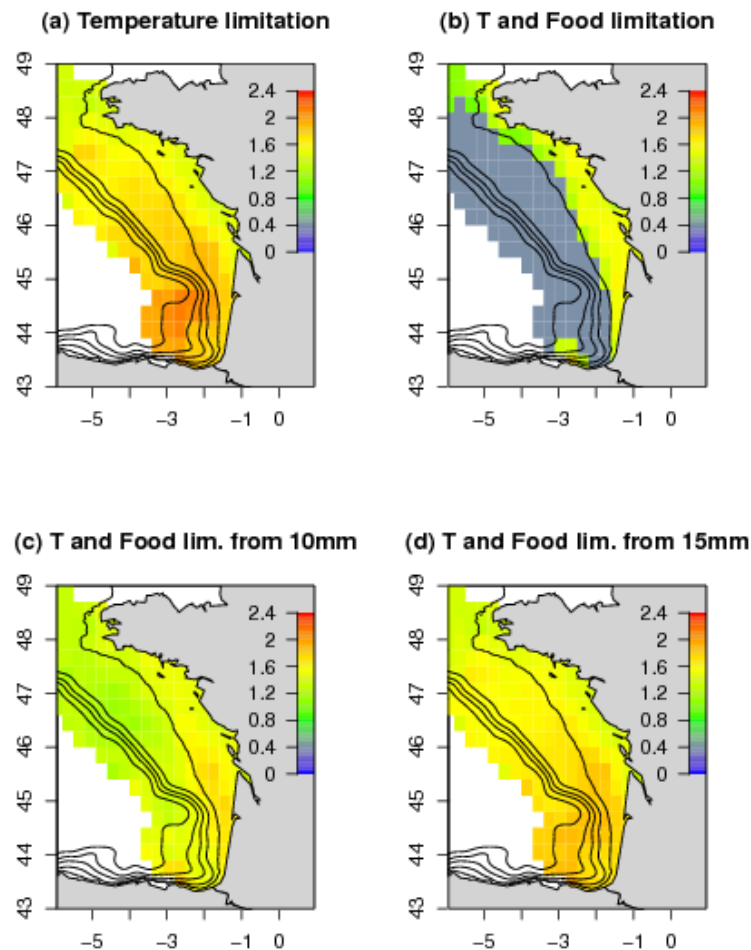


Fig. 7. Larval size at 50 days post-fertilisation under different limitation scenarios. (a) temperature limitation from the average temperature in spring (Fig. 4), (b) temperature and food limitation, (c) temperature and food limitation but the latter only from when larvae reach 10mm, (d) temperature and food limitation but the latter only from when larvae reach 15mm.

3-D experiment

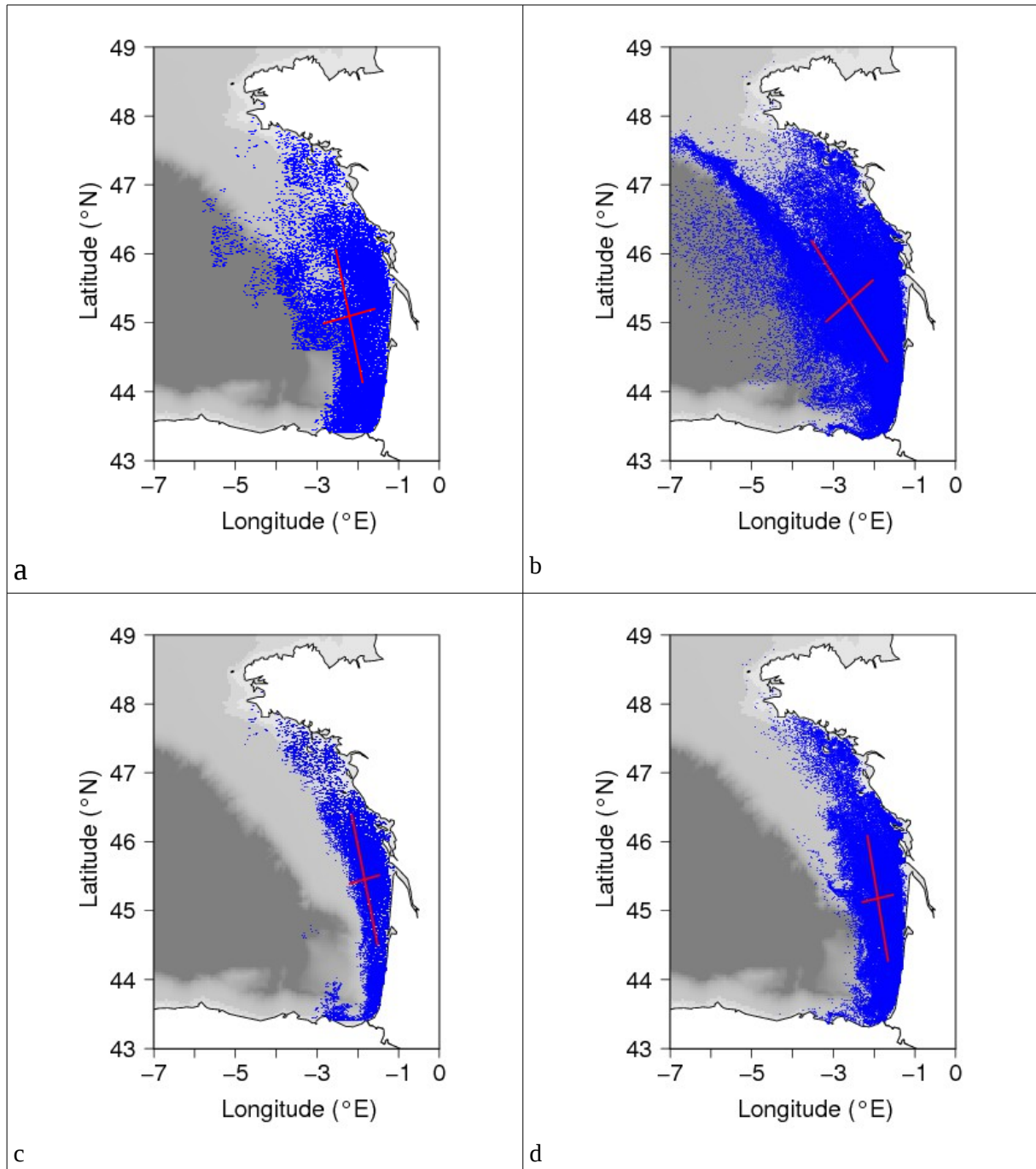


Fig. 8. Distribution of particles in the 3D-IBM at spawning (a,c) and after a 50 days drift (b,d). Top is all individuals, bottom is a selection of the survivors from the 3D DEB-IBM based on the mortality rule from starvation (see text). All particles from 2 releases per year from 2005 to 2007 are plotted. Red segments are minor and major axis of the variability of the distribution, with their cross-section being its centre of gravity.

Fig.8a is the climatology of spring spawning. Distribution after a 50 days-period drift (Fig.8b) shows a large dispersal of larvae towards the west and north. The centre of gravity remains onshelf though, with only a slight shift towards the north-west, even if some of the larvae end up off-shelf.

When growth and survival are considered, the successful spawning pool (Fig.8c) is considerably reduced to inshore 100m isobath. Only a very small fraction of the offshore spawning is successful in surviving until metamorphosis, around position 3°W-44.5°N. Those survivors distribution after drift

(Fig.8d) does not change significantly for the northern part of the bay, whereas in the southern part the particles end up over the slope or slightly offshore. The centre of gravity of the distribution also reveals a southern shift (from 45.5°N to 45°N).

Discussion

0-D experiment with prey and temperature climatology as forcing showed that prey availability is critical at early larval stage, especially until 10-15mm (Fig.5), with a clear separation between the habitat where survival is possible (along the coast) and the offshore region where prey availability is too low for that stage (Fig.6 and 7b). For bigger larvae, prey availability is higher and more homogeneous over the bay. The quality of the habitat then progressively increases offshore to become even more favorable in some locations than along the coast where temperature may be lower.

ELS transport experiments have shown that the mean drift from southern shelf is directed towards the offshore region (Huret et al., 2010) where a larger number of old larvae and juveniles are found (Irigoien et al., 2007). It appears that this drift patterns seems favorable for growth as best larval habitat switch from coastal to more offshore area. However spawning actually extends to the shelf break in the southern bay, and our model seems severe for early larvae located around the shelf break that all die before reaching a sufficient size to survive. Analysis with interannual forcing rather than climatology and extended to the whole spawning season should be conducted to assess the repeatability of these observations.

Previous modelling experiment also evidenced some accumulation of old larvae in the northern mid-shelf for some years (Allain et al. 2007a). The fact that this area is less efficient for larval growth than the southern offshore bay may explain that these old larvae and juveniles are not observed in survey data.

To our knowledge our 3D experiment is the first 3D-IBM modelling exercise in the area with growth simulated with a bioenergetic model. This study highlights the importance of considering interactions between growth and transport when studying connectivity patterns of marine species.

From this experiment, the pool of survivors, looking at their spawning location, is higher and extends further offshore in the south (Fig.8c) than estimated by the 0D model (Fig.7b). Food limitation implies less survival in the pool of larvae dispersed off-shore in the north, a really low food area, whereas in the south a slight dispersal offshore is allowed with higher food and temperature. This is important especially at that time of the year, when temperature can still be a strong limitation for growth.

This observation of general drift towards offshore, from the main spawning grounds onshelf in the south of the Bay, is consistent with observations of an increasing gradient in larval size towards offshore areas (Irigoien et al. 2008; Cotano et al., 2008). However, these authors indicates further offshore distribution of older larvae and juveniles, again in the south of the Bay. Complementary simulations with releases over the whole spawning season would tell whether our model overestimate mortality of drifting particles, or whether offshore habitats become more suitable for growth and survival as the season advances.

The small size of the larvae at age of 50 days may seem underestimated (Fig.7). We have actually very few data to validate this early spawned individuals development. Indeed, early May is the start of the spawning season (ending in July-August), and very few juveniles are found later in the season with birth date corresponding to early May (unpublished data). This may be then that even when these early spawned individuals can avoid starvation, their slow growth may induce strong mortality from predation. This latter process is not taken into account in our modelling exercise, which is still a limitation in the estimation of real connectivity patterns. And we were constrained to that period of the year from zooplankton prey field availability. Solutions for extending the availability of such information over the whole ELS development season will be investigated.

Another limitation is the use of a 2D prey field, without any vertical resolution of food availability potentially interacting with larval vertical distribution. For that we were constrained by the correction of the LOPC zooplankton data towards vertically integrated WP2 abundances (see methodology section). However when corrected, LOPC integrated abundance could then be redistributed with respect to the vertical profile, considering a correlated distribution of living and non-living particles.

Acknowledgements

This study was carried out with support from the project REPROdUCE of the ERA-NET MARIFISH (Contract ERAC(CT-2006-025989)) and ANR (French Research National Agency).

References

- Allain, G., Petitgas, P., Grellier, P., Lazure, P., 2003. The selection process from larval to juvenile stages of anchovy (*Engraulis encrasicolus*) in the Bay of Biscay investigated by Lagrangian simulations and comparative otolith growth. *FISHERIES OCEANOGRAPHY* 12, 407–418.
- Allain, G., Petitgas, P., Lazure, P., 2007. The influence of environment and spawning distribution on the survival of anchovy (*Engraulis encrasicolus*) larvae in the Bay of Biscay (NE Atlantic) investigated by biophysical simulations. *Fisheries Oceanography* 16, 506–514.
- Allain, G., Petitgas, P., Lazure, P., Grellier, P., 2007. Biophysical modelling of larval drift, growth and survival for the prediction of anchovy (*Engraulis encrasicolus*) recruitment in the Bay of Biscay (NE Atlantic). *FISHERIES OCEANOGRAPHY* 16, 489–505.
- Augustine, S., Litvak, M.K., Kooijman, S.A.L.M., 2011. Stochastic feeding of fish larvae and their metabolic handling of starvation. *Journal of Sea Research* 66, 411–418.
- Catalan, I., Folkvord, A., Palomera, I., Quilez-Badia, G., Kallianoti, F., Tselepides, A., Kallianotis, A., 2010. Growth and feeding patterns of European anchovy (*Engraulis encrasicolus*) early life stages in the Aegean Sea (NE Mediterranean). *ESTUARINE COASTAL AND SHELF SCIENCE* 86, 299–312.
- Conway, D., Coombs, S., Smith, C., 1998. Feeding of anchovy *Engraulis encrasicolus* larvae in the northwestern Adriatic Sea in response to changing hydrobiological conditions. *MARINE ECOLOGY-PROGRESS SERIES* 175, 35–49.
- Cotano, U., Irigoien X., Etxebeste, E., Alvarez, P., Zarauz, L., Mader, J. and Ferrer, L. 2008. Distribution, growth and survival of anchovy larvae (*Engraulis encrasicolus* L.) in relation to hydrodynamic and trophic environment in the Bay of Biscay. *Journal Of Plankton Research*. 30, 467-481.
- Cowen, R.K., Sponaugle, S., 2009. Larval Dispersal and Marine Population Connectivity. *Annual Review Of Marine Science* 1, 443–466.
- Daewel, U., Peck, M.A., Kuhn, W., St John, M.A., Alekseeva, I., Schrum, C., 2008. Coupling ecosystem and individual-based models to simulate the influence of environmental variability on potential growth and survival of larval sprat (*Sprattus sprattus* L.) in the North Sea. *Fisheries Oceanography* 17, 333–351.
- Daewel, U., Peck, M.A., Schrum, C., St John, M.A., 2008. How best to include the effects of climate-driven forcing on prey fields in larval fish individual-based models. *Journal Of Plankton Research* 30, 1–5.
- Gaines, S.D., Gaylord, B., Gerber, L.R., Hastings, A., Kinlan, B.P., 2007. Connecting Places. The Ecological Consequences of Dispersal in the Sea. *Oceanography* 20, 90–99.
- Gallego, A., North, E., Petitgas, P., 2007. Introduction: status and future of modelling physical-biological interactions during the early life of fishes. *MARINE ECOLOGY-PROGRESS SERIES* 347, 122–126.
- Gallego, A., North, E.W., Houde, E.D., 2012. Understanding and quantifying mortality in pelagic, early life stages of marine organisms — Old challenges and new perspectives. *Journal of Marine Systems* 93, 1–3.
- Garcia, A., Palomera, I., 1996. Anchovy early life history and its relation to its surrounding environment in the Western Mediterranean basin. *SCIENTIA MARINA* 60, 155–166.

- Hjort, J., 1914. Fluctuations in the great fisheries of northern Europe viewed in the light of biological research. *Rapp. P.-V.Reun. Cons. Int. Explor. Mer* 20, 1–228.
- Huret, M., Petitgas, P., Woillez, M., 2010. Dispersal kernels and their drivers captured with a hydrodynamic model and spatial indices: A case study on anchovy (*Engraulis encrasicolus*) early life stages in the Bay of Biscay. *Prog. Oceanogr.* 87, 6–17.
- Irigoiien, X., Fiksen, O., Cotano, U., Uriarte, A., Alvarez, P., Arrizabalaga, H., Boyra, G., Santos, M., Sagarminaga, Y., Otheguy, P., Etxebeste, E., Zarauz, L., Artetxe, I., Motos, L., 2007. Could Biscay Bay Anchovy recruit through a spatial loophole? *Progress In Oceanography* 74, 132–148.
- Irigoiien, X., Cotano, Boyra, G., Santos, M., U., Alvarez, P., OrtheGuy, P., Etxebeste, E., Uriarte, A., Ferrer, L. and Ibaibariaga, L. 2008. From egg to juvenile in the Bay of Biscay: spatial patterns of anchovy (*Engraulis encrasicolus*) recruitment in a non-upwelling region. *Fisheries Oceanography*. 37, 446-462.
- Kooijman, S.A.L.M., Pecquerie, L., Augustine, S., Jusup, M., 2011. Scenarios for acceleration in fish development and the role of metamorphosis. *Journal of Sea Research* 66, 419–423.
- Kristiansen, T., Lough, G.R., Werner, E.F., Broughton, A.E., Buckley, J.L., 2009. Individual-based modeling of feeding ecology and prey selection of larval cod on Georges Bank. *Marine Ecology Progress Series* 376, 227–243.
- Kuhn, W., Peck, M.A., Hinrichsen, H.H., Daewel, U., Moll, A., Pohlmann, T., Stegert, C., Tamm, S., 2008. Defining habitats suitable for larval fish in the German Bight (southern North Sea): An IBM approach using spatially- and temporally-resolved, size-structured prey fields. *Journal Of Marine Systems* 74, 329–342.
- Lough, R.G., Buckley, L.J., Werner, F.E., Quinlan, J.A., Edwards, K.P., 2005. A general biophysical model of larval cod (*Gadus morhua*) growth applied to populations on Georges Bank. *Fish Oceanogr* 14, 241–262.
- Morote, E., Olivar, M.P., Villate, F., Uriarte, I., 2010. A comparison of anchovy (*Engraulis encrasicolus*) and sardine (*Sardina pilchardus*) larvae feeding in the Northwest Mediterranean: influence of prey availability and ontogeny. *ICES Journal of Marine Science* 67, 897–908.
- Nogueira, E., Gonzalez-Nuevo, G., Bode, A., Varela, M., Moran, X., Valdes, L., 2004. Comparison of biomass and size spectra derived from optical plankton counter data and net samples: application to the assessment of mesoplankton distribution along the Northwest and North Iberian Shelf. *ICES JOURNAL OF MARINE SCIENCE* 61, 508–517.
- Palomera, I., Morales-Nin, B., Lleonart, J., 1988. Larval growth of anchovy, *Engraulis encrasicolus*, in the Western Mediterranean Sea. *Marine Biology* 99, 283–291.
- Peck, M.A., Hufnagl, M., 2012. Can IBMs tell us why most larvae die in the sea? Model sensitivities and scenarios reveal research needs. *Journal of Marine Systems* 93, 77–93.
- Pecquerie, L., 2008. Bioenergetic modelling of growth, development and reproduction of a small pelagic fish : the Bay of Biscay anchovy.
- Pecquerie, L., Petitgas, P., Kooijman, S.A.L.M., 2009. Modeling fish growth and reproduction in the context of the Dynamic Energy Budget theory to predict environmental impact on anchovy spawning duration. *Journal of Sea Research* 62, 93–105.
- Platt, T., Denman, K., 1977. Organisation in the pelagic ecosystem. *Helgoland Marine Research* 30, 575–581.
- Regner, S., 1996. Effects of environmental changes on early stages and reproduction of anchovy in the Adriatic Sea. *SCIENTIA MARINA* 60, 167–177.
- Sinclair, M., 1988. *Marine populations : an essay on population regulation and speciation*. Washington University Press, Seattle, WA.
- Sourisseau, M., Carlotti, F., 2006. Spatial distribution of zooplankton size spectra on the French continental shelf of the Bay of Biscay during spring 2000 and 2001. *J. Geophys. Res.* 111, 12 PP.
- Tudela, S., Palomera, I., Quilez, G., 2002. Feeding of anchovy *Engraulis encrasicolus* larvae in the north-west Mediterranean. *JOURNAL OF THE MARINE BIOLOGICAL ASSOCIATION OF THE UNITED KINGDOM* 82, 349–350.
- Vandromme, P., Nogueira, E., Huret, M., Gonzales-Nuevas, G., Lopez-Urrutia, A., Petitgas, P., Sourisseau, M. Spatial and vertical distribution of springtime zooplankton size-spectra in the Bay of Biscay from LOPC and Zooscan data analysis. In prep.

Werner, F.E., Cowen, R.K., Paris, C.B., 2007. Coupled Biological and Physical Models Present Capabilities and Necessary Developments for Future Studies of Population Connectivity. *Oceanography* 20, 54–69.