Modelling and numerical simulations of larval migration of the sole (*Solea solea* (L.)) of the Bay of Biscay. Part 1: modelling

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Abstract – A spatio–temporal model describing the dynamics of a population of sole is presented. The model is an extension to a 2D-space structure of a 1D model published by the three first authors. Spatial migration is modelled by an advection–diffusion second order operator with constant coefficients. The physical domain is represented by a half-plane with the coast as its boundary. A formula for estimating the proportion of eggs reaching the juvenile stage, depending upon climatic, transport, growth and mortality processes, is derived. Numerical results are deferred to elsewhere. © 2001 Ifremer/CNRS/IRD/Éditions scientifiques et médicales Elsevier SAS

Résumé – Modélisation et simulations de la migration des larves de sole, *Solea solea* (L.), du golfe de Gascogne, 1[re] partie : modélisation. Un modèle spatio–temporel de dynamique de population pour la sole du golfe de Gascogne (*Solea solea* (L.)) est présenté. C'est une extension 2D d'un modèle 1D proposé par les trois premiers auteurs. La migration spatiale par diffusion–advection est décrite par un opérateur du second ordre à coefficients constants. Le domaine physique est identifié à un demi-plan, limité sur son bord par la côte. Le modèle distingue les œufs, les larves, les juvéniles et les adultes, mais l'étude se focalise sur le stade larvaire. La croissance larvaire est modélisée par une fonction de la température. Un seuil de taille est imposé pour le passage au stade juvénile, en même temps qu'une contrainte de proximité suffisante de la côte. L'intégration de la partie « migration » peut être explicitement menée et permet d'aboutir à une formule calculable du taux de recrutement. Les résultats numériques sont détaillés dans un second article. © 2001 Ifremer/CNRS/IRD/Éditions scientifiques et médicales Elsevier SAS

population dynamics / diffusion and advection processes / recruitment

dynamique de population / processus de diffusion et d'advection / recrutement

1. INTRODUCTION

This paper is a follow-up of a previous work (Arino et al., 1996) where a mathematical model of the dynamics of

the larva of the Dover sole, *Solea solea* (L.), of the Bay of Biscay was first described. The main objective was to investigate the possible role of diffusion in the process by which the sole born in well identified spawning grounds, 80 to 100 kilometres from the coast, migrate to the shore until they reach such places as sheltered bays or estuaries, the nurseries where they mature until the adult stage. An

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excellent presentation of a variety of ways diffusion acts in biological and ecological phenomena is made in the classic (Okubo, 1980). The model considered is one-dimensional in space, the spatial variable being roughly the distance to the coast. The model consists of three equations, for the larval, the juvenile and the adult stage respectively. In each stage, the age within the stage is another structuring variable. The egg stage is treated as an input. Larval growth is modelled as a function of the daily average temperature with a threshold size regulating the completion of the metamorphosis of the larvae into flatfish and their passing into the juvenile stage.

In the present work we deal with a two-dimensional model for the sole. The model is roughly built on the same principles as in Arino et al. (1996), with the non-trivial complication introduced by the fact that we are working in two dimensions and also in that we are using no-flux boundary conditions instead of the zero-population boundary conditions. The main purpose of the present work is the calculation of the spatio–temporal evolution of larva distribution and an estimate of the proportion of spawned eggs reaching the juvenile phase at a given time. A formula estimating the recruitment rate of larvae depending upon various biotic and abiotic parameters of the model is established (section 4.1). Numerical simulations are presented in another paper.

The organization of the paper is as follows. Section two introduces our model. Section three is devoted to solving the equations. Mathematical aspects have been reduced to a minimum, essentially to a rigorous description of the formulae. It is also assumed that the equation describing the movement of the larvae has constant coefficients, and the domain where they move is a half-plane, $[0, +\infty[\times \mathbb{R}$. Section four is the main part of the work; it is devoted to estimating the recruitment rate in the juvenile stage. Recruitment is understood here as the arrival in a given stage. In this work, arrival in the juvenile stage is understood as initiation of metamorphosis and is concluded in terms of a threshold size to be reached by the larva. A formula for the recruitment rate is first established; then, estimates of the main parameters or functions entering the definition of the formula are obtained. The formula is based on two principal ingredients: $a_*(s)$, the age of recruitment for larvae in the juvenile stage at time t, and the migration parameters, K and u. The fact that a^* is a function of time only is a direct consequence of the simplifying assumption made about the size growth rate, modelled as a function of the average temperature only. The function $a_*(t)$ is expressed in terms of the development period from the egg to the juvenile stage, a function of the temperature determined in laboratory experiment (Fonds, 1979) see also; Amara et al. (1993) for some field data. We will also consider the function $a_*(s)$; the age at recruitment as a function of the birth date. It is shown that under some assumptions which allow the approximation of the movement as purely Gaussian, it is possible to relate the parameters K and u to the mean value and the variance of the spatial distribution of the concentration of the larvae, expressed as the ratio of the actual density of larvae of a same age and space cohort to the density of the patch of eggs from which the cohort originates. The final section, section five, discusses amply the conditions and the body of hypotheses which underlie the work, and the perspectives brought up by recent experimental as well as field findings, to conclude on the possible significance of our work within this new context and on its prospective future development.

2. THE MODEL

The problem is formulated in a region of the ocean surface enclosing in its interior the spawning grounds and the nurseries. For simplicity, we assume vertical homogeneity (as a result of averaging over the water column) and also that the coast is rectilinear. This makes possible to arrive at tractable formulae.

2.1. State variables

Two variables are considered for space parameterisation:

x_1 represents the direction perpendicular to the coast and measures the distance to the coast, $x_1 \in [0, +\infty[$.

x_2 represents the direction parallel to the coast and measures the distance to the origin arbitrarily chosen on the coast.

Ω_i, $i = 1, 2, ..., I_\Omega$ denotes the spawning areas, supposed subdivided into disjoint patches (D_i, $i = 1, 2, ..., I_D$ denotes the nursery areas, similarly subdivided into disjoint patches respectively). Let $\Omega = \bigcup_{i=1}^{I_\Omega} \Omega_i$ and $D = \bigcup_{i=1}^{I_D} D_i$.

At a given time t, we denote by: $L(a, t, x_1, x_2)$, $J(a, t, x_1, x_2)$ and $M(a, t, x_1, x_2)$: (respectively) the lar-

val, juvenile and adult density with respect to age and position, $B(t, x_1, x_2)$: the egg spawning rate density.

The function B links the mature and larva compartments via the birth equation (1).

2.2. Model equations

In general, the observed phenomena are almost identically reproduced each year. Time is counted in fractions of a year and, in a given year, initialised at the first of January. Spawning occurs in a period of the year represented by a time interval $[p_1, p_2]$, $(0 < p_1 < p_2 < 1)$.

2.2.1. Equation of reproduction

The reproduction period covers approximately three months starting from mid-January to mid-April, a period during which adult females spawn gradually. A few days after being spawned, eggs hatch giving birth to larvae. Egg mortality is presumably very high. The egg production equation is given by:

$$B(t, x_1, x_2) = \int_{a_{\min}}^{a_{\max}} \beta(a, t, x_1, x_2) e(a) M(a, t, x_1, x_2) \, da \quad (1)$$

$\beta(a, t, x_1, x_2)$ is the proportion of adult individuals aged a participating in the reproduction at time t and location (x_1, x_2). The function β is equal to zero outside of both the reproduction period and the spawning grounds. $e(a)$ is the egg number average produced per time unit, per adult female aged a.

$a_{\min}$ and $a_{\max}$ denote respectively the minimum and maximum age of reproduction.

2.2.2. Larvae dynamics

2.2.2.1. Larval growth equation
The growth of larvae is described as a function of the temperature. If $w(a, t)$ is the length at a time t of a larva aged a, $t \geq a$, then its evolution is modeled according to the equation:

$$\left(\frac{\partial}{\partial a} + \frac{\partial}{\partial t} \right) w(a, t) = \tilde{f}(t) g(w(a, t)) \quad (2)$$

where $\tilde{f}(t) = f(T(t))$, $T(t)$ is the temperature at a time t. f and g are positive continuous functions.

Integrating equation (2) along the 'characteristic lines', we obtain:

$$w(a, t) = w_0 + \int_{t-a}^{t} \tilde{f}(s) g(w(s - (t - a), s)) \, ds, \ (t \geq a)$$

where w_0 is the size at birth.

We assume that the recruitment in the juvenile stage is subject to reaching a threshold size w^* (Amara and Lagardère, 1995). What we consider here is not really the beginning of the juvenile stage, but rather the initiation of metamorphosis, that is to say, the transformation of the larva from a round fish into a flatfish. The possible role of this transformation as regulating the recruitment is discussed in (Amara et al., 2000): experimental evidence, notably regarding to the nutritional condition of metamorphosing larvae, seems to indicate that this period is not such a crucial one. The model we describe does not counteract the above-mentioned evidence. No increased mortality is attached to the period when w is near w^*: We denote as $a^*(t)$ the function that determines uniquely the value of a satisfying the condition:

$$w(a^*(t), t) = w^* \quad (3)$$

$a^*(t)$ is the age at metamorphosis of a larva recruited in the juvenile stage at time t. Size was used instead of weight because it is a more reliable, less fluctuating, data than weight. Weight should reflect a balance of the food eaten and the energy consumed in various respects: in searching food, in body maintenance, excretion of unused substances, etc. Finally, very often, data in the literature relating the stage to a certain global feature of an individual use length as the distinctive feature (Koutsikopoulos et al., 1991; Horwood, 1993). The threshold size is the average size at the beginning of metamorphosis.

2.2.2.2. Transport of larvae
During the pelagic phase, eggs and larvae are considered passive and are submitted to both mortality and water movement effects. Their displacement has two components: a diffusive component and an advective component, which are related to winds and marine currents. Then the dynamics of larvae are described by a Lotka–Von Foerster type model:

$$\left(\frac{\partial}{\partial a} + \frac{\partial}{\partial t} \right) L(a, t, x_1, x_2) = \nabla \cdot [K \nabla L(a, t, x_1, x_2)]$$
$$- \nabla \cdot (u L(a, t, x_1, x_2)) - \mu_L(a) L(a, t, x_1, x_2),$$
$$a < a^*(t) \quad (4)$$

with the following boundary conditions:

$$L(0, t, x_1, x_2) = B(t, x_1, x_2); \qquad (5)$$

$$L(a, i, x_1, x_2) = 0 \ \text{ for } \ i = 1, 2, \ldots$$

and

$$(-K\nabla L + uL) \cdot \vec{\eta} = 0 \text{ on the boundary} \qquad (6)$$

$\nabla = \begin{pmatrix} \dfrac{\partial}{\partial x_1} \\ \dfrac{\partial}{\partial x_2} \end{pmatrix}$ and the notation $\nabla.v$ denotes the divergence of v.

$K = (k_{ij})_{i,j=1,2}$ is a symmetric positive definite matrix.

The quantity $\int_{\mathcal{R}} \nabla \cdot [-K\nabla L(a, t, x_1, x_2)] \, dx_1 \, dx_2$ represents the larva flux due to diffusion through the boundary of any given region $\mathcal{R}$. In fact, according to Fick's law, the flux vector is equal to $-K\nabla L$ and its divergence integrated over any region gives the flux through the boundary of this region (Green–Stokes' formula).

u is the velocity vector of marine currents (all components included: winds, tidal currents, etc.) and it is assumed to be averaged throughout the period of the larval stage.

$\mu_L(a)$ is the age specific rate mortality from which we deduce the survival probability up to age a:

$$S_L(a) = \exp\left(-\int_0^a \mu_L(s) \, ds\right) \qquad (7)$$

The equation '$L(a, i, x_1, x_2) = 0$' reflects the fact that time was initialised on the first of January of a referential year, 'the year zero', and it is supposed that there is no larva alive at the beginning of each year. This hypothesis requires supplementary conditions on larval mortality and we admit that larvae cannot survive as larvae beyond their year of birth. Then, there is a maximum age that larvae should not reach, denoted $\bar{a}_L$ and satisfying the following singular condition:

$$\int_0^{\bar{a}_L} \mu_L(s) \, ds = +\infty \ \text{ and } \int_0^a \mu_L(s) \, ds < +\infty$$
$$\text{for every } 0 < a < \bar{a}_L \quad (8)$$

Given that reproduction occupies the period $[p_1, p_2]$ of each year, individuals born at time p_2 should not survive up to the beginning of the following year. Then, the following condition:

$$\int_0^{1-p_2} \mu_L(s) \, ds = +\infty \qquad (9)$$

must be satisfied. Taking (8) into account, the following condition should be checked:

$$\bar{a}_L \leq 1 - p_2 \qquad (10)$$

The boundary condition $(-K\nabla L + uL) \cdot \vec{\eta} = 0$ in (5), expresses that there is no fish flux through the limits between the sea and the land, where $\vec{\eta}$ is the normal vector to the coast. This condition should be satisfied at all fish stages and particularly for larvae:

$$-k_{11} \frac{\partial}{\partial x_1} L(a, t, 0, x_2) - k_{12} \frac{\partial}{\partial x_2} L(a, t, 0, x_2) +$$
$$u_1 L(a, t, 0, x_2) = 0 \quad (11)$$

2.2.3. Dynamics of juveniles

The juvenile stage is supposed to start when larvae reach the threshold size w^* related to their metamorphosis. We assume that only those whose metamorphosis occurs inside the nurseries are recruited in this stage. This assumption is in agreement with repeated observations reported for example in (Koutsikopoulos et al., 1991) showing that few juveniles were caught out of the nurseries.

The newly recruited juveniles remain in the nurseries, for a period of approximately two years, moving to estuaries in summer towards bays in winter, with a tendency more and more pronounced towards deeper zones. The recruitment of juveniles in nurseries at a time t, when it effectively occurs, is quantified by the entry rate density:

$$J(0, t, x_1, x_2) = (1 - (a^*)'(t)) L(a^*(t), t, x_1, x_2) \chi_D$$
$$(x_1, x_2) \quad (12)$$

where the function χ_D is such that:

$$\chi_D(x_1, x_2) = \begin{cases} 1 & \text{for } (x_1, x_2) \in D \\ 0 & \text{otherwise} \end{cases}$$

We assume that the displacements of juveniles in the nurseries have no influence on the demography. As a

consequence, the spatial distribution is supposed to be uniform, and is given by the following averaged expression:

$$J(0, t) = \frac{[1 - (a*)'(t)]}{A(D)} \int_D L(a*(t), x_1, x_2) \, dx_1 \, dx_2 \quad (13)$$

where $A(D)$ is the whole surface of the nurseries D and $J(0, t)$ represents the instantaneous flux per surface unit of larvae entering the juvenile stage at time t per unit time. The relationship (13) can be stated, as in (Arino et al. 1996), by establishing a balance of exchanges between the larval and juvenile compartments.

Consequently, the equation for the juveniles is reduced to an age-structured one, only accounting for the ageing and mortality processes, and reads:

$$\begin{cases} \left(\dfrac{\partial}{\partial a} + \dfrac{\partial}{\partial t}\right) J(a, t) &= -\mu_j(a) \, J(a, t) \\ J(a, 0) &= J_0(a); t > 0, 0 < a < 2 \end{cases} \quad (14)$$

where J_0 is the initial juvenile distribution at year 0. The equation is completed by formula (13) which gives the boundary condition at age $a = 0$.

The description of the dynamics of adults is skipped.

3. SOLVING OF THE MODEL EQUATIONS

The whole system is composed of three equations satisfied respectively by L and J; with initial and boundary conditions. We restrict our attention to two: (4), (5), (6) for L and (12), (14) for J:

3.1. Solving the equation for the larvae

The solving of equation (4) can be accomplished in two steps: 1) the equation with the right hand-side restricted to the diffusion term and boundary condition (6) is considered first: a parabolic equation, with constant coefficients, on a half-plane can be solved explicitly, using an extended version of the reflection method. In this step, the transport is cancelled, $u = 0$. 2) Coming back to the general case, $u \neq 0$, the first order expression in the right hand-side of (4) can be absorbed by a change of the unknown L to $\bar{L}$ given by:

$$\bar{L}(a, t, X) = \exp\left(-\frac{u^T K^{-1} X}{2}\right) L(a, t, x)$$

A brief explanation of the reflection method is as follows: given a solution L of equation (4); the goal is to extend it into a solution of the same principal equation on the whole plane. If this can be done, the extended solution can be computed in terms of the initial value, using the Fourier transform on $\mathbb{R}^2$. It is indeed possible to determine such an extension, using a transformation of the plane into itself, which maps the positive half-plane $x_1 > 0$ onto the negative one, $x_1 < 0$. The matrix of the transformation is:

$$T = T^{-1} = \begin{bmatrix} -1 & 0 \\ -2\dfrac{k_{12}}{k_{11}} & 1 \end{bmatrix} \quad (15)$$

For the sake of conciseness, the following notations are adopted: $X = (x_1, x_2)^T$ and $\tilde{X} = TX$, where 'T' denotes the transpose operator. As usual, K^{-1} denotes the inverse of matrix K and $\det(K)$ its determinant. Note that $T^T K^{-1} T = K^{-1}$.

3.1.1. Case (u = 0)

We use the method of lines (Webb, 1985) to reduce the study to age-cohorts; that is to say, we follow the larvae born at a same given moment. For these larvae, time and age are related as follows: $t = t_0 + a$, where t_0 is the birth date; so, one can substitute $t_0 + a$ for t in the equation, thus keeping only one time variable. The physical domain is considered a half-plane, with $x_1 = 0$ as a boundary. This, of course, is a simplification, justified by the size of the domain: it allows to us to obtain explicit formulae in the same way as was done in (Arino et al., 1996). The boundary condition reduces to:

$$\left(k_{11} \frac{\partial L}{\partial x_1} + k_{12} \frac{\partial L}{\partial x_2}\right)(a, t, 0, x_2) = 0$$

The solution can be explicitly written as follows:

$$L(a, t, X) = S_L(a) \int_{[0,+\infty[\times\mathbb{R}]} k_L(a, X, Y) \, B(t - a, Y) \, dY,$$
$$\text{for } t > a \quad (16)$$

where S_L is the larva survival function (7), and:

$$k_L(s, X, Y) = \frac{1}{4\pi \sqrt{\det(K)}}$$
$$[\exp(-H(s, X - Y)) + \exp(-H(s, \tilde{X} - Y))] \quad (17)$$

with

$$H(s, X) = \frac{X^{\mathrm{T}} K^{-1} X}{4s} \qquad (18)$$

It should be noted that this formula is valid only for $a < a^*(t)$, where $a^*(t)$ is given by (3). Relationship (16) is interpreted as follows: larvae of age a occupying the position X at time t, are those among larvae born at time $t–a$, whose density is $B(t–a, Y)$, which have survived up to age a with survival probability $S_L(a)$; and which have transited from birth position Y to the actual position X. The function $k_L(a, X,Y)$ gives the transition probability, during a period of time equal to a, of movement from a position Y to a position X.

3.1.2. Case (u ≠ 0)

We return to the first case by substituting the function $\tilde{L}$ to L as explained above. Straightforward computations lead to the following expression for L:

$$L(a, t, X) = S_L(a) \int_{\Omega} k_L(a, X, Y; u) \, B(t - a, Y) \, dY,$$
$$\text{for } t > a \quad (19)$$

where

$$k_L(a, X, Y; u) = \exp\left(-\frac{u^{\mathrm{T}} K^{-1} u}{4} a\right)$$
$$\exp\left(\frac{1}{2} u^{\mathrm{T}} K^{-1}(X - Y)\right) k_L(a, X, Y) \quad (20)$$

3.2. Solving of the equation for the juveniles

According to (12):

$$J(0, t, X) = (1 - (a^*)'(t)) \, L(a^*(t), t, X) \text{ for } X \text{ in } D$$

The expression of L is given in (19).

Using the method of lines, (14) leads to the following expression:

$$J(a, t, X) = \begin{cases} \dfrac{S_J(a)}{S_J(a-t)} J_0(a-t, X), & \text{for } t < a < 2 \\ S_J(a) \, J(0, t - a, X), & \text{for } a < t \end{cases} \quad (21)$$

where $S_J(a)$ is the survival function of juveniles which can be expressed in terms of μ_J by a formula similar to (7), and $J(0, t–a, X)$ is given by relationship (12).

4. ESTIMATE OF THE RATE OF RECRUITMENT

Some observations have permitted us to justify the hypothesis that only the larvae metamorphosing in nurseries are susceptible to become adults. In fact, a very small number of juveniles have been found outside the nurseries (Koutsikopoulos et al., 1993). The proposed model allows us to evaluate the fraction of larvae reaching the nurseries at the moment of their metamorphosis. A formula giving an estimate of the rate of recruitment will be established, involving the transport parameters K and u, biological related parameters as μ and a^*, and some geographic characteristics of the nurseries and spawning grounds.

Consider now a microcohort arriving at the juvenile stage in an infinitesimal time interval $[t, t + dt]$. Then, individuals of this microcohort were born during the interval time $[t - a^*(t), (t + dt) - a^*(t + dt)]$ whose length is $(1 - a^{*\prime}(t)) \, dt$. Then, the total number of individuals born in this time interval is equal to:

$$(1 - a^{*\prime}(t))\left(\int_{\Omega} B(t - a^*(t), Y) \, dY\right) dt \quad (22)$$

The number of individuals entering the juvenile stage in the time interval $[t, t + dt]$ is given by the formula:

$$S_L(a^*(t))(1 - a^{*\prime}(t))\left(\int_D \int_{\Omega} k_L(a^*(t), X, Y; u)\right.$$
$$\left. B(t - a^*(t), Y) \, dY \, dX\right) dt \quad (23)$$

Then, the fraction of larvae recruited in the juvenile stage is given by the following formula:

$$R(t) = S_L(a^*$$
$$(t)) \frac{\int_D \left(\int_{\Omega} k_L(a^*(t), X, Y; u) \, B(t - a^*(t), Y) \, dY\right) dX}{\int_{\Omega} B(t - a^*(t), Y) \, dY}$$
$$(24)$$

The proportion arriving at a given nursery D_i from all the larvae born (on any of the admissible spawning grounds) is:

$$R_i(t) = S_L(a^*(t))$$

$$\frac{\int_{D_i}\left(\int_\Omega k_L(a^*(t), X, Y; u) B(t - a^*(t), Y)\, dY\right) dX}{\int_\Omega B(t - a^*(t), Y)\, dY} \quad (25)$$

such that:

$$R(t) = \sum_{i=1}^{I_D} R_i(t) \quad (26)$$

$R(t)$ is, at time t, the fraction of eggs spawned at time $t - a^*(t)$ that become juveniles in nurseries at time t.

Now, to compute the recruitment rate over a period $[t_1, t_2]$, corresponding to the birth period $[t_1 - a^*(t_1), t_2 - a^*(t_2)]$, we integrate both (23) and (22) and divide the first quantity by the latter one. We arrive at the following expression:

$$R_{tot} = \frac{\int_{t_1}^{t_2}\iint_{D\times\Omega} S_L(a^*(t)) k_L(a^*(t), X, Y; u) B(t - a^*(t), Y)\, dY\, dX (1 - (a^*)'(t))\, dt}{\int_{t_1}^{t_2}\left(\int_\Omega B(t - a^*(t), Y)\, dY\right)(1 - (a^*)'(t))\, dt}$$

or equivalently, changing the time variable from t to s defined by:

$$t - a^*(t) = s$$

$$a_*(s) = a^*(s + a_*(s)) \quad \text{and} \quad a^*(t) = a_*(s)$$

$$R_{tot} = \frac{\int_{s_1}^{s_2} S_L(a_*(s))\left(\int_D\left(\int_\Omega k_L(a_*(s), X, Y; u) B(s, Y)\, dY\right) dX\right) ds}{\int_{s_1}^{s_2}\left(\int_\Omega B(s, Y)\, dY\right) ds} \quad (27)$$

where $s_i = t_i - a_*(t_i)$, $i = 1, 2$ and $a_*(s)$ is the period spent in the larval stage by a larva born at time s (thus, recruited in the juvenile stage at time t such that $t - a^*(t) = s$). R_{tot} gives the rate of recruitment for a season in terms of the spawning distribution and model

parameters. Then, if one can estimate the egg distribution (from data sampling), the model can be used for recruitment prediction.

4.1. A lower estimate of the rate of recruitment

From formula (27), one deduces immediately a lower estimate of the rate of recruitment into the juvenile stage:

$$R_{low}(s) = \int_D S_L(a_*(s)) \inf_{Y\in\Omega} k_L(a_*(s), X, Y; u)\, dX \quad (28)$$

With the variable s standing for the birth date, (28) gives a value inferior or equal to the actual instantaneous time rate of the proportion of larvae born at time s recruited in the juvenile stage. If we assume that the time birth rate over the spawning ground is constant within a time interval $[s_1, s_2]$, that is,

$$B_\Omega(s) =_{def} \int_\Omega B(s, Y)\, dY = \overline{B_\Omega} = \text{constant,}$$

$$\text{for } s_1 \le s \le s_2$$

then,

$$\left(\int_{s_1}^{s_2} R_{low}(s)\, ds\right)\overline{B_\Omega}$$

gives a value inferior or equal to the actual number of larvae born within the time interval $[s_1, s_2]$ which start metamorphosis (in the admissible domain). Therefore,

$$\frac{\int_{s_1}^{s_2} R_{low}(s)\, ds}{s_1 - s_2} \quad (29)$$

is a lower estimate of the instantaneous time rate of recruitment in the juvenile stage, for those larvae born within the time interval $[s_1, s_2]$, providing the assumption of a constant time birth rate holds during the same time interval. The assumption of a constant birth rate allows us to use (29) as a lower estimate of the recruitment, rather than:

$$\min_{s_1\le s\le s_2} R_{low}(s)$$

thus, yielding a better estimate. Assessment of the value rests on the computation of a_* and the parameters K and

u. These computations are the subject of the next subsection. The above estimates can be adapted so as to pinpoint a particular spawning patch or/and a particular nursery.

4.2. Estimating some model parameters

4.2.1. An estimate for $a^*(t)$

In order to evaluate the function $a^*(t)$, it is necessary to determine the functions f and g. This may be done by using the functional relationship giving the development period in terms of the temperature. In Arino et al. (1996), the following model is considered:

$$D(T) = aT^b, \quad a > 0 \text{ and } b < 0 \tag{30}$$

where $D(T)$ is the development period from the egg to the juvenile stage, at constant temperature T. The condition $b < 0$ stands for the fact that the development period is decreasing with respect to temperature: the higher the temperature, the faster the growth and the shorter the development period. The coefficients a and b can be estimated by linear regression of larval growth data.

Now, let us suppose for a moment that the temperature T is constant during larval development. Equation (2) reads along characteristic lines:

$$\frac{dw}{ds}(s) = f(T) \, g(w(s))$$

and

$$\int_0^{D(T)} \frac{dw(s)}{g(w(s))} = f(T) \, D(T)$$

If the function $\frac{1}{g}$ has an antiderivative G, then:

$$G(w^*) - G(w_0) = f(T) \, D(T)$$

thus, the expression of f is given by:

$$f(T) = \frac{G(w^*) - G(w_0)}{D(T)}$$

Integrating the above relationship from time $t - a$ to t, we obtain:

$$G(w(a,t)) - G(w_0) = (G(w^*) - G$$
$$(w_0)) \int_{t-a}^t \frac{1}{D(T(s))} \, ds$$

The function $a^*(t)$ is obtained when the following integral condition is satisfied:

$$\int_{t-a^*(t)}^t \frac{1}{D(T(s))} \, ds = 1$$

$$\text{or, equivalently} \int_t^{t+a_*(t)} \frac{1}{D(T(s))} \, ds = 1$$

The term $\dfrac{1}{D(T(t))}$ represents the fraction of size gained, per time unit, at time t and temperature $T(t)$. Finally, to estimate the development period, we need to choose a model for the evolution of temperature. We use a sinusoidal function model for the temperature, of the type:

$$T(t) = T_0 + T_m \sin(\alpha t + \gamma)$$

We then proceed to a discretization of time with step δt 'small enough' for estimating the function $a^*(t)$. We approach the value of the integral:

$$I(n) = \int_{t-n\delta t}^t \frac{1}{D(T(s))} \, ds \simeq \delta t \sum_{i=1}^n \frac{1}{D(T(s_i))},$$
$$\text{for} \quad n = 1, 2, \dots$$

The stopping test for n, denoted n^*, is the smallest n such that $I(n) \leq 1$ and $I(n+1) > 1$. Then, $a^*(t)$ is estimated by $\left(n^* + \dfrac{1}{2}\right) \delta t$.

4.2.2. Estimating transport parameters

In order to estimate the transport parameters K and u, we assume that the spawning is concentrated in tiny patches, sufficiently distant one from the other. Choose one of them located in the vicinity of a point X^0, occupying a small area ω_{X_0} around X_0, with the egg density equal to $B(t, X_0)$ all over the patch; then, the spatio–temporal distribution of the larvae initiated from this patch is approximated by:

$$L(a,t,X) \approx S_L(a) \, k_L(a, X, X^0; u) \, B(t-a, X^0) \, \omega_{X_0}$$

The quantity:

$$\pi_{X_0}(a, X) = \frac{L(a,t,X)}{B(t-a, X^0) \, \omega_{X_0}} = S_L(a) \, k_L(a, X, X^0; u)$$

gives the spatial distribution, relative to the initial egg patch, of larvae of age a, counting the mortality. Thus, leaving the mortality out, the quantity $k_L(a, X, X^0; u)$ reads as the probability density for a larva born near X_0

to reach the point X at age a. To say a little more about this probability, it is necessary to look at it in more detail. Using formula (20), a straightforward computation leads to:

$$k_L(a, X, X^0; u) = \mathbb{P}(a, X) + \mathbb{P}(a, \tilde{X})$$

where

$$\mathbb{P}(a, X) = \frac{1}{4\pi a \sqrt{\det(K)}} \exp\left\{ -\frac{(X - (X^0 + au))^T K^{-1}(X - (X^0 + au))}{4a} \right\}$$

$\tilde{X} = TX$, and T is given by formula (15).

We have:

$$\pi_{X_0}(a, X) = S_L(a) \left[\mathbb{P}(a, X) + \mathbb{P}(a, \tilde{X}) \right]$$

We note that $\mathbb{P}(a, X)$ is a normal probability law. If $\mathbb{P}(a, \tilde{X})$ can be neglected in comparison to $\mathbb{P}(a, X)$, then, for each time $t \geq 0$, the 'relative' spatial distribution $\pi_{X_0}(a, X)$ of larvae of the same cohort aged a, born in the same point X^0, is assimilated to a normal distribution of mean $m_a = S_L(a)(X^0 + au)$ and covariance matrix $\Gamma_a = 2a(S_L(a))^2 K$. So, knowing the survival function $S_L(a)$ and the eggs and larvae distribution (e.g. using data sampling), one can estimate X^0, u and K.

In the case of many spawning points, one can use the same principle but the time and the area of dispersion must be shorter and closer to the time and the area of spawning so that no mixing occurs between larvae born in different spawning points.

Let us now check conditions under which $\mathbb{P}(a, \tilde{X})$ can be neglected with respect to $\mathbb{P}(a, X)$. Denote by:

$$r = \frac{\mathbb{P}(a, \tilde{X})}{\mathbb{P}(a, X)} =$$
$$\exp -\frac{1}{4a} \left\{ (\tilde{X} - X)^T K^{-1}(\tilde{X} - X) + 2(\tilde{X} - X)^T K^{-1} (X - (X^0 + au)) \right\}$$

Direct computation of the above expression yields:

$$r = \exp -\frac{x_1(x_1^0 + au_1)}{ak_{11}}$$

where $X^0 = (x_1^0, x_2^0)^T$ and $u = (u_1, u_2)^T$.

Note that the quantity $x_1^0 + au_1$ is certainly positive and large, for a reasonable range of values of x_1^0, a and u_1. So,

the bigger the ratio $\frac{x_1}{a}$, the smaller r and the better the approximation of $\mathbb{P}(a, X) + \mathbb{P}(a, \tilde{X})$ by $\mathbb{P}(a, X)$. Furthermore, if a is sufficiently small, most larvae would not have time to diffuse far from their birth position X^0. So, if we proceed by a sampling strategy where the stations are close to spawning points, namely, $x_1 \approx x_1^0$, then:

$$r \approx \exp\left(-\frac{(x_1^0)^2}{ak_{11}} \right)$$

will tend exponentially to zero if $\frac{(x_1^0)^2}{ak_{11}}$ becomes large. The condition that x_1^0 be large or a small leads to the same observation, that the spawning areas can be considered sufficiently far from the coast that the spatial boundary effects can be neglected. In this case, one can do as if there were no boundary, thus the spatial distribution follows a normal law.

5. DISCUSSION AND CONCLUSION

The results presented in this paper are based on the same general hypotheses as those that were used in Arino et al. (1996). With regard to physical processes, repeated observations made by (Koutsikopoulos et al. 1993) indicate that drift by currents is weak and roughly parallel to the coast, therefore it would not explain the transport of larvae to the nurseries. Residual tidal currents have roughly the same effect (Le Cann et al., 1992). So, it has been suggested that the transport of a probably very small fraction of the spawning biomass towards the nurseries should be the result of an essentially diffusive process, both biological and physical on a very small scale. Arino et al. (1996) has dealt with the one-dimensional case, considering that the principal spatial coordinate was the distance to the coast. Introducing the coordinate parallel to the coast was felt a necessity in view of the heterogeneity of the coast and the fact that, as was mentioned above, the current tends to act along the coast. Regarding the life history of the sole, the scheme was: the egg stage followed by the early larval stage, both essentially passive, then an active feeding larval period preceding the metamorphosis into a juvenile flat fish which should occur within immediate vicinity of a nursery. The rationale for the geographic localization of the onset of the juvenile stage was a series of observations showing that nearly no juvenile has ever been captured out of the

nurseries (Koutsikopoulos et al., 1991). The model proposed in Arino et al. (1996) was built on these hypotheses. The model still suffers from several drastic simplifications, such as taking averages of all the parameters (including the velocity) and state variables instead of their local values. Vertical movement is an important component of fish dynamics. After a few days, the larva starts to adopt the usual circadian rhythm, being near the surface at night while reaching the lower part of the column during daylight. Compared to the mean span of the larval stage (between 40–60 days (Koutsikopoulos et al., 1991)), daily processes may be considered fast and are susceptible to be approximated using the theory of the aggregation of variables (the reader can look at Antonelli and Auger, 1998, for example, for getting a view on this theory and some applications). Such an approach was used in (Arino et al., 1999) in a study of the vertical displacement of fish larvae. A mean value of the horizontal velocity emerges from the aggregation of the velocity at various levels of the water column, associated with vertical mixing. This is not however the way it was carried out in (Arino et al., 1996) nor is it so in the present work. The possible role of vertical migration, combined with depth-differential advection, on the horizontal displacement will be investigated in a coming paper, using a 3D model fed with some real oceanographical data.

With regards the description of the life cycle, the emphasis in Arino et al. (1996) as well as here was put on the larval stage. In contrast, there are important gaps in the modelling of other stages: for the juvenile stage, for example, no space variability was accounted for. Although the movements of the juveniles are indeed quite limited, compared to those of the adults and larvae, one cannot however neglect their potential impact on their dynamics.

The main purpose in Arino et al. (1996) and in the present work was to explore by a mathematical model the combined role of diffusion-driven migration and temperature-dependent growth in the recruitment of larvae in the juvenile stage. The link between the physical and physiological processes is that a supposedly existing size threshold for metamorphosis is to be reached within close vicinity of a nursery. The unique feature of both our earlier work and this one is the same: it is to propose analytic formulae, which can be computed numerically and can also be used for sensitivity analysis.

How does the present work compare to Arino et al. (1996)? It would not be exact to consider that it is just the same as Arino et al. (1996) in the 2D setting instead of 1D. This very fact introduces non trivial complications in the mathematical treatment which are well reflected in paragraph 4.4.2: the fundamental solution, that is, the solution describing the time change of the concentration of a property which initially was concentrated in a single point, is not monotonic and it has been necessary to introduce an approximation to recover the more familiar concept of a normal distribution. The model incorporates some new features, such as for example assuming no-flux spatial boundary conditions, which is more realistic a hypothesis than assuming no population on this part of the boundary, but adds a little more to the difficulty of dealing with two dimensions. The model also accounts for the possible subdivision of the spawning or the nursery area into separate patches. A special effort was invested in the modelling of larval growth and in computing the growth function in terms of experimentally obtained functions (section 4).

What has been done in Arino et al. (1996) and in the present work is essentially based on experimental and field studies made in the eighties and early nineties (Dorel et al., 1991; Koutsikopoulos et al., 1989, 1991; Le Cann et al., 1992; Koutsikopoulos et al., 1993). Recent progress in sampling techniques as well as in the analysis of biological data has led experts on the Dover sole to modulate some of the hypotheses, which play a fundamental role in the models we have elaborated. There are several new aspects, regarding both the ecology of the sole and the identification of the nurseries and the spawning grounds that would need to be taken into account. We now mention a few of these.

It has been assumed in this paper that only the larvae completing metamorphosis within the nurseries are susceptible to reach sexual maturity: this hypothesis has been verified in each field study (Koutsikopoulos et al., 1989, Amara et al., 1993; Lagardère et al., 1999). However, it has been observed (Amara et al., 1993), see also Lagardère et al., 1999), that metamorphosing larvae were more abundant in the area 30–40 m deep than previously reported. These observations, favoured by the development of more powerful samplers Amara et al., 1994), suggest that additional mechanisms apart from diffusion play a role in the transport of larvae into the 20 m deep area and the nurseries. This leads us to mention a point which is gaining favour in the present

ideas on the ecology of the sole, that is, the idea of subdividing the migration of the sole into two distinct processes: a first one, essentially driven by diffusion, would select in a mostly random fashion the larvae which have the potential to become adults, the ones which by diffusion are transported within 20–40 km from the coast; then, a second mechanism, involving active movement of the larvae, notably in the water column, and tidal currents (Champalbert and Koutsikopoulos, 1995), would allow the successful individuals to reach the nurseries. Some physiological changes occurring during the development of the larva would then play a crucial role: for example, the use of an inflated swim bladder, viewed more as an energy saver than a device essential for the sole to ascend in the water column (Blaxter, 1980), would give *Solea solea* an advantage over the thickback sole, *Microchirus variegatus*, to reach coastal nurseries (Amara et al., 1998). In fact, the combination of vertical movement and horizontal transport could be enough to explain the migration of the larvae from the spawning ground to the 20–40 km offshore area. Finally, the type and characteristics of the nurseries become an important feature of the success, and recent advances in the analysis of chemical constituents of otoliths have permitted the determination of environmental imprints, which should be useful in exploring the relationships between the various nurseries and spawning grounds, and possibly estimating the distinctive role and importance of each nursery in the recruitment.

In conclusion, we want to stress two points: 1) migration from the spawning ground to within 20–40 km from the coast can be explained by a combination of diffusion and SE–NW drift, both horizontal, viewed as an average of corresponding properties throughout the water column. This is in agreement with the suggestion that was made notably in (Koutsikopoulos et al., 1991), and that stimulated (Arino et al., 1996) and the present work. What our paper adds to the intuition is that this mechanism can produce significant recruitment only if the drift is suitably small and the diffusion is big enough, and it provides formulae that can be used to estimate how small the drift should be and how big the diffusion. 2) For the perspectives: the mechanisms in action in the 20–40 km distance to the coast combine diffusion with possibly more prominent physical factors, notably tidal currents, concurrently with physiological features of the metamorphosing larvae which allow them to exploit the vertical movement to reach the nurseries. This part of the dynamics requires the development of a new model, possibly three dimensional, in order to account for the increased impact of the vertical movement in it together with its conceivably greater heterogeneity when nearing the 20 m or less deep waters. Future work is envisaged in this direction.

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