

## Growth performances of juvenile sole *Solea solea* under environmental constraints of embayed nursery areas

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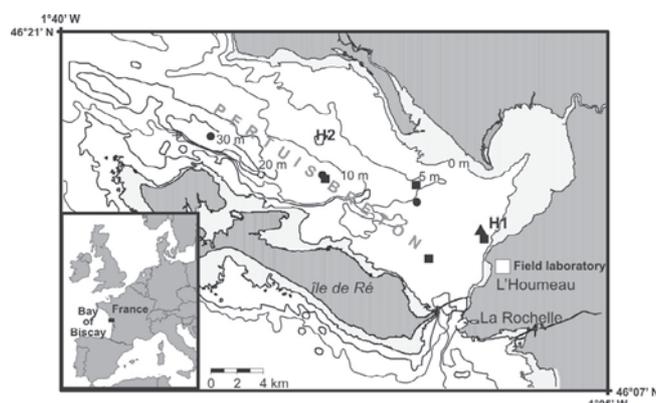
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**Abstract** – Tidal embayments in the Bay of Biscay (France) host nursery grounds where common sole, *Solea solea*, is the most abundant flatfish species. This study aimed to appraise the way those habitats function as nurseries through juvenile sole's responses in somatic growth and condition (Fulton's  $K$ ) during their first year of occupancy. Field data, two yearly trawling series, taken monthly, were compared with a 6-month-long mesocosm experiment involving reared fish of the same wild origin. Growth rates were compared with predicted maximum growth according to an experimentally established model in relation to temperature. In the field, 0-group sole total length (TL) averaged 130 mm from September onwards in 1999 and 2000. Mean growth rates were 0.7–0.9 mm day<sup>-1</sup> in summer and  $\leq 0.1$  mm day<sup>-1</sup> in autumn, when the model predicted 1.4 and 0.9 mm day<sup>-1</sup>, respectively. In the mesocosm, the growth rates were 0.9 and 0.4 mm day<sup>-1</sup> for the same seasons and for stocking densities (300 fish 1000 m<sup>-2</sup>) about 10 times higher than usually recorded in the field. Wild sole remained in medium condition ( $K$  ca. 1 g cm<sup>-3</sup>) during the entire growing season, whereas they attained a higher  $K$  after being released into the mesocosm (1.2–1.3 g cm<sup>-3</sup>). During the mesocosm experiment, growth was shown to be primarily temperature-controlled: fish reached 150–160 mm (TL) in November. From this investigation, it can be concluded that sole's responses in condition and growth are altered over the whole growing season on nursery grounds. The situation is exacerbated in autumn when the sum of abiotic constraints increases as the competitive biomass does. This indicates impairment of the nursery functioning which, in the context of fish habitat conservation, emphasises the particular vulnerability of embayments to the addition of any further constraint.

**Key words:** Coastal nursery / Habitat quality / 0-group fish / Growth / Condition factor / Mesocosm experiment / Flatfish / *Solea solea*

**Résumé** – Croissance des juvéniles de la sole *Solea solea* sous contraintes environnementales de nourriceries côtières. Les baies du golfe de Gascogne (France) hébergent des habitats où la sole, *Solea solea*, est le plus abondant des poissons plats. Cette étude vise à évaluer le fonctionnement des habitats pour leur rôle de nourriceries, en analysant la croissance et la condition des juvéniles de sole pendant leur première année. Les données de deux séries, 1999 et 2000, de chalutages mensuels sont comparées à celles acquises lors d'une expérience de 6 mois en mésocosme impliquant l'élevage de poissons originaires de la même nourricerie. La croissance observée est comparée à la croissance potentielle, en utilisant un modèle expérimental décrivant la croissance en fonction de la température. Les soles du groupe d'âge 0 capturées dans la nourricerie atteignent une taille moyenne de 130 mm en septembre. Le taux de croissance est de 0,7–0,9 mm jour<sup>-1</sup> en été et  $\leq 0,1$  mm jour<sup>-1</sup> en automne, alors que le modèle prédit respectivement 1,4 et 0,9 mm jour<sup>-1</sup>. En mésocosme, la croissance aux mêmes saisons est de 0,9 et 0,4 mm jour<sup>-1</sup> pour des densités (300 soles 1000 m<sup>-2</sup>) environ 10 fois supérieures à celles observées dans la nourricerie. Les soles sauvages maintiennent une condition moyenne ( $K$  env. 1 g cm<sup>-3</sup>) pendant toute la saison de croissance alors que ces mêmes poissons atteignent un facteur  $K$  plus élevé pendant l'élevage en mésocosme (env. 1,2–1,3 g cm<sup>-3</sup>). La croissance en mésocosme est dépendante principalement de la température : les poissons atteignent 150–160 mm (TL) en novembre. Nous montrons ainsi que la croissance et la condition des soles sur la nourricerie sont altérées pendant toute la saison de croissance. Cette situation est amplifiée à l'automne lorsque les contraintes abiotiques et la compétition sont accrues. Ceci montre une dégradation du fonctionnement de la nourricerie et indique la vulnérabilité de ces baies face à toute contrainte supplémentaire.

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**Fig. 1.** Map of the Pertuis Breton (northern part of the Pertuis Charentais complex) showing the location of fortnightly hydrological records (H1 and H2 for the stations Mid-Pertuis and Nearshore, respectively) and of the fish sampling stations with 1 to 4 otter-trawl hauls taken in: (triangle) July–October 1999 and July–September 2000; (circle) December 1999; (square) October 2000–January 2001.

## 1 Introduction

A nursery habitat is firstly defined by local structures which determine its role in juvenile fish concentration and survival (Beck et al. 2001). The role of the habitat also depends on dynamic components, the environmental changes, which determine the extent, functional value and production of the nursery (Peterson 2003). Coastal and estuarine areas are proven suitable nursery habitats for numerous fish species, including the common sole *Solea solea*. These areas allow juvenile fishes to exploit habitat resources, in order to grow and minimise mortality over the winter. When environmental constraints temporarily impair the nursery quality, fishes' responses, integrating the habitat degradation on the time scale appropriate for growth changes, may be a good indicator of ecosystem stress (Adams 2002).

The sole, a species of prime commercial value for European fisheries, displays a wide distribution in the Atlantic Ocean, from Norway to the north-western coasts of Africa, and the Mediterranean. In the Bay of Biscay, the main nursery grounds have been localised in estuaries and bays from yearly autumn surveys (Le Pape et al. 2003a). Comparison of various biological indicators indicated quality differences between nurseries, depending on the particular estuary or bay location (Le Pape et al. 2003b; Gilliers et al. 2006). In embayed nursery areas, and especially in the Pertuis Breton (Fig. 1), young sole were found in high densities but had a poorer condition and achieved smaller mean sizes than those living in estuarine nurseries. These differences questioned habitat functioning in embayment and their consequences on fishes' responses.

The Bay of Biscay sole was thus a good candidate to investigate the potential growth of juveniles in the mid-area of the species distribution. If optimal temperatures for growth prevail, both in terms of range and length of the growing season, juveniles should be allowed to store energetic reserves and maximise their size before winter. The present study aimed to understand the way an embayed nursery area functioned (1) by comparing juveniles' growth performances in the field to predicted maximal growth rates obtained from a previous model

based on laboratory experiments, and (2) by assessing the seasonal changes in growth of mesocosm-reared juveniles of the same wild origin. In addition, indicators of possible changes in fish condition and growth rates (Fulton's  $K$  and otolith mass) were used to investigate the relationships between fish growth and habitat features and better discriminate among factors liable to drive differences in growth.

## 2 Materials and methods

### 2.1 Study area and field collections

The Pertuis Breton (Fig. 1) is a macrotidal embayment sheltered by one island (I. de Ré) and covers 376 km<sup>2</sup>, with intertidal muddy flats mostly on the coast of the mainland. It is a part of the Pertuis Charentais complex. From subtidal to deeper areas, substrates encompass muddy banks and both sandy and coarse bottoms (*Crepidula* beds), muddy pits being restricted to depths of 35–50 m. Wide expanses of oyster and mussel cultures locally modify the features of the nursery habitat. Only small rivers flow into the bay and average runoff is 72 m<sup>3</sup> s<sup>-1</sup> of fresh and brackish waters. The tidal range is 6.4 m during spring tides, which guarantees a rapid renewal of marine water, particularly in the shallowest nursery areas.

Sampling strategy was based on previous knowledge of sole distribution in the Pertuis Breton. Sole have been shown to utilise restricted intertidal and nearshore nursery areas at depths less than 20 m (e.g. Dorel et al. 1991; Van der Veer et al. 2001). In summer, sole were sampled in nearshore stations where juveniles concentrated. Autumn–winter samplings were extended from the nearshore to the deepest areas of the bay.

Two series of trawls were carried out monthly in the Pertuis Breton from July to December 1999 and from July 2000 to January 2001, except in November (Fig. 1). A small fishing boat (10 m long) allowed us to sample the subtidal nursery areas monthly, including the shallowest stations, using an otter trawl (head rope and ground rope 13 m, one tickler chain and cod-end 40 × 40 mm mesh size), lined with an inner bag of 20 mm stretched mesh. The R/V “*Côte de la Manche*” (24.70 m long) was used during the December 1999 cruise, to reach the deepest zones of the Pertuis Breton. The gear was a modified shrimp trawl with a 12.4-m head rope, a 13.2-m ground rope, one tickler chain and a cod-end of 24 mm stretched mesh. Trawling was performed during daytime and under similar tide conditions (medium spring tides, during the flood or at high tide).

One to 4 hauls were undertaken per station and each trawl lasted about 10 min. On board, all sole were counted and either all young sole were retained or subsamples were taken (Table 1). Back at the laboratory, sole were measured to the nearest 1 mm for total length ( $TL$ ) and standard length ( $SL$ ), wet-weighted ( $W$ ) to the nearest 0.1 g and individually stored to be frozen (–20 °C), except on three dates (September, October and December 1999). These samples were thawed in order to be measured like fresh fish. Measurements were corrected using fresh vs. thawed fish linear regressions, computed for  $TL$ ,  $SL$  and  $W$  from July and August 1999 samples ( $Y_{(\text{fresh fish})} = a X_{(\text{thawed fish})} + b$ , with  $a = 1.064, 1.051$  and  $1.089$ ,

**Table 1.** *Solea solea*. conditions of 1999 and 2000–2001 sampling series: Number of hauls; Depth; Number of 0-groups in samples/subsamples, in brackets: total number of soles; Range of total lengths (*TL* in mm) for 0-groups and maximum *TL* in samples.

Date	Number of hauls	Depth (m)	Number of soles 0-groups (all soles)	Size Range (mm) 0-groups (maximum <i>TL</i> - all soles)	
1999	31 Jul.	1	2	120 (274)	66–95 (188)
	28 Aug.	1	2	118 (134)	81–116 (242)
	24 Sep.	1	2	221 (240)	88–168 (21)
	30 Oct.	2	2	153 (340)	75–168 (341)
	7–9 Dec.	3	8	47 (163)	81–168 (327)
		4	14	50 (114)	102–165 (362)
	4	34	7 (111)	117–160 (461)	
2000	8 Jul.	1	2	41 (190)	52–107 (175)
	28 Jul.	1	3	62 (78)	80–122 (235)
	19 Aug.	1	2	202 / 136 (209)	66–139 (248)
	29 Sep.	2	2	217 / 78 (641)	87–165 (270)
	20 Oct.	1	2	408 / 67 (469)	95–177 (262)
		1	3	22 (30)	111–160 (315)
		1	6	80 (107)	96–195 (297)
		1	15	18 (31)	104–175 (267)
		2 Dec.	1	2	11 (17)
		1	3	81 (89)	96–162 (307)
		1	8	53 (75)	90–181 (292)
	1	15	59 (69)	84–158 (281)	
2001	31 Jan.	1	2	10 (27)	140–168 (283)
		1	3	22 (36)	113–170 (278)
		1	12	27 (41)	97–163 (274)
		1	15	47 (59)	107–170 (375)

and  $b = -0.409$ ,  $-0.166$  and  $-0.135$  for *TL*, *SL* and *W*, respectively,  $n = 177$ ,  $R^2 = 0.99$ ,  $p < 0.001$ ).

Additional information on field growth was found in otolith mass vs. total length relationships, otolith mass being a sensitive indicator of growth histories, reflecting environmental changes (Folkvord and Mosegaard 2002). The method is based on no cessation of otolith growth when somatic growth is discontinuous, so that slow or null growth in length leads to allometric changes (coupling/decoupling) in these relationships. From 1999 and 2000 field samples, 50 fishes were taken at random within the range of *TL* distributions, and left sagittae were extracted to be weighed to the nearest  $10^{-3}$  mg (otolith mass, *OW* in mg). For each year, a linear regression was fitted to the  $\log_{10}$  *OW* as a function of  $\log_{10}$  *TL*, in order to consider regression residuals.

## 2.2 Mesocosm experiment

A growth experiment was carried out from June to November 2001, in a tidal earthen pond used as a mesocosm. This pond was 180 m<sup>2</sup> in surface area and had a clay and silt bottom. It was drained in winter and spring to enhance recycling of organic components and it was then allowed to fill to a minimum depth of 0.8 m during low tides, up to 1.8 m deep when totally filled during spring tides. Coastal water was supplied by a 1.3-km channel connected to the Pertuis Breton and was naturally renewed by the tidal cycles. A screen fitted on the top of the bunghole prevented the entrance or escape of large organisms but favoured the immigration of small marine

invertebrates and the production of potential benthic prey. Except for air diffusers used to maintain a correct oxygenation, there was no other modification of pond features.

Experimental fishes were obtained as previously, by trawling in nearshore stations of the Pertuis Breton nursery, on 21 June, 5 July and 21 July (batches *a*, *b* and *c*, respectively). Each individual was measured, wet-weighted as previously (*TL* and *SL* in mm; *W* in g) and then anaesthetised in a solution of phenoxy-ethanol (2.5 ml for 10 L of sea water) to be tagged. Soft VI-alpha tags, labelled with an alphanumeric code, were used (Northwest Marine Technology, Inc.). Each fish was implanted under the skin, on the left side and mid-part of the body, just below the dorsal fin. Each batch was successively released into the pond, constituting an initial set of 120 soles, which represented a stocking density of 660 soles 1000 m<sup>-2</sup> and a biomass of 2.65 g m<sup>-2</sup>. There was no food supply apart from the natural prey produced in the pond or brought by tide currents. Fish were re-captured about every 20 nights by emptying the pond, which allowed us to identify, measure and weigh most of the fish. The experiment ended on 14 November 2001, after a maximal duration of 160 days. Sole survival was 46%. The final stocking density was 300 soles 1000 m<sup>-2</sup> or 11.2 g m<sup>-2</sup>.

## 2.3 Field and mesocosm hydrological records

Water temperature (°C), salinity (psu) and turbidity (nephelometric turbidity units, NTU) were measured fortnightly at two locations in the Pertuis Breton: in a nearshore station 1 m

**Table 2.** Experimentally established growth rates ( $\text{mm day}^{-1}$ ) for young sole across 6 temperature treatments and a 3-degree polynomial equation based on the data:  $AGR = -0.3734 \times 10^{-3}T^3 + 0.0169T^2 - 0.1384T + 0.3235$  ( $R^2 \approx 1$ ;  $p < 0.01$ ).

Temperature (°C)	Observed AGR ( $\text{mm day}^{-1}$ )
6	0.023
10	0.253
14	0.680
18	1.141
22	1.486
26	1.601

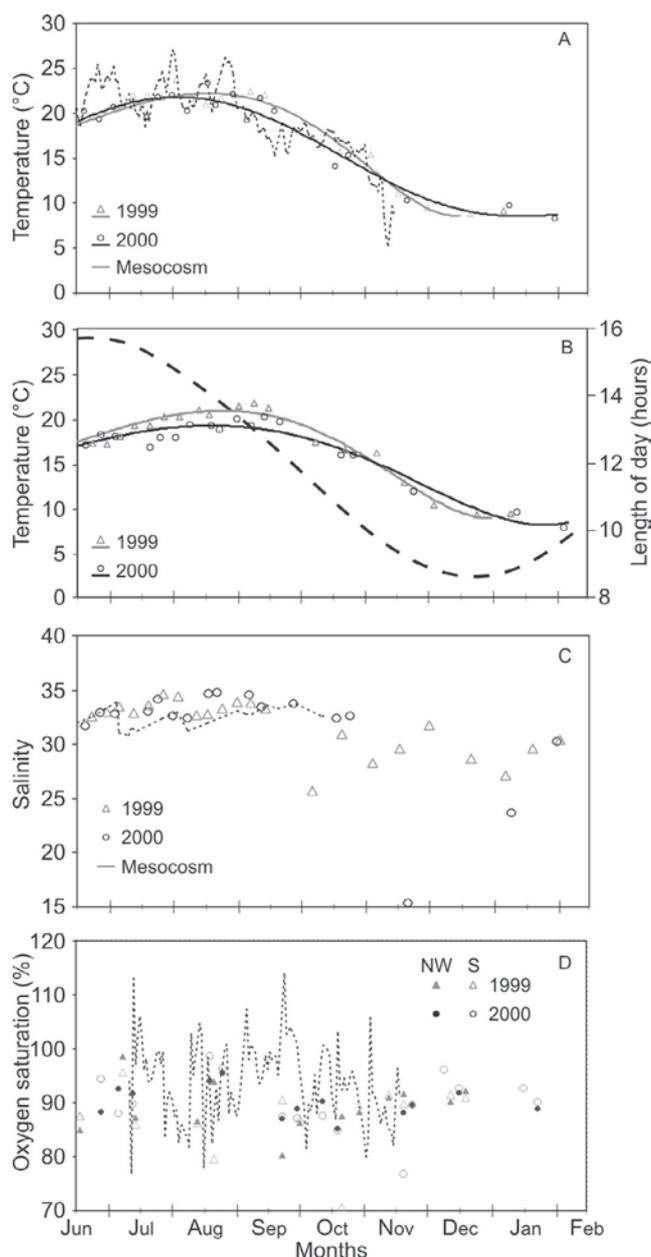
under the sea surface, close to the summer trawling area, and in a mid-Pertuis station, at a depth of 15 m (Fig. 1). No oxygen measurements were made in the Pertuis Breton when this study took place. However, a long-term series database exists for the southern area of the Pertuis Charentais (Soletchnik et al. 1998). During the mesocosm experiment, oxygen, temperature, pH and salinity were continuously recorded in the pond.

#### 2.4 Data analyses and statistics

To separate age groups which overlapped for fish sizes in the range 120–200 mm, otoliths (sagittae) were extracted. Readings were based on absence (age group 0) / presence (age group 1, 1 year) of one seasonal opaque zone (Vianet et al. 1989). Only 0-group fish were retained from samples; means and standard deviations were calculated for fish lengths and weights, both for field-sampled and mesocosm-reared fish. For both field- and mesocosm-reared young sole, we calculated the Fulton's condition index ( $\text{g cm}^{-3}$ ) as:  $K = 100 W / SL^3$  where  $W$ : wet body mass in g and  $SL$ : standard length in cm.

The mean increase in total length between two sampling dates,  $t_1$  and  $t_2$ , or absolute growth rates ( $\text{mm day}^{-1}$ ), was calculated as  $AGR = (TL_2 - TL_1) / (t_2 - t_1)$ . To compare measured AGR with values taken to describe maximal growth (rearing conditions under unlimited food supply) in relation to temperature, we used the experimentally determined relationships between growth rate and food requirement obtained across 6 temperature treatments and fitted a degree 3 polynomial equation (Table 2, after data from Rijnsdorp, pers. com. and experimental procedure given in Fonds and Saksena 1977; Fonds et al. 1992). Predicted mean seasonal growth rates were computed for the summer and autumn periods (Table 3), based on average daily temperatures measured in the mesocosm and derived from temperature models at the mid-Pertuis and nearshore stations (Figs. 2a-b).

Statistics were performed using the XLSTAT® software package. Normality and homoscedasticity were tested using, respectively, Kolmogorov-Smirnov (using Lilliefors corrected tables) and Bartlett tests. Multiple sample comparisons were performed by ANOVA with test analysis based on the Bonferroni  $t$ -test. When ANOVA assumptions (i.e. normality and homoscedasticity) were not respected, multiple sample comparisons were performed by non-parametric



**Fig. 2.** Main hydrological records taken at sea and in the mesocosm. A: Temperature fortnightly records and models (triangles/grey bold line and circles/black bold line for 1999 and 2000, respectively) in the Pertuis Breton nearshore stations and from the mesocosm (dotted line); B: Temperature at the mid-Pertuis station and changes in day length (broken line); C: Salinity measured at the nearshore field station and in the mesocosm; D: Oxygen variations (in percentage of air saturation) recorded in an embayment similar and close to the Pertuis Breton in a shallow area (plain symbol), mid-Pertuis area (open symbol) and in the mesocosm.

Kruskal-Wallis tests ( $H$  tests) followed by Dunn's test for paired comparisons. The Wilcoxon-Mann Whitney test ( $U$  test) was used for two-sample comparisons.

### 3 Results

#### 3.1 Hydrology

During the summer sampling periods, mean temperatures were 2–3 °C higher nearshore than in the mid-Pertuis stations, especially in 1999, and peaked at around 23 °C in August for both years (Fig. 2). Temperatures decreased from the autumn equinoctial changes in length of day, to stabilise at around 8–9 °C in the whole area in winter. During the 2001 mesocosm experiment, seasonal trends were similar although daily records were more variable, with maximal and minimal temperatures around 27 and 5 °C, respectively. The experiment was stopped when white frost events began in November.

In 1999 and 2000, mean salinity was relatively high in the bay and was less variable in summer as compared with autumn: 33.6 ( $\pm 0.6$ ) and 29.2 ( $\pm 7.2$ ), respectively ( $U$  tests  $p < 0.05$ ) (Fig. 2). In the mesocosm, the salinity ranged between 31 and 34 psu, and pH between 7.8 and 8.7.

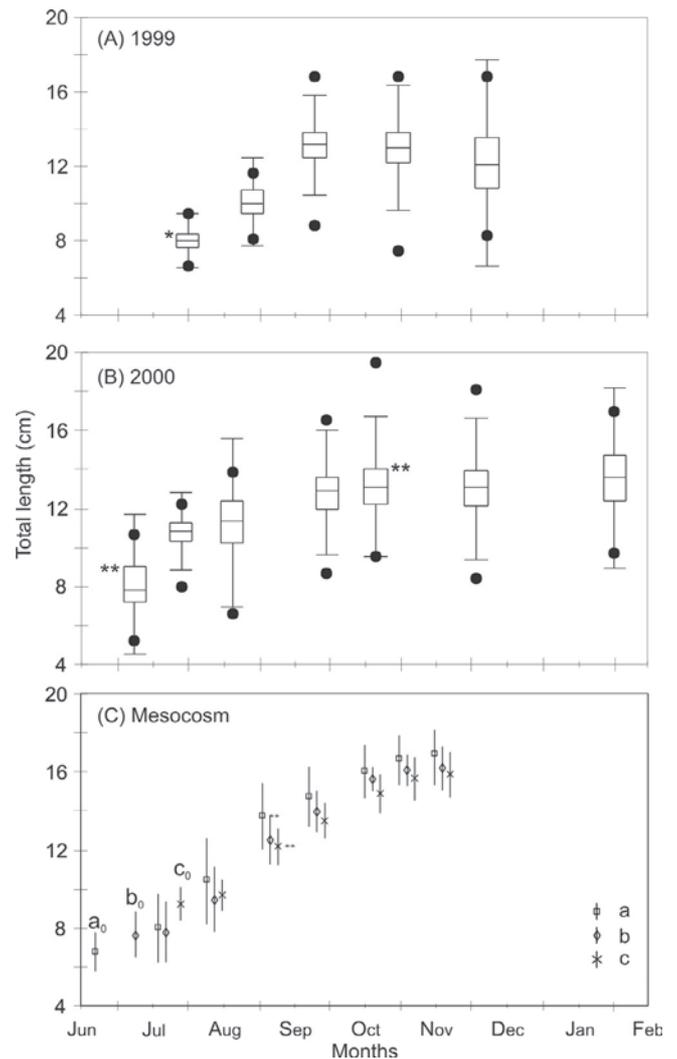
The daily mean oxygen levels usually remained above 90 and 80% air saturation in the field. In the mesocosm, daily mean oxygen levels roughly varied between 80 and 110% air saturation and three short-term hypoxic crises (under 60% for less than 4 h) were recorded, on the 27 July (min = 32%), 21–22 August (min = 29 and 49%), and 26–28 August (min = 57 and 58%) (Fig. 2). They were too brief to be significantly measured as somatic growth differences.

Concerning measurements of sea-water turbidity, those taken nearshore varied from 2.5 to 20 NTU, when mid-bay hydrological records were in the range 1.1–11 NTU (results not presented). However, no significant differences were discerned between years or seasons ( $U$  tests,  $p > 0.05$ ). Mean turbidity was 8.3 (standard deviation 4.8) NTU.

#### 3.2 Field vs. mesocosm 0-group sole growth

Box plots of total lengths indicated normal distributions, except in July 1999 and 2000 and in October 2000 (Kolmogorov-Smirnov tests,  $** p < 0.01$  and  $* p < 0.05$ ) (Fig. 3). Mean total lengths reached a plateau at ca. 130 mm in September for both years (128 and 132 mm). The highest summer mean growth rate was observed in 1999, around 0.9 mm day<sup>-1</sup>, whereas average autumn values were almost nil for both years ( $< 0.1$  mm day<sup>-1</sup>, Table 3). Expected AGR in relation to mean summer and autumn temperatures for each condition were higher than observed values, especially in autumn.

Regarding the 2001 mesocosm experiment, comparisons of  $TL$  distributions at release between dead and surviving soles did not show significant differences, which implied random mortality among the 3 initial batches ( $U = 234$  and  $335$ ,  $p > 0.05$  for the  $a$  and  $c$  batches, respectively; only 2 fish died in the  $b$  batch). When the experiment started in 2001, temperature and salinity values were similar to those measured in the field in June–July 1999 and 2000. However, each released fish batch showed a delay of at least 15 days in growth responses, compared with the following months (Fig. 3C). This indicated that wild sole needed to recover and acclimatise from trawling, tagging and capture. To take account of this recovery period, the beginning of the summer season was postponed to 18 July,



**Fig. 3.** Monthly changes in length increase of 0-group sole in the Pertuis Breton and during the mesocosm experiment. A: Box plots of total lengths (black circles represent minimum and maximum total lengths; test of normality:  $** p < 0.01$ ,  $* p < 0.05$ ); C: Mean total lengths of mesocosm-reared sole, considering three batches sea-sampled in June (batch  $a_0$ ) and July 2001 (batches  $b_0$  and  $c_0$ ). Significant differences between batches at each recapture date are given ( $** p < 0.01$ ). Vertical bars: standard deviations.

when growth resumed steadily for each batch, from 81 mm to reach 163 mm in mid-November 2001. Maximal mean growth rates were measured in August: 1.14 ( $\pm 0.28$ ), 1.18 ( $\pm 0.21$ ) and 1.01 (0.23) mm day<sup>-1</sup> for batch  $a$ ,  $b$  and  $c$ , respectively. For the summer and autumn periods, the overall mean AGR of 0.92  $\pm$  0.28 mm day<sup>-1</sup> and 0.40  $\pm$  0.25 mm day<sup>-1</sup>, respectively, were well below the expected maximal growth rates (Table 3).

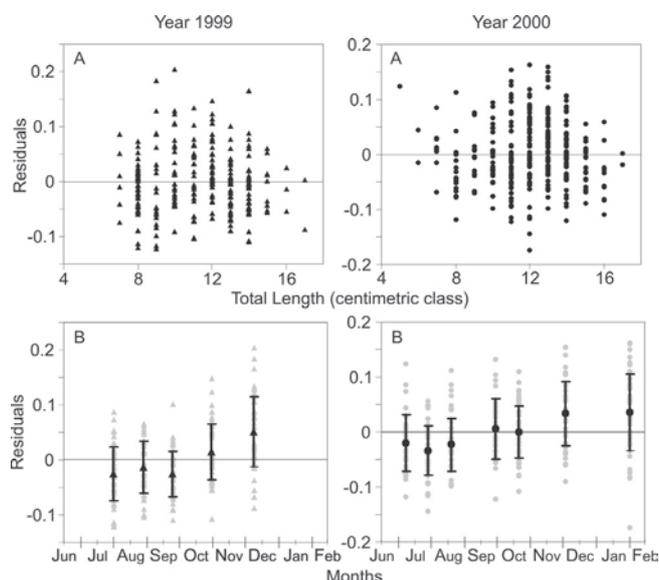
#### 3.3 Otolith vs. somatic growth (Fig. 4)

Sagitta-mass and total-length logarithmic values were linked by highly significant linear relationships ( $R^2 = 0.940$   $p < 0.01$  and  $R^2 = 0.924$   $p < 0.01$  for 1999 and 2000, respectively). ANOVA performed on residuals showed very low

**Table 3.** Changes in observed mean absolute growth rates (AGR) of wild and mesocosm-reared 0-group sole, depending on summer and autumn mean temperatures of the Pertuis Breton area and in the mesocosm, and comparisons with expected AGR computed for the same conditions.

	Period	Temperature (°C)		Absolute Growth Rate (mm day <sup>-1</sup> )		
		Mid-Pertuis	Nearshore	Observed	Expected	
					Mid-Pertuis	Nearshore
Field surveys	31 Jul.–24 Sep. 1999	20.5 (0.3)	21.7 (0.6)	0.93 (0.29)	1.38 (0.03)	1.46 (0.04)
	25 Sep.–8 Dec. 1999	15.1 (3.0)	14.4 (3.6)	0.10	0.81 (0.34)	0.73 (0.40)
	8 Jul.–29 Sep. 2000	18.8 (0.4)	20.7 (1.1)	0.65 (0.60)	1.22 (0.04)	1.39 (0.10)
	30 Sep.–2 Dec. 2000	15.8 (1.9)	13.9 (2.3)	0.09 (0.09)	0.81 (0.21)	0.67 (0.26)
Mesocosme	18 Jul.–21 Sep. 2001	21.5 (2.4)		0.92 (0.28)	1.41 (0.18)	
	22 Sep.–14 Nov. 2001	15.1 (3.4)		0.40 (0.25)	0.86 (0.34)	

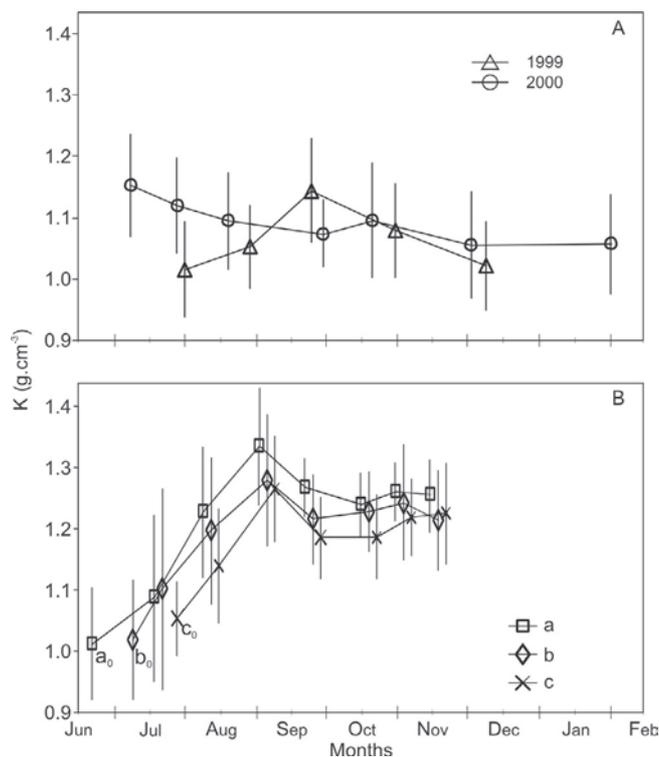
( ) Standard deviation of the mean value

**Fig. 4.** Residuals derived from the log<sub>10</sub> otolith weight vs. log<sub>10</sub> fish total length regressions plotted against fish total lengths (A) and dates (B), with seasonal trends given by mean residuals (vertical bars: standard deviations) for 1999 and 2000 field surveys.

or non-significant relationships of mean residuals against total length classes ( $R^2 = 0.047$ ;  $F = 2.370$ ;  $p = 0.04$  and  $R^2 = 0.022$ ;  $F = 1.424$ ;  $p = 0.215$  for 1999 and 2000, respectively). In contrast, relationships were significant when mean residuals were plotted against sample dates ( $R^2 = 0.254$ ;  $F = 20.652$ ;  $p \ll 0.01$  and  $R^2 = 0.217$ ;  $F = 14.242$ ;  $p \ll 0.01$  for 1999 and 2000, respectively). ANOVA analysis showed a significant difference in the monthly mean residuals for summer periods (lower, negative values), compared with autumn-winter periods (higher, positive values).

### 3.4 Field vs. mesocosm fish condition (Fig. 5)

In the field (Fig. 5A), the Fulton's condition index  $K$  in young sole varied significantly both monthly and yearly ( $H_{1999} = 228.2$ ,  $p \ll 0.01$ ;  $H_{2000} = 77.5$ ,  $p \ll 0.01$ ). Inverse trends appeared, with a maximum at the end of summer in 1999 ( $1.14 \pm 0.09$  g cm<sup>-3</sup>) and a continuous decrease from summer ( $1.15 \pm 0.08$  g cm<sup>-3</sup>) to winter in 2000. However, mean

**Fig. 5.** Comparisons between changes in Fulton's condition index ( $K$ ) measured in wild sole (A) and in mesocosm-reared 0-groups (B), with identification of the three  $a_0$ ,  $b_0$  and  $c_0$  batches as initial mean  $K$ . Vertical bars: standard deviations.

$K$  values remained within a range from 1.00–1.15 g cm<sup>-3</sup> in both years.

In the mesocosm (Fig. 5B), comparisons of  $K$  among recapture dates of pooled batches indicated significant differences ( $H = 244.5$ ,  $p \ll 0.01$ ). Mean  $K$  increased regularly from a medium initial value ( $1.01$ – $1.05$  g cm<sup>-3</sup>) to a maximum in early September ( $1.29 \pm 0.09$  g cm<sup>-3</sup>). In autumn, fish condition slowly declined and then stabilised until the end of the experiment to a narrow range of mean  $K$  values for the 3 batches, from  $1.20$ – $1.26$  g cm<sup>-3</sup> ( $H = 1.27$ ;  $1.11$ ;  $6.43$ ,  $p > 0.05$ , for the  $a$ ,  $b$  and  $c$  batches, respectively).

## 4 Discussion

Pertuis Breton represents one of the greater nursery grounds of the Bay of Biscay. However, 0-group sole are smaller in this area and this growth deficit is not compensated for in the following year, indicating durable effects of habitat constraints on fish size (Le Pape et al. 2003a). The field data presented here confirmed growth deficit and showed that wild 0-group sole did not meet their temperature-dependent physiological potential for growth. Recently, a re-appraised growth model for 0-group sole predicted a maximum possible growth rate of  $1.6 \text{ mm day}^{-1}$  (Van der Veer et al. 2001). Thermal conditions in the studied area allowed high maximal growth rates in summer (up to  $1.4 \text{ mm day}^{-1}$ ) and a protracted growing season in autumn. In contrast, lower values were observed for the summer period ( $0.6\text{--}0.9 \text{ mm day}^{-1}$ , on average) and *AGR* was close to zero in early autumn. The summer *AGR* estimated from our study was close to those reported in the same area and season from another study (Durieux et al. 2007:  $0.7 \text{ mm day}^{-1}$ ). Although summer values might be slightly underestimated due to sampling biases, wild fish often feed below laboratory conditions and have to face extra-energetic expenditures (e.g. when swimming for prey capture and predator escape), which partly explained non-maximal growth. The early growth arrest observed in autumn suggested either a photoperiod effect on growth, as suggested by Boeuf and Le Bail (1999), other non-temperature-dependent effects or fish movements. With regard to fish movements, the sampling strategy (see material and methods for details) and results based on otolith weight analysis reinforce the validity of the observed growth arrest. Due to the conservative nature of otoliths (e.g. Wright et al. 2001), changes in growth rates, and even more so a growth arrest, induce a modification of the ratio between somatic and otolith growth. This decoupling between somatic and otolith growth in autumn- and winter-sampled fish was observed for the two monthly surveys, indicating that only the otoliths continued to increase in mass while juveniles stopped growing.

The mesocosm demonstrated that fish can reach better growth than measured in the field ( $1.18 \pm 0.21 \text{ mm day}^{-1}$  when the temperature peaked in August) and maintain growth through autumn under ambient temperature and light conditions. Reared sole grew on average at lower rates than model predictions but no direct evidence allowed us to conclude on reasons for non-maximal growth (e.g. capture-recapture handlings, short-term hypoxic events or food quality). However, independently of *AGR* absolute values, the dynamic of growth variations followed the seasonal changes in temperature. In autumn, field and mesocosm situations greatly differed. Wild fish showed no growth concomitantly with a decrease in condition (Fulton's *K*). Mesocosm-reared sole both stabilised their *K* value and still increased their size, indicating that the sole were good at partitioning energy between vital functions and growth.

Comparisons of *K* between wild and mesocosm-reared sole are consistent with the conclusion that growth impairment in the field results from specific stress. In the Pertuis Charentais, *K* of around  $1.1 \text{ g cm}^{-3}$  (Durieux et al. 2007; this study) was a poor nutritional status, as shown experimentally (Fonds et al. 1989). In contrast, after being released into the

pond, the sole recovered a better condition and growth. Within 160 days, they reached the maximum *K* observed in the Bay of Biscay in late summer ( $\sim 1.3 \text{ g cm}^{-3}$  in Gilliers et al. 2006). Those high growth performances and condition level were achieved at high fish densities (300 sole  $1000 \text{ m}^{-2}$ ) as compared with commonly estimated densities on main nursery grounds (e.g. up to 31 sole  $1000 \text{ m}^{-2}$  in Pertuis Charentais, Dorel and Desaunay 1991). The reduction of some environmental constraints in the mesocosm probably contributed to enhancing sole performances (lower energy expenditures for predator avoidance and foraging, no tidal currents and limited wind stress and turbidity). Our results implied that the quantity and/or quality of available resources were sufficient in the mesocosm to sustain not only maintenance, but also biomass increase and energy store, which was not the case in the field.

In the changeable abiotic environment of coastal nurseries, complex interactions govern the level of habitat quality on which the capacity for fish to fulfil their requirements for growth and survival depends. With regard to temperature, it can be predicted from bioenergetics models that the elevation of temperatures may exert significant direct effects on growth by increasing the rates of metabolic processes (review in: Roessig et al. 2004). Temperatures toward the upper tolerance range of the fishes favour maximal growth only if other conditions are optimal and, in particular, food and oxygen supply. A metabolic scope model for sole juveniles showed that a thermal optimum for a maximal metabolic rate can be established at  $18.8 \text{ }^\circ\text{C}$  (Lefrançois and Claireaux 2003). Above this optimum, the maximal metabolic rate starts decreasing, to become nil at  $27 \text{ }^\circ\text{C}$ . The decrease in the maximal metabolic rate does not necessarily impair growth but reduces the scope for growth (see review in: Yamashita 2001). In the studied site, high summer thermal conditions (peak at  $24\text{--}25 \text{ }^\circ\text{C}$ ), beyond the optimal metabolic temperature for sole, could induce high growth rates but make fish very sensitive to any environmental constraint.

Nurseries in estuaries and bays combine chronic stress due to daily or seasonal changes not only in temperature, but also in numerous other abiotic constraints. Despite shallow-water areas being highly hydrodynamic, summer hypoxia has been recorded locally in the southernmost part of the Pertuis Charentais (Soletchnik et al. 1998). During the growing season, marine conditions develop until salinity reaches a maximum ca. 34–35 psu in August. There is no marked seasonal trend in turbidity (around 10–20 NTU, on average) but high turbidity (up to 40–80 NTU depending on the year) occurs during periods of wind-stress. Both hypoxia and elevated turbidity are intermittent events which temporally impact the nursery quality. In contrast, the salinity peak of late summer-early autumn, by adding osmoregulation costs (Boeuf and Payan 2001), seasonally enhances the effects of elevated temperature, which may partly explain progressive growth impairment.

In addition to abiotic-dependent effects in an embayed area, the Pertuis Charentais are characterised by reduced river inputs, young sole densities among the highest for the Bay of Biscay nurseries (Le Pape et al. 2003a) and intensively farmed areas. Reduced influence of river discharge has been shown to reduce young-of-the-year abundance (e.g. in the Vilaine Bay nurseries, Le Pape et al. 2003c), probably limiting

the extents of habitat and/or restraining food web production (Kimmerer 2002). The Pertuis Charentais area also hosts a considerable biomass of oysters and mussels which could modify the nursery quality (Jenkinson et al. 2007) and/or production (Leguerrier et al. 2004). Regarding density effects on young sole growth, authors have assumed from field studies that the carrying capacity of nurseries was never reached (e.g. Van der Veer et al. 2001). A nursery encompasses a multispecific community, which very probably reinforces food competition within the benthic-feeder assemblages (invertebrates and vertebrates) and contrasts with mesocosm conditions. Low inter-specific competition for food and habitat was hypothesised because of limited trophic overlap among flatfish species (e.g. Amara et al. 2001). However, juvenile fishes have a narrow potential prey range compared with older fishes (Piet et al. 1998) and prey abundance may readjust the degree of dietary overlap (Carter et al. 1991). Following Fonds and Saksena (1977), a 130-mm-long (TL) sole at 15 °C water (average fish size and autumnal temperature in the Pertuis Breton nursery) enhances its food consumption by almost 60% when compared with its summer status (80 mm long and 21 °C). It suggests a sole population energetic demand increase during nursery occupancy. If prey are limiting, they are throughout the seasons because a non-optimal condition index and non-maximal growth were measured over the whole growing season, and this limitation might be exacerbated in autumn when the competitive biomass reaches its maximal value and/or prey availability is minimal.

From this approach to growth in Bay of Biscay sole, it can be concluded that Pertuis Breton nursery offers non-optimal conditions for growth over the whole growing season. The fish condition status indicates that the way the habitat functions becomes altered in the course of the season of normal nursery occupancy, during which time the sum of environmental constraints tends to increase. The poor nutritional status could dramatically lower over-winter survival of the sole juveniles. Fish survival being tightly linked to growth, any environmental modifications that negatively impact growth could also lead to a negative impact on recruitment. The study suggests that, in the context of planning coastal management in shellfish-dominated bays, the addition of any further constraint could exceed the nursery capacity for conservation.

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