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**Aquatic
Living
Resources**

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

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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^{-1} in summer and $\leqslant 0.1$ mm day^{-1} in autumn, when the model predicted 1.4 and 0.9 mm day^{-1}, respectively. In the mesocosm, the growth rates were 0.9 and 0.4 mm day^{-1} for the same seasons and for stocking densities (300 fish 1000 m^{-2}) about 10 times higher than usually recorded in the field. Wild sole remained in medium condition (K ca. 1 g cm^{-3}) during the entire growing season, whereas they attained a higher K after being released into the mesocosm (1.2–1.3 g cm^{-3}). 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^{-1} en été et $\leqslant 0,1$ mm jour^{-1} en automne, alors que le modèle prédit respectivement 1,4 et 0,9 mm jour^{-1}. En mésocosme, la croissance aux mêmes saisons est de 0,9 et 0,4 mm jour^{-1} pour des densités (300 soles 1000 m^{-2}) environ 10 fois supérieures à celles observées dans la nourricerie. Les soles sauvages maintiennent une condition moyenne (K env. 1 g cm^{-3}) 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^{-3}). 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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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 TL - 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)	110–172 (282)
		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^2 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-weighed 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^{-2} and a biomass of 2.65 g m^{-2}. 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^{-2} or 11.2 g m^{-2}.

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

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 (± 0.6) and 29.2 (± 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^{-1}, whereas average autumn values were almost nil for both years (<0.1 mm day^{-1}, 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,
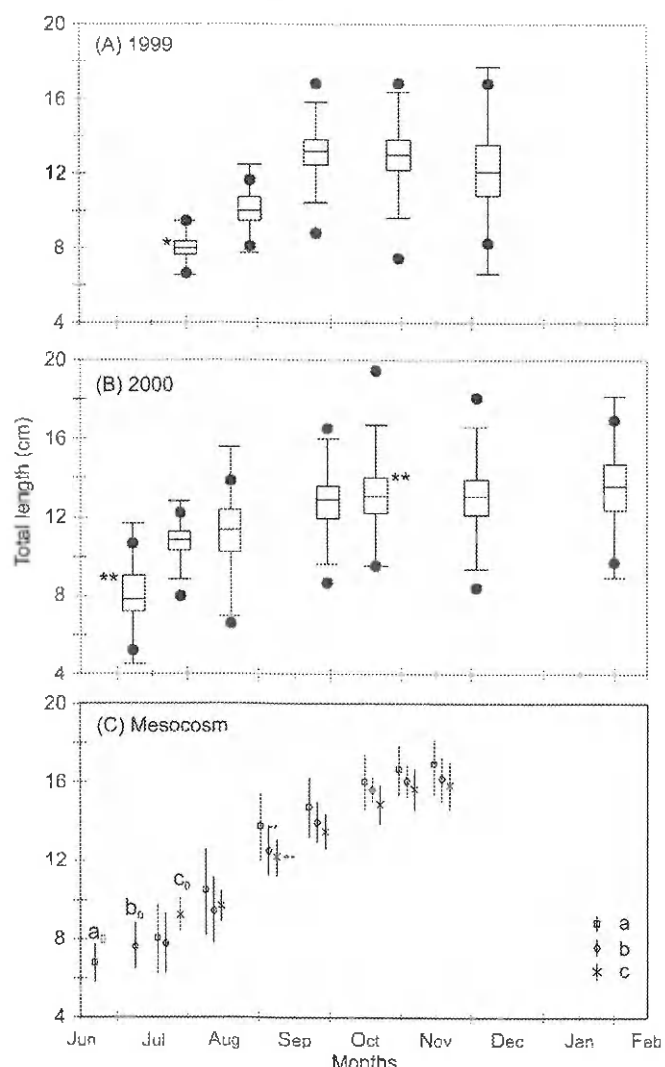
Fig. 3. Monthly changes in length increase of 0-group sole in the Pertuis Breton and during the mesocosm experiment. A: Box plots of total lengths (black circles represent minimum and maximum total lengths; test of normality: ** $p < 0.01$, * $p < 0.05$); C: Mean total lengths of mesocosm-reared sole, 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 (± 0.28), 1.18 (± 0.21) and 1.01 (0.23) mm day^{-1} for batch a, b and c, respectively. For the summer and autumn periods, the overall mean AGR of 0.92 ± 0.28 mm day^{-1} and 0.40 ± 0.25 mm day^{-1}, 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

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 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 mm day^{-1}) and a protracted growing season in autumn. In contrast, lower values were observed for the summer period (0.6–0.9 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 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 ± 0.21 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 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 (~1.3 g cm^{-3} in Gilliers et al. 2006). Those high growth performances and condition level were achieved at high fish densities (300 sole 1000 m^{-2}) as compared with commonly estimated densities on main nursery grounds (e.g. up to 31 sole 1000 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 °C (Lefrançois and Claireaux 2003). Above this optimum, the maximal metabolic rate starts decreasing, to become nil at 27 °C. The decrease in the maximal metabolic rate does not necessary impair growth but reduces the scope for growth (see review in: Yamashita 2001). In the studied site, high summer thermal conditions (peak at 24–25 °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

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