
Sedentary behaviour establishment in 0-group common sole *Solea solea*: a laboratory video-tracking study

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Abstract:

Spontaneous swimming activity of 0-group common sole (*Solea solea*) was evaluated using a video-tracking system under laboratory conditions. An experiment was conducted during two consecutive days on individuals sampled in June, July, September and November (2004) in a coastal nursery ground (Pertuis Charentais, Bay of Biscay, France). The measured behavioural variables were: distance travelled and frequency of occurrence of burying, swimming and immobility. 0-group sole showed a relatively clear circadian activity in line with the artificial light conditions (day, twilight and night). Swimming activity of 0-group sole decreased drastically from June to July, thereafter remaining at a very low level in September and November. Such important changes reflect the transition between the exploratory behaviour of the post-colonization period and a well established sedentary behaviour remaining until the onset of winter. These results highlight the potential limitation in habitat use capacities of 0-group sole once settled in coastal nursery grounds.

Keywords: behaviour; flatfish; juvenile; swimming activity; video-tracking

35 **Introduction**

36 Juveniles of many marine fishes and especially flatfishes inhabit coastal areas (*e.g.* estuaries
37 and shallow water bays) where they find generally more abundant food, lower predation risks
38 and higher temperatures than in offshore areas (Gibson, 1994). However, in these essential
39 habitats, fish juveniles have also to face highly variable environmental factors and
40 superimposed anthropogenic activities that may jeopardize survival and influence recruitment
41 into the adult population (Beck *et al.*, 2001). Fish habitat utilization reflects trade-offs
42 between spatial distribution of essential resources, the internal state of the organism, and
43 tolerance to ambient conditions (Huntingford, 1993). In order to achieve habitat conservation
44 and sustainable fisheries management, it is therefore critical to understand fish juveniles
45 behaviour in term of spatio-temporal dynamics within these coastal habitats (Rice, 2005).

46

47 Common sole, *Solea solea* (L.) is a widely distributed and most economically important
48 flatfish species of the North East Atlantic region. Most common sole stocks are reported to be
49 overexploited (ICES, 2005). Previous both field and laboratory studies have focused on the
50 behavioural processes occurring in 0-group juveniles during the short colonization phase
51 (Champalbert & Koutsikopoulos, 1995, Amara *et al.*, 2000). Once settled in shallow coastal
52 areas individuals have to face a variety of natural and anthropogenic stressors that may impact
53 their survival. However, apart from field studies that have focused on their spatio-temporal
54 distribution till autumn (Dorel *et al.*, 1991, Rogers, 1992, Jager *et al.*, 1993) and some other
55 rare studies that have inferred indirectly about their movements capacities using conventional
56 (Coggan & Dando, 1988) or natural (Vinagre *et al.*, 2008) tags, little is known on 0-group
57 sole behavioural activities during the post-colonization period.

58

59 Therefore, the present study aimed at bringing new insights on 0-group sole swimming
60 behaviour during the sensitive post-colonization period in order to better understand
61 dynamics of individuals in shallow coastal areas. A laboratory video-tracking system was
62 developed to measure the spontaneous swimming and burying activity. Since behavioural
63 patterns in fishes generally vary on a diel cycle, experimental set up was designed to measure
64 behavioural activities during two consecutive days according to light period of the day (day-
65 twilight-night). 0-group common sole were caught throughout four different months after
66 colonization until the onset of winter (*i.e.* June to November) in an Atlantic nursery ground
67 (Pertuis Charentais, Bay of Biscay, France). In this region, colonization is centred around
68 May so that, it is likely that individuals belong to the same cohort. Therefore, it was
69 hypothesized that sampling month may be used as proxy of age / ontogenetic status. The
70 objectives were to establish the baseline levels of these natural activities in 0-group sole (*i.e.*
71 normal/spontaneous behaviour) and test the effect of the ontogenetic status (sampling month)
72 on these activities according to light periods under constant experimental conditions
73 throughout the post-colonization period.

74

75 **Materials and methods**

76 This study was conducted under the approval of the Animal Care Committee of France under
77 the official licence of M.L. Bégout (17-010).

78

79 **Fish origin and maintenance**

80 Thirty-one wild 0-group juveniles were caught in the Pertuis Charentais, a main sole nursery
81 ground for the Bay of Biscay (Le Pape *et al.*, 2003), in June, July, September and November
82 2004 in a mussel pole-culture area (46° 15' 80"N, 1° 13' 40"W) using a push net to avoid

83 injuries to the fish (Durieux *et al.*, 2007). At the video-tracking laboratory, fish were
84 maintained in aerated tanks (45x30x35 cm) with filtered sea water (temperature: 20 ± 1 °C;
85 salinity: 35 ± 1 ; oxygen concentration: 100 % air saturation) and a sand substratum (light
86 colour). Both temperature and salinity were set to constant value as a mean of disconnecting
87 the experiment from field conditions in a consistent way for all the fish. Fish were fed daily
88 with frozen *Tubifex*. They were maintained under these conditions for at least 10 days
89 acclimatization prior experimentation in order to avoid tidal rhythm effects (Gibson, 1973,
90 Burrows, 1994) that could eventually prevent comparisons between months. An artificial
91 photoperiod was applied: daylight period (8:00 – 21:00), a twilight transition period (7:00 –
92 8:00 and 21:00 – 22:00) and a night period (22:00 – 07:00).

93

94 **Video-tracking set-up and experimental protocol**

95 In the video tracking laboratory (isolated from external disturbances): three black circular
96 arenas of 60 cm diameter, with walls drilled regularly with 5 mm diameter holes to allow
97 water circulation, were placed individually in a 400 l tank with aeration and water filters that
98 maintained a continuous water flow around the arena. A 5 cm deep layer of black sand (100
99 to 300 μm) was placed on the bottom of the arena in order to allow sole to bury and to
100 provide an adequate colour contrast to allow fish detection by the image analysis system.
101 Water was maintained at temperature around 20 ± 1 °C (by an air conditioning system in the
102 laboratory); salinity at around 35 ± 1 psu (by regularly changing sea water and when needed
103 adjusting salinity with freshwater to compensate for evaporation); and oxygen concentration
104 at around 100% air saturation (using air aerator systems). The arenas were illuminated
105 laterally by artificial light with the same photoperiod used during maintenance of the fish:
106 daylight period (8:00 – 21:00; white light: 0.3×10^{15} $\text{Q}\cdot\text{cm}^{-2}\cdot\text{s}^{-1}$), a twilight transition period
107 (7:00 – 8:00 and 21:00 – 22:00; white light: 0.3×10^{14} $\text{Q}\cdot\text{cm}^{-2}\cdot\text{s}^{-1}$) and a night period (22:00 –

108 07:00; infrared light (PAR38 IR 175): $0.14 \times 10^{14} \text{ Q.cm}^{-2} \cdot \text{s}^{-1}$). Since fish are not sensitive to
109 infrared light (Douglas & Hawryshyn, 1990), nocturnal behaviour was considered un-altered
110 by the artificial lighting used to assess nocturnal swimming. Fish were not fed the day before
111 the experiment nor during the subsequent video recordings.

112 Above each arena, a digital black and white high sensitivity camera (Sony XCD-X700, XGA)
113 linked to a computer equipped with Visilog 6.2 software (NOESIS, France) was mounted.
114 Image acquisition proceeded with cyclic sub-sampling of each arena with 33 s duration
115 sequences of 1 image s^{-1} and each image was saved in .jpeg format. Successive sequences
116 relative to a same arena were separated by a time lag of 2 min because of a 7 s delay between
117 each sequence acquisition. The resulting sub-sampling factor (SSF) was 1/3.6. For each
118 month, at 11:00, the day of the beginning of recording, one fish was introduced per arena, so
119 that three fish were recorded at a time. Videos were then recorded for 48 hrs duration. After
120 video recording, fish were individually measured (to 1 mm, standard length SL) (Table 1). To
121 complete each month group, successive recordings took up to 8 days.

122 Fish detection was based on the colour contrast between the fish (appearing in white) and the
123 black sandy bottom using image analysis (Visilog 6.2). The XY coordinates (mm) of the
124 barycentre of the detected fish shape were extracted for each image / time. An integrated
125 VBA module to Visilog 6.2, developed by NOESIS for this experiment, allowed automation
126 of the acquisition and image treatment process.

127

128 **Data analysis**

129 Five to ten individuals per month (June, July, September, November) *i.e.* around 1, 500 hrs of
130 video-tracking were analysed (Table 1). Based on XY coordinates, four behavioural
131 endpoints could be obtained: the distance travelled between consecutive images (D_i) and the
132 frequency of occurrence of three different activities: swimming (S_i), burying (B_i), and

133 immobility (I_i). When the fish was not detected, XY coordinates equalled 0, and the fish was
 134 considered buried. When fish was detected but distance travelled between two consecutive
 135 images was $\leq 5 \text{ mm s}^{-1}$ (limit of motion detection of distance travelled between two
 136 consecutive images) fish was considered immobile. Alternatively when distance travelled was
 137 $> 5 \text{ mm s}^{-1}$ fish was considered swimming. Distance travelled were transformed in body
 138 length (Bl) to avoid any effect of size on swimming speed (Peck *et al.*, 2006). For each
 139 individual fish, hourly values of the four variables were calculated:

$$140 \quad D_h = \frac{1}{SSF} \sum_{i=1}^n D_i$$

$$141 \quad S_h = \frac{1}{n} \times 100 \sum_{i=1}^n S_i$$

$$142 \quad B_h = \frac{1}{n} \times 100 \sum_{i=1}^n B_i$$

$$143 \quad I_h = \frac{1}{n} \times 100 \sum_{i=1}^n I_i$$

144 with SSF: sub-sampling factor; n: number of observations per hour; i: individual observation
 145 per sec.

146 D_h is expressed in Bl h^{-1} and S_h , B_h and I_h are expressed in percentage.

147

148 Using all 48 hrs observations, individual data were averaged for specific light periods (day,
 149 twilight and night) prior analysis. Given the nature of the data, *i.e.*, non-independent light
 150 periods, one-way repeated measures ANOVAs was used to test differences for each
 151 behavioural variable (D, S, B and I) between month groups (between-subject factor: June,
 152 July, September, October) and light periods (within-subject factor: day, night, twilight) as
 153 well as interaction of both factors. Data were tested for normality with a Shapiro-Wilk test
 154 and for homoscedasticity with a Bartlett's test. Since data could not meet assumptions they
 155 were ranked prior analysis (Kane *et al.*, 2004). Homogeneous groups were determined with

156 the *a posteriori* multiple comparisons Newman and Keuls tests. Results are given as averages
157 \pm SE (Standard Error). Statistical tests were performed using XLStat software and Systat.
158 Tests were considered significant at $p < 0.05$.

159

160 For derived instantaneous swimming speeds, only values $> 5 \text{ mm s}^{-1}$ (limit of motion
161 detection of distance travelled between two consecutive images) were considered. Swimming
162 speed frequencies were calculated for the different month groups with individual speed
163 classes of 2 cm s^{-1} and a range of 0.5 to 20 cm s^{-1} .

164 **Results**

165 Significant differences were detected for both factors (*i.e.* sampled months and light periods)
166 for all measured behavioural variables D, B, S and I (Table 2; Figure 1). Independently of the
167 light periods, D and S decreased significantly between June and July, while B increased
168 significantly. Between July and September, D, S and I decreased significantly, while B
169 increased significantly. The pattern observed for these four variables was independent from
170 the light periods. Between September and November, B decreased significantly and I
171 increased significantly independently of the light periods for both variables whereas no
172 difference was detected for D and S. D and S were significantly higher at night and twilight
173 than during the day, B was significantly lowest at night, intermediate at twilight and highest
174 during the day independently of sampled months. I was significantly highest at night
175 independently of sampled months.

176 For fish sampled in June, swimming speed frequencies displayed a bimodal distribution
177 (Figure 2). The first mode for speed comprised between 0.5 - 2 cm s^{-1} (0.4 Bl s^{-1}) and a second
178 for speed of 8 - 10 cm s^{-1} (2.2 Bl s^{-1}), each representing 25% of the overall swimming speeds.

179 For fish sampled in July, September and November, swimming speed frequencies displayed a
180 unimodal distribution with 50-60 % of swimming speeds between 0.5-2 cm s⁻¹.

181

182 **Discussion**

183 Our data were obtained under experimental conditions using a video tracking system at a
184 scale of observation enabling the assessment of daily spontaneous swimming activities
185 (levels, rhythms) of 0-group common sole for the first time. This method appears to be one of
186 the only non-harmful methods of quantifying free activity of 0-group sole. However, caution
187 should be applied in extrapolating these data to field observations. Swimming activity over
188 two days showed relatively high inter individual variability as often observed for fish (Bourke
189 *et al.*, 1997, Salvanes & Hart, 1998, Mehner, 2006). Body size is well known to influence fish
190 swimming activity so that in our study we used relative distance travelled in proportion of
191 body size in order to minimize size effect within and between sampled months. Alternatively
192 it is important to consider that the low sample size routinely employed in behavioural studies
193 (here five to ten replicates per sampled month) and often due to technical constraints might
194 also have the effect of rising the variability. Nevertheless, some clear temporal trends in the
195 behavioural activities from the post-colonization period till autumn were observed.

196

197 0-group sole showed a relatively clear circadian activity in line with the artificial light
198 conditions of the experiment, with higher swimming activity at night and twilight than during
199 the day and alternatively more burying activity during the day than during the night. This
200 nocturnal activity pattern is consistent with previous studies on young 0-group sole
201 (Macquart-Moulin *et al.*, 1991, Champalbert & Marchand, 1994, Champalbert &
202 Koutsikopoulos, 1995), older 2-group (Lagardère *et al.*, 1988, Laffargue *et al.*, 2006) and in
203 general in other flatfishes (Gibson, 1973, Burrows, 1994, Hurst & Duffy, 2005). Champalbert

204 et al. (1991) demonstrated that sole > 30 mm were photonegative at most light intensities
205 except at twilight. In the field, in addition to circadian rhythms, flatfishes display tidal
206 rhythms in swimming activity which has been shown for juveniles to correspond to a trade-
207 off between foraging, predator avoidance and the selection of suitable environmental
208 conditions (Burrows, 1994, Gibson *et al.*, 1998). In our study, fish were acclimatize for ten
209 days prior experiment in order to prevent any confounding effect of tidal rhythms between
210 sampled months.

211

212 Burying behaviour represented 80% of the activity in autumn months (September and
213 November). This behaviour is linked to a strategy for predation avoidance (Gibson, 1997) but
214 also energy saving with lower basal metabolism while buried (Howell & Canario, 1987). Sole
215 from June and July buried clearly less than fish from September and November. The later
216 were often immobile at the surface of the substratum, especially at night. As burying capacity
217 of juvenile flatfish is a strong logistic function of body size relative to the sediment grain size
218 (Gibson & Robb, 1992), June and July fish, due to their relatively small size, are likely to
219 have been limited by the size of the sand grains used in the experiment (100-300 μm).

220

221 The 0-group sole showed a strong decline in swimming activity from June to July (around 8
222 fold in distance travelled and 4 fold in % swimming), with very low activity remaining until
223 November. This drastic change was also observed in term of swimming speed frequency
224 distributions. Individuals sampled in June displayed a high proportion of fast swimming
225 speeds (around 10 cm s^{-1} or 2 Bl s^{-1}) that typically corresponds to off bottom swimming with
226 large scales movements (Champalbert & Koutsikopoulos, 1995, Hurst & Duffy, 2005)
227 whereas from July onwards the majority of swimming speeds were lower than 2 cm s^{-1} which
228 is characteristic of the foraging behaviour of juvenile flatfish searching for benthic prey

229 (Lagardère *et al.*, 1994, Hill *et al.*, 2000, Hill *et al.*, 2002). Both environmental (i.e. current,
230 salinity, light, and food availability) and endogenous factors are considered to play a
231 determinant role in nursery colonization (Champalbert & Koutsikopoulos, 1995). Here,
232 experimental conditions were the same for all sampled months so that we assume that our
233 observations reflect an ontogenetic change in swimming activity. 0-group sole juveniles in the
234 Bay of Biscay colonize nursery grounds around May (Amara *et al.*, 2000). Around one month
235 post-colonization, 0-group sole juveniles still demonstrate a relatively high swimming
236 activity. This behaviour may be a relic of an exploratory behaviour associated with
237 colonization of new habitat (Hurst & Duffy, 2005). Low activity from July onwards may
238 reflect the transition to a well established sedentary behaviour. From an ecological point of
239 view, this behaviour may be interpreted as giving a relatively high resiliency of 0-group sole
240 in confined areas of the shallow coastal habitat. This is consistent with field observations of
241 potential 0-group sole movements in different nursery grounds based on density distributions
242 (Dorel *et al.*, 1991, Rogers, 1992, Jager *et al.*, 1993), recapture of tagged individuals (Coggan
243 & Dando, 1988) and use of natural tags (Vinagre *et al.*, 2008).

244

245 In the field it has been reported that 0-group sole operate migration to deeper waters prior to
246 winter in order to avoid very low water temperature occurring in shallow part of the habitat at
247 this time (Dorel *et al.*, 1991, van der Veer *et al.*, 2001). Since we did not observe any
248 increase in swimming activity at this time under constant experimental conditions, this
249 suggests that such migratory behaviour prior to winter is mainly influenced by hydro climatic
250 factors.

251

252 In conclusion, using a laboratory video-tracking system this study provides a quantified
253 spontaneous swimming activity baseline levels of 0-group common sole through their first

254 period of life in coastal shallow areas. 0-group sole showed a clear ontogenetic change in
255 swimming activity between June and July, demonstrating the transition between the
256 exploratory behaviour of late colonization and the well established sedentary behaviour till
257 the onset of winter. These results highlight the potential movements limitation of 0-group sole
258 in coastal areas during this highly critical period.

259

260

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268

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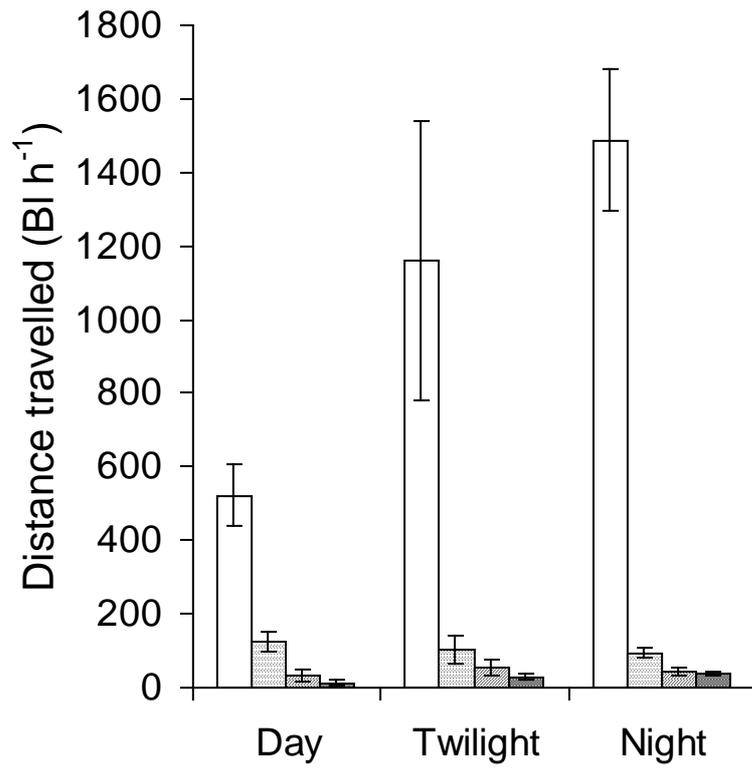
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372

372 Fig. 1. Average distance travelled (Bl h^{-1}) (A) and frequency occurrence (%) for the three
373 different types of activity swimming (B), burying (C) and immobility (D) per sampled month
374 and light period for 0-group common sole *Solea solea* captured in 2004 in the Pertuis
375 Charentais area (France). Artificial light time period was set as: Day: 8:00 – 21:00; Twilight:
376 7:00 – 8:00 and 21:00 – 22:00; Night: 22:00 – 7:00. Values were calculated on the total 48
377 hours observation period.

378

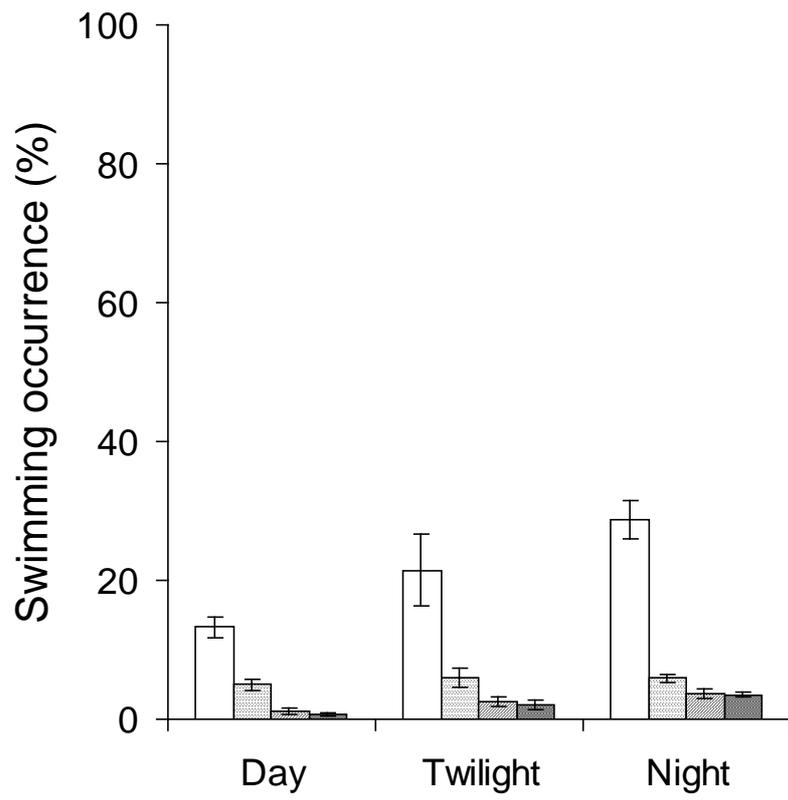
379 Fig. 2. Swimming speed (cm s^{-1}) frequency distribution calculated on the total 48 hours
380 observation period for each sampled month of wild-caught individuals captured in the Pertuis
381 Charentais area (France). 10 cm s^{-1} corresponds to 2.2, 2.0, 1.4 and 0.9 Bl s^{-1} in June, July,
382 September and November respectively.



383

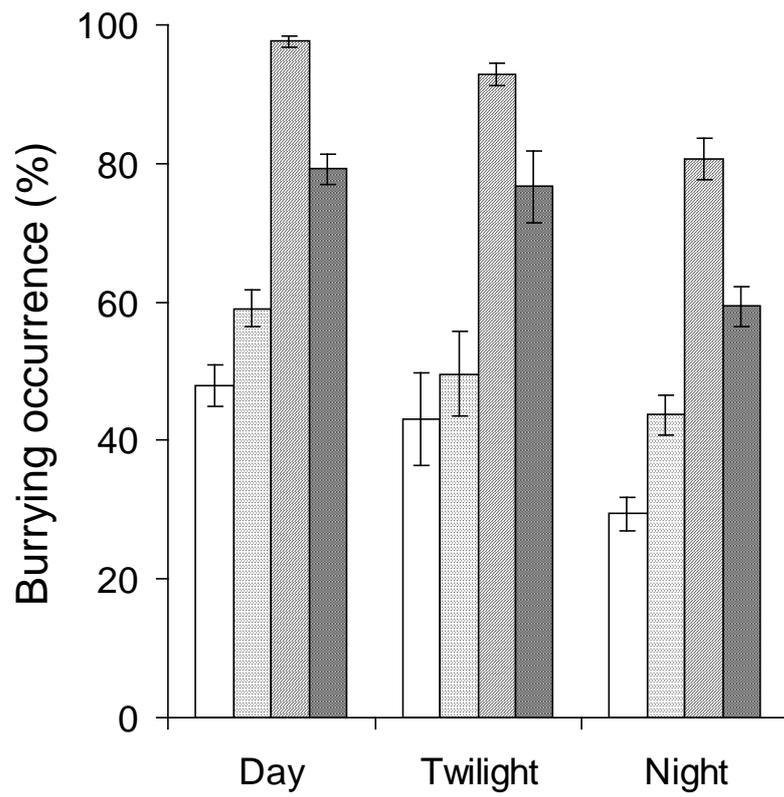
384 Fig. 1A.

385



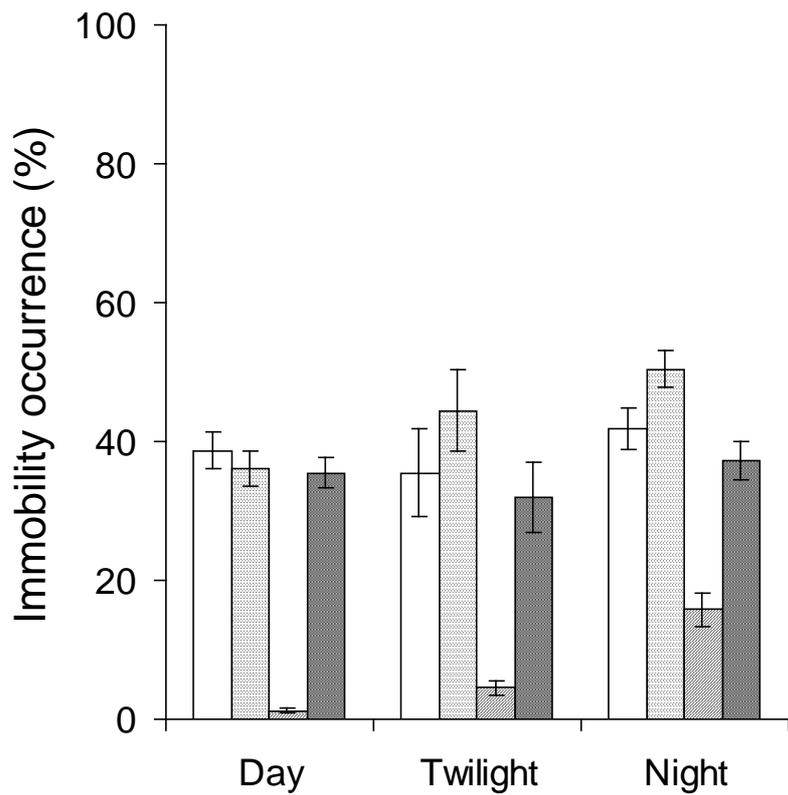
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386 Fig. 1B.



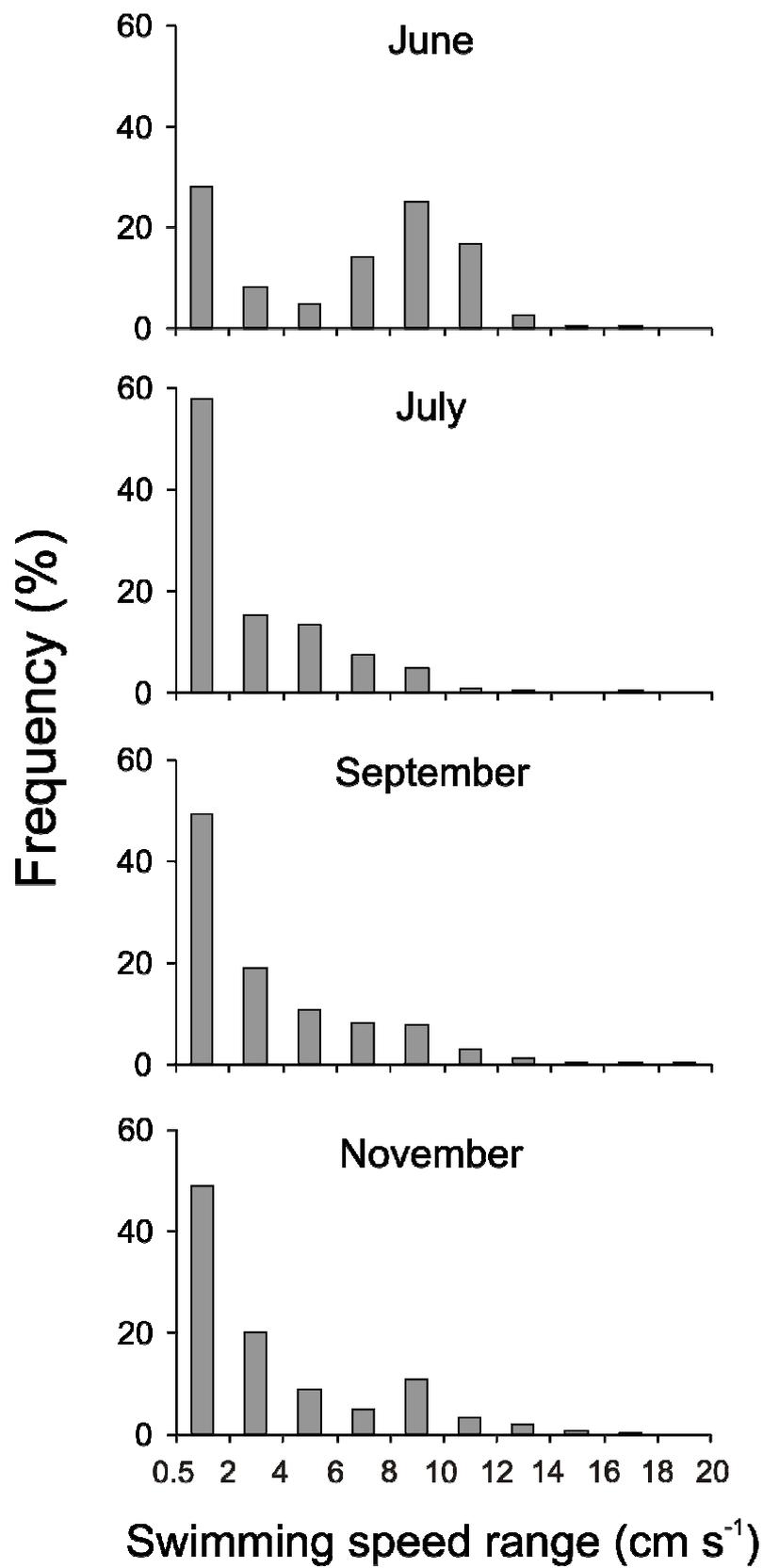
387

388 Fig. 1C.



389

390 Fig. 1D.



391

392 Fig. 2.

393 Table 1. Sample size (n), mean standard length (SL \pm SE (mm)), and size range of 0-group
 394 common sole, *Solea solea* sampled in 2004 in the Pertuis Charentais nursery ground (France)
 395

Sampled month	n	SL \pm SE (mm)	Range (mm)
June	7	46.00 \pm 1.23	41 - 50
July	9	51.22 \pm 1.97	44 - 63
September	5	72.20 \pm 1.43	69 - 76
November	10	108.80 \pm 3.21	96 - 125

396

397 Table 2. Results of one-way repeated measures ANOVAs testing differences in mean behavioural variables (Distance travelled and Swimming,
 398 Burying and Immobility occurrences; ranked transformed data) between months (between-subject factor), light periods (within-subject factor)
 399 and interaction of both factors for 0-group common sole, *Solea solea* sampled in the Pertuis Charentais nursery ground (France). Multiple
 400 comparisons Newman and Keuls tests posthoc Abbreviations are as follows: Jn: June, Jl: July, Sept: September, Nov: November; Twi: Twilight
 401 period.

<i>Distance travelled (Bl h⁻¹)</i>					<i>Swimming occurrence (%)</i>			
<i>Source</i>	<i>df</i>	<i>F</i>	<i>P > F</i>	<i>Newman and Keuls</i>	<i>df</i>	<i>F</i>	<i>P > F</i>	<i>Newman and Keuls</i>
Month	3 - 27	10.48	<0.001	Sept = Nov < Jl < Jn	3 - 27	12.37	<0.001	Sept = Nov < Jl < Jn
Period	2 - 54	5.72	0.006	Day < Twi = Night	2 - 54	11.99	<0.001	Day < Twi = Night
Month x Period	6 - 54	1.14	0.354	ns	6 - 54	1.38	0.236	ns

<i>Burying occurrence (%)</i>				<i>Immobility occurrence (%)</i>				
<i>Source</i>	<i>df</i>	<i>F</i>	<i>P > F</i>	<i>Newman and Keuls</i>	<i>df</i>	<i>F</i>	<i>P > F</i>	<i>Newman and Keuls</i>
Month	3 - 27	7.33	0.001	Jn < Jl < Nov < Sept	3 - 27	5.11	0.006	Sept < Nov < Jl = Jn
Period	2 - 54	17.54	<0.001	Night < Twi < Day	2 - 54	11.54	<0.001	Day = Twi < Night
Month x Period	6 - 54	0.46	0.834	ns	6 - 54	1.49	0.200	ns

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