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1 **Amphidromous Fish School Exploratory and Instantaneous Swimming Speeds in**
2 **Shallow Water Coastal Lagoon Channels**

3
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25 **Abstract** Although the estimation of *in situ* swimming speed of a fish school remains seldom
26 documented, this elementary information is needed concerning gregarious fish species
27 behavioural purposes, ecological and management studies. This study analyses data collected
28 *in situ* for small pelagic fish schools in two shallow water lagoon channels using multibeam
29 sonar. In horizontal beaming, the high resolution sonar covers the whole cross part of the
30 channels, providing dynamic echo traces of mobile fish schools which permit the gathering of
31 information on them during their passage inside the channels. Two school swimming speed
32 indicators are distinguished: the average of a series of instantaneous speed values (ISS, based
33 on successive measurements) and the exploratory speed (ESS, based on the total observation
34 time). These swimming speeds are estimated for each observed fish school according to their
35 Euclidian position within the sonar beam and the ID ratio defined as the average of ISS values
36 divided by the ESS, is calculated as an indicator of the trajectory of the displacement of the
37 school. The amphidromous fish schools average ISS values per school vary from 0.15 m.s^{-1} to
38 a maximum of 4.46 m.s^{-1} while on the other hand; ESS per school varies at lower level
39 amplitude from 0.04 m.s^{-1} to a maximum of 3.77 m.s^{-1} . A majority of fish schools exhibit an
40 ID value demonstrating an oriented swimming behaviour through the channel related to the
41 migration process. This trend appears as an intrinsic property of school movements according
42 to the sampling period, while 36% differ from this general trend. This result comforts the
43 ‘multi-transit’ hypothesis, as all schools do not show a directional trajectory assumed as
44 representative of active migration behaviour. This result, however, does not allow a
45 quantitative estimation of the part of schools migrating actively (*i.e.* the migration flow), but
46 it permits a qualitative interpretation of this pattern. However, the sampling design should
47 allow one to obtain a quantitative estimation of the flow. The presentation of this
48 methodology and the continuous improvements multibeam sonar technologies foresee, allow
49 henceforth the measurements of fish school swimming speed in their habitat at a small spatio-

50 temporal scale, as well as for large individual fish and marine megafauna. Our methodology
51 can be carried out to analyse movement characteristics of large fishes and small schools in
52 their habitat and has a wide range of applications in the scope of behavioural studies in an
53 ecosystemic approach such as for management purposes.

54

55 **Keywords:** gregarious fish · migration · multi-transit · behaviour · lagoon · sonar.

56

57

58 **Introduction**

59

60 The use of the active underwater acoustics has significantly increased over the course of time,
61 enabling nowadays the study of both single fish and fish school behaviours in various aquatic
62 ecosystems. In lakes, rivers and estuaries, *in situ* studies (counting, swimming behaviour,
63 geographical distribution in the habitat, circadian behaviour) of both fishes and schools using
64 echosounder, have increased over the past few years (*e.g.* Gerlotto et al. 1992; Duncan and
65 Kubecka 1996). Moreover, the development of the technology has allowed a shift from
66 descriptive to quantitative studies (*e.g.* Stieg and Johnston 1996; Gauthier et al. 1997; Maes et
67 al. 1999). Subsequently, due to the use of split-beam sounders in a fixed location,
68 measurements of movement characteristics of both individual fish and schools (swimming
69 speed and trajectory, within horizontal and vertical habitat dimensions) were carried out *in*
70 *situ* (*e.g.* Mulligan and Keiser 1996; Arrhenius et al. 2000; Mulligan and Chen 2000; Guillard
71 and Colon 2000; Cech and Kubecka 2002; Lilja et al. 2003). The swimming speed capabilities
72 could be estimated in controlled conditions using laboratory aquaria (Wardle 1975), video in
73 water tank (Soria et al. 2007), swim tunnel (Lee et al. 2003) or in the aquatic environment
74 using an electronic tag on individual fishes (Fängstam 1993; Dagorn et al. 2006). Electronic
75 tags sometimes affect the swimming performance, particularly on small fish (Stakenas et al.
76 2009), and in any case are unable to provide information on the whole school movements.

77 Quantitative results of migrating ichthyofauna between sea and lagoon have been obtained
78 (Miller et al. 1990; Gonzalez and Gerlotto 1998; Bardin and Pont 2002) emphasising the
79 importance of migratory flows between the two ecosystems. Coastal lagoons have a great
80 ecological importance and their functions as nurseries, refuge zones and feeding zones are
81 well recognized (Beck et al. 2001). Previous studies demonstrate that fish school behaviours
82 can be accurately described using multibeam sonar in horizontal beaming (*e.g.* Misund and

83 Algen 1992; Nøttestad et al. 1996; Onsrud et al. 2005; Brehmer et al. 2006a, b), even in
84 shallow waters (Guillard 1998), because this acoustic device displays a continuous
85 visualization of fish school movements (Pitcher et al. 1996).

86 In this paper we present *in situ* observations of fish schools performed at a short range in
87 shallow waters, using multibeam sonar in horizontal beaming in a fixed position. This allows
88 the measurement of fish school swimming speed values at two different temporal scales: for
89 short time periods of the school in the acoustic beam (instantaneous speeds) and the global
90 time of the presence of the school inside the acoustic beam (exploratory speed). From these
91 observations, we discuss the schools' migration behaviour in a lagoon channel and its
92 consequences on the school counting methodology using acoustic remote systems in
93 horizontal beaming and fixed position.

94

95 **Material and Methods**

96

97 The study areas: two Mediterranean shallow water lagoon channels

98

99 Our research takes place within two channels that link coastal lagoons of Ingril (549 ha) and
100 Prévost (380 ha) to the Mediterranean Sea. These two lagoons are part of a series of shallow
101 ponds located along the coastal area of the Hérault area in the south of France (43°44' N;
102 03°79' E and 43°52' N; 03°90' E). The Ingril channel has a 'bank to bank' width of 25 m and
103 the Prévost ones 17 m, both having a maximum depth of around 1.5 m (Brehmer et al. 2006a).
104 Artisanal fisheries in Mediterranean lagoons are considered as an ancient activity dating back
105 to Gallo-Roman times using fishing methods practically unchanged over the course of time
106 (Gourret, 1897; Bourquard 1985; Bach 1992). The most abundant species according to
107 landings, in biomass, is the eel (*Anguilla anguilla*), but other species such as big-scale sand

108 smelt (*Atherina boyeri*), the bass (*Dicentrarchus labrax*), the gilthead sea bream (*Sparus*
109 *aurata*), and various mugilidae (*Liza ramada*, *Liza aurata*, *Mugil cephalus*, *Chelon labrosus*)
110 are also abundant in captures for seasonal periods (Brehmer et al., 2006a). In this work, only
111 pelagic aggregative species in schools (Pitcher 1984) have been studied: the major species
112 encountered are the bass, the gilthead sea bream and the mullets (Brehmer et al. 2006a). All of
113 these species are known to migrate between the lagoons and the sea, due to their trophic
114 behaviour (from sea to lagoon during the spring) and/or for both physiological and spawning
115 reasons (from lagoon to sea during the autumn). Cast net sampling carried out during acoustic
116 surveys has shown the presence of fish with fork length sizes ranging from a minimum of 52
117 mm (Mugilidae juvenile) to a maximum of 169 mm (*D. labrax*).

118 Data analysed in this study came from two acoustic sampling surveys of 24 hours each,
119 performed consecutively during the autumnal migration season in September 1999 inside both
120 lagoon channels (Brehmer et al. 2006a).

121

122 The high resolution multibeam sonar dynamic observations

123

124 The RESON Seabat 6012 multi-beam sonar used for data acquisition emits on 60 contiguous
125 beams of 1.5° each. For reception, the efficient horizontal angle is 90° with a vertical angle of
126 15°. The sonar frequency was 455 kHz with pulse duration of 0.06 ms; all the data were
127 continuously stored on S-VHS videotapes. The sonar characteristics and the environmental
128 parameters determine the threshold of the sonar resolution, in our case 45 cm (Brehmer et al.,
129 2006b). A preliminary study of acoustic data, intended to quantify the migratory fish school
130 flows collected from the school echo traces (Olsen 1969; Scalabrin and Massé 1993; Moreno
131 et al. 2007) counted from acoustic imagery, was accomplished using the same acoustic
132 equipment used in horizontal beaming (Brehmer et al. 2006a).

133 The S-VHS video recordings are replayed at the laboratory to select the sonar sequences
134 including fish school echo traces (Brehmer et al. 2006b), which correspond to specific
135 detections of homogeneous continuous responses well discriminated on the screen. For both
136 sampling areas, we were able to observe mobile echo traces (Brehmer et al. 2006a) and
137 stationary ones. We then differentiated the dynamic echo traces, characteristic of fish schools
138 detection (vs. fixed bottom echo traces). In this way, each selected series of sonar images
139 corresponding to a detection of a school on which we attribute an individual code were stored
140 in a fish school library (Fig. 1). The echo traces observed within the sonar acoustic beams less
141 than two seconds were removed from the analysis as well as some schools exhibiting
142 particular behaviours (*i.e.* splitting/merging phenomenon). Finally, we selected and extracted
143 information on 164 fish schools, 41 and 123 observed in the channels of the Ingril lagoon and
144 the Prévost lagoon, respectively.

145

146 Sonar data processing of fish school echo traces

147

148 Each separate fish school data is extracted from the sonar images using the ‘Infobancs’
149 software (Brehmer et al. 2006c). For each fish school we obtain the number of consecutive
150 echo traces ‘N’, the total time of observation of echo traces within the beam (in seconds) and
151 the Euclidian position (x; y) of the centre of the fish school, defined as the centre of gravity of
152 the surface defining the detected biological structure. From this information and the scale
153 factor of observations on the screen (Brehmer et al. 2006b) we calculate the Instantaneous
154 Swimming Speed values of the fish school, (ISS in $\text{m}\cdot\text{s}^{-1}$), outlined on the basis of the
155 difference between two successive positions of the geometric centre of the fish school divided
156 by the time interval between observations. Moreover, we estimate the Exploratory Swimming
157 Speed (ESS in $\text{m}\cdot\text{s}^{-1}$) outlined on the basis of the rectilinear distance between the first and the

158 last positions of the fish school divided by the time interval separating these two observations.
159 From this data, we calculated: the mean of ISS values for each school (ISSm), and the
160 indicator of the trajectory of the displacement ID defined as the ratio between ISSm and ESS.
161 The ID index is derived from the 'IHM' Index of Horizontal Movement (Misund, 1991;
162 Brehmer et al. 2006). It is used as an indicator of the horizontal school displacement: above
163 0.9 we assume the displacement as straightforward and the lower the ID is, the higher is the
164 sinuosity of the displacement (Epstein, 1989). Non parametric tests and Pearson's correlation
165 analysis between indices were performed with the Statistica software
166 (<http://www.statsoft.com/>).

167

168 **Results**

169

170 For the 164 fish schools analysed the number of consecutive echo trace observations per
171 school varied from three to eight sonar images. The total of echo traces sampled reaches 621,
172 of which 174 and 447 concern schools detected in Ingril and Prévost lagoon channels,
173 respectively. The number of observations for each school varies from 3 to 8 around a mean of
174 4 for both lagoons (Table 1). The time of the school presence in the acoustic beam varies from
175 2 s to 31 s around an average of 10 s for Ingril and from 2 s to 34 s around an average of 10 s
176 for Prévost (Tab. 1). The distance travelled by a school across the acoustic beam varies from 1
177 m to 27.9 m around an average of 10 m for Ingril and from 2.2 m to 50.8 m around an average
178 of 12.2 for Prévost (Table 1). The relationship between the distance travelled by a school and
179 the residence time of this school in the acoustic beam shows a logarithmic shape for both
180 lagoons (Pearson's correlation coefficient $R = 0.55$, $p < 0.001$ for Ingril and $R = 0.64$, p
181 < 0.001 for Prévost) (Fig. 2).

182

183 Fish school swimming speed

184

185 The mean of ISS values (ISSm) ranged between 0.15 m.s^{-1} and 2.93 m.s^{-1} around an average
186 value of 1.31 m.s^{-1} (SD = 0.77) in the Ingril channel. For the Prévost lagoon, ISSm ranged
187 between 0.31 m.s^{-1} and 4.46 m.s^{-1} around an average value 1.51 m.s^{-1} (SD = 0.86) (Table 1).
188 The ESS varied between 0.04 m.s^{-1} and 2.72 m.s^{-1} around a mean value of 1.19 m.s^{-1} (SD=
189 0.77) for the Ingril channel. It ranged from 0.23 m.s^{-1} to 3.77 m.s^{-1} with an average of 1.34
190 m.s^{-1} (SD = 0.79) for the Prévost lagoon (Table 1). The scatter plot of ESS values versus
191 ISSm values shows that the major part of observations are distributed along the 1:1 line (*i.e.* x
192 $= y$), indeed the trend lines for both lagoons were close to it (Fig. 3).

193

194 Characteristics of the displacement

195

196 The index ID differs between 0.12 and 1.17 around an average value of 0.9 (SD= 0.77) for
197 Ingril channel. It ranged from 0.31 to 1.25 around an average of 0.89 (SD= 0.86) for the Ingril
198 lagoon channel (Table 1). As suggested by the Figure 3, for a majority of schools the ID value
199 is equal or close to 1. Then, 36 % of schools display displacements (ID value below 0.9)
200 which differ with the general trend (Fig. 4). We could envisage that this characteristic would
201 depend on the distance travelled by the school or the time of the observation of the school as
202 ISSm and ESS are correlated. However, this general trend of displacement of schools in both
203 channels was observed whatever the distance travelled (Fig. 5).

204

205 **Discussion**

206

207 The amplitude of variation of the observation time (Fig. 2) between fish schools came from
208 the loss of detection due to (i) swimming behaviour (*i.e.* the fish school trajectories can cross
209 the acoustic beams in different manners: horizontally, vertically or slantwise), and (ii) bottom
210 or surface reverberations during the passage of schools within sonar beams which prevent any
211 clear discrimination. The fish school ISSm and ESS calculations were obtained for a minimal
212 number of three observations of the school in the acoustic beam, set on a timing interval
213 which should be defined according to the target speed and the sonar performances (range and
214 pulse length). In our case study, the selected time interval was set at one second for the
215 shortest observation, without restriction in the total time of observation above three seconds
216 (Fig. 2). Within this first investigation, we decided to keep all available information relative
217 to the whole set of digitized sonar sequences selected for each fish school.

218 Our study demonstrates the ability to estimate the average instantaneous speed (ISSm) *in situ*
219 of fish schools, which differ in the channels between 0.15 to 4.46 m.s⁻¹. However the ESS
220 varies between 0.04 m.s⁻¹ and 3.77 m.s⁻¹. Such an extent of values could be due to the length
221 of individuals inside the school and an appropriate approach to interpret speed values would
222 be to consider the speed value relative to the length. Unfortunately, we could not translate
223 these swimming speeds into body length per second 'Bl.s⁻¹' (Bainbridge 1958), as the specific
224 identification from the echo trace was not feasible and because the size of the individual fish
225 within the school could be suspected to be not directly correlated to the fish school swimming
226 speed; obviously inferior to the one of an isolated fish (*i.e.* not in school) of a same size.
227 Nevertheless we can notice that the maximum value observed could not be related to juvenile
228 fish, as those caught during the experiment. Indeed Wardle (1975) found on individual fish in
229 laboratory aquaria that small fish (0.1 m) can reach 25 Bl.s⁻¹, while for the smaller fish of 52
230 mm sampled in this study the maximum speed value observed of 4.46 m.s⁻¹ would be
231 converted in 85 Bl.s⁻¹ which is biologically unreliable. For the bigger fish of 169 mm sampled

232 by fishing, this maximum speed value would be converted in 26 Bl.s^{-1} which is biologically
233 reliable. ISSm values can be clustered in four groups (Fig. 6), with a constant swimming
234 speed interval of 1.25 m.s^{-1} except for the highest values, which were only observed in the
235 Prevost lagoon. This assumption of a fish group discrimination makes sense according to
236 biological reliable swimming speeds expressed in Bl.s^{-1} and unpublished data showing a
237 higher value of individual TS on isolated fish (the TS is related to relative individual fish size
238 (Guillard et al. 2004)) from Prévost lagoon (Brehmer 2002, unpublished data); we could
239 assume that would be the same for gregarious fish as the species diversity remains the same
240 between both lagoons (Mouillot et al. 2005). Indeed, the first group could be related to
241 juveniles of mugilidae ($< \text{Lf } 7.5 \text{ cm}$), the second group to *S. aurata* ($\text{Lf} \sim 13 \text{ cm}$), the third
242 group to *D. labrax* ($\text{Lf} \sim 20 \text{ cm}$) and the last group which is only present in Prevost (the
243 deeper lagoon vs. Ingril) to adults of *D. labrax*, *S. aurata* or from the Mugilidae group.

244 The swimming behaviour is quite variable, even on small spatial and temporal scales, as
245 demonstrated in our analysis. Future study should explore more precisely the fish school
246 kinematic using adapted analysis (e.g. Benhamou 2004; 2006) on larger time scales (i.e.
247 several hours) obtained from different sampling protocols (e.g. mobile transducer along the
248 channel to track the school). The maximum time of observation recorded during this study of
249 34 s does not permit achieving this goal.

250 The multi-transit hypothesis assumes that the same fish school can be recorded several times
251 by the sonar system according to its swimming behaviour (Brehmer et al. 2006a). Cronkite *et*
252 *al.* (2007) confirm the multi-transit hypothesis with a study led on a river using split beam
253 echosounder data on individual fish. If we assume that the oriented swimming behaviour
254 corresponds to a certain form of an active migration (continuous swimming activity),
255 considering an ID value above 0.9 as an indicator of this oriented swimming behaviour, our
256 results allow us to estimate that 64 % (Fig. 4) of fish schools exhibit an active migration

257 movement through the channel. Then, this active migration movement appears as an intrinsic
258 property of observed school during our study, as such a general trend of displacement of
259 schools in both channels was observed whatever the distance travelled (Fig. 5). This
260 estimation is reliable under the hypothesis that schools exhibit this swimming behaviour all
261 along their transfer inside the lagoon channel during the well known autumnal migration
262 period of mugilidae, sparidae and centrarchidae fishes. Fish schools not having a well defined
263 migration behaviour regarding their ID value are susceptible to be detected several times in
264 the acoustic beam. They reach 36 % of fish schools which could represent resident fish in
265 lagoons or migratory fish which present rather an exploratory behaviour than a migratory one.
266 The swimming speed of fish schools is an elementary indicator which has an interest in many
267 aspects of the ecology of aggregative fish species (*e.g.* Gillanders et al. 2003). To gather our
268 data the operating system carried out was time consuming (Fig. 1; video sequences selection
269 and fish school identification, then, sonar image digitization, import of digitized sequences
270 through a software solution and configuration) and an automation of working sequences
271 through a post process of sonar data using dedicated software is in progress. However, these
272 operations need further developments. Indeed, analysed echo traces are easily identifiable,
273 allowing developing a discrimination algorithm of useful echoes to be validated in a second
274 step by an expert (Weill et al. 1993; Brehmer et al. 2006a). The development of both acoustic
275 technologies and data analysing process might be allow to quantify behavioural pattern of
276 fishes at small scale. Consequently, impacts of both fishing and management activities (*e.g.*
277 shallow water stock assessment as well as marine protected areas, artificial reefs) would be
278 evaluated more accurately.

279

280 **Conclusions**

281

282 The multibeam sonar in horizontal beaming allows an analysis of fish school displacement, at
283 short range in shallow water and allows their swimming speed measurements which are
284 precious sources of elementary information for ecological studies or landscaping of shallow
285 water surroundings. In the way of an ecosystemic approach (Garcia et al. 2003; Misund and
286 Skjoldal 2005; Cury and Christensen 2005), the control and the management of the ecological
287 quality of such ecosystems as well as their fisheries components (Sherman and Duda 1999),
288 our methodologies permit to consider free fish school swimming speeds. This elementary
289 information enhances our knowledge of fish school displacement and migration processes
290 which are essential to better our understanding of ecosystem functioning (Gillanders et al.
291 2003) and finally, to formulate management measures of the seashore. Our methodology can
292 be extended to other fish target types in aquatic ecosystems, such as large isolated fish in the
293 open ocean (elasmobranchii, marine mammals) obviously subject to the reverberation of the
294 focused target (*i.e.* above the required threshold and resolution). The development of the
295 acoustic methodology should lead to numerous *in situ* measures in aquatic ecosystems, such
296 as on large marine animals swimming behaviour in their natural habitat, or within ecological
297 and anthropogenic perturbation situations (*e.g.* habitat eutrophication). The swimming speed
298 should be used to propose indicators to discriminate fish school species or characterise their
299 behavioural motivation (feeding, spawning, and migration). Lastly the morphological
300 characteristics of the fish school (shape, surface, size of individual fish) can be related to the
301 swimming speed measurements in order to improve our understanding of aggregative fish
302 displacement.

303

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308

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- 443

444 **Table 1**

445 Summary of school swimming speeds (ESS: Exploration Swimming Speed. ISS:
 446 Instantaneous Swimming Speed) descriptors values per lagoon (Ingril and Prévost), with their
 447 total time and 'N' number of observations, their distance travelled across the beams and their
 448 ratio ID (*i.e.* average ISS divided by the ESS).

449

Lagoon		Total time (s)	N	ESS (m.s ⁻¹)	ISSm (m.s ⁻¹)	Distance (m)	ID
Ingril	Mean	10	4	1,19	1,31	10	0,89
	Max.	31	8	2,72	2,93	27,9	1,25
	Min.	2	3	0,05	0,15	1,1	0,31
Prévost	Mean	10	4	1,34	1,51	12,6	0,9
	Max.	34	8	3,77	4,46	50,8	1,17
	Min.	2	3	0,23	0,31	2,2	0,12

450

451

452 **Fig. 1** Scheme representing the sonar data collection, their treatment, which include several
453 steps (selection of sonar sequence, digitalization, identification of echo traces on sonar
454 images, data extraction and then exportation for final analysis on ad hoc software), and their
455 analysis to obtain the swimming speed measurements.

456

457 **Fig. 2** The relationship between the school observation time and the distance travelled inside
458 the sonar beams (grey triangle, dotted line: Ingril lagoon; black empty circle, full line: Prévost
459 lagoon) shown a logarithmic shape, higher for the Prévost values than the Ingril ones.

460

461 **Fig. 3** The relationship between the 'ISSm' and the 'ESS' (grey triangle: Ingril lagoon; black
462 empty circle, Prévost lagoon) shown a linear shape (grey line $y = x$. Ingril trend line black
463 dotted $y = 0.916 x$; $R^2 = 0.87$. Prévost trend line full black $y = 0.872 x$; $R^2 = 0.83$) which were
464 comparable for both lagoons.

465

466 **Fig. 4** Cumulative frequency of the fish school ID defined as the average of instantaneous
467 swimming speed 'ISS' divided by the exploration swimming speed 'ESS'. The schools having
468 an ID below 0.9 represent 36 % of the total.

469

470 **Fig. 5** Relationship between the distance travelled inside the beams by the fish school and the
471 ID (grey triangle: Ingril lagoon; black empty circle, Prévost lagoon). The ID values appear as
472 not linked to the distance travelled.

473

474 **Fig. 6** Histogram of average of instantaneous swimming speed of the fish schools from the
475 Prévost (black) and Ingril (grey) lagoons, where 4 groups can be distinguished at a regular
476 swimming speed interval (1.25 m.s^{-1}).