

# Exploratory and instantaneous swimming speeds of amphidromous fish school in shallow-water coastal lagoon channels

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► **To cite this version:**

Patrice Brehmer, Jean Guillard, P. I. C. Pinzon, Pascal Bach. Exploratory and instantaneous swimming speeds of amphidromous fish school in shallow-water coastal lagoon channels. *Estuaries and Coasts*, Springer Verlag, 2011, 34 (4), pp.739-744. <10.1007/s12237-011-9409-3>. <ird-00607866>

**HAL Id: ird-00607866**

**<http://hal.ird.fr/ird-00607866>**

Submitted on 11 Jul 2011

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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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24

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  $0.15 \text{ m}\cdot\text{s}^{-1}$  to  
38 a maximum of  $4.46 \text{ m}\cdot\text{s}^{-1}$  while on the other hand; ESS per school varies at lower level  
39 amplitude from  $0.04 \text{ m}\cdot\text{s}^{-1}$  to a maximum of  $3.77 \text{ m}\cdot\text{s}^{-1}$ . 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 (Fångstam 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  $0.15 \text{ m.s}^{-1}$  and  $2.93 \text{ m.s}^{-1}$  around an average  
186 value of  $1.31 \text{ m.s}^{-1}$  (SD = 0.77) in the Ingril channel. For the Prévost lagoon, ISSm ranged  
187 between  $0.31 \text{ m.s}^{-1}$  and  $4.46 \text{ m.s}^{-1}$  around an average value  $1.51 \text{ m.s}^{-1}$  (SD = 0.86) (Table 1).  
188 The ESS varied between  $0.04 \text{ m.s}^{-1}$  and  $2.72 \text{ m.s}^{-1}$  around a mean value of  $1.19 \text{ m.s}^{-1}$  (SD=  
189 0.77) for the Ingril channel. It ranged from  $0.23 \text{ m.s}^{-1}$  to  $3.77 \text{ m.s}^{-1}$  with an average of  $1.34$   
190  $\text{m.s}^{-1}$  (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<sup>-1</sup>. However the ESS  
220 varies between 0.04 m.s<sup>-1</sup> and 3.77 m.s<sup>-1</sup>. 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<sup>-1</sup>' (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<sup>-1</sup>, while for the smaller fish of 52  
230 mm sampled in this study the maximum speed value observed of 4.46 m.s<sup>-1</sup> would be  
231 converted in 85 Bl.s<sup>-1</sup> which is biologically unreliable. For the bigger fish of 169 mm sampled

232 by fishing, this maximum speed value would be converted in  $26 \text{ Bl.s}^{-1}$  which is biologically  
233 reliable. ISSm values can be clustered in four groups (Fig. 6), with a constant swimming  
234 speed interval of  $1.25 \text{ m.s}^{-1}$  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  $\text{Bl.s}^{-1}$  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

304 **Acknowledgements** This work has been supported by a state-regional grant 'CPER XI' and  
305 the GIS Europole Mer. We are grateful to Thang Do Chi (CNRS, UMR Ecolag), Marc Soria,

306 François Gerlotto and Laurence Vicens (IRD, UMR Eme) for their help during the project and  
307 all the participants of the field missions.

308

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310

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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<br>(s) | N | ESS<br>(m.s <sup>-1</sup> ) | ISSm<br>(m.s <sup>-1</sup> ) | Distance<br>(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 ( $1.25 \text{ m.s}^{-1}$ ).