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STOREFISH: a new database dedicated to the reproduction of temperate freshwater teleost fishes

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Abstract. - There is currently an increasing demand for the diversification of the production in fish aquaculture and the domestication of new species, which may display highly divergent strategy of reproduction. Yet, today, the domestication of a new species is still essentially realized by a long, costly, and usually empirical zootechnical process. Within this context, a research program has been launched to establish a functional typology, focusing on the function of reproduction, in order to cluster species displaying similar reproductive strategies, and thus apply or adapt rearing systems (zootechnical practices) already in use in species belonging to the same group. This research has been restricted to some temperate freshwater teleost species inhabiting Europe and North America. This objective has required the development of a new database, namely STOREFISH (acronym for STRategies Of REproduction in FISH), which currently comprises 50 reproductive traits for 80 species (distributed into 19 families). The 50 characters are classified into four main categories: 7 characters for egg, 7 for larvae, 21 for breeders and 15 for spawning conditions. Overall, 70 % of the character/species cells were successfully fulfilled, corresponding to 1000 biographical references. The potential applications of this database for the study of the domestication process in fish aquaculture are further discussed.

Résumé. - **STOREFISH : une nouvelle base de données dédiée à la reproduction des poissons téléostéens d'eau douce tempérée.**

Il existe à l'heure actuelle une demande croissante pour une diversification de la production en pisciculture et la domestication de nouvelles espèces, qui peuvent présenter des stratégies de reproduction très différentes. Or, à ce jour, la domestication d'une nouvelle espèce s'effectue essentiellement par une approche zootechnique souvent empirique, longue et coûteuse. Dans ce contexte, une recherche a été engagée dans le but d'établir une typologie fonctionnelle, en se concentrant sur le fonction de reproduction, afin de regrouper les espèces présentant des stratégies reproductives similaires, pour ensuite appliquer ou adapter des systèmes d'élevage (approches zootechniques) déjà éprouvés aux espèces appartenant au même groupe. Cette recherche a été limitée à quelques espèces de poissons téléostéens d'eaux douces tempérées d'Europe et d'Amérique du Nord. Cet objectif a nécessité le développement d'une nouvelle base de données, STOREFISH (acronyme de STRategies Of REproduction in FISH), qui comprend actuellement 50 caractères liés à la biologie de la reproduction pour 80 espèces (réparties sous 19 familles). Ces 50 caractères sont regroupés en 4 grandes catégories : 7 caractères liés à l'œuf, 7 à la larve, 21 aux géniteurs et 15 aux conditions de ponte. D'une manière générale, 70% des cellules caractère/espèce ont été remplies, ce qui correspond à 1000 références bibliographiques. Les applications potentielles de cette base de données pour l'étude du processus de domestication en pisciculture sont discutées.

Key words. – Reproductive strategies - Database - Freshwater - Teleost fish - STOREFISH - Aquaculture.

There is currently an increasing demand for the diversification of the production of fish in aquaculture, yielding particularly to the rearing of new species (Naylor *et al.*, 2000; Fontaine, 2004; Muir, 2005). Presently, however, species domestication usually results from a

53 long, costly and empirical zootechnical process. Undertaking to manage such a process on a
54 new species thus appears somewhat uncertain, taking into account the about 29,300
55 potentially available wild species (Froese and Pauly, 2006), the diversity of their life history,
56 and the lack of knowledge about the underlying biological mechanisms involved in the
57 domestication process. One possible way to lower uncertainty is to take advantage of the
58 available information in various species regarding characteristics of their life history, to
59 establish a functional typology (i.e., cluster species displaying similar life histories and
60 identify few fish-models), to try answering the three following questions:

- 61 1) Is it possible to extrapolate, for an aquacultural purpose, the knowledge acquired on
62 one species to another?
- 63 2) If yes, which methods can be used?
- 64 3) Among the available biological features, which main ones must be taken into account
65 in the process of selection/domestication of fishes?

66 In order to evaluate the reliability of such a generic approach, it appeared logical to first
67 focus on the function of reproduction because its control is critical in the domestication
68 process of teleost fishes and it is usually admitted that the similarity of reproductive traits is
69 much more important for phylogenetically close species, i.e., those belonging to the same
70 genus or family (Fostier and Jalabert, 2004). For instance, if a species X, which displays a
71 relative fecundity of 200,000 eggs/kg is the sister species of Y, then one expects that the
72 species Y possesses a similar fecundity, for example 150-250,000 eggs/kg.

73 However, no database gathering reliable and relevant data characterizing the reproductive
74 biology of a large number of species is currently available. Indeed, the main accessible
75 database used by ichthyologists, namely FishBase (Froese and Pauly, 2000) is too general,
76 albeit containing few reliable reproductive features for some species, and the few attempts of
77 clustering species using reproductive traits were either too subjective (Balon, 1975) or too
78 narrow, focusing only on specific groups such as salmonids (Crespi and Teo, 2002).

79 Within this context, the goal of the present work was to develop a new database
80 focusing on the function of reproduction, i.e., from the onset of gametogenesis to the end of
81 larval stages (including spawner features and spawning conditions) of some freshwater teleost
82 species from Europe (both native and introduced) and, to a lesser extent, from North America.
83 We chose to target these species as the main outcomes of this work are directed to the
84 domestication of new species in European countries. The development and the completeness
85 of this new database, called STOREFISH (acronym for STrategy Of REproduction in FISH)
86 are further described in the present article.

87

88

MATERIALS AND METHODS

89

90 **Targeted species**

91 This database primarily focused on freshwater fish species inhabiting European waters
92 (both native and introduced) (Table 1). The initial choice of species was based on reference
93 books (Billard, 1997; Bruslé and Quignard, 2001; Keith and Allardi, 2001) and FishBase
94 (Froese and Pauly, 2005). Additional species living in North American freshwaters, in similar
95 habitats and latitudes, were also included to enlarge the database, thus allowing
96 supplementary comparisons (e.g. species belonging to the Clupeidae, Esocidae, Moronidae, or
97 Salmonidae). All targeted species are gonochoristic.

98

99 **Targeted reproductive traits**

100 Reproductive characters were chosen in order to describe as much as possible the
101 entire reproductive strategy of each species, i.e., from the onset of gametogenesis to the end
102 of larval stages. Four main categories of characters were initially identified, those dealing
103 with egg, larvae, spawners and spawning conditions. A preliminary set of 135 characters
104 (Appendix 1) was established based on the exhaustive literature search (i.e., character cited at
105 least by one author). Then, within each category, the more reliable particular characters were
106 chosen depending on the ability to discriminate reproductive strategies and the occurrence in
107 literature. These characters could be divided into two main categories: the numerical or
108 quantitative variables displaying continuous values between species, such as egg diameter
109 (character 1), initial larval size upon hatching (character 8), and the categorical or qualitative
110 variables displaying few discrete states between species, such as egg buoyancy (character 3),
111 spawning substrates (character 44).

112

113 **Literature search**

114 An extensive literature search was performed mainly based on the Aquatic Sciences
115 and Fisheries Abstracts bibliographic database (ASFA) (<http://www.fao.org/fi/asfa/asfa.asp>).
116 Reproductive data for each targeted species were then obtained from two main sources: peer-
117 reviewed journal articles and various books that summarize large amounts of information for
118 individual species, e.g., the northern pike *Esox lucius* (Linnaeus, 1758) (Billard, 1983) or the
119 walleye *Sander vitreus* (Mitchill, 1818) (Coldy *et al.*, 1979), or for several species (Pennel
120 and Barton, 1996; Craig, 2000; Bruslé and Quignard, 2001). Information were preferentially

121 collected from natural field studies, albeit some were issued from rearing facilities,
122 particularly for characters dealing with larval stages. Besides, information coming from
123 different sources for the same species were gathered to (i) better evaluate both the validity of
124 each character and the reliability of data and (ii) assess the intra-specific variability
125 (ecological plasticity). Yet, when no consistent data were found concerning a particular trait,
126 the corresponding cell within the matrix (species X reproductive traits) was left blank. All
127 references used have been entered within Endnote. The matrix is written in English and
128 currently hosted within Microsoft Excel software.

129

130

RESULTS

131

General remarks

132
133 This literature search revealed to be relatively difficult because most relevant
134 references are dispersed and ancient (thus usually not available on-line). This thus implies that
135 since these pioneer times, much basic information has not been updated, confirmed or refuted
136 by recent works and highlight the need for new field studies. Besides, it also emerged that the
137 definition of some characters varies between authors, thus rendering the utilization of their
138 data tricky, e.g., the use of the term “egg diameter”, being either the oocyte diameter, the
139 fertilized egg diameter or the swollen fertilized egg diameter (see characters 1 and 2).
140 Nevertheless, reliable and accurate information were obtained for most of the 50 reproductive
141 characters selected for the 80 species finally retained (70% of overall completeness), which
142 corresponds to 1000 bibliographical references. However, the percentage of completeness
143 greatly varies depending on species and characters.

144

145

List of the species kept

146
147 The number of targeted species was initially set at 150. Yet, because for almost half of
148 them only a few relevant information were found, 80 species were kept in the final database.
149 Among these 80 species, 57% belong to two out of a total of 19 families (in brackets the
150 number of species per family): Anguillidae (1), Balitoridae (1), Centrarchidae (4), Clupeidae
151 (3), Cobitidae (2), Cottidae (1), Cyprinidae (28), Cyprinodontidae (1), Esocidae (3),
152 Gasterosteidae (2), Ictaluridae (2), Lotidae (1), Moronidae (4), Osmeridae (1), Percidae (5),
153 Poeciliidae (1), Salmonidae (18), Siluridae (1) and Valenciidae (1) (Table 1). As indicated
154 above, the number of available data varies greatly between species. For instances, thirteen

155 species display more than 80% of completeness, namely *Micropterus salmoides*, *Cyprinus*
156 *carpio*, *Gobio gobio*, *Rutilus rutilus*, *Tinca tinca*, *Exox lucius*, *Perca flavescens*, *Perca*
157 *fluviatilis*, *Sander lucioperca*, *Sander vitreus*, *Oncorhynchus mykiss*, *Salmo salar*, and
158 *Thymallus thymallus*. On the opposite, nine species exhibit between 35 and 50% of
159 completeness, i.e., *Ambloplites rupestris*, *Cobitis paludica*, *Alburnus alburnus*,
160 *Mylopharyngodon piceus*, *Aphanius iberus*, *Valencia hispanica*, *Coregonus clupeaformis*,
161 *Coregonus lavaretus*, and *Oncorhynchus nerka*. Between these two extremes, the percentage
162 of completeness mostly varies between 50-70%.

163

164 **Definitive list of reproductive characters**

165 Overall, the percentage of completeness varies greatly between characters, from a
166 minimum of 18% for the character 34 (Spermatogenesis duration) to a maximum of 99% for
167 the characters 1 (Oocyte size) and 39 (Spawning season). Between these two extremes, most
168 characters display a percentage comprised between 60-80%. Significant differences between
169 the four main categories of characters were observed (in brackets the overall percentage of
170 completeness): 7 characters for egg (85%), 7 for larvae (52%), 21 for breeders (55%) and 15
171 for spawning conditions (73%). Among these fifty characters, thirty three are quantitative or
172 numerical, namely characters 1, 2, 5-8, 11, 13-17, 19, 20, 22-29, 31-37, 39-41, and 43, the
173 seventeen remaining are discrete or qualitative, namely nine characters displaying two states
174 (4, 9, 10, 12, 18, 30, 38, 42 and 49) and height characters displaying three to five states (3, 21,
175 44, and 45-48 and 50). Data corresponding to the characters 22-26 and 31-35 were either
176 obtained directly from articles when available or determined from graph displaying the annual
177 changes in gonadosomatic index GSI (%GSI= (GW/BW) X 100, where GW is the gonad
178 weight and BW the body weight). The full description of each of the 50 characters is given
179 below, followed by the character-states for discrete characters in brackets, and the current
180 percentage of completeness in bold.

181

182 *Egg features:*

- 183 (1) Oocyte size: corresponds to the average diameter of the unfertilised egg, i.e., mature,
184 fully yolked ovarian oocyte ready to be or just released (in mm): **99%**
- 185 (2) Egg size after water-hardening: corresponds to the average diameter of the fertilized
186 egg after swelling, due to water uptake (in mm): **60%**
- 187 (3) Egg buoyancy: of the fertilized swollen egg, being either demersal (sinks to the
188 bottom), semi-pelagic (remains for a short period in the water column, then sinks) or

189 pelagic (floats on or near the surface of the water and could derive for a long
190 distance, several kilometers), scored as a three-state variable [Demersal, Semi-
191 pelagic, Pelagic]: **86%**

192 (4) Egg adhesiveness: of the fertilized egg after water-hardening. Eggs which are
193 slightly sticky only prior to water-hardening were considered as non-adhesive,
194 scored as a binary variable [Non-adhesive, Adhesive]: **84%**

195 (5) Incubation time: average number of days required in natural conditions from
196 fertilization to hatching, period designed as “incubation”: **96%**

197 (6) Temperature of incubation: corresponds to the average temperature, in degree
198 Celsius (°C), encountered during the incubation period of egg: **91%**

199 (7) Degree-days for incubation: average Degree-Days (temperature*time, with
200 temperature in degree Celsius (°C) and time in days), required for the entire
201 incubation of egg: **89%**

202

203 *Larval features:*

204 (8) Initial larval size: average larval size upon hatching (in mm): **85%**

205 (9) Larvae behaviour: corresponds to the behaviour of the larvae prior to exogenous
206 feeding, being either demersal (remain near the bottom) or pelagic (swim actively
207 near the surface), scored as a binary variable [Demersal, Pelagic]: **62%**

208 (10) Reaction to light: larvae during the first days after hatching are either negatively
209 (photophobic) or positively (photopositive) attracted to light, scored as a binary
210 variable [Photophobic, Photopositive]: **42%**

211 (11) Temperature during larval development: average temperature, in degree Celsius (°C),
212 encountered until the post-larvae stage (i.e., while starting exogenous feeding): **45%**

213 (12) Sibling intracohort cannibalism: corresponds to the intra-specific predation of
214 members of the same cohort during the post-larval growth, scored as a binary variable
215 [Absent, Present]: **29%**

216 (13) Full yolk sac resorption: corresponds to the average period of time, in Degree-Days,
217 required for the complete resorption of the yolk-sac: **26%**

218 (14) Onset of exogenous feeding: corresponds to the average period of time, in Degree-
219 days, required for the beginning of the exogenous feeding: **25%**

220

221 *Mature female and male features*

222 Female

- 223 (15) Age at sexual maturity: average age at maturity (in years): **96%**
- 224 (16) Length at sexual maturity: average total body length at maturity (in cm): **81%**
- 225 (17) Weight at sexual maturity: average body weight at maturity (in kg): **50%**
- 226 (18) Female sexual dimorphism: females of some species develop secondary sexual
227 characters during the breeding season, scored as a binary variable [Absent, Present]:
228 **21%**
- 229 (19) Relative fecundity: average number of eggs (in thousands) per kilogram of body
230 weight: **70%**
- 231 (20) Absolute fecundity: average number of eggs (in thousands) recorded by individual
232 female: **90%**
- 233 The six following characters aimed at describing the main events within the reproductive
234 cycle:
- 235 (21) Oocyte development: synchronous (all oocytes present within the ovary are at the
236 same stage of development), group-synchronous (at least two distinct populations of
237 oocytes at different development stages) and asynchronous (oocytes at all stages of
238 development), scored as a three-state variable [Synchronous, Group-synchronous,
239 Asynchronous]: **64%**
- 240 (22) Onset of oogenesis: defined as the months in the year when an initial significant
241 inflexion and increase in the GSI is observed. This period corresponds to the onset of
242 the active vitellogenesis, mainly endogenous: **55%**
- 243 (23) Intensifying oogenesis activity: defined as the months in the year when the GSI
244 displays the largest increase. This period mainly corresponds to the end of the active
245 vitellogenesis, prior to the final maturation of oocytes (i.e., oocyte meiotic resumption
246 and ovulation): **50%**
- 247 (24) Maximum GSI value: corresponds to the average maximal GSI value (%) observed
248 within the entire reproductive cycle: **63%**
- 249 (25) Oogenesis duration: corresponds to the total duration of the oogenesis process from
250 the initial significant inflexion and increase in GSI until ovulation (in months): **25%**
- 251 (26) Resting period: corresponds to the duration of gonadal quiescence between two
252 consecutive reproductive cycles when the ovaries are recovering from the spawning
253 act (in months): **49%**
- 254
- 255 Male
- 256 (27) Age at sexual maturity: average age at maturity (in years): **95%**

- 257 (28) Length at sexual maturity: average total body length at maturity (in cm): **71%**
258 (29) Weight at sexual maturity: average body weight at maturity (in kg): **39%**
259 (30) Male sexual dimorphism: males belonging to certain species develop secondary sexual
260 characters during the breeding season, scored as a binary variable [Absent, Present]:
261 **51%**

262 The five following characters aimed at describing the main events within the reproductive
263 cycle of male:

- 264 (31) Onset of spermatogenesis: defined as the months in the year when a significant
265 increase in the GSI is observed. This period mainly corresponds to the initial
266 proliferation of spermatogonia through repeated mitotic divisions, and primary
267 spermatocytes differentiation: **35%**
268 (32) Main spermatogenesis activity: defined as the months in the year when the GSI
269 displays a sharp increase. This period mainly corresponds to the transformation of
270 spermatocytes into mature spermatozoa (including the spermiogenesis process) and
271 prior to spermiation: **32%**
272 (33) Maximum GSI value: corresponds to the average maximal GSI value (%) observed
273 within the entire reproductive cycle: **50%**
274 (34) Spermatogenesis duration: corresponds to the total duration of the spermatogenesis
275 process from the initial proliferation of spermatogonia to spermiation (in months):
276 **18%**
277 (35) Resting period: corresponds to the duration of gonadal quiescence between two
278 consecutive reproductive cycles when the testis are recovering from the spawning act
279 (in months): **36%**

280

281 *Spawning features:*

- 282 (36) Spawning migration distance: corresponds to the average distance run by adults to get
283 to the spawning grounds (in km): **39%**
284 (37) Spawning migration period: corresponds to the months in the year when some species
285 display extensive spawning run: **46%**
286 (38) Homing: defines as the accurate returning behaviour of some teleosts to their natal
287 areas to spawn, scored as a binary variable [Absent, Present]: **35%**
288 (39) Spawning season: corresponds to the usual months of the presence of spawners on the
289 spawning ground: **99%**
290 (40) Spawning period duration: corresponds to the period of time when spawners are

- 291 present on the spawning ground (in weeks): **73%**
- 292 (41) Spawning temperature: average temperature observed during the spawning period
293 (°C): **86%**
- 294 (42) Spawning water type: corresponds to the kind of water frequented during the
295 spawning season, could be either stagnant water such as ponds or lakes (with no or
296 slight current) or rivers and streams (with much more current), scored as a binary
297 character [Stagnant water, Flowing or turbulent water]: **87%**
- 298 (43) Spawning depth: defines at the average depth at which spawning occurs (meters):
299 **79%**
- 300 (44) Spawning substrate: teleost species either scatter their eggs in the water column
301 (pelagophils), or deposit their eggs (i) on a rock or gravel bottom (lithophils), (ii) on
302 plants (phytophils), (iii) on roots or grass above the sandy bottom or on the sand itself
303 (psammophils) or (iv) into gill cavity of mussels (ostracophils). This character is
304 mainly derived from Balon's (1975) classification of reproductive guilds of teleost
305 fishes, and scored as a five-state variable [Pelagophils, Lithophils, Phytophils,
306 Psammophils, Ostracophils]: **90%**
- 307 (45) Spawning site preparation: teleost species scatter their eggs either in the water column,
308 directly over the substrates, or within a nest, which is a depression dug into the
309 substrate by either the male, the female or both parents, scored as a five-state variable
310 [Open water/substratum scatter, Substrate chooser, Nest built by male, Nest built by
311 female, Nest built by both parents]: **95%**
- 312 (46) Nycthemeral period of oviposition: corresponds to the main period during the day
313 when mass spawning occur, scored as a four-state variable [Night, Dawn, Day, Dusk]:
314 **56%**
- 315 (47) Mating system: teleost species display three main kind of mating system:
316 monogamous (one male and one female), polygamous (an individual, either the male
317 or the female, has several mates), and promiscuity (both sexes have multiple partners
318 within a single season), scored as a four-state variable [Monogamy, Polygyny,
319 Polyandry, Promiscuity]: **68%**
- 320 (48) Spawning release: teleost species display three main kind of egg release during the
321 breeding season: total (all eggs are shed at the same time), fractional (several batches
322 of eggs are released at intervals, usually over several days or weeks, but the potential
323 breeding season fecundity is fixed before spawning, also known as determinate
324 fecundity) or multiple (several batches of eggs are shed more than once through a long

325 spawning season, and there is a recruitment to the stock of spawnable oocytes during
326 the entire spawning season, also known as undermature fecundity), scored as a three-
327 state variable [Total, Fractional, Multiple]: **92%**

328 (49) Parity: teleost species are either iteroparous (most individuals survive after the
329 spawning act, i.e., several reproductive cycles during a lifetime) or semelparous (most
330 or all individuals die, i.e., only one reproductive cycle during a lifetime), scored as a
331 binary variable [Semelparous, Iteroparous]: **57%**

332 (50) Parental care: defines as the association between one or both parents and offspring that
333 enhances offspring development and survival (e.g. males of some species guards and
334 aerates their eggs and larvae for several weeks), scored as a four-state variable [No
335 care, Male parental care, Female parental care, Biparental care]: **90%**

336

337

DISCUSSION

338

Assessment of the Database

340 Overall, more than 70% of the 4000 species/character cells were successfully fulfilled,
341 i.e., ~ 2800, corresponding to the exploitation of 1000 biographical references. Yet,
342 considerable differences in the number of available data were observed depending on
343 characters and species, which may provide a good picture of the current knowledge acquired
344 on the biology of reproduction in teleost fishes inhabiting European waters. For instances,
345 much more information is clearly available concerning egg than larval stages (85% vs 53%)
346 or from female than from male (63% vs 47%), especially concerning the description of the
347 gametogenesis cycle. Such differences were also observed between species, e.g., only 2
348 pertinent references were found for *Cobitis paludica* and 3 for *Mylopharyngodon piceus*,
349 whereas 25 were retrieved for *Cyprinus carpio* and 27 for *Perca fluviatilis*. This implies that
350 the evaluation of the intraspecific variability (ecological plasticity) varies significantly
351 between species, as for some up to ten references (coming from different populations) for a
352 given trait were found whereas for others only one piece of data was obtained (issued from
353 one population).

354 Thus it appeared that most studies had focused on only about a dozen species, which
355 are the most used in fisheries and aquaculture (e.g., *Anguilla anguilla*, *Micropterus salmoides*,
356 *Cyprinus carpio*, *Tinca tinca*, *Esox lucius*, *Dicentrarchus labrax*, *Perca fluviatilis*,
357 *Oncorhynchus mykiss*, *Salmo salar*), and that virtually nothing is known concerning the
358 reproductive biology of numerous others, as already highlighted for marine species in the

359 fisheries management field by King and MacFarlane (2003).

360

361 **Reappraisal of the reliability of selected characters**

362 Among the 50 reproductive characters finally kept in the database, 40 are directly
363 based on data provided by authors, i.e., characters 1-21, 27-30, 36-50. The other ten, namely
364 characters 22-26 and 31-35, aiming at describing the main events within the reproductive
365 cycle of female and male respectively, were either obtained directly from articles when
366 available or determined from graph displaying the annual changes in gonadosomatic index.
367 For this reason, the consistency of these ten character is much questionable than the other 40
368 because they usually result from an interpretation of graph.

369 Besides, the definition of some characters was particularly tricky as it could vary
370 between authors, particularly at the larval stages: character 13 (Full yolk sac resorption) and
371 14 (Onset of exogenous feeding), but see Urho (2002) for a more completed review. This
372 mainly explains why we usually chose the term ‘average’ in the definition of most characters
373 in order to illustrate the actual nature of data in the literature.

374

375 **Preliminary analysis of the database**

376 Once the literature search was considered as completed, we tried to determinate, for
377 each numerical character, few character-states. Indeed, we considered that such approach,
378 compared to the use of a single average or mean value for each species, might better allow
379 taking into account both the “true” intra-specific variability (differences due to latitude,
380 environment, ...) and the variability due to differences in measures and definitions of
381 characters employed (as indicated above). Thus, for each numerical characters, a thorough
382 analysis of the variability both within and among species was performed based on available
383 data. Minimal and maximal values for each species were plotted on the same graph, and the
384 most unambiguous gaps within the distribution were searched in order to establish the
385 character states having the most biological sense (encompassing most of the intra-specific
386 variability while being sufficiently different between them). Yet, such operation proved much
387 more tricky than expected, as most numerical characters were clearly continuous, showing no
388 clear-cut states between species. For this reason, we now also plan to use an average value for
389 each numerical characters and compare the results of both approaches. The use of average
390 values is actually the most currently used method in comparative analysis of life traits
391 between species. For instances, Growns (2004) while comparing 13 life history traits of 54
392 freshwater fishes inhabiting south-eastern Australia, used the mean of the minimum and

393 maximum unfertilized egg size recorded for each species. King and McFarlane (2003), while
394 studying the life history strategies of 42 marine fish species inhabiting the west coast of
395 Canada, used for fecundity the mid-point of the reported range of number of eggs per
396 individual. Similarly, Winemiller and Rose (1992) chose to determinate for each species the
397 average or modal value of traits by using data from populations located near the centre of
398 species' ranges. When limited data were available near the centre of the range, they sought
399 estimates from peripheral populations in an incremental fashion (working outward from the
400 centre of the range). For example, if a freshwater species ranged from Central Canada to
401 Tennessee River, they first sought studies conducted near the latitudes of the Great lakes
402 (Winemiller and Rose, 1992). Such approach allowed them to find comparable values
403 between species, particularly for those displaying a wide geographical distribution. In our
404 case, the most pertinent values are clearly those obtained first in north-western Europe
405 (France, Belgium, Germany, ...), then those obtained from Spain and Norway.

406 Either based on average values or classes, three main kind of analyses are planned on
407 both each of the four main categories of characters separately and on the full dataset, namely
408 (i) Pearson's correlation coefficients and Spearman's rank correlation coefficients to evaluate
409 the bivariate relationships among reproductive traits, (ii) a series of Principal Component
410 Analysis (PCA) to explore patterns of association among reproductive traits and ordination of
411 species and (iii) cluster analysis using uncorrected distances and the Neighbour-Joining
412 method to group species according to their reproductive strategy.

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414

415 **Potential applications**

416 The three main potential applications of this new database lay in the aquaculture,
417 fisheries and aquatic management fields. The main interest of STOREFISH in aquaculture is
418 to present a functional typology focusing on reproduction, i.e., cluster species displaying
419 similar reproductive strategies, in order to define functional groups and one fish-model per
420 group. Then, based on this clustering, evaluate if it is possible to apply or adapt rearing
421 systems (zootechnical practices) already in use in species belonging to the same group. Such
422 approach should allow answering the three questions asked in introduction, and thus renders
423 current practices more efficient, particularly for the domestication of new species. Within the
424 fisheries field, STOREFISH could help to provide a conceptual framework based on
425 reproductive traits that could be used for the management of newly exploited species for
426 which virtually no information is available, as already proposed by Winemiller and Rose

427 (1992) and King and McFarlane (2003). Lastly, STOREFISH could also be used to help
428 aquatic management, such as the identification of the main biological characters leading to
429 successful invasion of non-native fish species (Vila-Gispert *et al.*, 2005).

430

431 **STOREFISH Planned Evolution**

432 This database is planned to be extended into two main directions. First, new species
433 will be included, particularly (i) tropical species both marine and freshwater, (ii) more species
434 inhabiting North American freshwaters and (iii) marine species living in the Northern
435 hemisphere, for which quite of lot of information is already available. This will particularly
436 allow increasing the number of reproductive strategies (e.g., hermaphrodite species).

437 Second, the database is planned to be extended to the entire life cycle of species
438 including growth, nutrition function, and behavior of adult, by including additional characters
439 such as maximum length, weight and age ever reported, trophic level of adult phase,
440 gregariousness of adult (gregarious, solitary), behaviour of adult (sedentary, migratory),
441 stenotherm or eurytherm, main habitat of adults (lakes, ponds, rivers ...), feeding behaviour
442 (carnivorous, herbivorous)... These data will be issued mainly from the same sources and also
443 from FishBase www.fishbase.org, particularly for trophic levels.

444

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446 Mathieu Andro (MNHN, Paris) who greatly helped us during the literature search.

447

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493

493 Table 1.

494 Species studied, with family and common french and FAO names (Species name and families
 495 are based on Froese and Pauly, 2006; French and FAO common names primarily on Keith
 496 and Allardi, 2001 and ftp://ftp.fao.org/FI/stat/data/ASFIS_sp.zip respectively, or on Froese
 497 and Pauly, 2006 if not available, indicated by*).

498

Species	Family	French common name	FAO common name
<i>Anguilla anguilla</i> (Linnaeus, 1758)	Anguillidae	Anguille européenne	European eel
<i>Barbatula barbatula</i> (Linnaeus, 1758)	Balitoridae	Loche franche	Stone loach
<i>Ambloplites rupestris</i> (Rafinesque, 1817)	Centrarchidae	Crapet de roche	Rock bass
<i>Lepomis gibbosus</i> (Linnaeus, 1758)	Centrarchidae	Perche-soleil	Pumpkinseed
<i>Micropterus dolomieu</i> Lacepède, 1802	Centrarchidae	Black-bass à petite bouche*	Smallmouth bass
<i>Micropterus salmoides</i> (Lacepède, 1802)	Centrarchidae	Achigan à grande bouche	Largemouth black bass
<i>Alosa alosa</i> (Linnaeus, 1758)	Clupeidae	Grande alose	Allis shad
<i>Alosa fallax fallax</i> (Lacepède, 1803)	Clupeidae	Alose feinte	Twaite shad
<i>Alosa sapidissima</i> (Wilson, 1811)	Clupeidae	Alose canadienne*	American shad
<i>Cobitis paludica</i> (de Buen, 1930)	Cobitidae		
<i>Cobitis taenia</i> Linnaeus, 1758	Cobitidae	Loche épineuse	Spine loach*
<i>Cottus gobio</i> Linnaeus, 1758	Cottidae	Chabot commun	Bullhead*
<i>Abramis brama</i> (Linnaeus, 1758)	Cyprinidae	Brème commune	Freshwater bream
<i>Alburnoides bipunctatus</i> (Bloch, 1782)	Cyprinidae	Spirilin	Chub
<i>Alburnus alburnus</i> (Linnaeus, 1758)	Cyprinidae	Ablette	Bleak
<i>Aristichthys nobilis</i> (Richardson, 1845)	Cyprinidae	Carpe à grosse tête	Bighead carp
<i>Aspius aspius</i> (Linnaeus, 1758)	Cyprinidae	Aspe	Asp
<i>Barbus barbus</i> (Linnaeus, 1758)	Cyprinidae	Barbeau fluviatile	Barbel
<i>Blicca bjoerkna</i> (Linnaeus, 1758)	Cyprinidae	Brème bordelière	White bream
<i>Carassius auratus auratus</i> (Linnaeus, 1758)	Cyprinidae	Carassin doré	Goldfish
<i>Carassius carassius</i> (Linnaeus, 1758)	Cyprinidae	Carassin commun	Crucian carp
<i>Chondrostoma nasus</i> (Linnaeus, 1758)	Cyprinidae	Hotu	Common nase
<i>Chondrostoma toxostoma</i> (Vallot, 1837)	Cyprinidae	Toxostome ou Sofie	
<i>Ctenopharyngodon idella</i> (Valenciennes, 1844)	Cyprinidae	Amour blanc	Grass carp(=White amur)
<i>Cyprinus carpio carpio</i> (Linnaeus, 1758)	Cyprinidae	Carpe commune	Common carp
<i>Gobio gobio gobio</i> (Linnaeus, 1758)	Cyprinidae	Goujon	Gudgeon*
<i>Hypophthalmichthys molitrix</i> (Valenciennes, 1844)	Cyprinidae	Carpe argentée	Silver carp
<i>Leucaspis delineatus</i> (Heckel, 1843)	Cyprinidae	Able de Heckel	Belica
<i>Leuciscus cephalus</i> (Linnaeus, 1758)	Cyprinidae	Chevaine	Chub
<i>Leuciscus idus</i> (Linnaeus, 1758)	Cyprinidae	Ide mélanote	Orfe(=Ide)
<i>Leuciscus leuciscus</i> (Linnaeus, 1758)	Cyprinidae	Vandoise	Common dace
<i>Mylopharyngodon piceus</i> (Richardson, 1846)	Cyprinidae	Carpe noire*	Black carp
<i>Phoxinus phoxinus</i> (Linnaeus, 1758)	Cyprinidae	Vairon	Eurasian minnow
<i>Pimephales promelas</i> Rafinesque, 1820	Cyprinidae	Tête de boule	Fathead minnow
<i>Pseudorasbora parva</i> (Temminck & Schlegel, 1846)	Cyprinidae	Pseudorasbora	Stone moroko
<i>Rhodeus sericeus</i> (Pallas, 1776)	Cyprinidae	Bouvière	Bitterling
<i>Rutilus rutilus</i> (Linnaeus, 1758)	Cyprinidae	Gardon	Roach
<i>Scardinius erythrophthalmus</i> (Linnaeus, 1758)	Cyprinidae	Rotengle	Rudd
<i>Tinca tinca</i> (Linnaeus, 1758)	Cyprinidae	Tanche	Tench
<i>Vimba vimba</i> (Linnaeus, 1758)	Cyprinidae	Vimbe	Vimba bream
<i>Aphanius iberus</i> (Valenciennes, 1846)	Cyprinodontidae	Aphanius d'Espagne	Spanish toothcarp
<i>Esox masquinongy</i> Mitchell, 1824	Esocidae	Maskinongé*	Muskellunge*
<i>Esox niger</i> Lesueur, 1818	Esocidae	Brochet maillé*	Chain pickerel*
<i>Esox lucius</i> Linnaeus, 1758	Esocidae	Brochet	Nothern pike
<i>Gasterosteus aculeatus aculeatus</i> Linnaeus, 1758	Gasterosteidae	Epinoche	Three-spined stickleback
<i>Pungitius pungitius</i> (Linnaeus, 1758)	Gasterosteidae	Epinochette	Ninespine stickleback
<i>Ameiurus nebulosus</i> (Lesueur, 1819)	Ictaluridae	Barbotte brune*	Brown bullhead
<i>Ictalurus punctatus</i> (Rafinesque, 1818)	Ictaluridae	Barbue de rivière*	Channel catfish
<i>Lota lota</i> (Linnaeus, 1758)	Lotidae	Lote	Burbot
<i>Dicentrarchus labrax</i> (Linnaeus, 1758)	Moronidae	Bar européen*	European seabass
<i>Morone americana</i> (Gmelin, 1789)	Moronidae	Baret*	White perch
<i>Morone chrysops</i> (Rafinesque, 1820)	Moronidae	Bar blanc*	White bass
<i>Morone saxatilis</i> (Walbaum, 1792)	Moronidae	Bar rayé*	Striped bass
<i>Osmerus eperlanus</i> (Linnaeus, 1758)	Osmeridae	Eperlan	European smelt
<i>Gymnocephalus cernuus</i> (Linnaeus, 1758)	Percidae	Grémille	Ruffe
<i>Perca flavescens</i> (Mitchill, 1814)	Percidae	Perchaude*	American yellow perch

<i>Perca fluviatilis</i> Linnaeus, 1758	Percidae	Perche	European perch
<i>Sander lucioperca</i> (Linnaeus, 1758)	Percidae	Sandre	Pike-perch
<i>Sander vitreus</i> (Mitchill, 1818)	Percidae	Doré jaune*	Walleye
<i>Gambusia affinis</i> (Baird & Girard, 1853)	Poeciliidae	Gambusie	Mosquitofish
<i>Coregonus albula</i> (Linnaeus, 1758)	Salmonidae	Corégone blanc*	Vendace
<i>Coregonus clupeaformis</i> (Mitchill, 1818)	Salmonidae	Grand corégone*	Lake(=Common)whitefish
<i>Coregonus lavaretus</i> (Linnaeus, 1758)	Salmonidae	Corégone	European whitefish
<i>Hucho hucho</i> (Linnaeus, 1758)	Salmonidae	Huchon	Huchen
<i>Oncorhynchus gorbuscha</i> (Walbaum, 1792)	Salmonidae	Saumon rose*	Pink(=Humpback)salmon
<i>Oncorhynchus keta</i> (Walbaum, 1792)	Salmonidae	Saumon keta*	Chum(=Keta=Dog)salmon
<i>Oncorhynchus kisutch</i> (Walbaum, 1792)	Salmonidae	Saumon coho*	Coho(=Silver)salmon
<i>Oncorhynchus mykiss</i> (Walbaum, 1792)	Salmonidae	Truite arc-en-ciel	Rainbow trout
<i>Oncorhynchus nerka</i> (Walbaum, 1792)	Salmonidae	Saumon rouge*	Sockeye(=Red)salmon
<i>Oncorhynchus tshawytscha</i> (Walbaum, 1792)	Salmonidae	Saumon chinook*	Chinook salmon
<i>Salmo salar</i> Linnaeus, 1758	Salmonidae	Saumon atlantique	Atlantic salmon
<i>Salmo trutta trutta</i> Linnaeus, 1758	Salmonidae	Truite de mer	Sea trout
<i>Salvelinus alpinus alpinus</i> (Linnaeus, 1758)	Salmonidae	Omble chevalier	Arctic charr
<i>Salvelinus fontinalis</i> (Mitchill, 1814)	Salmonidae	Omble de fontaine	Brook trout
<i>Salvelinus namaycush</i> (Walbaum, 1792)	Salmonidae	Cristivomer	Lake trout(=Char)
<i>Stenodus leucichthys</i> (Güldenstädt, 1772)	Salmonidae	Inconnu*	Sheefish
<i>Thymallus arcticus arcticus</i> (Pallas, 1776)	Salmonidae	Ombre arctique*	Arctic grayling
<i>Thymallus thymallus</i> (Linnaeus, 1758)	Salmonidae	Ombre commun	Grayling
<i>Silurus glanis</i> Linnaeus, 1758	Siluridae	Silure glane	Wels(=Som)catfish
<i>Valencia hispanica</i> (Valenciennes, 1846)	Valenciidae	Cyprinodonte de Valence	Valencian toothcarp*

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APPENDIX

Table 2. List of the discarded reproductive traits (either because of insufficient reliable data or lack of consistency in our context).

<i>Egg features</i>	Photoperiod during the intensifying oogenesis
Egg dry weight	Variation of photoperiod during the intensifying oogenesis
Egg wet weight	Months in the year corresponding to the resting period
Egg colour	Growth between two consecutive reproductive cycle
Egg shape	Degree-days required for the entire oogenesis
Oil globule (if present: number)	Optimum period between consecutive ovulations
Oil globule (if present: size)	Basal serum levels of sexual steroids
Structure/ultrastructure of the chorion	Highest serum levels of sexual steroids
Thickness of the chorion	Basal serum levels of vitellogenin
Resistance to manipulation	Highest serum levels of vitellogenin
Shape of the micropyle	Male
Salinity tolerance	Morphology of the testis
Light intensity tolerance	Number of testis
pH tolerance	Length of the spermiduct
Oxygen requirement	Additional organs (if present)
Post-ovulation survival of egg	Where are the spermatozoa stored prior ejaculation
<i>Larval features</i>	Viability of spermatozoa in water
Initial wet weight	Extreme values of sperm volume released per stripping
Presence of cement glands	Number of spermatozoa per individual
Days for resorption of yolk-sac	Sperm concentration
Length at resorption of yolk-sac	Volume ejaculated
Days for first feeding	Period of the first increase in GSI
Length at first feeding	Period of the second increase in GSI (if present)
Kind of first natural food	Period of the third increase in GSI (if present)
Size of first prey	Period of the fourth increase in GSI (if present)
Optimal photoperiod	Period of the first decrease in GSI (if present)
Duration of the larval period	Period of the second decrease in GSI (if present)
Larval growth rate	Temperature during the onset of spermatogenesis
<i>Mature female and male features</i>	Variation of temperature during the onset of spermatogenesis
Female	Photoperiod during the onset of spermatogenesis
Ovary morphology	Variation of photoperiod during the onset of spermatogenesis
Number of ovary	Temperature during the main spermatogenesis activity
Length of the oviduct	Variation of temperature during the main spermatogenesis activity
Additional organs (if present)	Photoperiod during the main spermatogenesis activity
Period of the first increase in GSI	Variation of photoperiod during the main spermatogenesis activity
Period of the second increase in GSI (if present)	Months corresponding to the resting period
Period of the third increase in GSI (if present)	Spermiation period
Period of the fourth increase in GSI (if present)	Basal serum levels of sexual steroids
Period of the first decrease in GSI (if present)	Highest serum levels of sexual steroids
Period of the second decrease in GSI (if present)	Spawning features
Temperature during the onset of oogenesis	Role of the photoperiod
Variation of temperature during the onset of oogenesis	Role of the temperature
Photoperiod during the onset of oogenesis	Duration of the mating act
Variation of photoperiod during the onset of oogenesis	Egg size heterogeneity between batches
Temperature during the intensifying oogenesis	Other feature
Variation of temperature during the intensifying oogenesis	Genetic determinism of sex

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