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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

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

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

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

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

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

MATERIALS AND METHODS

Targeted species

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

Targeted reproductive traits

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

Literature search

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

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

RESULTS

General remarks

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

List of the species kept

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

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

Definitive list of reproductive characters

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

Egg features:

(1) Oocyte size: corresponds to the average diameter of the unfertilised egg, i.e., mature, fully yolked ovarian oocyte ready to be or just released (in mm): **99%**

(2) Egg size after water-hardening: corresponds to the average diameter of the fertilized egg after swelling, due to water uptake (in mm): **60%**

(3) Egg buoyancy: of the fertilized swollen egg, being either demersal (sinks to the bottom), semi-pelagic (remains for a short period in the water column, then sinks) or

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

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

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

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

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

Larval features:

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

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

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

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

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

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

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

Mature female and male features

Female

(15) Age at sexual maturity: average age at maturity (in years): **96%**

(16) Length at sexual maturity: average total body length at maturity (in cm): **81%**

(17) Weight at sexual maturity: average body weight at maturity (in kg): **50%**

(18) Female sexual dimorphism: females of some species develop secondary sexual characters during the breeding season, scored as a binary variable [Absent, Present]: **21%**

(19) Relative fecundity: average number of eggs (in thousands) per kilogram of body weight: **70%**

(20) Absolute fecundity: average number of eggs (in thousands) recorded by individual female: **90%**

The six following characters aimed at describing the main events within the reproductive cycle:

(21) Oocyte development: synchronous (all oocytes present within the ovary are at the same stage of development), group-synchronous (at least two distinct populations of oocytes at different development stages) and asynchronous (oocytes at all stages of development), scored as a three-state variable [Synchronous, Group-synchronous, Asynchronous]: **64%**

(22) Onset of oogenesis: defined as the months in the year when an initial significant inflexion and increase in the GSI is observed. This period corresponds to the onset of the active vitellogenesis, mainly endogenous: **55%**

(23) Intensifying oogenesis activity: defined as the months in the year when the GSI displays the largest increase. This period mainly corresponds to the end of the active vitellogenesis, prior to the final maturation of oocytes (i.e., oocyte meiotic resumption and ovulation): **50%**

(24) Maximum GSI value: corresponds to the average maximal GSI value (%) observed within the entire reproductive cycle: **63%**

(25) Oogenesis duration: corresponds to the total duration of the oogenesis process from the initial significant inflexion and increase in GSI until ovulation (in months): **25%**

(26) Resting period: corresponds to the duration of gonadal quiescence between two consecutive reproductive cycles when the ovaries are recovering from the spawning act (in months): **49%**

Male

(27) Age at sexual maturity: average age at maturity (in years): **95%**

(28) Length at sexual maturity: average total body length at maturity (in cm): **71%**

(29) Weight at sexual maturity: average body weight at maturity (in kg): **39%**

(30) Male sexual dimorphism: males belonging to certain species develop secondary sexual characters during the breeding season, scored as a binary variable [Absent, Present]: **51%**

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

(31) Onset of spermatogenesis: defined as the months in the year when a significant increase in the GSI is observed. This period mainly corresponds to the initial proliferation of spermatogonia through repeated mitotic divisions, and primary spermatocytes differentiation: **35%**

(32) Main spermatogenesis activity: defined as the months in the year when the GSI displays a sharp increase. This period mainly corresponds to the transformation of spermatocytes into mature spermatozoa (including the spermiogenesis process) and prior to spermiation: **32%**

(33) Maximum GSI value: corresponds to the average maximal GSI value (%) observed within the entire reproductive cycle: **50%**

(34) Spermatogenesis duration: corresponds to the total duration of the spermatogenesis process from the initial proliferation of spermatogonia to spermiation (in months): **18%**

(35) Resting period: corresponds to the duration of gonadal quiescence between two consecutive reproductive cycles when the testis are recovering from the spawning act (in months): **36%**

Spawning features:

(36) Spawning migration distance: corresponds to the average distance run by adults to get to the spawning grounds (in km): **39%**

(37) Spawning migration period: corresponds to the months in the year when some species display extensive spawning run: **46%**

(38) Homing: defines as the accurate returning behaviour of some teleosts to their natal areas to spawn, scored as a binary variable [Absent, Present]: **35%**

(39) Spawning season: corresponds to the usual months of the presence of spawners on the spawning ground: **99%**

(40) Spawning period duration: corresponds to the period of time when spawners are

present on the spawning ground (in weeks): **73%**

(41) Spawning temperature: average temperature observed during the spawning period (°C): **86%**

(42) Spawning water type: corresponds to the kind of water frequented during the spawning season, could be either stagnant water such as ponds or lakes (with no or slight current) or rivers and streams (with much more current), scored as a binary character [Stagnant water, Flowing or turbulent water]: **87%**

(43) Spawning depth: defines at the average depth at which spawning occurs (meters): **79%**

(44) Spawning substrate: teleost species either scatter their eggs in the water column (pelagophils), or deposit their eggs (i) on a rock or gravel bottom (lithophils), (ii) on plants (phytophils), (iii) on roots or grass above the sandy bottom or on the sand itself (psammophils) or (iv) into gill cavity of mussels (ostracophils). This character is mainly derived from Balon's (1975) classification of reproductive guilds of teleost fishes, and scored as a five-state variable [Pelagophils, Lithophils, Phytophils, Psammophils, Ostracophils]: **90%**

(45) Spawning site preparation: teleost species scatter their eggs either in the water column, directly over the substrates, or within a nest, which is a depression dug into the substrate by either the male, the female or both parents, scored as a five-state variable [Open water/substratum scatter, Substrate chooser, Nest built by male, Nest built by female, Nest built by both parents]: **95%**

(46) Nycthemeral period of oviposition: corresponds to the main period during the day when mass spawning occur, scored as a four-state variable [Night, Dawn, Day, Dusk]: **56%**

(47) Mating system: teleost species display three main kind of mating system: monogamous (one male and one female), polygamous (an individual, either the male or the female, has several mates), and promiscuity (both sexes have multiple partners within a single season), scored as a four-state variable [Monogamy, Polygyny, Polyandry, Promiscuity]: **68%**

(48) Spawning release: teleost species display three main kind of egg release during the breeding season: total (all eggs are shed at the same time), fractional (several batches of eggs are released at intervals, usually over several days or weeks, but the potential breeding season fecundity is fixed before spawning, also known as determinate fecundity) or multiple (several batches of eggs are shed more than once through a long

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

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

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

DISCUSSION

Assessment of the Database

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

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

fisheries management field by King and MacFarlane (2003).

Reappraisal of the reliability of selected characters

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

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

Preliminary analysis of the database

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

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

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

Potential applications

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

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

STOREFISH Planned Evolution

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

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

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Table 1.

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

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

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

APPENDIX

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

Egg features	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
Larval features	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
Mature female and male features	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