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The European sea bass: a key marine fish model in the wild and in aquaculture

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Summary

The European sea bass (*Dicentrarchus labrax* L.) is a marine fish of key economic and cultural importance in Europe. It is now more an aquaculture than a fisheries species (>96% of the production in 2016), although modern rearing techniques date back only from the late 1980s. It also has high interest for evolutionary studies, as it is composed of two semispecies (Atlantic and Mediterranean lineages) that have come into secondary contact following the last glaciation. Based on quantitative genetics studies of most traits of interest over the past 10–15 years, selective breeding programs are now applied to this species, which is at the beginning of its domestication process. The availability of a good quality reference genome has accelerated the development of new genomic resources, including SNP arrays that will enable genomic selection to improve genetic gain. There is a need to improve feed efficiency, both for economic and environmental reasons, but this will require novel phenotyping approaches. Further developments will likely focus on the understanding of genotype-by-environment interactions, which will be important both for efficient breeding of farmed stocks and for improving knowledge of the evolution of natural populations. At the interface between both, the domestication process must be better understood to improve production and also to fully evaluate the possible impact of aquaculture escapees on wild populations. The latter is an important question for all large-scale aquaculture productions.

Keywords dicentrarchus labrax, genetics, heritability, population genetics

Background: biology, economic importance and domestication

The European sea bass is a coastal marine fish that lives in shallow waters (<100 m) from the north-eastern Atlantic Ocean to the Mediterranean and the Black Sea. The sea bass is euryhaline (0–40 ppt salinity) and eurythermal (2–32 °C) and is often found foraging in estuaries and lagoons from spring to fall, especially at the juvenile stage. During winter, juvenile and adult sea bass migrate from the coastline to deeper waters, where the temperature is more stable, as they prefer temperatures above 9–10 °C (Pickett & Pawson 1994). The sea bass normally matures at two to three years of age for males, and three to four years of age for females (Perez-Ruzafa & Marcos 2014). Reproduction happens in groups, between December and March in the Mediterranean and between March and June in the Atlantic. Females spawn an average of 200 000 eggs/kg, which are fertilized externally. Eggs hatch after three to five days, and larvae (4 mm at hatching) reach the post-larval stage (>22 mm) in two to three months while migrating to inshore nursery areas and lagoons. The European sea bass is an opportunistic predator, feeding on plankton at the larval stage and on fish and crustaceans at the juvenile and adult stages.

The European sea bass is highly regarded for capture and recreational fisheries. The fishing grounds are the north-eastern Atlantic Ocean, especially the English Channel, the Irish Sea and the Gulf of Biscay (Pickett & Pawson 1994), as well as the Mediterranean. Captures in the two areas have been historically comparable, although in recent years the catches have been higher in the Atlantic Ocean. Recreational fisheries have a major share in capture fisheries, as they can account for 30% to 50% of the total catch in the Atlantic (ICES 2018). However, in economic terms, European sea bass is now clearly an aquaculture species. Aquaculture has been producing more than fisheries since

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1992 and has accounted for 96% of the total production in 2016 (aquaculture 165 915 tons vs. fisheries 6919 tons in 2016; FAO 2018). Contrary to fisheries, sea bass culture is essentially located in the Mediterranean area, which accounts for 94% of the production, mostly in Turkey, Greece, Egypt and Spain. Aquaculture production is in two phases: first a hatchery-pregrowing phase, which produces fish of 1 to 20 g in three to eight months, and then an ongrowing phase to 250–450 g in 12 to 20 months. Hatcheries are typically inland, in temperature-controlled systems, whereas the bulk of the ongrowing is in sea cages in natural waters. The main market product is the 250–400 g pan-sized fish, but there is growing interest in the production of larger fish (800 g to 1 kg) to sell whole or as processed fillets (EUMOFA 2018).

The domestication of sea bass is very recent, like for most marine aquaculture species. It was the first non-salmonid marine species commercially cultured in Europe (Bagni 2005). The first intensive rearing trials started in the early 1970s, based on wild-captured juveniles (Fig. 1). In the early 1980s, controlled reproduction in spawning tanks and larval rearing were developed, mainly in France and Italy, and made domestication possible (Bagni 2005; Chatain & Chavanne 2009). Mostly wild-caught broodstock was used in the hatcheries, and the first selective breeding programs using exclusively hatchery-born broodstock (and thus domestication in its genetic meaning) started only in the 1990s (Chatain & Chavanne 2009). In 2016, it was estimated that approximately 50% of farmed sea bass came from selective breeding programs (Janssen *et al.* 2017). However, domestication remains recent, and in 2016, the sea bass strains with the longest history of domestication were eight generations away from the wild populations of origin (Chavanne *et al.* 2016).

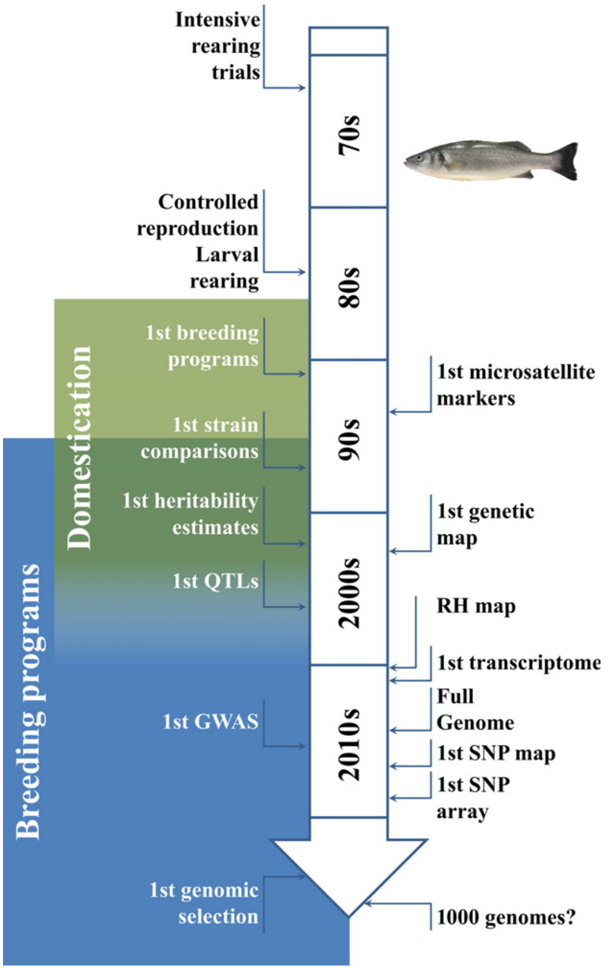

Figure 1 Development over time of genetic/genomic tools and their application in European sea bass.

Phenotypes of interest

As in all farmed fish species, growth is a key trait, especially because sea bass need 18 to 24 months to reach commercial size. Improvement in growth rate is thus highly demanded by farmers, although some recent studies tend to show that growth itself is of little interest compared to feed efficiency (Besson *et al.* 2016). As in many (especially marine) fish species, deformities can reach a high incidence and are thus an important trait, as they have an impact on fish welfare and economic value (Boglione *et al.* 2013).

Resistance to diseases is also a major category of phenotypes that require improvement for farming. The main disease affecting sea bass is viral nervous necrosis (VNN), for which there is still no efficient vaccine (Doan *et al.* 2017b). Other diseases that cause significant concern are bacterial diseases, such as vibriosis and tenacibaculosis, and parasitic diseases caused by *Diplectanum* spp. or isopods (Vendramin *et al.* 2016). A second key category of phenotypes in terms of production efficiency is processing yields (gutted carcass yield and fillet yield). These attract less attention because most fish are sold whole, but the foreseen development of the fillet market makes them more and more interesting. Finally, as in all farmed species, feed efficiency is a key parameter for the improvement of profitability and the reduction in the environmental footprint (Besson *et al.* 2017). However, feed efficiency is difficult to approach, as there is presently no way to precisely estimate individual feed intake in fish in farming conditions (see de Verdal *et al.* 2018, for a review). One important point, in the context of the reduction of fishmeal and fish oil use in fish feeds, is the ability of sea bass to adapt to plant-based diets.

Control of the sea bass population sex ratio is presently difficult. Although in the wild the sex ratio is balanced in young fish and biased toward females in older fish (Vandeputte *et al.* 2012), farmed sea bass show a clear bias toward males (75%–95%). This is because sea bass sex is determined by a polygenic system with approximately equal influences of genetics and environment, the latter mostly through larval rearing temperature (reviewed by Vandeputte & Piferrer

2019). As hatcheries use higher temperature to obtain faster growth, farmed populations are mostly males, which grow 20%–30% less than do females and have advanced puberty, two unfavorable characteristics for farming (Saillant *et al.* 2001).

Other 'functional' phenotypes, such as behavior, coping styles, tolerance of stress, swimming capacities and tolerance of hypoxia, have raised some interest. There are also variations in body shape, which may be important for predicting processing yields but also as consumers tend to prefer 'wild-like' elongated shapes when buying whole fish. Muscle fat content is also important as a key trait for organoleptic quality. Finally, the only known color variant is a recessive albinism.

Genetic variation

The European sea bass shows a moderate level of nucleotide diversity ($\pi = 0.25\%$; Tine *et al.* 2014), which is quite similar between Atlantic and Mediterranean sea bass populations and slightly higher than in the spotted sea bass (*Dicentrarchus punctatus*), the closest relative to *D. labrax* (Tine *et al.* 2014). Although the two species are sympatrically distributed in some regions and display a net genetic divergence of only 0.5%, they do not seem to hybridize at present in nature, although they can hybridize by artificial fertilization (Ky *et al.* 2012).

Natural populations structure and phenotypic variation

Genetic diversity in the European sea bass is spatially structured. Early population genetic studies have reported substantial genetic differentiation between Atlantic and Mediterranean regions (Allegrucci *et al.* 1997; Caccone *et al.* 1997; Naciri *et al.* 1999). A marked genetic discontinuity between these two regions occurs in the Alboran Sea (the westernmost part of the Mediterranean Sea, close to the Strait of Gibraltar) and has been attributed to the existence of a hybrid zone between two evolutionary lineages that likely originated through allopatric isolation between Atlantic and Mediterranean basins during the Pleistocene (Lemaire *et al.* 2005). There is a striking contrast among markers in the extent of genetic differentiation across this hybrid zone. A sharp gradient in mitochondrial haplotype frequencies has been observed in the Atlantic–Mediterranean transition zone (Lemaire *et al.* 2005), whereas nuclear markers usually display very low genetic differentiation in the same region (Quéré *et al.* 2012; Souche *et al.* 2015). A population genomic study including more than 200 000 SNPs mapped along the 24 chromosomes of the reference genome has described such heterogeneous divergence patterns at the genome scale (Tine *et al.* 2014). This study revealed that despite a low genome-wide average differentiation between Atlantic and Mediterranean sea bass ($F_{ST} = 0.028$), some regions of the genome display fixed differences between the two lineages. An intriguing finding was that regions of increased differentiation most often mapped to central chromosomal regions, forming large (sometimes megabase-scale) genomic islands of differentiation above the background level. Historical demographic reconstruction based on whole-genome resequencing revealed that this situation results from the differential erosion of past divergence accumulated in allopatry for about 300 000 years (Duranton *et al.* 2018). Since the end of the last glacial period, the two lineages have come into secondary contact, resulting in asymmetric introgression mostly from the Atlantic into the Mediterranean background. Introgressed genomic fragments of Atlantic origin are often neutral when they enter the Mediterranean lineage. However, some are slightly or mildly deleterious and are therefore progressively removed by selection following introgression. Selection against introgressed tracts was shown to be more efficient within central chromosomal regions, which are characterized by reduced crossover rates. This is because genes involved in reproductive isolation between the two lineages add their individual effects more efficiently in low-recombining regions (Duranton *et al.* 2018). This suggests that a high number of small effect genes, rather than a few genes of large effect, are responsible for partial reproductive isolation between Atlantic and Mediterranean sea bass lineages. This also implies that the two lineages should not be considered simply as differentiated populations of the same species but, rather, as semi-isolated species (i.e. semispecies), which have not finished to speciate (and perhaps never will). The biological functions of the genes underlying partial reproductive isolation between the two lineages has not been identified yet. However, phenotypic differences of potential interest for selection and domestication are expected at the molecular level (e.g. protein function, gene regulation) due to this cryptic species subdivision.

Another consequence of the two hybridizing lineages in sea bass concerns the spatial population structure within each lineage. A lower level of genetic subdivision has been described between the western and eastern Mediterranean (Caccone *et al.* 1997; Bahri-Sfar *et al.* 2000; Souche *et al.* 2015) and also to a lower extent within each Mediterranean basin (Garcia De Leon *et al.* 1997; Castilho & Ciftci 2005). By contrast, no study has yet revealed any biologically meaningful pattern of spatial genetic structure in the North Atlantic (Fritsch *et al.* 2007; Coscia & Mariani 2011; Souche *et al.* 2015). Such an asymmetry between the obvious longitudinal population structure in the Mediterranean and the absence of any detectable pattern in the Atlantic partly reflects the asymmetry in gene flow between the two lineages. Asymmetrical introgression generates an allele frequency gradient within the Mediterranean but almost none in the Atlantic. Moreover, introgressed Atlantic alleles can enter the Mediterranean only from the western side, after which migrant DNA fragments are progressively removed by selection as they diffuse from west to east (Duranton *et al.* 2018). Consequently, many genes show a longitudinal gradient in allele frequency due to the opposite effect of gene flow and selection within the Mediterranean. This spatial introgression process has the potential to amplify any genetic differentiation pattern due to an underlying neutral population structure (Gagnaire *et al.* 2015). Therefore, signals of introgression between lineages are important for illuminating fine-scale population connectivity patterns for the conservation and management of wild sea bass populations.

Considering this hierarchical genetic structure, comparing natural populations for their phenotypes really makes sense in sea bass, both to understand the evolution of the natural populations and to make informed choices in order to establish base populations for farming. A first experiment (Gorshkov *et al.* 2004) showed a higher condition factor, a higher proportion of females but also a higher proportion of deformed fish, in western Mediterranean fish compared to eastern Mediterranean populations but no heterosis in population crosses. Then, a large-scale common garden comparison of North Atlantic (NAT), South Atlantic, western Mediterranean (WEM), north-eastern Mediterranean (NEM) and south-eastern Mediterranean (SEM) fish and their crosses showed moderate between-population variation for growth, body shape and carcass yield and zero variation for fillet yield (Costa *et al.* 2010; Vandeputte *et al.* 2014). Higher variation was found for muscle fat content, for which NAT and SEM were fatter than the others, as well as for sex ratio. Heterosis was found in population crosses between the Atlantic and Mediterranean lineages for sex ratio and general survival but not for other traits (Guinand *et al.* 2017). The most spectacular difference between those populations was the resistance to VNN, for which the expected survival between SEM, NEM, WEM and NAT was estimated to be 99%, 94%, 62% and 44% respectively (Doan *et al.* 2017a). This might be explained by natural selection due to a higher prevalence of VNN, a warm water disease, in the eastern Mediterranean, where temperatures are higher. It also nicely reflects the longitudinal gradients in Atlantic allele frequencies described in the Mediterranean (Duranton *et al.* 2018), especially if Atlantic sea bass carry sensitivity to VNN.

Genetic variation for phenotypic traits

Apart from differences between populations, estimating within-population genetic variation of traits and covariation among traits is crucial for optimizing the design of breeding programs. During the last decade, many studies have investigated genetic parameters for growth, processing traits, deformities, feed efficiency, welfare, behavior, health or reproduction traits in European sea bass (Table S1). The heritability of growth traits ranges from 0.30 to 0.60 for body weight at a given age and from 0.15 to 0.45 for growth rate at specific periods, depicting their high potential for genetic improvement. Minor- to moderate-effect QTL have also been found for these traits (Chatziplis *et al.* 2007; Massault *et al.* 2010b) but with little potential for practical application. Processing yields show low phenotypic variability and moderate heritability ($h^2 = 0.21$ for fillet yield, 0.57 for carcass yield; Vandeputte *et al.* 2017). General body shape is rather heritable ($h^2 = 0.40$–0.50 with some low values) but little predictive of processing yields. Conversely, heritability of spine deformities is low to moderate (ranging from 0.13 to 0.33) with large differences according to experimental conditions. These differences sometimes may be caused by the difficulty to occur sufficiently commonly to produce accurate heritability estimates but also by the fact that the genetic basis may differ depending on the main deforming factor, as seen in salmonids (Kause *et al.* 2007). Thus, efficient selection against deformities might be difficult. Regarding feed efficiency and feeding behavior, very few studies have been able to properly address the genetic variation of such traits due to the practical impossibility of recording individual feed intake in commercial conditions (de Verdal *et al.* 2018). An indirect trait, tolerance to fasting, which is phenotypically linked to feed efficiency, has been shown to be moderately heritable ($h^2 = 0.23$; Grima *et al.* 2010), quite similar to the heritability of feed conversion ratio, which could only be estimated in individual aquaria ($h^2 = 0.26$; Besson *et al.* 2018). Welfare and behavior traits display low to moderate heritability (from 0.19 to 0.48). In this mass spawning, prolific species, a low priority has been given to estimating the heritability of most reproduction traits. The sex of sea bass is determined as a polygenic trait governed by several low-effect QTL (Palaiokostas *et al.* 2015), with some of the QTL specific to some natural populations (Faggion *et al.* 2018), but with high heritability of the underlying sex tendency ($h^2 = 0.47$–0.62, Vandeputte *et al.* 2007; Palaiokostas *et al.* 2015). As sex tendency is genetically correlated with growth ($r_A = 0.50$), it is expected that selection for growth will lead to a higher proportion of females in farmed populations (Vandeputte *et al.* 2007). Finally, the heritability of resistance to VNN is moderate (0.26–0.27) but sufficient to expect its improvement by selective breeding. Again, some QTL for VNN resistance have been found, but with small effects (Palaiokostas *et al.* 2018). Some remarkable genetic correlations between traits, such as positive correlations between growth and lipid deposition and negative correlations between growth and disease resistance, have to be considered in breeding programs to avoid unfavorable correlated responses. Correlations between growth (the main trait selected) and other important traits are shown in Fig. 2.

Genotype-by-environment interactions

Genotype-by-environment (G × E) interactions are also important to consider in a selective breeding context to

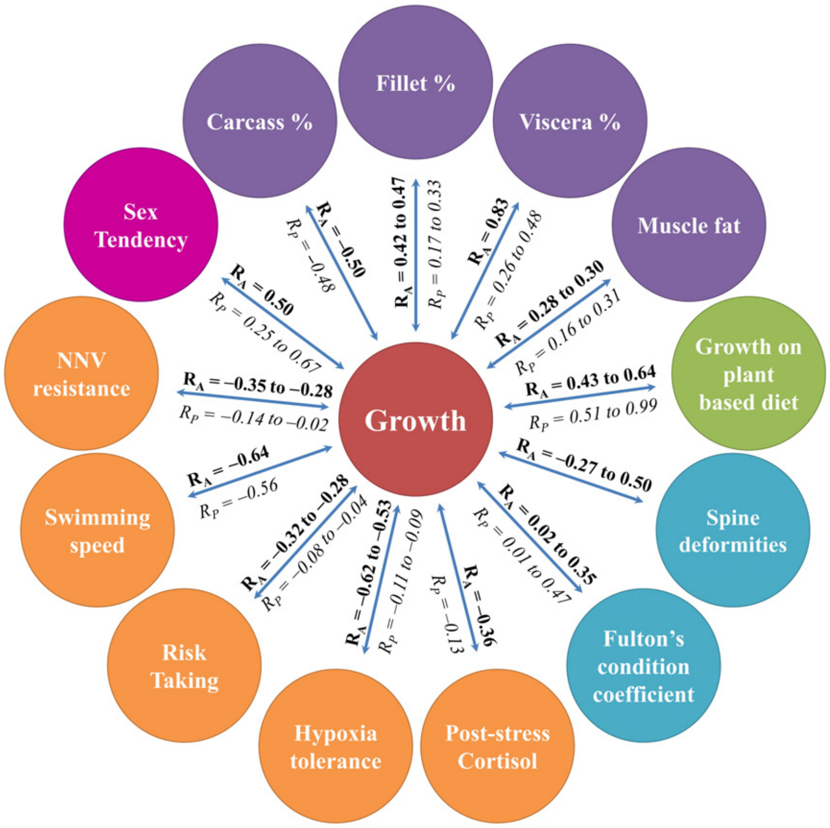

Figure 2 Genetic (R_A) and phenotypic (R_P) correlations between growth and other traits of interest in European sea bass.

assess the stability of performances across different environments. In sea bass, this is especially relevant due to the high variation of environmental conditions between farming systems and farming areas. At the population level, there was no impact of G × E interactions on the traits tested except for growth rate, for which SEM fish performed better than did others in warm water conditions in the Red Sea, whereas they were poor growers in other conditions (Vandeputte *et al.* 2014). There was also moderate G × E interaction on carcass yield but not on fillet yield, muscle fat content or condition factor. At the family level, G × E interaction is measured by the genetic correlation between the same trait measured in different environments. Low correlations (and thus high G × E interactions) were evidenced for growth rate (but not final body weight) between different farming environments. Genetic correlations between the most extreme environments were as low as 0.38, but never negative (Dupont-Nivet *et al.* 2010; Vandeputte *et al.* 2014). G × E interactions were moderate ($r_G > 0.70$) for quality traits and deformities (Haffray *et al.* 2007; Karahan *et al.* 2013).

A specific type of G × E interaction is the genotype-by-feed interaction, which has been evaluated to estimate the potential to adapt sea bass to plant-based diets, as there is limited availability (in terms of volume and price) of fishmeal and fish oil to produce aquaculture feeds. It was shown that the genetic correlation between a marine and a 100% plant-based diet was significantly lower than 1 for body weight, growth rate and muscle fat content (Le Boucher *et al.* 2011, 2013). However, response to selection failed to show trans-generational adaptation to the plant diet, probably due to the fact that the 100% plant-based diet used was too challenging for the sea bass due to the absence of long chain omega3 fatty acids (M. Vandeputte, unpublished).

Effects of domestication, selected lines and specific genotypes

As domestication is very recent, its effects are not well documented. Reduced genetic variability was shown in Greek hatchery populations compared to the wild (Loukovitis *et al.* 2014), probably due to low effective population sizes. At the phenotypic level, several studies have compared wild caught to farmed sea bass, showing less flight response and anti-predator behavior in domesticated fish (Malavasi *et al.* 2004; Benhaïm *et al.* 2012), but this includes ontogenic effects of domestication (early rearing in hatchery vs. in the wild) and not only the genetic effect. Comparison of contemporary groups from domesticated and wild parents has been done so far only at the first generation and has showed no effect on growth, stress response or maximum swimming speed (Vandeputte *et al.* 2009, 2016; Millot *et al.* 2010). Some effects were seen in swimming and exploratory behavior as well as in feeding rhythms, showing that domesticated fish were more tolerant of stress and exhibited less anti-predatory behavior (Millot *et al.* 2011). A last documented effect of domestication is that there are more females in the offspring of domesticated sea bass when the sex ratio of the parents was strongly biased toward males, consistent with what is expected from frequency-dependent selection (Vandeputte 2012; Vandeputte & Piferrer 2019). The expectation is that, without changing the hatchery environment, balanced sex ratios should be achieved in domesticated populations in seven to eight generations, even in the absence of selection (Vandeputte *et al.* 2007).

Although selective breeding of European sea bass is relatively recent, several privately owned breeding programs operate in Europe. In 2016, seven sea bass breeding programs were identified in Greece, France and Turkey (Chavanne *et al.* 2016). The traits selected are growth, morphology, disease resistance and product quality. Half of the programs use individual selection, whereas the other half use family and combined selection. The average number of generations selected is 4.2 (range 1–8), and most programs use fewer than 400 parents per generation. One program has reported 23% genetic gain per generation for harvest weight over 2.3 generations (Thorland *et al.* 2017). Experimental lines selected for growth, tolerance of fasting, female ratio, VNN resistance, albinism as well as wild western Mediterranean and Atlantic reference populations are available for research at Ifremer in Palavas-les Flots, France (https://wwz.ifremer.fr/mediterranee_eng/aquaculture/Cheptels-experimentaux-de-bar). Response to selection has been demonstrated on growth (23–42% per generation, Vandeputte *et al.* 2009; Thorland *et al.* 2017) and tolerance of fasting (Daulé *et al.* 2014). Selection for growth-induced correlated with response on sex ratio (more females; Vandeputte 2012) but not on post-stress cortisol and maximal swimming speed (Vandeputte *et al.* 2016) or on muscle fat, carcass yield and fillet yield (M. Vandeputte, M. Dupont-Nivet, H. Chavanne, P. Haffray, A. Vergnet and B. Chatain, unpublished). Selection for tolerance of fasting over one generation failed to produce the expected correlated response in feed efficiency, for which fasting tolerant fish would be expected to be more efficient (Daulé *et al.* 2014).

Chromosome set manipulation and uniparental reproduction exploit the external fertilization and developmental plasticity of fish. In European sea bass, by applying temperature or pressure shocks at specific times after fertilization, triploids (3n chromosomes) may be obtained by the retention of the second polar body (Colombo *et al.* 1995; Felip *et al.* 1997; Peruzzi & Chatain 2000) and tetraploids (4n chromosomes) by suppression of the first cell division (Piferrer *et al.* 2009). Meiotic gynogenetic fish (leading to uniparental dam progeny) may be produced by irradiated sperm-induced egg activation and further retention of the second polar body (Peruzzi & Chatain 2000). Mitotic gynogenetic fish (leading to double haploid progeny) can be obtained by ultra violet (UV) irradiated sperm-induced egg activation (Bertotto *et al.* 2005; Colleter *et al.* 2014). UV irradiation of eggs, fertilization by normal sperm and suppression of the first cell division normally permit the production of androgenetic double haploids. However, in sea bass, Colleter *et al.* (2014) reported lack of efficiency of UV inactivation of egg DNA due to the presence of gadusol, a UV-screening component, at the surface of sea bass eggs—thus preventing the use of androgenesis.

Uniparental progenies and double haploids are useful for gene and centromere mapping (Oral *et al.* 2017), genome assembly and duplication assessment (Tine *et al.* 2014), construction of isogenic lines (Bertotto *et al.* 2005; Quillet *et al.* 2007) and identification of QTL at low frequency in a population (Verrier *et al.* 2012). Production of triploid sea bass, which are sterile (Peruzzi *et al.* 2004), may be a potential solution to protecting genetic gain or preventing the genetic impact of aquaculture escapees on wild populations.

Molecular resources

Whole genome sequence

The sea bass reference genome was sequenced and *de novo* assembled from an Adriatic meiogynogenetic male using a mix of whole genome shotgun, mate pair and BAC-end sequencing strategies assisted by linkage map anchoring (Tine *et al.* 2014). It has a total length of 675 Mb, 575 of which are assembled into 24 chromosomes showing high collinearity with the stickleback (*Gasterosteus aculeatus*) genome. This high-quality chromosome-scale assembly was annotated using a combination of gene-prediction, homology-search and transcript-mapping strategies. It contains about 21% of repetitive DNA sequences (e.g. transposable elements) and more than 26 000 annotated genes. The sea bass genome is also characterized by expansions of gene families playing a role in adaptation to euryhalinity, including claudins, aquaporins, arginine-vasotocin receptors, prolactin and its receptors. Overall, the sea bass genome shows a high number of gene copies involved in osmoregulation compared to other sequenced teleosts. This observation is consistent with an increased retention in the sea bass ancestral lineage of gene copies favoring tolerance to rapid salinity changes, following the teleost-specific whole genome duplication.

Sequence polymorphism is highly heterogeneous across the sea bass genome, with large-scale variation patterns of nucleotide diversity being found within most chromosomes (Tine *et al.* 2014). The general pattern corresponds to an increased diversity near chromosomal extremities ($\pi = 0.5\%$) in comparison to central chromosomal regions ($\pi = 0.1\%$). Such a chromosome-center-biased loss of diversity has been attributed to the effect of linked selection, which removes neutral variants more efficiently in chromosome centers compared to peripheries. This effect is due to a generally reduced crossover rate in central chromosomal regions, which is a common feature of fish genomes (Bradley *et al.* 2011; Roesti *et al.* 2012) and a possible consequence of crossover interference and male heterochiasmy. The apparent pervasiveness of linked selection in the sea bass genome makes the local nucleotide diversity level strongly negatively correlated to the local recombination rate. This property was exploited for the design of sea bass SNP arrays (see below), in order to select variants that are homogeneously spaced along the recombination map.

Markers, genotyping arrays and transcriptomes

Following the development of microsatellite markers for population genetics and linkage mapping studies (e.g. Garcia De Leon *et al.* 1995; Chistiakov *et al.* 2005), SNP markers that were first developed from expressed sequenced tags progressively have replaced microsatellites (e.g. Souche *et al.* 2015). Large numbers of randomly distributed SNP markers became available more recently with the implementation of restriction-site-associated DNA (RAD) sequencing approaches. For instance, more than 200 000 SNPs were genotyped by Tine *et al.* (2014) thanks to the use of a frequent cutter enzyme (BamHI), whereas linkage mapping studies used enzymes with a longer restriction site (SbfI) or ddRAD-seq to generate smaller-scale SNP datasets (Palaiokostas *et al.* 2015, 2018; Oral *et al.* 2017). More recently, the development of SNP markers has been taken a step further with the use of whole-genome resequencing in wild samples that were crossed to generate 24 genomes from eight parent–offspring trios (Duranton *et al.* 2018). This approach not only permitted the discovery of genome-wide SNP variation but also allowed for the verification of the correct Mendelian transmission of those makers within family trios to filter false variation and the determination of the phase of variants located on the same chromosome. This approach generated a genome-wide variation map containing 2 628 725 SNPs phased into chromosome-wide haplotypes (Duranton *et al.* 2018). At the time of this writing, the sequencing of 60 additional genomes has more than tripled the number of variants that are mapped and validated in *D. labrax*, and one genome of *D. punctatus* has also been sequenced to analyze the extent of shared polymorphism between the two species (unpublished data).

The first low-density linkage maps were based on a few hundred microsatellite and AFLP markers (Chistiakov *et al.* 2005, 2008). In 2010, a radiation hybrid (RH) map of 1581 markers was produced (Guyon *et al.* 2010), but with the publication of the sea bass genome (Tine *et al.* 2014) and the recent advances of next generation sequencing, this RH map has not been used much. Higher density maps, including a map from gynogenetic families that enabled centromere mapping (Oral *et al.* 2017), have been produced with RAD-sequencing (Palaiokostas *et al.* 2015, 2018).

In the genomic toolbox of a species of interest, SNP arrays are important tools for genetics, as they allow repeatable investigations of known loci, enabling the merging of multiple generations or experiments, which is not obvious when applying genotyping-by-sequencing or RAD genotyping. In European sea bass, a growing interest in developing such tools has arisen after the publication of the genome and the massive subsequent SNP discovery (Tine *et al.* 2014; Palaiokostas *et al.* 2015, 2018; Duranton *et al.* 2018). To our knowledge, two arrays have been developed for European sea bass: an Illumina iSelect Custom Infinium® 3K SNP array (Faggion *et al.* 2018) and a Thermofisher Axiom™ 'DlabCHIP' 57K custom array (F. Allal, M. Duranton, R. Morvezen, S. Brard-Fudulea, C. Poncet, E. Belmonte, R. Griot, J.-S. Bruant, S. Cariou, A. Bajek, B. Peyrou, M. Vandeputte, C. Jaimet, P. Haffray and P.-A. Gagnaire, unpublished). Both these arrays were produced from the above-mentioned genome-wide variation map containing 2 628 725 SNPs phased into chromosome-wide haplotypes discovered from the resequencing of Atlantic and Mediterranean individuals (Duranton *et al.* 2018). Both chips were designed to include markers spread along each chromosome with a variable density of SNPs depending on the estimated local nucleotide diversity (π). The Axiom DlabCHIP displayed high design quality, with an average genotype call rate for passing samples of over 99.7% estimated over 2300 sea bass from two French commercial populations (F. Allal, M. Duranton, R. Morvezen, S. Brard-Fudulea, C. Poncet, E. Belmonte, R. Griot, J.-S. Bruant, S. Cariou, A. Bajek, B. Peyrou, M. Vandeputte, C. Jaimet, P. Haffray and P.-A. Gagnaire, unpublished). We anticipate that this 57K SNP array will soon become a standard genomic tool for implementation of genomic selection in European sea bass breeding programs.

Although initial expression studies used candidate gene PCR-based approaches (Blázquez & Piferrer 2004; Navarro-Martín *et al.* 2009), the first transcriptome of sea bass was produced in 2010 and comprised 18 196 putative unigenes from 14 normalized tissue-specific libraries including liver, ovary, testis, bone/cartilage, brain/pituitary, heart/vessels, adipose, head/kidney, trunk/kidney, gill, intestine, spleen, muscle and skin (Louro *et al.* 2010). Then, microarrays were generated to study, for example, larval development (Ferraresso *et al.* 2010), effect of a plant-based diet on the hepatic transcriptome (Geay *et al.* 2011) and the transcriptomic basis of egg quality (Zarski *et al.* 2017). Currently, *de novo* sequencing of transcriptomes is more routinely used and has generated a large amount of data: 35 073 transcripts from a brain and liver transcriptome (Magnanou *et al.* 2014); 69 794 transcripts expressed during egg development and at hatching (Kaitetzidou *et al.* 2015); 31 842 transcripts from skin and 20 423 transcripts from scales (Pinto *et al.* 2017); and 47 071 transcripts from brain, liver and white muscle in growing fish (Louro *et al.* 2019). Several datasets were integrated in an assembled transcriptome in 2016, providing 68 790 contigs with a mean size of 2125 bp and an N50 of 2966 bp, available at http://sea.ccmar.ualg.pt (Louro *et al.* 2016).

Perspectives

Genetic studies of European sea bass really started in 1995 with the development of microsatellite markers. This enabled the description of the structure of natural populations as well as the first quantitative genetics studies, as it became possible to set up common garden experiments with many families to estimate the heritability of traits. This is quite different from other major fish species (Atlantic salmon, Nile tilapia) for which selective breeding and genetic studies rely mostly on breeding programs with separate rearing of families for historical (Atlantic salmon) or reproductive biology (Nile tilapia) reasons. The reliance on molecular pedigrees is shared with the gilthead sea bream, which has followed a similar track as European sea bass for quantitative genetics studies (first heritability estimates by Navarro *et al.* 2009; first QTL by Massault *et al.* 2010a). However, in gilthead sea bream, there was no explicit exploration of the phenotypic variation between natural populations—which are also less clearly structured (De Innocentiis *et al.* 2004). The use of parentage assignment rather than separate rearing in sea bass and sea bream breeding programs is induced by the frequent use of mass spawning to produce selection candidates (Chavanne *et al.* 2016) but also by the will to limit environmental tank effects between families in the larval and juvenile phases, even when artificial fertilization is used (Vandeputte & Haffray 2014).

With the advent of the full genome sequence, the evolutionary history of sea bass, including the mechanisms of divergence and admixture between Atlantic and Mediterranean lineages, are becoming better understood. In farmed populations, the genetic variation of most traits of economic importance is now well described and breeding programs have been set up. The next development will certainly be the use of genomic selection to accelerate genetic gain, thanks to the development of convenient SNP genotyping arrays. Genomic selection has already started in salmonids and provides significant improvement over traditional pedigree-based approaches (Ødegård *et al.* 2014; Tsai *et al.* 2016; Vallejo *et al.* 2017), whereas in sea bass and sea bream, the first experimental genomic evaluations have only started (Palaiokostas *et al.* 2015, 2016, 2018). In terms of genetic improvement, there is a pressing need to improve feed efficiency, both for economic and environmental reasons (Besson *et al.* 2017), but this will require novel phenotyping approaches. Further developments will likely focus on adaptation and on G × E interactions, which will be important both for efficient breeding of aquaculture stocks (e.g. specific stocks for warmer/colder temperatures, interaction of disease resistance with evolution of feeds) and for better modeling of the evolution of natural stocks. At the interface between evolution and aquaculture, such knowledge will improve the understanding of the domestication process and the possible impact of aquaculture escapees on wild populations, which is an important question for all large-scale aquaculture productions. Introgression of natural stocks by domesticated genomes has been documented on a large scale in Atlantic salmon (Glover *et al.* 2013; Karlsson *et al.* 2016) and locally in sea bass (Šegvić-Bubić *et al.* 2017). Beyond introgression *per se*, the key question is how it may impact the life history of wild populations, as documented for age and size at maturity in Atlantic salmon (Bolstad *et al.* 2017).

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Conflict of interest

The authors declare no conflict of interest.

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Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. Heritability estimates for different traits in European sea bass.