POPULATION STRUCTURE AND INTROGRESSION

IN WILD POPULATIONS OF EUROPEAN SEABASS

(DICENTRARCHUS LABRAX)

DISSERTATION

submitted in fulfilment of the requirements for the degree of MSc by Research in Marine Biology By

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Statement of originality:

I declare that, with the exception of any statements to the contrary, the contents of this report/dissertation are my own work, that the data presented herein has been obtained by experimentation and that no part of the report has been copied from previous reports/dissertations, books, manuscripts, research papers or the internet.

Signed: *Sophia Webb* Print name: SOPHIA WEBB Date: 04/05/2023

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<u>Abstract</u>

Escapes of domesticated fish from aquaculture followed by interbreeding with wild conspecifics pose a threat to the genetic integrity of natural populations. In addition to disease and competition, wild populations can become inundated with genetic material from domesticated peers, leading to the introduction of deleterious alleles that can reduce fitness and survivability. Extensive work has focused on the interaction between farmed and wild Atlantic salmon, Salmo salar, within rivers, while little attention has been given to marine farmed species. European seabass (Dicentrarchus labrax) is a critical species for aquaculture in the Mediterranean Sea. However, levels of introgression among the wild populations are unclear. With wild stocks under ever-growing fishing pressure, it has become evident that more needs to be done to understand the extent and effects of introgression of farmed genes into the wild. In this study, 1,994 samples were taken from 19 farms and 33 locations in the wild and screened at 1,742 SNPs generated using double-digest RAD (ddRAD). Population structure and individual admixture were assessed using statistical approaches such as Principal Component Analysis (PCA), Discriminant Analysis of Principal Components (DAPC) and FastStructure. Results elucidate previously unknown patterns of differentiation among Mediterranean populations and reveal a complicated picture of the genomic make up of farmed sea bass. Movement of broodstock between the Atlantic and Mediterranean Sea is evident and domestication and domestication has left a strong impact on farmed genomes. Genomics is a valuable tool in discovering patterns of differentiation in marine fish populations, while highlighting how unregulated and long-term farming practices can affect natural populations diversity.

Introduction

Aquaculture is the fastest-growing global food production system, and now provides half of all fish consumed by humans, with at least 600 million livelihoods at least partially dependent on fisheries and aquaculture (FAO, 2022; Nakajima et al., 2019; Yang et al., 2019). Common carp (*Cyprinus carpio*) farming for human consumption dates back 8,000 years to Henan Province in China (Nakajima et al., 2019), and Nile tilapia (*Oreochromis niloticus*) farming dates back to 3500 years ago in Egypt (Nakajima et al., 2019; Teletchea, 2021). The greatest expansion of fish aquaculture worldwide occurred in the 1960s, since the introduction of marine net pens, with an estimated 543 marine species farmed globally (Diserud et al., 2022; Gkagkavouzis et al., 2021; Houston et al., 2020; Teletchea, 2021). Eighty percent of global aquaculture production volume is supported by farming approximately 70 of these species, compared with the major terrestrial livestock species of pigs, chickens, and cows, which make up 80% of global meat production (Houston et al., 2020). The FAO reports that in 1974, only 4% of fish consumed were domesticated, but that number has now risen to 49.2% (FAO, 2022).

Marine genomics and fisheries

Genetic tools are invaluable to inform sustainable management of fisheries and the health of not only farmed stocks, but also their natural wild conspecifics. Next Generation Sequencing (NGS) and Restriction-site Associated DNA markers (RAD) have been proven effective for the detection of hidden population structure, subdivision, and differentiation in fish, according to Maroso et al., (2021). Most notably for this study, NGS and RAD allow for detailed comparison of wild and farmed populations to predict the potential impact of aquaculture on natural populations, a recommended practice since the early '90s (Arechavala-Lopez et al., 2018; Jackson et al., 2015; Maroso et al., 2021).

DNA-based analysis, such as microsatellites, mitochondrial DNA, and single nucleotide polymorphisms (SNPs), have been used extensively in research for the following aquaculture species, notably salmon, cod, Nile tilapia, rainbow trout, and, to a lesser extent, seabass (Consuegra et al., 2011; Seddon et al., 2014; Bolstad et al., 2017; Maduna et al., 2017; Wringe, Anderson, et al., 2018; Bernaś et al., 2020; Nabaes Jodar, Cussac, and Becker, 2020;

Nayfa et al., 2020; O'Sullivan et al., 2020; Wenne et al., 2020; Jensen et al., 2021; Quinn, 2021).

Single Nucleotide Polymorphisms occur upon the change of a single base in DNA sequence and are a highly abundant source of genetic variation in and among species (Peñaloza et al., 2021; Ruperao & Edwards, 2015) allowing for genome-wide coverage of the targeted individual. SNPs have often been used in marine species which often have low levels of population structure and have become an exceptionally useful tool in determining effective population size, spatial connectivity, population structure, and admixture between and across populations (Arechavala-Lopez et al., 2012; Glover et al., 2013; Polovina et al., 2020; Robinet et al., 2020; Souche et al., 2015)

Breeding practices

In aquaculture, selective breeding programmes play an ever-increasing role in production. Despite more recent developments than most terrestrial livestock, it is seen in salmonids, shrimp, tilapia, carp, sea bream, seabass, turbot, sturgeons, oysters and more (Boudry et al., 2021). The term selective breeding, also known as artificial selection, can be defined by the various methods that humans use to select organisms with desirable traits by using selected parents to make controlled crosses (Chavanne et al., 2016). Common commercial traits selected for fish breeding are increased growth, disease resistance, reduced aggression, absence of malformations, adaptation to density and utilisation of feed and fillet quality (Arechavala-Lopez et al., 2013; Karlsson et al., 2016; Wringe, Jeffery, et al., 2018; Almodóvar, Leal, et al., 2020; Bradbury et al., 2020). Consistent selection of characteristics over generations leads to significant genetic differences between domesticated individuals and the wild (Glover et al., 2017). Non-genomic effects of aquaculture can also affect the surrounding ecosystem by eutrophication, release of chemicals and medicines, and modification of benthos (Porporato, Pastres and Brigolin, 2020).

In Europe, the six main cultured finfish species are Atlantic salmon (*Salmo salar*), rainbow trout (*Oncorhynchus mykiss*), gilthead seabream (*Sparus aurata*), European seabass (*Dicentrarchus labrax*), common carp (*Cyprinus carpio*) and turbot (*Scophthalmus maximus*) (FAO, 2022). Of the total European aquaculture production, 80-83% originate from selective breeding (Janssen et al., 2017), with family-based breeding schemes predominant (Chavanne

et al., 2016). Family-based designs require tracing the family origin of the breeding pairs, often allowing flexibility in the number and type of desired traits (Chavanne et al., 2016; Delomas & Campbell, 2022; Janssen et al., 2017; Waters et al., 2020).

Breeding populations can be established from wild and farmed individuals. Breeding success heavily depends on the genetic integrity and variability of the selected individuals, and therefore it is necessary to determine the relatedness between them to control inbreeding, so that long-term sustainability of the farm and the natural populations can be ensured (Villanueva et al., 2022; Boudry et al., 2021; Chavanne et al., 2016; Janssen et al., 2017; Robledo et al., 2018; Waters et al., 2020; You et al., 2020; Loukovitis et al., 2015). A key means of controlling excessive inbreeding, as Chavanne et al., (2016) suggest, is to ensure a sufficiently large effective breeding size, usually above 50, that can contribute to the next generation. Domestication can be evaluated by the number of generations in a breeding program. When comparing the domesticated individuals to the wild through genetic techniques it can be seen that the more generations of selective breeding, the greater the difference in genetics and performance. In the case of our target species, the number of selected generations varied between two and eight for European seabass (Villanueva et al., 2022; Chavanne et al., 2016; Janssen et al., 2017).

Many fish species are highly fecund, meaning many individuals can be produced from a small proportion of brood stock, decreasing effective population size and increasing inbreeding; a problem hard to control in marine species that exhibit mass-spawning behaviour, as a large variance parental contribution to offspring can occur (Villanueva et al., 2022; Bylemans et al., 2016; Chavanne et al., 2016; Janssen et al., 2017; Superio et al., 2021).

The performance of a farmed individual depends on the interaction between its genotype and the environment (Houston et al., 2020). This interaction can vary in aquaculture, both within and across the farm. Bylemans et al., (2016), and Novel et al., (2010), found that reared individuals often have a loss of genetic variability and lower evolutionary potential. This could be due to poor selection in the breeding processes or the use of strains that are not locally adapted to the surrounding wild environment (Delomas & Campbell, 2022). Small effective population sizes and founder effects that occur when using only a few limited individuals for broodstock are the main contributing factors for this decline (Glover et al.,

2013; Loukovitis et al., 2015; Vandeputte et al., 2019). Domesticated fish can compete for food, space, and breeding opportunities, influence predation, interbreeding with native populations, spread parasites and diseases, and increase fishing pressure on wild populations due to the assumption of increased stocks (Arechavala-Lopez et al., 2013; Atalah & Sanchez-Jerez, 2020; Clavelle et al., 2019; Fragkoulis et al., 2017; Lorenzen et al., 2012; Šegvić-Bubić et al., 2017).

A common method of rearing in the coastal environment are sea cages (Figure 1). Escapees are a major threat to natural biodiversity, likely due to events such as net failure, predators, sabotage, deliberate release in restocking, collisions with seagoing vessels, human error, storms and other severe environmental factors (Bylemans et al., 2016; Clavelle et al., 2019; Jackson et al., 2015).



Figure 1: Seabass and Seabream farm located in Greece (Sonesson, 2022)

Frequent low-level leakage escape events can represent average production losses between 1-5% annually, leading to a steady flow of potentially invasive fish entering the local ecosystem (Atalah & Sanchez-Jerez, 2020; Jackson et al., 2015). Polovina et al., (2021), suggests that domestication can introduce new alleles allelic combinations that may change the genetic structure of the natural populations and damaging local adaptations. Genes from one genome of a population or species become permanently embedded into the other genome, also known as introgression (Ghosh et al., 2012; Harrison & Larson, 2014). Broodstock such as fry and fingerlings, which are exchanged between farms from varying geographic regions, have entirely different genetic backgrounds to the local wild populace (Polovina et al., 2021).

Aquaculture icons - Salmon and Salmonids

Salmonids is a subsector that has experienced the most dramatic growth and is at the forefront of aquaculture practices. Atlantic salmon *(Salmo Salar)*, are an iconic and high value species and is considered to be one of the most domesticated and most researched fish in aquaculture (Almodóvar et al., 2020; Beacham et al., 2021; Bertolotti et al., 2020; Bolstad et al., 2017, 2021; Boulding et al., 2008; Bradbury et al., 2020; Gao et al., 2020; Glover et al., 2013; Karlsson et al., 2016; Keyser et al., 2018; Wringe, Anderson, et al., 2018; Wringe, Jeffery, et al., 2018) *S.Salar* are decreasing in the wild due to anthropogenic effects such as overexploitation and habitat degradation and as such, their farmed counterparts make up over 70% of production globally (Almodóvar et al., 2020; Bolstad et al., 2021; Naylor et al., 2005).

Scotland and Norway began the first farming of Atlantic Salmon in the 1970s taking advantage of their suitable coastal habitat with deep-water columns and ideal temperature ranges (Barton et al., 2023) with commercial breeding programmes introduced in Norway in 1997 (Boudry et al., 2021; Diserud et al., 2022). However, concerns about escapees have been long known, with the first study published by Maitland in 1986. Since then, the number of farmed escapees in Norway, based off growth patterns in the scales, has increased to more than 470, 000 since 1989 (Diserud et al., 2022).

Although this is consistent across many aquaculture species, farmed salmon grow significantly faster, display lower fitness, have differing anti-predator behavioural responses and transcribe genes differently (Clavelle et al., 2019; Glover et al., 2020; Yang et al., 2019). Introgression between domesticated and wild individuals has been well recorded in salmonids (Glover et al., 2008; Ozerov et al., 2016; Wringe, Anderson, et al., 2018; Wringe, Jeffery, et al., 2018). Glover et al, 2008, conducted the first study into Atlantic Salmon escapees, which successfully assigned 21 out of 29 escaped individuals back to a single farm. Hybridisation of escaped farmed salmon with wild Atlantic salmon has resulted in an average level of farmed introgression of 6.4% in 109 rives across Norway, of which 25% had introgression levels above 10% (Karlsson et al., 2016). Reduced life expectancy, altered sizes when reaching maturity, reduced spawning success and low survival rates in the wild have been shown for individuals with a high level of introgression in salmon (Bolstad et al., 2017; Glover et al., 2021).

Additionally, sea lice spread from salmon farms can greatly increase mortality, reduce population size, and resilience to the changing climate (Thorstad et al., 2021). Glover et al., (2012), showed that 28% of genetic changes in microsatellite DNA in studied populations of the wild population could be linked to introgression from farmed counterparts. Over a 12-year period, Diserud et al., (2022), found that increasing farming intensity increases the number of escapees, and concurrently states that as long as non-sterile fish can escape, all wild populations are at risk.

European sea bass (Dicentrarchus labrax)

Marine fish species European sea bass (Dicentrarchus labrax) ranges from Africa to southern Norway in the Atlantic, throughout the Mediterranean and the Black Sea (Robinet et al., 2020) (Figure 2).

Consumption of marine species dates back to the 15th century. Italy exploits the natural migration of species such as sea bass, gilthead seabream, grey mullets and European eel, and confining them in lagoons known as 'vallicoltura' (Boudouresque et al., 2020; Ciccotti et al., 1995; Teletchea, 2021). At present, sea bass is one of the most important fish in Mediterranean and Atlantic aquaculture, producing more than 191,000 tons annually, 95% of which come from farms (Šegvić-Bubić et al., 2017). Of the farmed production of European seabass, 50% consists of individuals from selective breeding programmes (Superio et al.,



Figure 2: European Seabass - Dicentrarchus labrax. Image: © Hans Hillewaert / CC BY-SA 4.0 (European Seabass, 2021)

2021). Based on fish sampled in the West-Mediterranean and Adriatic Sea, the first captive broodstock of European sea bass was established in France and Italy in the 1990's. Most domesticated stocks fall between two and eight generations, with the oldest known breeding program having individuals bred in captivity for eight generations without the input of the wild (Villanueva et al., 2022; Boudry et al., 2021; Chavanne et al., 2016).

European seabass hatcheries rely on spontaneous mass spawning and communal rearing of the produced progeny for production purposes, with four to five breeding programs available (Villanueva et al., 2022). Mating patterns and reproductive success of each breeder in a mass spawning event are difficult to quantify, and a successful breeding program requires many parents to participate in each spawn (Boudry et al., 2021; Superio et al., 2021; Vandeputte & Haffray, 2014). Superio et al., (2021), investigated parental assignment in European seabass *(Dicentrarchus labrax)*, a known mass spawner, and found that only four females produced up to 80% of the analysed eggs, and of those eggs, where a single male may sire up to 57%, allowing progeny to be skewed towards one or few families, thus increasing the risk of an inbreeding depression.

Escapes are not new. Some studies have estimated that up to 10-15% of fish in aquaculture escape. However, little is known about the impacts this has on the wild population in seabass (Villanueva et al., 2022, Brown et al., 2015; Polovina et al., 2020; Šegvić-Bubić et al., 2011). 1.5 million fish (90% *Dicentrarchus labrax*, 10% *Sparus aurata*) escaped in La Palma, Spain after repeated severe storms between December 2009 and January 2010 (Toledo-Guedes et al., 2014). Jackson et al., (2015), has also documented numerous escapes of ~ 600,000 seabream and seabass across three years causing significant economic losses of €42.8 million (Izquierdo-Gomez & Sánchez-Jerez, 2016; Jackson et al., 2015; Toledo-Guedes et al., 2014).

Despite the financial losses and possible impact on natural populations, many countries in the Mediterranean, such as Croatia, Turkey, Greece, provide no specific regulations of farming to avoid or limit escapes. Natural populations of sea bass are already under great pressure from fishing and habitat changes, with 62.5% of Mediterranean stocks exploited at unsustainable levels and Atlantic stocks in decline. If aquaculture is found to be adding to the impact on them, implications for wild sea bass could be disastrous (FAO, 2022; Souche et al., 2015).

New genomic resources have been developed for *D.labrax*, such as SNP arrays and quality

reference genomes, like the combined ~60K SNP array 'MedFish' and a 57K array known as 'DlabChip' (Griot et al., 2021; Peñaloza et al., 2021). Such developments have allowed the investigation of the population structure of wild and/or farmed European seabass using both microsatellite data and SNPs (Coscia et al., 2012; Coscia & Mariani, 2011; Hillen et al., 2017; Loukovitis et al., 2015; Polovina et al., 2020; Robinet et al., 2020; Šegvić-Bubić et al., 2017).

Advances in genetics over the past decade have allowed for the detection of three regional groupings found in the north-eastern Atlantic, the western Mediterranean and the eastern Mediterranean (Villanueva et al., 2022; de Pontual et al., 2019; Peñaloza et al., 2021; Robinet et al., 2020). Partial reproductive isolation occurs between the Atlantic and Mediterranean populations with a potential hybrid zone located near Gibraltar in the Alboran Sea (Duranton et al., 2018, 2020; Souche et al., 2015; Vandeputte et al., 2019).

However, the aforementioned investigations are much smaller compared to this study. Both Villanueva et al, (2022) and Peñaloza et al., (2021), sequenced 516 individuals belonging to 24 populations restricted to the Mediterranean. In the Atlantic Oceans, Robinet et al., (2020), studied 827 wild individuals for population connectivity. And Souche et al., (2015), sequenced 644 individuals from 22 sites across the sea bass native range, which had a greatly reduced number of SNPs at 49 loci. Furthermore, studies focused on the nature of escapees have been limited in nature, either looking solely at the Adriatic Sea with six farmed and ten wild populations used (Šegvić-Bubić et al., 2017) or have been investigated solely in Cyprus, which compared wild caught individuals against three hatcheries (Brown et al., 2015). What cannot be underestimated is the importance of this research project. Never before has *D.labrax* been investigated at this scale for both population structure and potential introgression of farmed genes into the wild.

More needs to be done to understand the dynamics of sea bass stocks and populations, given that wild stocks are under ever-growing fishing pressure, in addition to the stresses of climate change. This study aims to i) characterise the genetic structure of natural populations of sea bass across its distribution range ii) estimate the genetic diversity across all farmed and wild samples and iii) try to characterise farmed sea bass using genetic tools, to assess introgression into wild populations, and evaluate the use of genetic tools for traceability of escapees. This study will complement the literature surrounding *Dicentrarchus labrax*, enable targeted

conservation efforts to maintain genetic purity in natural populations, and show critical areas in which mitigation measures to reduce fish escapes are essential.

Methods

Samples of *Dicentrarchus labrax* were collected in 2016 by research surveys and fishing vessels throughout their range in the Atlantic and Mediterranean as part of the European-funded project AquaTrace. Coordinates were recorded for points where fish were captured or collected from markets, as well as for the length of each individual. Tissue samples were then extracted from muscle or fin clips. Samples were processed (DNA extraction, library preparation and sequencing) at the Laboratory of Biodiversity and Evolutionary Genomics (LBEG), KU Leuven, Belgium, as described by Hillen et al., (2017). In short, a RAD protocol was used using a modified salt extraction procedure and sequenced on an Illumina HiSeq2500 in paired-end mode at the Genomics Core of the University of Leuven. It should be noted that only the subsequent raw ddRAD data file created in 2016 at KU Leuven was used for this analysis at the University of Salford, no wet laboratory work was performed.

Sampling locations



Figure 3: Map of the collection location for samples used in analyses. Due to confidentiality, only the samples belonging to the wild populations are displayed.

More than fifty locations were selected to ensure the most comprehensive and representative collection of samples across the Mediterranean and Atlantic (Fig. 3). Natural populations were selected according to their geographical location to ensure full coverage. Criteria for farms included high domestication, high annual production levels, geographical location and origin of the brood stock used.

 Table 1: Summary of sea bass populations sampled, including origin, region, country, population ID and number of individuals (N) in each population.

Origin Country ID N Origin Region Country ID N Wild Norway NOR 33 Wild West Spain SPA_5 20 Bangor UK_1 26 France FRA_7 12 Bristol UK_2 53 Italy FRA_7 12 Belgium BEL 40 FRA_2 21 FRA_2 21 France FRA_1 30 FRA_4 44 FRA_5 51 FRA 54 70 71 71 71 71 71 71 71 71 71 71 71 71 71 71 73 70 71 <td< th=""><th></th><th>Atlanti</th><th>ic</th><th></th><th></th><th>Mee</th><th>literranear</th><th>1</th><th></th></td<>		Atlanti	ic			Mee	literranear	1	
Wild Norway NOR 33 Wild West Spain SPA_5 20 Bangor UK_1 26 France FRA_7 12 Bristol UK_2 53 Italy ITA_1 12 Belgium BEL 40 ITA_2 21 France FRA_1 30 ITA_3 60 FRA_3 30 FRA_3 0 ITA_4 44 FRA_5 51 East Italy ITA_5 19 FRA_6 53 SPA_1 56 Greece GRE_1 19 SPA_3 17 SPA_3 ITA_6 42 GRE_6 43 SPA_4 33 SPA_4 33 GRE_6 45 Farmed ATL_1 66 GRE_6 45 ATL_2 75 Turkey TUR_1 24 WM_3 26 WM_4 63 WM_5 8 WM_4 51 8	Origin	Country	ID	N	Origin	Region	Country	ID	Ν
$ Bangor UK_1 26 \\ Bristol UK_2 53 \\ Belgium BEL 40 \\ FRA_2 30 \\ FRA_2 30 \\ FRA_4 30 \\ FRA_5 51 \\ FRA_6 53 \\ Spain SPA_1 56 \\ Spain SPA_1 56 \\ SPA_2 17 \\ SPA_3 17 \\ Portugal OL 33 \\ Farmed ATL_2 75 \\ Farmed West \\ $	Wild	Norway	NOR	33	Wild	West	Spain	SPA_5	20
		Bangor	UK_1	26			France	FRA_7	12
$ Belgium BEL 40 & ITA_2 21 \\ France FRA_1 30 & ITA_3 60 \\ FRA_2 30 & ITA_4 44 \\ FRA_3 30 & FRA_4 30 \\ FRA_5 51 & East Italy ITA_5 19 \\ FRA_6 53 & Greece GRE_1 39 \\ SPA_2 17 & GRE_3 43 \\ SPA_4 33 & GRE_4 11 \\ Portugal OL 33 & GRE_6 45 \\ GRE_7 37 & ITRev TUR_1 24 \\ TUR_2 32 \\ Farmed West & WM_1 74 \\ WM_2 44 \\ WM_3 26 \\ WM_4 63 \\ WM_5 18 \\ WM_6 28 \\ WM_7 8 \\ WM_8 47 \\ East & EM_1 52 \\ East & EM_1 52 \\ Em_3 82 \\ EM_4 58 \\ EM_5 83 \\ EM_5 83 \\ EM_5 6 \\ EM_9 78 \\ EM_8 56 \\ EM$		Bristol	UK_2	53			Italy	ITA_1	15
$ \begin{array}{cccccccccccccccccccccccccccccccccccc$		Belgium	BEL	40				ITA_2	21
FRA_2 30 ITA_4 44 FRA_3 30 Tunisia TUN 7 FRA_4 30 ITA_6 42 9 9 9 9 17 6 42 17 17 6 42 17 17 6 42 17 17 6 42 17 17 6 42 17 17 17 6 42 12 17 17 14 4 4 17 16 42 17 16 42 13 16 16 14 16 17 16 17 16 16 16 16 16 16 16 16 16 16 16 16 16 16 16 16		France	FRA_1	30				ITA_3	60
$\begin{array}{cccccccccccccccccccccccccccccccccccc$			FRA 2	30				ITA 4	44
$\begin{array}{cccccccccccccccccccccccccccccccccccc$			FRA 3	30			Tunisia	TUN	7
$\begin{array}{cccccccccccccccccccccccccccccccccccc$			FRA_4	30					
$\begin{array}{cccccccccccccccccccccccccccccccccccc$			FRA 5	51		East	Italy	ITA_5	19
Spain SPA_1 56 SPA_2 Greece GRE_1 39 GRE_2 12 I2 SPA_3 17 SPA_3 GRE_3 43 GRE_3 GRE_4 11 GRE_5 19 GRE_6 45 GRE_7 37 TURkey GRE_7 37 TURL 24 TUR_2 32 Farmed ATL_2 75 Turkey TUR_1 24 TUR_2 32 Farmed West WM_1 74 WM_2 44 WM_3 26 WM_4 63 WM_5 18 WM_6 28 WM_7 8 WM_7 8 WM_7 8 WM_6 28 WM_7 8 WM_6 28 WM_7 8 WM_8 47 East EM_1 52 EM_3 EM_4 58 EM_5 83 EM_6 12 EM_7 75			FRA 6	53			-	ITA 6	42
SPA_2 17 GRE_2 12 SPA_3 17 GRE_3 43 SPA_4 33 GRE_1 11 Portugal OL 33 GRE_6 45 Farmed ATL_2 75 Turkey TUR_1 24 TUR_2 32 Farmed West WM_1 74 WM_2 44 WM_3 26 WM_4 63 WM_4 63 WM_7 8 WM_7 8 WM_6 28 WM_7 8 244 458 EM_5 83 EM_5 83 EM_6 12 EM_7 75 EM_9 78 24		Spain	SPA 1	56			Greece	GRE 1	39
$\begin{array}{cccccccccccccccccccccccccccccccccccc$		-	SPA_2	17				GRE 2	12
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TUR_2 32 Farmed West WM_1 74 WM_2 44 WM_3 26 WM_4 63 WM_5 18 WM_6 28 WM_7 8 WM_7 8 WM_8 47 Em_1 52 Em_2 15 EM_3 82 EM_4 58 EM_5 83 EM_5 83 EM_5 83 EM_6 12 EM_7 75 EM_8 56 EM 9 78			ATL 2	75			Turkey	TUR 1	24
Farmed West WM_1 74 WM_2 44 WM_3 26 WM_4 63 WM_5 18 WM_6 28 WM_7 8 WM_8 47 East EM_2 15 EM_3 82 EM_4 58 EM_5 83 EM_5 83 EM_6 12 EM_7 75 EM_8 56 EM_9 78			-					TUR 2	32
Farmed West WM_1 74 WM_2 44 WM_3 26 WM_4 63 WM_5 18 WM_6 28 WM_7 8 WM_8 47 East EM_1 52 EM_2 15 EM_3 82 EM_4 58 EM_4 58 EM_5 83 EM_6 12 EM_7 75 EM_8 56 EM_9 78								-	
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WM_3 26 WM_4 63 WM_5 18 WM_6 28 WM_7 8 WM_8 47 East EM_2 15 EM_3 82 EM_4 58 EM_5 83 EM_5 83 EM_6 12 EM_7 75 EM_8 56 EM_9 78								WM ₂	44
WM_4 63 WM_5 18 WM_6 28 WM_7 8 WM_8 47 East EM_1 52 EM_2 15 EM_3 82 EM_4 58 EM_5 83 EM_6 12 EM_7 75 EM_8 56 EM_9 78								WM 3	26
WM_5 18 WM_6 28 WM_7 8 WM_8 47 East EM_1 52 EM_2 15 EM_3 82 EM_4 58 EM_5 83 EM_6 12 EM_7 75 EM_8 56 EM_9 78								WM 4	63
WM_6 28 WM_7 8 WM_8 47 East EM_1 52 EM_2 15 EM_2 15 EM_3 82 EM_4 58 EM_5 83 EM_6 12 EM_7 75 EM_8 56 EM_9 78								WM 5	18
WM_7 8 WM_8 47 East EM_1 52 EM_2 15 EM_3 82 EM_4 58 EM_5 83 EM_6 12 EM_7 75 EM_8 56 EM_9 78								WM ₆	28
WM_8 47 EM_1 52 East EM_2 15 EM_3 82 EM_4 58 EM_5 83 EM_6 12 EM_7 75 EM_8 56 EM_9 78								WM 7	8
East EM_1 52 EM_2 15 EM_3 82 EM_3 82 EM_4 58 EM_5 83 EM_6 12 EM_7 75 EM_8 56 EM_9 78								WM 8	47
East EM_1 52 East EM_2 15 EM_3 82 EM_4 58 EM_5 83 EM_6 12 EM_7 75 EM_8 56 EM_9 78								-	
East EM_2 15 EM_3 82 EM_4 58 EM_5 83 EM_6 12 EM_7 75 EM_8 56 EM_9 78								EM 1	52
EM_3 82 EM_4 58 EM_5 83 EM_6 12 EM_7 75 EM_8 56 EM_9 78						East		EM ₂	15
EM_4 58 EM_5 83 EM_6 12 EM_7 75 EM_8 56 EM_9 78								EM 3	82
EM_5 83 EM_6 12 EM_7 75 EM_8 56 EM_9 78								EM 4	58
EM_6 12 EM_7 75 EM_8 56 EM_9 78								EM 5	83
EM_7 75 EM_8 56 EM_9 78								EM 6	12
EM_8 56 EM_9 78								EM 7	75
EM 9 78								EM 8	56
								EM 9	78

Populations were ordered according to their geographical location: first in the Atlantic and

then from West to East (Table 1). Farm sites are confidential and therefore labelled according to region. For example, WM_1 is West Mediterranean Farm 1 and EM_1 East Mediterranean Farm. Broodstock can strongly influence population structure and compare population indices. The use of brood stock is a well-established practice in fisheries to improve health, genetic diversity, and desirable breeding characteristics. Four populations included in this analysis are known to have individuals of varying geographic origin, ATL 2 and WM 6-8.

Data Preparation

Samples underwent a tailored bioinformatics pipeline using GBSX v1.2 (Herten et al., 2015), BOWTIE v2.2.4 (Langmead & Salzberg, 2012), SAMTOOLS v1.1 (H. Li et al., 2009) and BEDTOOLS v2.23.0 (Quinlan & Hall, 2010). Samples were demultiplexed, mapped to the sea bass genome (sea bass _ V1.0, GenBank: GCA_000689215.1). FREEBAYES v1.02.-33 (Garrison & Marth, 2012) was then used to call SNP variants in all samples simultaneously, with minimum mapping quality and minimum base quality set to 15 and 15. The resulting variant call format (VCF) data file used in this study consisted of 172,000 markers and 2349 D. labrax individuals across wild and farmed locations.

To achieve a quality dataset, stringent filters were applied using vcftools 0.1.15 (Danecek et al., 2011). First, indels were removed and only bi-allelic SNPs were kept. Second, sites with a minimum allele frequency greater than or equal to 0.05 had a minimum quality score above 40, and a mean depth value of 3 were retained. Individuals and SNPs with missing data of more than 20% have also been removed. A final filtering step included removing duplicates and two populations due to unknown geographical locations and origins. This resulted in 1,994 individuals on 52 geographic locations and 1,742 SNPs, 1% of the original genetic markers. To ensure maximum population structuring in the data, loci that do not meet the expectations of Hardy-Weinberg equilibrium were not removed. Pearman et al., 2022 show that the removal of loci that exhibit deviations from HWE can significantly reduce the degree of inferred population structure.

Genetic Diversity

R package ADEGENET (Jombart et al., 2010; Jombart & Ahmed, 2011) was used to calculate heterozygosity (expected H_E and observed HO), heterozygosity was then tested for significance using Bartlett's test to compare variances. ADEGENET was further used to

calculate the inbreeding coefficient (F_{IS}) and pairwise F_{ST} coefficients (Weir and Cockeram, 1984), bootstrapped 1000 times by R package *hierfstat*. The fixation index ranges from zero (without differentiation) to one (different alleles in the other population). When comparing groups of individuals of the same species, F_{ST} values below 0.05 generally indicate little evidence of genetic differentiation, while an FST value above 0.15 can be considered significant in differentiating populations (Frankham, 2010).

In addition to genetic diversity, the effective population size (N_e) also contributes significantly to the viability of a population. N_e identifies the number of individuals within the population that contribute to the next generation of offspring. Fluctuations in the population size studied, the sex ratio of breeding individuals, and subsequent reproductive success can influence Ne. Estimates of the current effective population size (N_e) were obtained from linkage disequilibrium between groups, as implemented in N_eEstimator v2.1 software (Do et al., 2014).

Population Structure

Principal Component Analysis (PCA), which reduces extensive data to fewer dimensions known as the Principal Components (PCs) of Variation, is widely used to investigate population structure. PCs capture the maximum variability of the data while being free of Hardy Weinberg Equilibrium (HWE) and linkage equilibrium (LD) assumptions, demonstrating the geographical origin of populations without assuming a predefined number of expected clusters (Gaspar & Breen, 2019; Visscher et al., 2014). PCA was conducted using FactoMineR (Lê et al., 2008). R package ADEGENET v.2.1.3 (Jombart et al., 2010; Jombart & Ahmed, 2011) was used to perform DAPC on clusters predefined by sampling location using the *dapc()* function. DAPC summarizes genetic differences between sampling sites by transforming the data via PCA and performing discriminatory analyses of the number of main components retained (Jombart et al., 2010). Jombart et al., (2010), and Miller et al., (2020) found that results typically maximise distance and minimise the variance between groups, while making no assumptions about population genetic processes, such as genetic drift. DAPCs were calculated without prior spatial information, with the inferred number of genetic clusters using the *find.clusters()* function in ADEGENET. *Find.clusters tests* successive K-means with increasing clusters (k) up to 10 and repeated 100 times. The selection of optimal k was carried out by applying the lowest Bayesian Information criterion (BIC) score,

as recommended by Jombart et al. (2010). For DAPC, the number of principal components to retain was determined using the cross-validation approach using function *xvalDapc()*, with the maximum number of PCs being N/3. Following this, *optim.a.score()* was used to determine the optimal number of principal components to retain. Once the optimal number of PCs was determined, subsequent DAPC for both prior and no prior analyses was conducted using this value.

A Bayesian cluster analysis was carried out in fastSTRUCTURE (Raj et al., 2014) to assess the potential number of genetic clusters. This software uses a model-based algorithm that simultaneously estimates the frequency of population alleles with ancestry proportions. The tested K values ranged from 1 to 10 under the admixture model, with 10 replicates per run. To determine the number of population results from fastSTRUCTURE runs, the Structure Selector web server analysed the resultant Qmatrix files (Evanno et al., 2005; Li & Liu, 2018; Puechmaille, 2016). Structure Selector implements the methods of Puechmaille (2016) and Evanno et al. (2005) to identify the most likely number of clusters. Of these estimators, Puechmaille was used, as they account for uneven sample sizes in the dataset. Interactive R package *Pophelper* was used to visualise the chosen runs (Francis, 2017). R package *FSTruct* measured ancestry differences in the conclusion of population structure based on the membership clusters found in Structure Selector (Morrison et al., 2022). The resulting pairwise F_{ST}/F_{ST}^{max} were bootstrapped 1000 times and tested for significance using a Wilcoxon rank-sum test.

Results

Genetic Diversity

On average, all locations had a lower observed heterozygosity compared to expected, with the largest differentiation between the wild Western Mediterranean (Supplementary Table 1 & 2). H_0 was higher in wild populations than in aquaculture species, except in the Eastern Mediterranean (EM). H_E greater in the western Mediterranean and Atlantic wild populations compared to their farmed conspecifics, and lower in the wild eastern populations compared to their domesticated counterparts. Averaging F_{IS} across regions had values ranging from 0.041 to 0.101. F_{IS} was lower in the Atlantic and Western Mediterranean wild populations compared to their domesticated counterparts but was higher in the wild individual's Eastern Mediterranean basin (0.101) than in the nearby farms (0.096) (ST1 & 2). When applying Bartletts test of homogeneity of variances between the two heterozygosity measures and considering the 95% confidence intervals, only the Atlantic demonstrated significance.

Table 2: Estimates of genetic diversity in both the Atlantic and Mediterranean populations of European sea bass. uH_E (unbiased expected heterozygosity) and H_O (observed heterozygosity). Bartlett's test of homogeneity of variances was used to determine significance between expected and observed values. $* = \le 0.05$, $** = \le 0.01$, $*** = \le 0.001$ and $**** = \le 0.0001$

		A	tlantic			West M	Mediterrane	an	I	East Medi	iterranean	
Origin	ID	Ho	He	(Drigin	ID	Ho F	le	Origin	ID	Ho	He
Wild	NOR	0.222	0.251	1	Wild	SPA_5	0.231	0.268	Wild	ITA_5	0.235	0.257
	UK_1	0.243	0.252	**		FRA_7	0.247	0.258 ****		ITA_6	0.218	0.249
	UK_2	0.234	0.248			ITA_1	0.239	0.261 *		GRE_1	0.210	0.239
	BEL	0.266	0.253	***		ITA_2	0.245	0.260 **		GRE_2	0.214	0.232
	FRA_1	0.254	0.248	***		ITA_3	0.249	0.260 *		GRE_3	0.202	0.235
	FRA_2	0.263	0.259	***		ITA_4	0.236	0.261		GRE_4	0.236	0.235 ****
	FRA_3	0.292	0.261	***		TUN	0.202	0.273		GRE_5	0.200	0.225
	FRA_4	0.239	0.256	**						GRE_6	0.221	0.237
	FRA_5	0.237	0.253	1	Farmed	WM_1	0.232	0.248		GRE_7	0.224	0.234
	FRA_6	0.236	0.254	**		WM_2	0.253	0.259 ****		TUR_1	0.232	0.234 **
	SPA_1	0.259	0.259	****		WM_3	0.233	0.246 ***		TUR_2	0.204	0.221
	SPA_2	0.227	0.258			WM_4	0.232	0.248				
	SPA_3	0.262	0.256	****		WM_5	0.224	0.259	Farmed	EM_1	0.233	0.245 **
	SPA_4	0.252	0.264	***		WM_6	0.227	0.248		EM_2	0.234	0.260
	POR	0.259	0.273	***		WM_7	0.230	0.235 ****		EM_3	0.241	0.261
						WM_8	0.226	0.228 *		EM_4	0.254	0.268 *
Farmed	ATL_1	0.221	0.243							EM_5	0.250	0.255 **
	ATL_2	0.261	0.272							EM_6	0.209	0.242
										EM_7	0.246	0.265
										EM 8	0.256	0.265 **
										EM_9	0.232	0.246

At a population level (Table 2), observed heterozygosity ranged from 0.2 to 0.292, and

expected heterozygosity (H_E) ranged 0.228 to 0.273. Significant differences between the two measures of heterozygosity were found in 25 of the sampling sites with the most significance seen in the Atlantic locations. Observed heterozygosity was lower than expected across all sites, except in BEL, FRA_1-3, SPA_1, SPA_3 and GRE_4. Inbreeding coefficients (F_{IS}) below zero, demonstrating heterozygote excess (Table 3). By contrast, positive F_{IS} values indicate a slight deficiency of heterozygotes, as shown in all other samples. Significant findings can be seen in UK 2, FRA 4, SPA 4, POR, ATL 2, EM 7 and EM 8.

Table 3: Estimates of the inbreeding coefficient (F_{1S}) according to Nei (1987) and 95% confidence intervals in both the Atlantic and Mediterranean populations of European sea bass. IL shows the lower confidence limits and uL the higher.

* Indicates significance.

			Atlantic			West Mediterranean					East Mediterranean			
Origin	ID	Fis I	L u	L	Origin	ID	Fis 1	L ı	ıL	Origin	ID	Fis 1	L (ıL
Wild	NOR	0.103	0.099	0.114	Wild	SPA_5	0.111	0.1221	0.1385	Wild	ITA_5	0.077	0.0715	0.0874
	UK_1	0.037	0.024	0.039		FRA_7	0.031	0.0233	0.0406		ITA_6	0.116	0.1086	0.1231
	UK_2	0.057	0.045	0.057 *		ITA_I	0.071	0.0692	0.0866		GRE_1	0.113	0.1086	0.1211
	BEL	-0.029	-0.063	-0.051		ITA_2	0.05	0.0419	0.0572		GRE_2	0.065	0.0594	0.0804
	FRA_1	-0.014	-0.035	-0.023		ITA_3	0.047	0.0327	0.0435		GRE_3	0.125	0.1213	0.1363
	FRA_2	-0.002	-0.032	-0.016		ITA_4	0.092	0.0848	0.098		GRE_4	-0.002	-0.0261	-0.0055
	FRA_3	-0.079	-0.133	-0.117		TUN	0.179	0.2172	0.2464		GRE_5	0.095	0.0907	0.1097
	FRA_4	0.065	0.050	0.065 *							GRE_6	0.063	0.0542	0.0665
	FRA_5	0.057	0.053	0.065	Farmed	WM_1	0.066	0.0527	0.0642		GRE_7	0.046	0.0313	0.0446
	FRA_6	0.069	0.055	0.072		WM_2	0.028	0.0094	0.0219		TUR_1	0.021	-0.0027	0.0118
	SPA_1	0.009	-0.014	-0.003		WM_3	0.049	0.0336	0.0519		TUR_2	0.07	0.0585	0.0744
	SPA_2	0.107	0.104	0.122		WM_4	0.059	0.0481	0.0609					
	SPA_3	-0.015	-0.039	-0.024		WM_5	0.113	0.1177	0.1338	Farmed	EM_1	0.058	0.0328	0.0476
	SPA_4	0.059	0.032	0.045 *		WM_6	0.078	0.0682	0.0835		EM_2	0.081	0.0823	0.1005
	POR	0.054	0.039	0.052 *		WM_7	0.002	-0.0029	0.0239		EM_3	0.071	0.0646	0.0757
						WM_8	0.01	-0.0064	0.0097		EM_4	0.048	0.0369	0.0492
Farmed	ATL_1	0.089	0.0779	0.0923							EM_5	0.032	0.0053	0.0171
	ATL_2	0.042	0.0295	0.0406 *							EM_6	0.119	0.1163	0.1366
											EM_7	0.075	0.062	0.0731 *
											EM_8	0.039	0.0215	0.0342 *
											EM_9	0.058	0.0479	0.0582

Estimated Population Size

Estimates of Ne, as executed by NeEstimator v 2.1, could not be defined for many which showed wide ranges with upper confidence limits of infinity (Table 3). However, comparing the estimated population sizes can still be of interest. In addition to the higher heterozygosity estimates in the Atlantic, all wild populations in this region had an effective population size over 100. The site with the largest N_e with reliable CI values was FRA_6 (1009, [95% CI 572 - 1935]), followed closely by FRA_1 (938, [95% CI 378 - 1041]).

The lowest N_e was found in WM_3 with a very low estimation of 10 (95% CI 6.3-16). N_e is much higher in wild populations than compared to aquaculture. Notable exceptions were WM $_$ 5 and WM $_$ 6 with surprisingly high estimates of 1616 (95% CI 195 - inf) and 946 (95% CI 568 - inf), GRE $_$ 5 (28 [95% CI 17 - 56]) and TUR $_$ 1 had very low values (57 [95% CI

20 - inf]). TUN also showed a low Ne estimate of 76 [95% CI 15 - inf], however, this is unsurprising due to the small sampling size of 6 individuals. It should be noted that 14 of the 19 farms examined had an effective population size of less than 50.

Table 4: Effective population size (N_e) and 95% confidence intervals (CI) for all populations of European Seabass

		Atlantic				Mediterranean			
Origin	Population ID	Ne	Lower CI	Upper CI	Origin	Population ID	Ne	Lower CI	Upper CI
Wild	NOR	1270	259	00	West	SPA_5	252	79	00
	UK_1	537	274	1197		FRA_7	595	122	446
	UK_2	353	114	00		ITA_1	144	95	00
	BEL	493	316	48960		ITA_2	641	252	767
	FRA_1	938	378	1041		ITA_3	974	589	00
	FRA_2	153	60	00		ITA_4	1298	810	00
	FRA_3	547	325	1675		TUN	76	15	00
	FRA_4	130	40	00					
	FRA_5	1103	442	00		WM_1	61	43	90
	FRA_6	1009	572	1935		WM_2	15	10	21
	SPA_1	817	610	39364		WM_3	8	4	13
	SPA_2	604	125	00	Farmed	WM_4	23	20	27
	SPA_3	985	212	1267		WM_5	1619	195	00
	SPA_4	249	124	52862		WM_6	946	568	00
	POR	517	219	30		WM_7	26	10	30
						WM_8	18	15	22
Farmed	ATL_1	16	12	21					
	ATL_2	50	38	68		ITA_5	467	412	00
					East	ITA_6	102	44	00
						GRE_1	874	374	00
						GRE_2	2919	166	00
						GRE_3	1429	593	00
						GRE_4	109	44	00
						GRE_5	28	17	56
						GRE_6	878	455	6482
						GRE_7	872	377	30
						TUR_1	57	20	00
						TUR_2	1784	557	x 0
						EM 1	10	6	14
					Farmed	EM 2	20	13	40
						EM 3	18	15	21
						EM 4	30	22	42
						EM 5	19	16	24
						EM_6	29	11	00
						EM_7	25	19	31
						EM_8	22	17	29
					 	EM_9	62	52	77

Population structure

Slight differentiation could be found between the Atlantic wild populations with many values close to 0. However, significant differences in F_{ST} values could be seen between Norway and SPA_2, and Norway and POR. The Western Mediterranean populations similarly follow suit, and slight differences can be seen between the wild EM populations, especially in GRE_5, GRE_6, TUR_1 and TUR_2 with their fellow cohorts. Varying differentiation was found between the West and East Mediterranean, ranging from a weak F_{ST} of 0 to 0.05, with most values falling somewhere between. East Mediterranean farms showed varying differences between themselves and their native cohort, the greatest of which can be seen between



Figure 4: Pairwise F_{ST} calculated via R package *dartR*. F_{st} values scale from ivory which demonstrates the lowest and red which demonstrates the highest. The black line indicates the Mediterranean/Atlantic Split and the yellow, the Western/Eastern Mediterranean. Atlantic individuals are shown by the light green for wild and darker green for domesticated fish. Following suit, West Mediterranean populations are shown by light blue for wild and darker blue for farmed. Finally, Eastern Mediterranean samples are shown by red for wild and dark burgundy for farmed.

TUR_2 and EM_5 at 0.135. Most evidently in Figure 2 is the 0.3 F_{ST} found between WM_6-8 and the Mediterranean populations. The use of Atlantic broodstock in these farms is exceptionally clear, showing lower differentiation with the Atlantic populations; the lowest of which is seen in WM_6 having an F_{ST} of 0. Mediterranean broodstock use is also present within the Atlantic with ATL_2 showing higher differentiation compared to the wild Atlantic than the Mediterranean farms.

Principal component analysis (PCA) explained 13.2% of the total variance for all the populations explored in the dataset across PC 1 and 2 (Figure 5a). PCA reveals that the Atlantic and Mediterranean populations are two distinct groups, and there is great overlap between the wild conspecifics and farmed populations within the same basin. When considering only wild individuals (Figure 5b)

Farmed fish in the Western Mediterranean are indistinguishable from their wild conspecifics, while individuals that identify with the Eastern Mediterranean farms are well distributed across the entire Mediterranean (Fig. 5a). Domesticated individuals that geographically align with the Atlantic can be found in the Eastern Mediterranean, and farmed individuals located in the Western Mediterranean can be found grouping with the Atlantic. As expected, these domesticated individuals belong to ATL_2 and WM_6-8 (SF1). When removing these populations from the picture, one fish from the West Mediterranean wild, one from the West Mediterranean farm and one from the Atlantic can still be seen collating with the East Mediterranean Farms (SF 2).

In wild populations, PCs 1 and 2 accounted for 14.7% of total variance for all wild populations across both regions (Figure 5b), 3.3% of variation for those belonging to the Mediterranean (Figure 6a), and 1.7% for the Atlantic (Figure 6b). Interestingly individuals from the western Mediterranean wild populations can be seen grouping with the Atlantic wild and vice versa. This could be a potential hybrid zone between the wild Atlantic and Western Mediterranean individuals (from POR and SPA_5; Fig. 5) between the two or a case of migration. Additionally, a subtle genetic differentiation can be seen between the Western and Eastern Mediterranean at 2.7%, forming two clusters along PC2 with overlap of individuals around Italy.



Figure 5: Principal component analysis (PCA) of individuals (dots) and samples (labels) across all 1742 SNPs. Each individual was grouped according to whether they were wild or farmed and to broad geographic regions. a) shows both wild and farmed conspecifics whereas b) shows only wild. Each individual is coloured according to sampling location (or farm). For colour reference, please see the appropriate legend.



Figure 6: Principal component analysis (PCA) of wild individuals (dots) across all 1742 SNPs with a) being the Mediterranean and b) the Atlantic with extreme outliers removed. Each individual is marked according to their populations a) show Mediterranean samples and b) shows only Atlantic. Each individual is coloured according to sampling location (or farm). For colour reference, please see the appropriate legend.



Figure 7: Optimum number of clusters as assumed by the Bayesian Information Criterion (BIC) for wild Atlantic and Mediterranean seabass via *find. clusters* in R package ADEGENET.



Figure 8: Discriminant Analysis of Principal Component (DAPC) conducted demonstrating K = 3 clusters as indicated by Bayesian Information Criterion (BIC). Each individual is a dot, and each dot is coloured according to its assigned cluster.

Adegenet recommends that principal components do not exceed N/3 or 664 in this study (Jombart & Ahmed, 2011). Cross validation showed that with a maximum retention of five hundred principal components, individuals assigned back to their populations had a success rate of 97.4%, with a root mean squared error of 0.544. To avoid overfitting of the data, *optim-a-score* retained seventy-three principal components for both prior and non-prior population analysis (Supplementary Figure 3). When adjusting for 73 PC's, only 28.3% of individuals were assigned back to their original populations.

Assignment success greatly increases when considering the wild populations. BIC revealed 3 genetically distinct clusters with an assignment probability of 99.61% (Figure 7 & Figure 8). Assignment probability for K1 and 2 was 100%, with individuals' assignment to cluster 3 being 98.1% (Supplementary Table 2). Contrastingly, Structure Selector (Figure 9b) determined 4 or 5 groups to represent the population structure of the wild individuals. However, when visualised, the true representation is in accordance with BIC, DAPC and literature at 3 (Fig 11).



Figure 9: Alternative method of choosing K via. MedMeanK, MaxMeanK, MedMedK, MaxMedK (Threshold=0.5) according to Puechmaille (2016) using Structure Selector for (a) domesticated *Dicentrarchus labrax* and (b) for the wild. Red lines indicate the optimal K (Y-axis) after removing spurious clusters.

BIC revealed a lack of population structure when investigating farmed populations. Structure Selector, however, identifies the ideal number of populations of either 8 or 9 (Figure 9a). A DAPC (Figure 10) correctly assigned 89.8% of individuals to these 9 clusters. 2 out of the 9 clusters (4 and 6) had an assignment success rate of 100%. K=4 houses ATL_1 individuals and K =6, WM_2 and WM_3. The remaining ranged between 72.3% to 96.27% (Supplementary Table 4). Assignment probability outside of these 9 clusters drastically falls to 64.59% (SF 5).



Figure 10: Discriminant Analysis of Principal Component (DAPC) conducted demonstrating K = 9 clusters as indicated by Bayesian Information Criterion (BIC). Each individual is a dot, and each dot is coloured according to its assigned cluster.

Wild Atlantic populations are genetically homogeneous, with no substructure detected. In direct contrast, the Atlantic/Mediterranean split gives a strong genetic signal. (Figure 11). Mixing can clearly be seen between the two clades around the Strait of Gibraltar (POR AND SPA_5), with little introduction from the Atlantic into the Eastern Mediterranean except in TUN, ITA_5 and ITA_6. POR is the most affected and shows evident Mediterranean markers either from migration or historical mixing events. It is also clear that one individual

categorised with SPA_4 shows introgression from the Mediterranean and an individual from SPA_5 showing Atlantic genomes (Figure 11 and 13), these individuals were also identified during Principal Component Analysis in Figure 5b. (Figure 11 and 13). TUN also demonstrates some Atlantic material.

Substructure can also be seen in the wild Mediterranean between the East (Tunisia to Greece) and Western groups (Sicily to Gibraltar) (Figure 11). When comparing the two Mediterranean regions, it is clear that the Eastern Mediterranean has impacted the West, with at least one full wild Eastern Mediterranean individual present in ITA_1 and a potential domesticated escapee at ITA_4. Western Mediterranean markers can also be seen across ITA_5, ITA_6 and GRE_1, showing that gene flow is still very present between the two clades. GRE_5 also demonstrates high levels of introgression with the EM farms, similar in genetic composition to EM_3 (Figure 11 and 13) most likely to be from domesticated escapees. A hybrid of 50% ancestry may also be present in GRE_7, which could have originated from numerous sources.

Farms also had homogeneous populations, and therefore showed similar patterns, such as WM_2-5, EM_1 and ATL_1 and EM_4,5 and 7 (Figure 12 and 13). However, domesticated farms like WM_7-8 have a very distinct genetic structure, despite grouping with the Atlantic in the PCA's (Figure 14). WM_6 seems entirely made up of wild Atlantic individuals and may be early in their selection process. EM_9 is also entirely distinct from the other aquaculture sites. Overall, long-term selection of strains and the use of brood stock was very apparent.


Figure 11: FastSTRUCTURE plots demonstrating wild samples demonstrating K= 3 graphically represented by R package *Pophelper*. K was chosen by the Bayesian Information Criterion Analysis [Figure 9]. Population codes are shown on the x-axis and each individual is resented by a thin vertical line partitioned into coloured segments showing the proportion of each individual assigned to the K different genetic clusters.



Figure 12: FastSTRUCTURE plots demonstrating farmed sampling locations across K = 8 and K = 9 graphically represented by R package *Pophelper*. K was chosen by the Puechmaille method (2016) using Structure Selector [SF 6]. Population codes are shown on the x-axis and each individual is resented by a thin vertical line partitioned into coloured segments showing the proportion of each individual assigned to the K different genetic clusters.





Figure 13: FastSTRUCTURE plots demonstrating all 52 sites across K = 8 and K = 9 graphically represented by R package *Pophelper*. K was chosen by the Puechmaille method (2016) using Structure Selector [Figure 7]. Population codes are shown on the x-axis and each individual is resented by a thin vertical line partitioned into coloured segments showing the proportion of each individual assigned to the K different genetic clusters.



Figure 14: Stacked bar plot demonstrating FastSTRUCTURE ancestry in all 52 sampling sites of *D. labrax* across all 9 clusters identified by BIC and Structure Selector. Each colour on the bar plot corresponds to a specific cluster as shown in the legend.

Locations with samples from multiple sources or populations recently mixed are expected to have higher variable ancestry (FST/FST^{max}), while populations with few mixing events are expected to have more homogeneous ancestry and a lower FST/FST^{max} score. FST/FST^{max} was computed for the 3 wild clusters, measuring the ancestry variability of the inferred cluster memberships. FST/FST^{max} ranged from 0.01 to 0.272 (Figure 14). Pairs of bootstrap distributions are significantly different $p < 2e 10^{-16}$ for all combinations via a Wilcoxon rank-sum test (Supplementary Table 5). The lowest ancestry variability was found in clusters K2 at 0.01 (West Mediterranean), while the highest was found in K1 (East Mediterranean) with the Atlantic (K2) falling in the middle at 0.119.



Figure 14: (a) Stacked bar plot demonstrating FastSTRUCTURE ancestry in all wild sampling sites of *D. labrax* and (b) bootstrapped distributions of the ancestry variability measure, FST/FST^{max} from R program *FSTruct*, across 3 clusters identified by BIC and Structure Selector. Each colour on the bar plot corresponds to a specific cluster as shown in the legend.

Discussion

Anthropogenic events, such as overfishing or climate change, can reduce population size variation, leading to reduced genetic variation (Glover et al., 2012; Loukovitis et al., 2015; Vandeputte et al., 2019). Furthermore, aquaculture practices typically increase inbreeding and change gene frequencies due to genetic drift and selection (Hillen et al., 2017; Lorenzen et al., 2012; Novel et al., 2010, 2013). When combining these factors, it is no wonder that the Mediterranean Sea is described as "under siege" (Boudouresque et al., 2020; Coll et al., 2012).

Wild Population Structure

Populations of *D. labrax* form three genetic clusters: the Atlantic from Gibraltar to Norway, the Western Mediterranean from the Alboran Sea to the Sicily Strait, and the Eastern Mediterranean from the Sicily Strait to the Black Sea. Immediately apparent is that the Atlantic samples have weak population structure and are near homogeneous; a finding consistent with Coscia et al., (2012), Coscia & Mariani (2011), and Souche et al., (2015). As such, the ability to assign individuals to the wild Atlantic cluster was extremely high.

Early population genetic studies support the strong genetic differentiation found between the Atlantic and Mediterranean regions at the Strait of Gibraltar, as seen throughout this study (Lemaire et al., 2005; Vandeputte et al., 2019 and Villanueva et al., 2022). Such a strong phylogeographic break between the Atlantic and Mediterranean has also been proven for numerous other species, such as the European green crab (*Carcinus maenas*, Roman & Palumbi, 2004), red seaweed (*Asparagopsis taxiformis*, Andreakis et al., 2004), the common dentex (*Dentex dentex*, Bargelloni et al., 2003) and *Sagitta setosa* (Peijnenburg et al., 2004).

Wild Atlantic and Mediterranean populations of European sea bass diverged 300,000 years ago (Novel et al., 2010; Patarnello et al., 2007; Robinet et al., 2020; Tine et al., 2014). However, this break is not absolute and is a permeable barrier. Our study finds that the natural exchange of the Atlantic and Mediterranean genomes is localised around Gibraltar. Duranton et al., (2018), discovered asymmetrical gene flow with Atlantic genomes influenced by around 5% of Mediterranean material, while Western Mediterranean genomes contained around 31% of the Atlantic. While Duranton et al., (2018), found that 13% of Atlantic ancestry was present in the Eastern Mediterranean, it should be noted that none was demonstrated in this study past the Sicily-Tunisian strait.

Phylogenetic breaks between the Western and Eastern Mediterranean have been successfully identified, such as in swordfish, which was previously thought to be a panmictic unit (*Xiphias gladius*, Vias et al., 2010). Since Bahri-Sfar et al., (2000), this split in seabass has led only a few studies, which found significant divergence between the two basins at six microsatellite loci in 19 samples. Mixing is very present from the Eastern Mediterranean into the Western populations in our data. The Eastern Mediterranean is very pure, while the West can be seen as a face to introgression from two fronts. Such findings are in line with Quéré et al., (2012), who discovered that the West Mediterranean had dual evolutionary origins from both the Atlantic and Eastern Mediterranean, leading to the emergence of an entirely new reproductive population in the West.

Introgression between Wild and Farmed populations

Effective population size being larger in the wild than farmed populations of seabass has been seen in previous literature (Villanueva et al., 2022; Šegvić-Bubić et al., 2017) and it is expected. Some Ne CI estimates could not be accurately determined, suggesting that either there was little power to make any inferences, or more likely that the wild populations are exceptionally large, which is not uncommon in natural populations of marine fish (Marandel et al., 2019). That being said, Ne could be seen as smaller than the 500 proposed to maintain long-term genetic diversity in marine populations (Frankham, 2010; Wang et al., 2016) or the 100 individuals suggested solely for aquaculture (Hillen et al., 2017). Numerous estimates were even below 50, most notably WM_3, which had an effective populations listed, are based on their sampling locations and are arbitrary. Therefore, I urge them to be taken with caution. For those wanting to repeat this analysis, it would be far more informative to group sampling locations to the three clades when conducting estimates of population size for the wild populations.

Regardless, low estimates of Ne can allow the effects of genetic drift to outweigh the influence of selection, making it difficult for populations to respond to environmental change (Lehnert et al., 2020). Further challenges can arise in domesticated stock from the typical breeding practice of mass spawning. While many commercial farms aim to use many breeders (typically 200), the number of contributing parents to the next generation may be

unknown, and much smaller than the number of individuals present in the tank (Brown et al., 2015; Chavanne et al., 2016; Hillen et al., 2017).

Surprisingly, the inbreeding coefficient F_{IS} was higher in the East Mediterranean populations than in their domesticated populations. Another possible explanation for these results is the Wahlund effect. This explains positive F_{IS} values with the presence of undetected (or unaccounted for) population substructure, which is not thought to be the case here. Additionally, F_{IS} assumes an island model. An island model contains populations calculated by a balanced migration rate, random mating, and equal mating chances, which are likely violated in uncontrolled conditions. Populations of sea bass in the wild occur in large numbers allowing for over 5998 tons to be captured globally in 2020 (FAO 2022). The likelihood of natural populations being inbred is extremely low thanks to reproductive traits, such as mass spawning where sexually mature females can spawn on average 200, 000 eggs/kg (Vandeputte et al., 2019).

Both wild and farmed sampled had locations with higher expected heterozygosity than observed indicating a reduction in fitness. Higher H_E can be found if the population was established relatively recently, if there are increased numbers of kin through inbreeding and if the population was generated from numerous origins. F_{ST} also shows small to large differences between farms, depending on their composition and broodstock origin. Contrastingly, genetic investigations using SNPs and microsatellites performed prior to this study found reduced allelic richness, reduced genetic variability, and lower expected heterozygosity in aquaculture compared to wild populations (Bahri-Sfar et al., 2000; Brown et al., 2015; Loukovitis et al., 2015; Novel et al., 2013; Peñaloza et al., 2021; Šegvić-Bubić et al., 2017). Artificial gene flow can also influence low values between domesticated populations, as the same hatchery may be used, or individuals shared, to reduce the risk of inbreeding depression. Indeed, haplotype sharing has been previously proven among Mediterranean farmed populations by Peñaloza et al (2021).

Farmed populations with genetic compositions similar to those in wild populations (as seen in WM_6) may be in the initial stages of their selective breeding program, or that the practice of broodstock has been re-implemented, where wild individuals are used to mitigate inbreeding by matching the genetic diversity of the wild (Polovina et al., 2020; Villanueva et al., 2022). High relatedness in farms signifies a great degree of inbreeding, and along with low population estimates, the introduction of broodstock may not be enough to avoid deleterious

effects. The genetic background of farmed fish plays a key role in assignment, as assignment is more robust when larger differences are present (Glover et al., 2012). There is convincing evidence of Atlantic fish being present in Mediterranean farms and of Mediterranean individuals present in one Atlantic Farm (ATL_2). Due to the varying geographic composition of domesticated samples, admixture composition of farms differs between great similarity to the native fish to signatures of high selection intensity. While high selection intensity is an asset for tracing fish back to the source farm, it is impossible to identify a unique genetic profile for each farm with this current dataset. As such, individuals can only be traced to native or domesticated populations.

Escapees and introgression

FastStructure detected few events of genetic introgression from domesticated individuals in wild populations of European seabass, with the exception of GRE_5. This could be explained in three ways: 1) good farming practices (no or little escapees); 2) escapees low survival rate and no reproduction in the wild 3) low rate of escapees and introgression into a very big wild population (genetic signal gets diluted or lost). Below I discuss these options in detail.

Escaped sea bass has the potential to survive for extended periods, as shown by Arechavala-Lopez et al (2012). After escaping, they often swim to nearby fishing grounds, coastal habitats, and protected areas where they feed on prey and compete for natural resources. A considerable influence of domesticated sea bass on the local wild population was found by Šegvić-Bubić (2017), with the middle Adriatic showing such high degrees of admixture that no true wild individuals remained. There is a high probability of genetic change in the population if an escape incidence is 10% or higher (Castellani et al., 2018).

That being said, given the power of this dataset, we are confident that there are very few escapees from farms in the wild populations. Numerous factors can allow limited introgression between wild and farmed populations. First, it is possible that escapees could have been missed in the sampling effort at the wild locations, or that they are not able to be distinguished genetically. Secondly, farmed individuals may lack survival in the wild. Lower survival rate could be due to reduced foraging ability, greater predation risk, and lower swimming performance. Farmed seabass may not be well adapted to the local environment conditions, given the genetic, phenotypic, and behavioural changes that result from breeding programs (Bernaś et al., 2020). Reduced fitness of hybrids from escapees has been

extensively documented in seabream, salmon, trout and cleaner fish (Bernaś et al., 2020; Bolstad et al., 2017, 2021; Castellani et al., 2018; Faust et al., 2018, 2021; Glover et al., 2018; Naylor et al., 2005; Solarte-Murillo et al., 2020; Wringe, Jeffery, et al., 2018; Žužul et al., 2019).

Toledo-Guedes, Sanchez-Jerez and Brito., (2014), suggest that sexual maturity is usually not reached in sea cages. As such escapees could potentially be reproductively viable but unable to successfully interbreed with wild conspecifics and become a self-sustaining population. Conversely, large female escapees up to 6kg were identified by Brown, Miltidou, and Tsigenopoulos., (2015), who found that they could interact with the surrounding wild after an escape, including mature eggs. Reduced reproductive success in domesticated fish relative to wild individuals may be due to changes in mating behaviour. If mating does occur, offspring could be nonviable or maladapted to the local environment due to genetic differences. Typically, offspring that are farmed have a lower lifetime survival than offspring that are wild, with hybrid groups falling between the two (Karlsson et al., 2016). Furthermore, Naylor et al., (2005) found that the lifetime success of hybrids was significantly reduced compared to wild individuals (by a reduction between 27 and 89%) and that 70% of second-generation embryos did not survive. Finally, although survival is thought to be low in the larval stage, and establishment in the environment unlikely, a final potential route of introgression is for eggs to escape during spawning (Brown et al., 2015).

Furthermore, restocking, a practice most commonly known in Atlantic salmon but widespread in aquaculture, could have additional effects. Restocking aims to compensate for population declines by releasing fry into the natural environment. Arechavala-Lopez et al., (2013) discovered that intentionally released domesticated sea bream, were rediscovered mixed with wild individuals, and showed the same spawning behaviour after just one year. *D.labrax* instances such as this are unknown and would require further study. It is clear, however, that precautions must be taken to avoid escapees that could affect native populations, and only native individuals should be used in restocking practices.

Reducing the number of escapees significantly is an appropriate approach to protect native populations. Three methods for reducing escapes were reviewed by Dempster et al., (2018). (1) Introduce programs for the effective recapture of escapes in habitats where they are known to school. (2) Encourage the establishment of predatory fish around sea cages to predate upon smaller escapees. Castellani (2018) highlights the effectiveness of

implementing a grid between the escaped farm and a known river location of wild salmon. Although these grids may not be viable for ocean cages, shoals of escapees rarely travel more than 3 km from their escape point (Arechavala-Lopez et al., 2018). (3) Enact technical standards so that fish farmers invest in preventive technologies to minimize escape (Dempster et al., 2018). (5) Sterilisation of aquaculture species. A recent report by Nofima (the Norwegian food research institute) focused on comparing production traits between sterilised and fertile farmed salmon (Andersen et al., 2022). Sterilised salmon had their embryonic germ cells inactivated through ablation and were studied between 2018-2022. Andersen et al., (2022), found that compared to their non-sterilised conspecifics they showed similar growth performance in freshwater, normal osmoregulatory processes, seawater tolerances and no significant differences in stress responses.

This study was unable to trace escapees to their origin, though this is a technique that has been successfully used in salmon, rainbow trout and Atlantic cod to trace them back to their farmed source (Glover et al., 2018; Karlsson et al., 2016; Polovina et al., 2020). A technique successfully used in at least one study of European Seabass was implemented by Šegvić-Bubić et al., (2017). With only 3.2% of fish being misclassified, they found significant genetic differences between farmed fish of different origins and wild conspecifics enabled the identification of seabass escapees to their farmed source without prior knowledge of pedigree. Categorising seabass correctly remains a top priority for preserving natural stocks and is an avenue that should be further explored.

Further investigation is warranted on the reduced genetic diversity observed through introgression, with studies focused on the fitness effects of hybridisation, specifically in *Dicentrarchus labrax*. New avenues to explore are programs such as NEWHYBRIDS (Wringe, Anderson, et al., 2018) which in addition to RStudio package could allow for the further investigations into outlier loci, allelic diversity, and hybridisation. Loukovitis et al., (2015) found that allelic diversity is a more sensitive measure of genetic variation than heterozygosity for bottleneck events such as founder events, and allelic loss can occur faster. Whether through the development of new equipment or further behavioural analysis of escaped seabass, research on the mitigation of escapees is vital. Comprehensive management programmes are also crucial in relation to broodstock and breeding programmes. An invaluable asset to the scientific community would be a public data set covering broodstock, breeding pairs and their offspring, in order to genetically characterize individual farms.

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Supplementary Materials

Supplementary Table 1: Average estimates of genetic diversity in both the Atlantic and Mediterranean populations of wild European sea bass. H_E (expected heterozygosity), H_O (observed heterozygosity) and F_{IS} (Inbreeding Coefficient) (Nei, 1987) and 95% confidence intervals. IL shows the lower confidence limits and uL the higher. * Indicates significance.

Region	Но	He	P-value	Fis	IL	uL
Atlantic	0.25	0.257	0.044 *	0.041	0.017	0.033 *
West Med	0.24	0.262	0.638	0.082	0.071	0.089
East Med	0.217	7 0.240	0.111	0.101	0.088	0.107

Supplementary Table 2: Average estimates of genetic diversity in both the Atlantic and Mediterranean populations of wild European sea bass. H_E (expected heterozygosity), H_O (observed heterozygosity) and F_{IS} (Inbreeding Coefficient) (Nei, 1987) and 95% confidence intervals for Fis. IL shows the lower confidence limits and uL the higher. ATL_2 and WMED 6-8 have been removed to reduce artifacts and bias.

Region	Ho	He		P-value	Fis	IL	uL	
ATL_1		0.221	0.243	0.560	().089	0.079	0.108
West Med Farms		0.237	0.259	0.445	().087	0.076	0.094
East Med Farms		0.244	0.269	0.098	().096	0.087	0.104

Supplementary Table 3: Percentage assignment to each of the 3 clusters identified by BIC and subsequent DAPC of the wild populations of European Seabass.

Cluster	1	2	3
Successful			
assignment %	100	100	98.1

Supplementary Table 4: Percentage assignment to each of the 9 clusters identified by BIC and subsequent DAPC of the farmed populations of European Seabass.

Cluster	1	2	3	4	5	6	7	8	9
Assignment Success %	85.90%	72.37%	74.39%	100.00%	81.25%	100.00%	95.53%	96.27%	92.59%

Supplementary Table 5: Wilcoxon rank-sum test for pairs of bootstrapped distributions of FST/FSTmax

	K1	K2
K2	<2e-16	-
К3	<2e-16	<2e-16

Supplementary Figure 1: PCA of European Seabass across the Atlantic and Mediterranean containing both wild and farmed populations. Each individual is a dot, and each colour represents a separate population as shown in the legend.



Supplementary Figure 2: PCA of European Seabass across the Atlantic and Mediterranean containing both wild and farmed populations. Populations ATL_2 and WM_6-8 have been removed. Each individual is a dot, and each colour represents a separate population as shown in the legend.



Supplementary Figure 3: Cross Validation (a) and a-score (b) of principal components performed via *Adegenet* in R Studio. xvalDAPC achieved assignment success of 97.4% at 500 PCs whereas the optimum number of principal components to retain without overfitting as shown by the optim a-score was 73.



Supplementary Figure 4: DAPC of European Seabass across the Atlantic and Mediterranean farmed populations. Each individual is a dot, and each colour represents a geographic location as shown in the legend.