

Memòria Treball Final de Grau

Títol del treball:

**Update on genetic studies that apply molecular markers
of recent development to fish of the genus *Mugil***

**Posada al dia dels estudis genètics que apliquin marcadors
moleculars de desenvolupament recent al peixos del gènere
*Mugil***

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Resum

El gènere *Mugil* (Linnaeus, 1758) són peixos coneguts comunament com a llisses (família Mugilidae). Són peixos marins costaners, amb un total de 17 espècies distribuïdes per tot el món. És un gènere d'alt valor comercial que es pesca globalment, destacant Mèxic i Xina. Per això, cal estudiar l'estructura poblacional i la diversitat genètica del gènere, ja que l'èxit en la gestió i la conservació de les pesqueries depèn de les poblacions de les espècies i de les seves localitzacions. L'objectiu de l'estudi és, per tant, revisar els estudis genètics del gènere *Mugil* que han utilitzat marcadors genètics d'última generació, perquè aquests ajuden a conèixer la dinàmica poblacional de l'espècie en una zona concreta i la seva estructura genètica, cosa que és especialment important per a la gestió de les pesqueries.

Per a aquest treball s'ha realitzat un estudi bibliogràfic utilitzant les bases de dades WOS i SCOPUS i la cerca booleana amb les paraules clau (*Mugil* and microsatellit*) o (*Mugil* and SNP*) o (*Mugil* and SSR*) per trobar els estudis relacionats amb els marcadors genètics més recents, microsatèl·lits o SSRs i SNPs, aplicats al gènere *Mugil*. Els resultats – 29 articles – es van recopilar i filtrar manualment, i es van seleccionar 15 articles finals per a la seva anàlisi.

En total, en aquest treball es van estudiar quatre espècies del gènere *Mugil*, centrant-se en les localitzacions i poblacions. En tres articles sobre *Mugil liza* es van analitzar zones d'Argentina, Brasil i el Carib colombià. *Mugil curema* en altres tres articles es va trobar i va estudiar al Golf de Mèxic i les seves zones més properes. Es van trobar vuit articles sobre *Mugil cephalus* i es van classificar en quatre localitzacions: Mar Mediterrani, Austràlia, Pacífic i Mèxic. Finalment, *Mugil incilis* va ser estudiat per un article, centrat al Carib colombià.

En les anàlisis de les quatre espècies, els microsatèl·lits es van utilitzar amb més freqüència que els SNPs, per la qual cosa es recomana que els futurs estudis se centrin en els SNPs per tancar la bretxa. A més, cal fer investigacions similars amb altres espècies del gènere *Mugil*. Finalment, caldria ampliar les zones estudiades, ja que l'anàlisi de més localitats ampliarà el nostre coneixement de l'estructura de les poblacions del gènere.

Resumen

El género *Mugil* (Linnaeus, 1758) son peces conocidos comúnmente como mujoles (familia Mugilidae). Son peces marinos costeros, con un total de 17 especies distribuidas por todo el mundo. Es un género de alto valor comercial que se pesca globalmente, destacando México y China. Por ello, es necesario estudiar la estructura poblacional y la diversidad genética del género, ya que el éxito en la gestión y conservación de las pesquerías depende de las poblaciones de las especies y de sus localizaciones. Por lo tanto, el objetivo del estudio es revisar los estudios genéticos del género *Mugil* que han utilizado marcadores genéticos de última generación, dado que estos ayudan a conocer la dinámica poblacional de la especie en una zona concreta y su estructura genética, lo que es especialmente importante para la gestión de las pesquerías.

Para este trabajo se ha realizado un estudio bibliográfico utilizando las bases de datos WOS y SCOPUS y la búsqueda booleana con las palabras clave (*Mugil* and microsatellit*) o (*Mugil* and SNP*) o (*Mugil* and SSR*) para encontrar los estudios relacionados con los marcadores genéticos más recientes, microsatellits o SSRs y SNPs, aplicados al género *Mugil*. Los resultados - 29 artículos - se recopilaron y filtraron manualmente, y se seleccionaron 15 artículos finales para su análisis.

En total, en este trabajo se estudiaron cuatro especies del género *Mugil*, centrándose en sus localizaciones y poblaciones. En tres artículos sobre *Mugil liza* se analizaron zonas de Argentina, Brasil y el Caribe colombiano. *Mugil curema* en otros tres artículos se encontró y estudió en el Golfo de México y sus zonas más cercanas. Se encontraron ocho artículos sobre *Mugil cephalus* y se clasificaron en cuatro localizaciones: Mar Mediterráneo, Australia, Pacífico y México. Por último, *Mugil incilis* fue estudiado por un artículo, centrado en el Caribe colombiano.

En los análisis de las cuatro especies, los microsatellits se utilizaron con más frecuencia que los SNP, por lo que se recomienda que los futuros estudios se centren en los SNPs para cerrar la brecha. Además, es necesario realizar investigaciones similares con otras especies del género *Mugil*. Por último, deberían ampliarse las zonas estudiadas, ya que el análisis de más localidades ampliará nuestro conocimiento de la estructura de las poblaciones del género.

Abstract

The *Mugil* genus (Linnaeus, 1758) are fish commonly known as mullets in the taxonomic family Mugilidae. These are coastal marine fishes, with a total of 17 species distributed around the world. It is a genus of high commercial value that is fished around the world, highlighting Mexico and China. Therefore, the population structure and genetic diversity of the genus have to be studied, as successful fisheries management and conservation depend on the populations of the species and their location. That being the case, the aim of the study is to review genetic studies of the genus *Mugil* that used the latest genetic markers, since these help understand the population dynamics of the species in a specific area and its genetic structure, which is particularly important for the management of fisheries.

For this paper, a bibliographic study has been carried out using the databases WOS and SCOPUS and using Boolean search with keywords (*Mugil* and microsatellit*) or (*Mugil* and SNP*) or (*Mugil* and SSR*) to find the studies related to the latest genetic markers, microsatellites or SSRs and SNPs, applied to the genus *Mugil*. The results - 29 articles - were compiled and filtered manually, with 15 selected final articles to analyse.

In total, four species of *Mugil* genus were studied in this paper, focusing on their location and populations. Three articles about *Mugil liza* analysed areas of Argentina, Brazil and Colombian Caribbean. *Mugil curema* in another three articles was found and studied in the Gulf of Mexico and its nearest areas. Eight articles about *Mugil cephalus* were found and categorized into four locations: Mediterranean Sea, Australia, Pacific and Mexico. Finally, *Mugil incilis* was studied by one article, focused on Colombian Caribbean.

In the analyses of these four species, microsatellites were more commonly used than SNPs, so it is recommended for the future studies to focus on SNPs to close the gap. Besides, similar research needs to be done with other species of the genus *Mugil*. Finally, the studied areas should be expanded, since analysing more locations will broaden our knowledge of the genus populations' structure.

Reflections on ethics, sustainability and gender perspective

Ethics

When conducting a literature search on genetic studies that apply molecular markers to fish, key considerations related to the ethics should be the potential impact on the species being studied, the handling of genetic information and cultural and social implications of the research. The researchers have to take steps to protect the privacy and confidentiality of the information. In addition, it is important to evade plagiarism to ensure honest and credible work acknowledging the contribution of others.

Sustainability

It is crucial that the researchers ensure that their work contributes positively to the goal of sustainability, advancing the well-being and safeguarding the world for future generations. They must assess how their work might affect ecosystems, biodiversity, and climate stability, striving to minimize any adverse effects on the environment.

No damage should be done to the natural behavior and habitat of fish populations, and appropriate measures must be taken to minimize possible negative impacts.

Gender perspective

The gender gap in science and research is a well-known phenomenon, with women underrepresented in many fields. Worldwide, women account for only 28.8% of researchers (UNESCO, 2021). The reasons for this imbalance are complex and include factors such as bias, discrimination and gender expectations.

A study by Kuehn, B. (2017) analyzed the gender balance of authors in research articles in genetics from 2008 to 2016 and showed that women represented only 27% of the first authors and 19% of the corresponding authors in the articles on genetics.

Another study examined the gender balance of the distinguished speakers at North American Ecology Conferences between 2000 and 2015. According to it, women accounted only for 15%–35% of distinguished speakers and were less likely to be invited than men as main speakers (Farr, C. *et al.*, 2017).

Therefore, women are still underrepresented both as authors of research articles and as speakers at scientific meetings. It poses an important challenge, as scientific research must not perpetuate discrimination against any group, including gender. Hence, it is crucial to accurately represent the diversity of human experiences and contribute to creating an equitable society.

1. Introduction

1.1 General description of Mugil species

Mugil (Linnaeus, 1758) is a genus of marine fish belonging to the family Mugilidae, commonly known as mullets. They are widely distributed in temperate and tropical waters worldwide. The genus consists of 17 species, with the next four as the most known ones: *Mugil curema*, *Mugil cephalus*, *Mugil liza* and *Mugil incilis* (Froese and Pauly, 2024). Eight species from Mugilidae family are found in the Mediterranean Sea (Turan *et al.*, 2005).

Generally, mullets are similar in appearance torpedo-shaped fish, with a moderately elongated, robust body, usually of silvery or olive coloration. Their body is covered with large cycloid, ctenoid or often both scales, generally, a pentagonal shape. The lateral line of mullet is incomplete or absent (Butova *et al.*, 2018).

Mullets have two short widely spaced dorsal fins, the first of which usually contains only four barbed rays, an anal fin and pectoral fins high on body. The tail is concave or weakly forked. The head is small but broad, flattened from above, the mouth is small, and the teeth are very small; the eyes in some species have a well-demarcated fatty eyelid (Figure 1) (Smithsonian Tropical Research Institute).

Maximum length of the genus is about 90 cm. They travel in schools and the main diet are fine algae, diatoms and detritus of bottom sediments.



Figure 1. Photography of an exemplar of *Mugil curema*, one of the most commonly known species of the family Mugilidae and genus *Mugil*. A – Detail of mouth displaying dentition. B – Details of scales located on ventral body region above anal-fin origin. Extracted from Menezes *et al.* (2015).

According to World Register of Marine Species (WoRMS) (2024), fishes belonging to *Mugil* genus follow the next taxonomic classification:

- *Kingdom:* Animalia

- *Phylum*: Chordata
- *Subphylum*: Vertebrata
- *Infraphylum*: Gnathostomata
- *Parvphylum*: Osteichthyes
- *Gigaclass*: Actinopterygii
- *Superclass*: Actinopteri
- *Class*: Teleostei
- *Order*: Mugiliformes
- *Family*: Mugilidae
- *Genus*: *Mugil*

1.2 Geographic distribution

Fishes from *Mugil* genus are coastal marine fishes of tropical, subtropical and moderately warm waters of all oceans (Figure 2). They can tolerate significant desalination and penetrate brackish and even quite fresh waters. There are among them true freshwater species inhabiting rivers and lakes in America, Australia, Indonesia and the Philippines, like *Mugil abu* (Safronov et al., 2006).

Mulletts can habit waters with temperatures from 8 to 30°C, even though the optimum temperature is between 20 and 30 degrees. Normally found on depths from 0 to 20 metres (Ocean Biodiversity Information System).

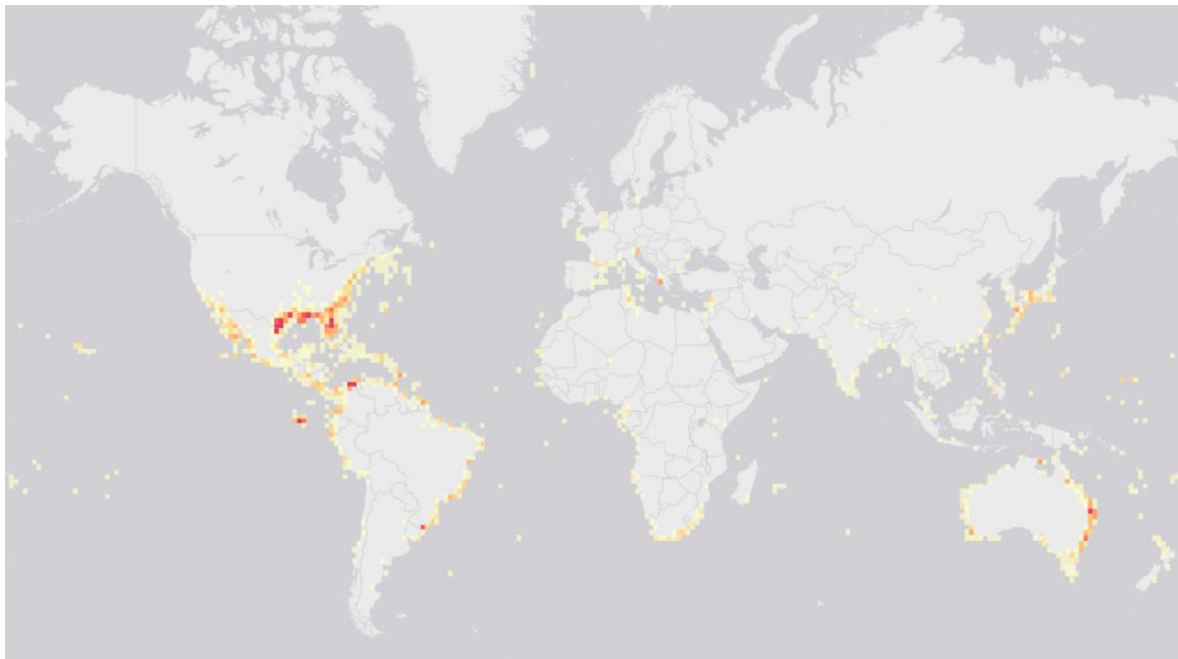


Figure 2. Map showing geographic distribution of genus *Mugil* around the world, extracted from Ocean Biodiversity Information System (OBIS).

1.3 Human use

Fish of genus *Mugil* play a significant role in the economics of fisheries and aquaculture in many regions due to their commercial value. Many mullet species are cultured for human consumption, with traditions dating back centuries (Crosetti, 2016). Mulletts are still gastronomically appreciated on the banks of the Nile and the Ganges delta, on the coasts of South-East Asia, Central and South America, Africa, Australia, on the islands of the Indian and Pacific Oceans. The ancient Greeks and Romans highly appreciated the taste qualities of mullets, praising them in literature and commemorating in sculptures (Fashchuk, 2019).

Among all the species of *Mugil* genus, *Mugil cephalus* is a highly commercially important one, especially for its salted and dried egg roe, which is a traditional luxury item in many regions of the world, currently sold at approximately 170€/kg in Spain.

Among the main countries where fishing for fish of genus *Mugil* is most common are China, Mauritania and Mexico (FAO, 2021). As an example, in Mexico, *M. curema* is the most abundant “fish mullet”, its commercial importance is fundamental on both coasts of the country (Pacheco-Almanzar *et al.*, 2017).

For the last 10 years, the global capture of fishes of genus *Mugil* has been higher than 100 000 tones (Figure 3), which is a further proof of their importance.

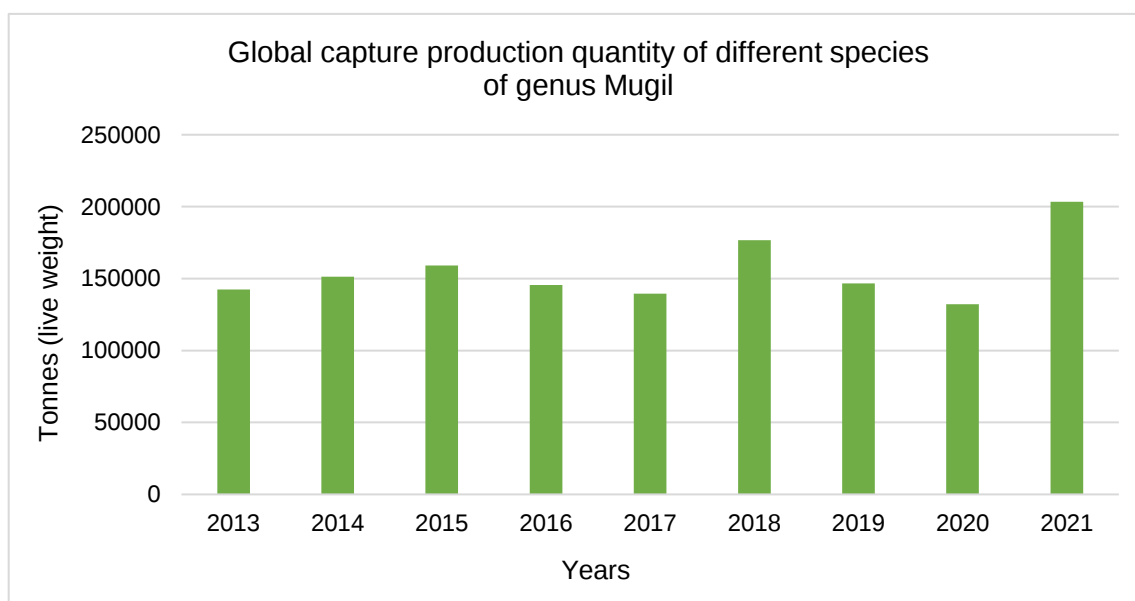


Figure 3. Graphic of own elaboration based on data of global capture production of 7 different *Mugil* species, extracted from FAO (2021).

1.4 Genetic studies

A study of population structure and genetic diversity of genus *Mugil* and the gene flow is extremely important for understanding the dynamics of population connectivity, for conservation purposes and for designing effective management strategies for aquaculture and fisheries.

Using genetic markers like microsatellites, also known as simple sequence repeats (SSRs) and single nucleotide polymorphisms (SNPs) it is possible to effectively study population

genetics and their structuring, gene flow and parentage. Thanks to their high polymorphism, microsatellites are a great cost-effective and simple tool to detect fine-scale genetic variations (Slatkin, 1995) (Pérez-González *et al.*, 2023).

On other hand, SNPs are a tool that are more abundant and uniformly distributed across the genome. They also present some advantages, like their precision or ability to consider local adaptation, and disadvantages, as they have lower allelic diversity (Zimmerman *et al.*, 2020).

In conclusion, both microsatellites and SNPs have their unique advantages and are often complementary in population genetics studies. While SNPs are better for long-term evolutionary processes, microsatellites are great for short-term because of their high variability. The choice between two should depend on the aims and objectives of the study.

2. Aims

This work focuses on a study of a collection of papers and discoveries in genetics and using molecular markers of latest development, such as microsatellites or SSRs and SNPs for the genus *Mugil* over the last 10 years, with the aim of:

- Gathering and analyzing the new data discovered in the last 10 years related to the population genetic studies of the genus *Mugil* using microsatellites or SSRs and SNPs in order to understand the current situation in different areas of the world.
- Identifying the existing gaps in our knowledge of the genus and its populations, and discussing possible ways of closing these gaps as a way to help to the conservation of the species and the management of human use of the resource.

3. Materials and methods

The search was done on November 1st, 2023, using FECYT (Fundación Española para la Ciencia y Tecnología) platform. This platform allows identified users access to two different search engines: WOS (Web of Science) and SCOPUS. For this study, both search engines found in FECYT were used, with the search being done using the Boolean method and containing the next keywords: (*Mugil* and microsatellit*) or (*Mugil* and SNP*) or (*Mugil* and SSR*). The results were filtered using a data range from January 1st, 2013 up to November 1st, 2023, a total of 10 years.

From each of the selected articles, an abstract was read, and the articles were filtered to remove those that did not fit the research topic. The remaining articles were identified into groups for detailed discussion and conclusions.

4. Results and discussion

The result of the search in the database of WOS were 26 articles. The platform also allows us to see under which categories the search results fall (Figure 4, Table 1).



Figure 4. Visual organization of existing categories for found articles, and the amount of these in each category, extracted from WOS.

In this case, 25 out of the 26 articles that were found fall under the category “Genetics Heredity”. Other important categories are “Zoology”, “Marine Freshwater Biology” and “Environmental Sciences Ecology”. At least 73% of the articles are related to these categories. On the other side, the least important categories are “Life Sciences Biomedicine other topics” and “Science Technology other topics”. Less than 35% of the articles are related to these two categories.

Table 1. Recompilation of the articles found in WOS classified according to the categories and with their references, in chronological order.

	References	Articles	Categories									
1	Durand et al. (2013)	Population genetic structure of <i>Mugil cephalus</i> in the Mediterranean and Black Seas: a single mitochondrial clade and many nuclear barriers	■	■	■	■	■	■	■	■	■	■
2	Krück et al. (2013)	New SNPs for population genetic analysis reveal possible cryptic speciation of eastern Australian sea mullet (<i>Mugil cephalus</i>)	■	■	■	■	■	■	■	■	■	■
3	Mai et al. (2014)	Microsatellite variation and genetic structuring in <i>Mugil liza</i> (Teleostei: Mugilidae) populations from Argentina and Brazil	■	■	■	■	■	■	■	■	■	■
4	Tessema et al. (2015)	Phylogeography of <i>var</i> gene repertoires reveals fine-scale geospatial clustering of <i>Plasmodium falciparum</i> populations in a highly endemic area	■	■	■	■	■	■	■	■	■	■
5	Rajan et al. (2016)	Design and evaluation of reverse transcription nested PCR primers for the detection of betanodavirus in finfish	■	■	■	■	■	■	■	■	■	■
6	Dor et al. (2016)	Identification of the sex-determining region in flathead grey mullet (<i>Mugil cephalus</i>)	■	■	■	■	■	■	■	■	■	■
7	Pacheco-Almanzar et al. (2017)	Diversity and genetic structure of white mullet populations in the Gulf of Mexico analyzed by microsatellite markers	■	■	■	■	■	■	■	■	■	■

From the Boolean search on WOS it was possible to obtain a citations graphic of these articles (Figure 5). In this graph, there is a large increase in citations starting in 2018, which reaches its peak of over 80 citations in 2021. In the following years, the number of citations drops by an approximate 25%. The increase proves the growing interest in the genetic studies of genus *Mugil*.

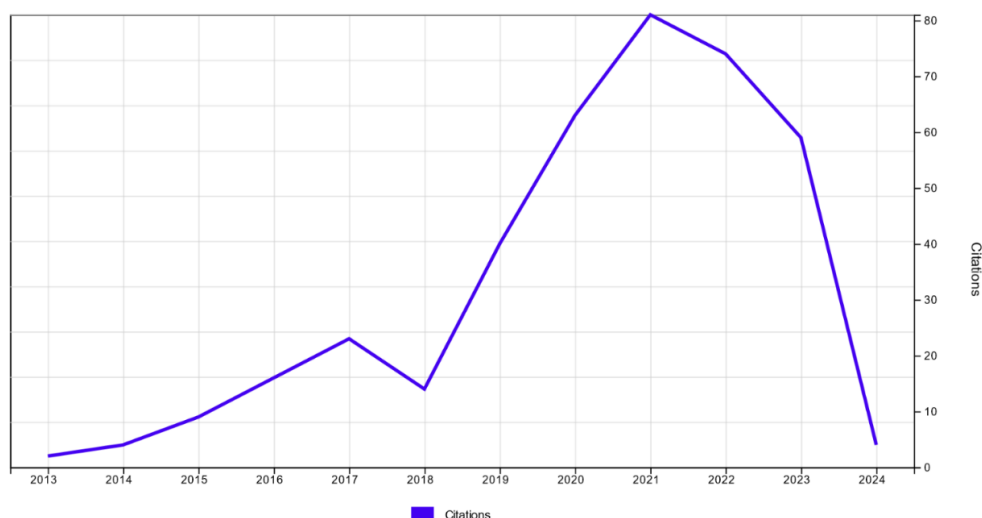


Figure 5. Graphic obtained from Web of Science, which visually summarizes the number of citations over time, beginning in 2013.

When repeating the same search in Scopus, 22 documents were found, 19 of which are also in WOS, and three are new, not mentioned previously articles (Table 2). These three (№ 27, 28 and 29) are listed under the category “Environmental science”, and articles number 28 and 29 are also in the category “Agricultural and Biological sciences”.

Table 2. Recompile of all articles found in Scopus using the same Boolean search, in chronological order.

	References	Articles
27	Huey et al. (2013)	Regional panmixia in the mullet <i>Mugil cephalus</i> along the coast of Eastern Queensland; revealed using six highly polymorphic microsatellite loci
28	Behrouz et al. (2018)	Microsatellite analysis of golden grey mullet <i>Chelon auratus</i> (Risso, 1810) in the fereydoon - kenar and ramsar coasts (South Caspian sea, Iran)
29	Vilasboa et al. (2021)	Genetic connectivity of mullets (<i>Mugil liza</i>) between Rodrigo de Freitas lagoon and a conservation unit in state of Rio de Janeiro, southeastern Brazil

After an in-depth review of all the articles, only 15 of them were selected for the analysis. The other thirteen (№ 4, 5, 6, 9, 11, 14, 16, 18, 20, 22, 24, 25, 26 and 28) were not related to population genetic studies of the genus *Mugil* or to the aim of the study and, therefore, were not suitable according to various parameters. Articles numbered 4 and 11 focus on the parasites *Plasmodium falciparum* and *Myxobolus* respectively. Articles number 5 and 20 were also eliminated; one studies the detection of a betanodavirus, and the other summarizes the existing information about tilapia lake virus. Studies under number 6, 16 and 18 were excluded since these are focused on the sex-determining region in genes in *Mugil*, which is not related to the aim of the study. Article number 14 does talk about *Mugil* genera, but there is no genetic analysis done in the study. Articles number 9, 22, 25, 26 and

28 study other subclass and species of fish: Elasmobranchii, *Oncorhynchus keta*, *Chelon ramada*, *Micropogonias furnieri* and *Chelon auratus*, and so, were filtered out. Finally, article number 24 was discarded since it is focused on a mammal, *Lutra lutra*, and fish are mentioned as its diet.

The remaining 15 articles that were used for the study are listed in Table 3.

Table 3. Final list of selected articles for the study.

1	Durand et al. (2013)	Population genetic structure of <i>Mugil cephalus</i> in the Mediterranean and Black Seas: a single mitochondrial clade and many nuclear barriers
2	Krück et al. (2013)	New SNPs for population genetic analysis reveal possible cryptic speciation of eastern Australian sea mullet (<i>Mugil cephalus</i>)
3	Huey et al. (2013)	Regional panmixia in the mullet <i>Mugil cephalus</i> along the coast of Eastern Queensland; revealed using six highly polymorphic microsatellite loci
4	Mai et al. (2014)	Microsatellite variation and genetic structuring in <i>Mugil liza</i> (Teleostei: Mugilidae) populations from Argentina and Brazil
5	Pacheco-Almanzar et al. (2017)	Diversity and genetic structure of white mullet populations in the Gulf of Mexico analyzed by microsatellite markers
6	Dor et al. (2018)	Genetic stock identification of the flathead grey mullet (<i>Mugil cephalus</i>) in lake Tiberias based on parent-offspring relationship
7	Mendoza-Ureche et al. (Jun 2019)	Low variability and population genetic differentiation in Colombian Caribbean "mullet", <i>Mugil incilis</i> (Teleostei: Mugilidae)
8	Colín et al. (2019)	Are striped mullet (<i>Mugil cephalus</i>) philopatric?
9	Krück et al. (2020)	Ocean currents and the population genetic signature of fish migrations
10	Bae et al. (2020)	A new perspective on biogeographic barrier in the flathead grey mullet (Pisces: Mugilidae) from the northwest Pacific
11	Cossu et al. (2021)	Genetic patterns in <i>Mugil cephalus</i> and implications for fisheries and aquaculture management
12	Avila-Herrera et al. (2021)	Past and recent connectivity of white mullet between the Gulf of Mexico and the Mexican Pacific inferred through sequences of the gene cytochrome c oxidase I and microsatellites
13	Vilasboa et al. (2021)	Genetic connectivity of mullets (<i>Mugil liza</i>) between Rodrigo de Freitas lagoon and a conservation unit in state of Rio de Janeiro, southeastern Brazil
14	Avila-Herrera et al. (2022)	Evidence of flow and low genetic structure between populations of the Gulf of Mexico and the Mexican Pacific of white mullet, <i>Mugil curema</i> (Pisces) inferred from single nucleotide polymorphisms
15	Aguirre-Pabon et al. (2022)	Population structure and low genetic diversity in the threatened lebranche <i>Mugil liza</i> in the Colombian Caribbean

After a thorough reading, these articles were grouped and classified into four different categories according to the studied species.

4.1 Genetic studies of *Mugil liza*

Between all the final articles, three are focused on *Mugil liza*: № 4, 13 and 15 (Table 3).

The starting point of this study is an article by Mai *et al.* (2014) that investigated the patterns of distribution of nuclear genetic diversity in South America *Mugil liza* populations, specifically the ones at Brazilian and Argentinean Atlantic coasts (Figure 6). A set of nine microsatellite loci for *Mugil cephalus* were used (Muce-9, Mcs17FM, Mcs16DM, Mcs2DM, Mce-4, Mce-11, Mce-14, Mce-24 and Mce-27), by Xu *et al.* (2010), Miggiano *et al.* (2005) and Shen *et al.* (2010), since the authors mentioned the lack of articles using microsatellites in the study of *Mugil liza* in South America.

With 131 alleles observed, there was no evidence found on homozygotes excess or recent reduction in population. However, what was found was an evidence of genetic differences at nuclear loci between one of the samples, Niterói (northern) and the other four, indicated by F_{ST} , hierarchical analyses, assignment tests and Bayesian analyses.

These results indicate an existence of two population clusters: a South American Atlantic Coast, represented by the Brazilian Niterói sample, and the other one, represented by Brazilian and Argentinian samples (Ubatuba, Laguna e Rio Grande, Lavalle and Buenos Aires Province). The authors, nevertheless, cannot conclude with certainty the cause of the differentiation, with the lack of significant correlation between genetic and geographic distance excluding the isolation-by-distance cause, and so, other factors have to be considered as a possible reason.

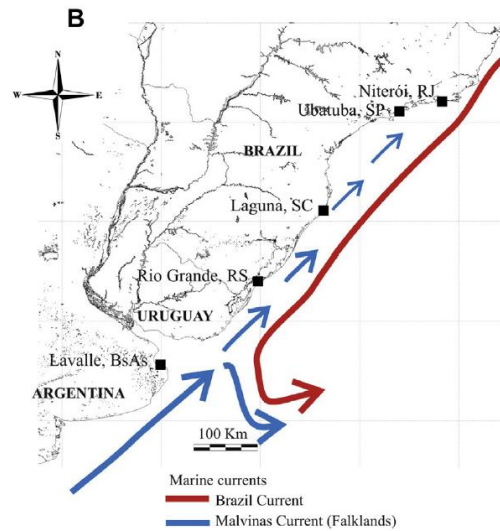


Figure 6. Map of the studied area, extracted from Mai et al. (2014)

Vilasboa et al. (2021) used seven heterologous microsatellites by Miggiano et al. (2005), same as in the previous article, with three of these later being excluded since they were monomorphic, to study the genetic connectivity of the *Mugil liza* population between two bodies of water: Rodrigo de Freitas lagoon and Cagarras Islands, both located in the Rio de Janeiro municipality, Brazil (Figure 7). The lagoon has been an enclosed from the sea area, with sporadic connections thanks to the rising tide, until the channel “Jardim de Alah” was constructed in the 1920s.

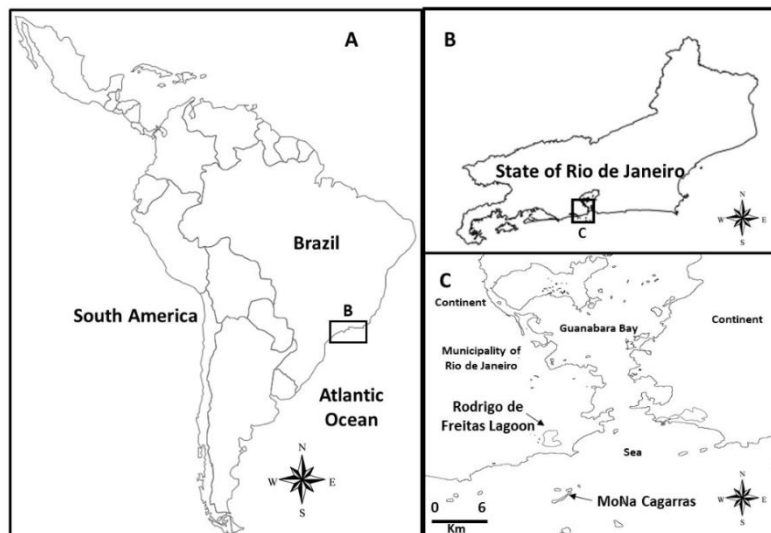


Figure 7. Map of the studies area, extracted from Vilasboa et al. (2021).

The analyzed data disclosed the occurrence of 41 alleles; 31 of these are present in populations from both of the areas. In addition, a high similarity in allelic frequencies and genetic diversity were found. A Factorial Analysis of Correspondence revealed a high similarity between the areas, which could indicate a panmixia case.

In closing, the article concludes that the samples from the Rodrigo de Freitas Lagoon are genetically very similar to the ones near the Cagarras Islands, which shows that the mullets from the Lagoon can migrate to the sea.

A study by Aguirre-Pabon *et al.* (2022) used nine microsatellite loci by Miggiano *et al.* (2005) and Shen *et al.* (2010), same as Mai *et al.* (2014), to analyse the *Mugil liza* populations found in Colombian Caribbean in order to find possible solutions for the overfishing and environmental damages in the area. The authors mention lack of knowledge about existing populations and so, strategies to implement on fishery management.

A total of 112 alleles were found, with all sites showing low genetic diversity, high inbreeding and high genetic potential. A deficit of heterozygotes was found, which could be related either to a drastic reduction of the population, lack of information about *Mugil liza* behaviour, the effect of null alleles, or a combination of all the above.

The authors conclude that there are two populations lowly or moderately differentiated without a clear relation between geographic barriers, and that the population structure is possibly affected by their behaviour, specifically by their biological cycle (Pelagic Larval Duration) and their migration along the coastline to reproduce.

Despite the information provided by these studies, there are still some gaps in our knowledge of the species populations and genetic structure. In the case of Mai *et al.* (2014), the authors themselves acknowledge potential limitations, such as low sampling and number of loci analysed, and the uncertainty with the cause of the differentiation. Additional studies should be done to solve the issues. In addition, the sampling area could be expanded for a better understanding of the populations of the area. Vilasboa *et al.* (2021) used the same nine microsatellites for *Mugil cephalus* for the study. More comparative analyses with the other regions and extra tests, for example using SNPs since none of these three used them, would be beneficial for the study to solve the inconsistency and to contextualize the connectivity findings into a greater picture of the Brazilian coast. Aguirre-Pabon *et al.* (2022) recognize the existent gaps in the knowledge of migration behaviour of *Mugil liza* and the need to study the lifecycle, which is significantly related to the populations. There is lack of information about the species in general and in the area of Colombian coast, so there is a necessity for further research in this area. Finally, none of the studies used SNPs for the analyses, which should be considered and solved in the future researches.

As it is known, world distribution of *Mugil liza* is concentrated on Western side of the Atlantic Ocean, especially USA's state of Florida, Bahamas and from Caribbean Sea to Argentina (Froese and Pauly, 2024). Bearing in mind the studied locations in the analysed articles, Florida and Bahama's areas could be used as next locations for a study.

4.2 Genetic studies of *Mugil curema*

Articles № 5, 12 and 14 (Table 3) focused their studies on *Mugil curema*.

First of the three articles is a research by Pacheco-Almanzar *et al.* (2017), which studied 11 different locations of the Gulf of Mexico for presence of different populations (Figure 8). The hypothesis was based on the difference in spawning points in Northern Gulf of Mexico, with one single spawning point in spring-summer, and Southern Gulf of Mexico, with two spawnings, in summer and in winter.

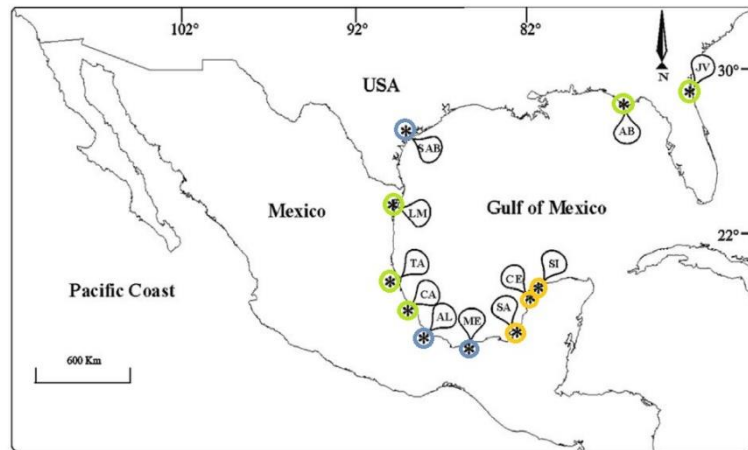


Figure 8. Map of the 11 studies locations in Gulf of Mexico: Apalachicola Bay (AB), San Antonio Bay (SAB), Madre Lagoon (LM), Tamiahua Lagoon (TA), Estero Cazon (CA), Alvarado Lagoon (AL), Mecoacán Lagoon (ME), Estero Sabancuy (SA), Estero Celestún (CE), Estero Sisal (SI), and Jacksonville (JV). Extracted from Pacheco-Almanzar *et al.* (2017).

For the study were used 10 microsatellite, originally designed for *Mugil cephalus* by Miggiano *et al.* (2005) and Shen *et al.* (2010), same as the previous articles, all being polymorphic and no null alleles were detected. F_{ST} values and Nei analysis of genetic distances between populations showed significant genetic differentiation.

Three genetically distinct groups were found, marked in orange, blue and green (Figure 8). The authors conclude that the formation of three different groups is related to the spawning temporality and the oceanographic conditions in Gulf of Mexico either creating larval dispersion or restricting the gene flow. In addition, the genetic differences of 2nd and the 3rd groups in regard to the 1st one may be caused by the environmental differences between the Gulf of Mexico and the Caribbean Sea, and a possible case of isolation, since there are previous cases recorded.

Avila-Herrera *et al.* (2021) used microsatellites and mitochondrial markers (COI) to evaluate genetic structure, connectivity and evolutionary history of *Mugil curema* in the Gulf of Mexico, Pacific Mexican coast and the Atlantic one. The authors studied the same locations as Pacheco-Almanzar *et al.* (2017) did, with an addition of the three locations of the Pacific Coast (Figure 9). Ten nuclear microsatellite marker loci were analyzed, following the Pacheco-Almanzar *et al.* (2017) procedure, who is also an author in this article.

Both microsatellites and COI markers showed clear differences between the populations of Gulf of Mexico and Pacific coasts. Thanks to the microsatellite study, four

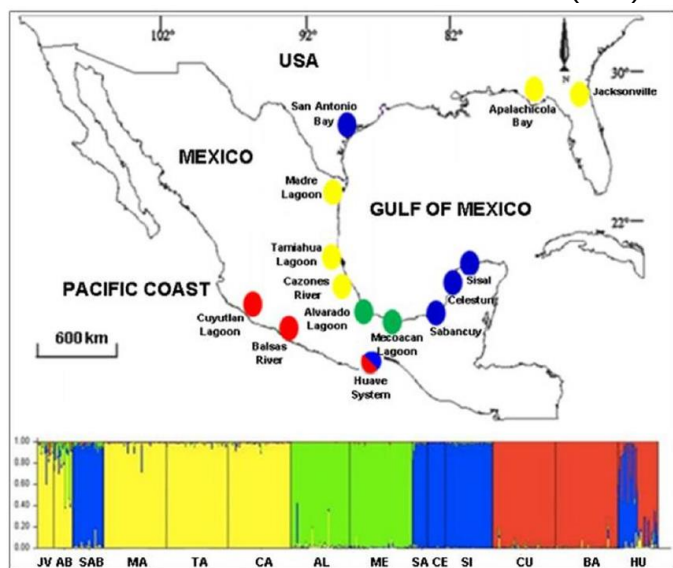


Figure 9. Map of the locations studied, with the populations marked in colours, in the Avila-Herrera *et al.* (2021).

different groups were found, marked as blue, yellow, green and red (Figure 9). The authors find that their grouping is consistent with the marine currents in Gulf of Mexico and the coasts, which means that these could have influenced the gene flow in the area.

COI analysis did find possible two cryptic species: *M. curema* “T2” in Atlantic and *Mugil* sp. O in the Pacific. In addition, the genetic divergences detected by the microsatellite markers, were not detected by COI analyses. Since the microsatellites can detect these divergences in a more recent time scale, the homogeneity described by the results of COI analysis could be influenced by the geological evolution of the Gulf of Mexico, and the formation of oceanographic currents, etc.

Finally, Avila-Herrera *et al.* (2022) was published, which is a study on population connectivity and genetic diversity of *Mugil curema* in 3 locations in Gulf of Mexico and 6 locations on Pacific Mexican Coast, approximately the same ones as the previous study (Figure 10).

To do so, 14172 SNPs markers were used, unlike the previous that used only microsatellites. Between the Gulf of Mexico (GOM) and the Mexican Pacific (MP) Coast locations, the differentiation values were high, singling out the difference between Celestun and Huave System. Celestun also showed a moderate sign of genetic isolation.

The authors detected three genetic groups of *Mugil curema*: the first included Madre Lagoon and Alvarado Lagoon in the Gulf of Mexico, connected with two of the Pacific Coast - Huave System and Puerto Escondido; the second one with the six localities of the Pacific Coast; and the third, containing only the location of Celestun (Figure 10). Celestun also is the population with the highest genetic differentiation, which could indicate a new cryptic species of *Mugil curema*.

On the other side, low genetic structure between the locations of GOM and MP could be considered as arguments against the possibility of two cryptic species corresponding to *M. curema* T2 in Atlantic and *Mugil* sp. O in the Pacific.



Figure 10. Map of the locations, colored bearing in mind the found genetic groups, studied by Avila-Herrera *et al.* (2022).

Finally, as for the gaps in these articles, it is observed that all three articles studied the same area of Gulf of Mexico, with some small alterations, using the same microsatellites, except the last article that also used SNPs, and the resulting groups are different. It is recommended that further research using these and other genetic markers be carried out. It is also recommended to increase the study area. Also, Avila-Herrera *et al.* (2022) themselves conclude the need for analyses of phenotypic, ecological, demographic data, and reproductive isolation tests for the delimitation of *Mugil curema* species. The discrepancy of the cryptic species need additional studies o

As for the species distribution, *Mugil curema* can be found in North Atlantic Ocean from Canada's Nova Scotia and Gulf of California to South Pacific Ocean's Argentina and Chile. It is also found in Eastern Atlantic Ocean, from Senegal River outlet to Namibia (Froese and Pauly, 2024). All the studied articles are concentrated on Gulf of Mexico, Gulf of California and Mexican Pacific, so the areas of Canada, Argentina and Africa need to be studied as well.

4.3 Genetic studies of *Mugil cephalus*

The most cosmopolitan and known *Mugil* species, *Mugil cephalus*, is studied in eight articles (№ 1-3, 6, 8-11) (Table 3) focusing on different regions of the world:

A) Mediterranean Sea

Three articles (№ 1, 6 and 11) focus on populations of *Mugil cephalus* in Mediterranean Sea.

The first one, by Durand *et al.* (2013), explored eastern and western basins of Mediterranean Sea in 18 locations to study the genetic differentiation in the area. To do so, cytochrome b, six microsatellite loci (MCS1EH, MCS2FH, MCS15AM, MCS 15CM, MCS 2DM and MCS16DM) by Miggiano *et al.* (2005) and the first intron of the prolactin 1 gene locus (prl-1) by Blé *et al.* (2010) were used.

By studying mitochondrial DNA (mtDNA), the authors detected a single clade over Mediterranean, Black Sea and parts of Atlantic Ocean (Portugal), but also there is a population differentiation between the Black Sea and the Mediterranean Sea, which needs a further study. No bottleneck was found, but there was a possible recent population expansion, probably in the Pleistocene.

Besides mtDNA, nuclear markers were used to find out that the North East Atlantic, the Mediterranean and the Black Sea populations are genetically differentiated units, most probably separated by the Almeria-Oran front, Siculo-Tunisian Strait and the south of the Greek Peninsula.

Another article, under № 6, (Table 3) by Dor *et al.* (2018) focused on identifying the taxonomic status and stock origin of a sample of 32 mullet individuals caught in the Sea of Galilee (Lake Tiberias), Israel. In that area, young mullet fingerlings are captured along the Israeli Mediterranean coast and are transferred into Lake Tiberias. They are also produced in commercial hatcheries and stocked in the same lake for an improvement of the regional fishing industry.

Since the main goal of the study was to identify the individuals, COI sequence analysis and 13 microsatellite markers (FHM550, MCE6, FHM255, MSC4GH, MCE4, 2D7GM, MUCE44, 204HH, 2D15FM, MCE25, MCE2, MCE3, MCE7) were redesigned from *M. cephalus* ones (Dor *et al.*, 2016) and used to check the authenticity of *Mugil cephalus*.

Based on both mitochondrial DNA barcoding and nuclear genetic markers analysis, out of 32 studied individuals, seven were from a morphologically similar species, *L. ramada*, and 25 were *M. cephalus*. Eight of these individuals were determined as the progeny of the three parental pairs, and so, the authors concluded that both the hatchery-reared fingerlings and the translocated ones survived in the Lake Tiberias.

Finally, article №11 by Cossu *et al.* (2021) studied the *Mugil cephalus* populations in the Western Mediterranean, specifically on the island of Sardinia, Italy. It is focused on four coastal ponds, which are relevant to the local fisheries: Cabras pond (CAB), Mistras pond (MIS), Porto Pino ponds (PPI) and Tortoli pond (TOR) (Figure 11).

In total, 14 microsatellites, originally designed by Miggiano *et al.* (2005), were used to investigate patterns of genetic variation in a Mediterranean area that harbor flourishing fisheries and practice semi-intensive farming of *Mugil cephalus*. Seven of them showed deviations from Hardy-Weinberg, possibly caused by null alleles and so, were excluded from the further study.

According to the homogeneity, the Bayesian clustering and the Discriminant Analysis of Principal Components (DAPC), the four populations might belong to the same single genetic stock. If so, it supports the hypothesis of high connectivity and gene flow among the ponds. This conclusion is consistent, with previous findings by other authors. However, significant differences in effective population sizes were observed, with Mistras pong being the smallest, and the Cabras one being the largest. This indicated that the environmental conditions and habitat sustainability influence the population size.

As conclusion, Sardinia Island can be managed as a single management unit in terms of fishery practices in order to preserve the genetic integrity of the *Mugil cephalus* population in the area.

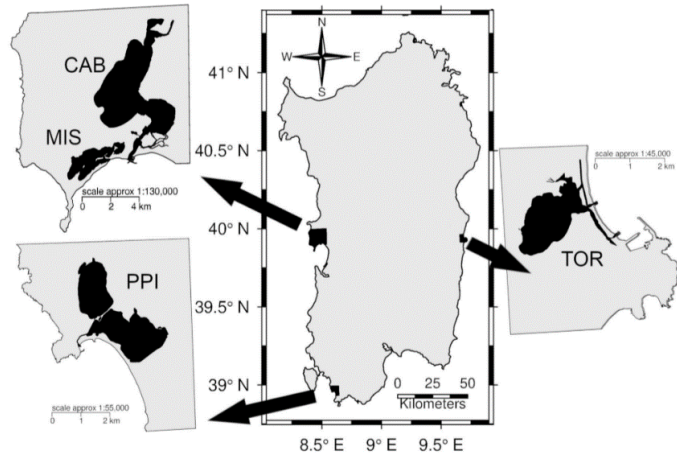


Figure 11. Map of the studies ponds of Sardinia Island; extracted from Cossu *et al.* (2021).

B) Pacific

The article № 10 (Table 3) by Bae *et al.* (2020) studied the *Mugil cephalus* lineages in 14 locations in Korea, Japan, China and Taiwan (Figure 12) using nine microsatellites and two partial mtDNA gene sequences (COI and 16S rRNA). The authors hypothesised about a possibility of existence of at least two *Mugil cephalus* lineages around Korea.

The microsatellites used were MCE3, MCE6, MCE10; MCE2, MCE7, MCE11, MCE4, MCE8, and MCE22, designed by Andree *et al.* (2010).

Two distinct lineages were described using a minimum spanning network based on distances among mtDNA haplotypes, with lineage 1 (L1) made up of haplotypes from all locations, and lineage 2 (L2) with haplotypes from the Jeju Island, Shanghai, Japan and Taiwan. A pairwise F_{ST} comparison showed that a significant differentiation was found between Japan, Taiwan and

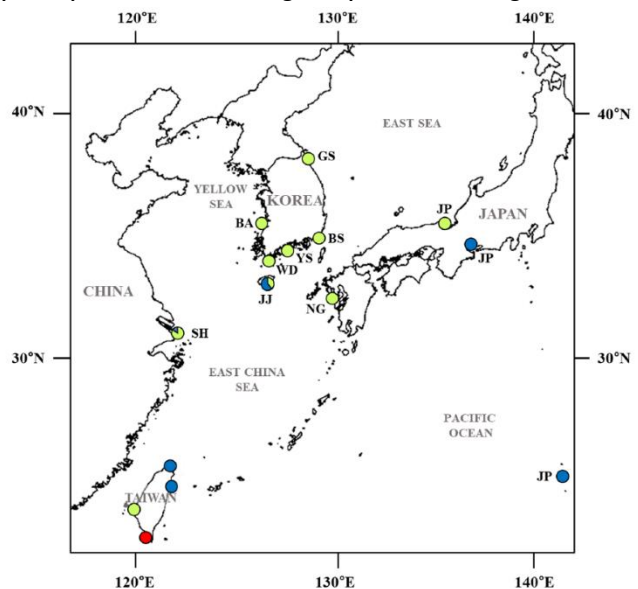


Figure 12. Map of the studied locations: Goseong (GS), Busan (BS), Yeosu (YS), Wando (WD), Buan (BA), Jeju-do (JJ), Shanghai (SH), Japan (JP), Nagasaki (NP) and Taiwan (TW); extracted from Bae *et al.* (2020)

Jeju Island and all the other locations, which could mean an existence of three barriers. The first one between Pacific side of Japan and Goseong, Busan and Nagasaki; the second one between Shanghai and Taiwan; and the third barrier located between the Jeju Island and Yeosu, Wando, Shanghai and Nagasaki.

The microsatellite analysis was done in the same locations excluding Goseong and Buan. Low migration rates and gene flow between the locations were found, which strong biogeographic barriers, like oceanic fronts, could cause.

In conclusion, these factors could lead to speciation, and the authors hypothesise that the lineage L1 could actually be *Mugil japonicas*, and L2 an undescribed species under *Mugil* genus. Therefore, a more profound and detailed study should be done to establish with accuracy what are the found lineages.

C) Australia

Australian population of *Mugil cephalus* were studied in the articles № 2, 3 and 9 (Table 3).

Article № 2 by Krück *et al.* (2013) is a research of the eastern Australian coast, specifically three regions: North Queensland (NQLD), South Queensland (SQLD), and central New South Wales (NSW) (Figure 13).

In this paper, the researchers used restriction site associated DNA next-generation sequencing (RAD-seq) to identify population genetic markers in eastern Australian sea *Mugil cephalus* populations.

Because of RAD-seq, 1267 single nucleotide polymorphisms (SNPs) and 1417 potential microsatellite loci were found. Out of these, 92 SNPs were confirmed as reliable and primers were developed for 27 microsatellites.

The genetic analysis by SNPs revealed significant genetic differentiation between northern and southern populations of *M. cephalus*, and CB being the most different from the others. Keeping in mind the high values of pairwise F_{ST} , there is a possibility of cryptic speciation between northern and southern regions. As a conclusion, it is necessary to introduce region-specific management strategies in fishery industry to maintain the genetic diversity in the studied populations.

The same year, Huey *et al.* (2013) published an article (№3, Table 3) studying the genetic structure of *Mugil cephalus* populations along the Queensland coast, Australia (Figure 14).

Eight microsatellites by Miggiano *et al.* (2005) were employed (Loci 15CM, 16DM, 17FM, 2DM, 2FH, 6DM, 15AM and 1EH), later excluding two (15AM and 1EH) since these failed to amplify.

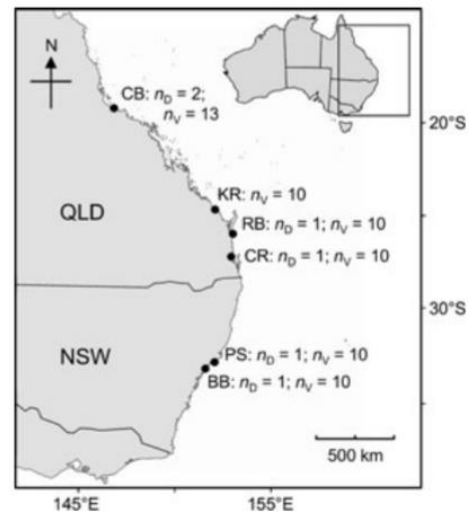


Figure 13. Map of the studied locations on the Australian coast: Cleveland Bay (CB), Kolan River (KR), Rainbow Beach (RB), Caboolture River (CR), Port Stephens (PS) and Blacksmith Beach (BB); extracted from Krück *et al.* (2013)

Despite the high diversity, no significant genetic structure was detected by the F_{ST} test. This suggests that the population along the coast is genetically homogenized and it shows the importance of connectivity between marine and freshwater habitats of the species.

Finally, the article № 9 is a research conducted by Krück *et al.* (2020) again focused on twelve sites of coast of Eastern Australia. The main aim of the research was to study the migration and spawning of *Mugil cephalus* in Australia by developing a simulation-based approach to test explicit fish migrations. The authors used 51 SNPs previously discovered by Krück *et al.* (2013) for genotyping, and based their study on the “contranant theory”, which says that the fish moves against the flow of the current to spawn, so the eggs and larvae get additional help and drift to suitable location to nurse. They also hypothesise that the genetic structure of a population will reflect their larval dispersion pattern.

Firstly, their hypothesis about the relationship between the larval dispersion and genetic structure was confirmed, so using genetic variations can be used to study different ecological processes of a population. Their findings argue against the simplification of migration patterns based on basic information like the ocean currents. The authors consider that using other species with a more complex migration pattern could be more complicated for their approach, and that the nearshore dynamics and the development and behaviour of the larvae should be considered as possible limitations for the method.

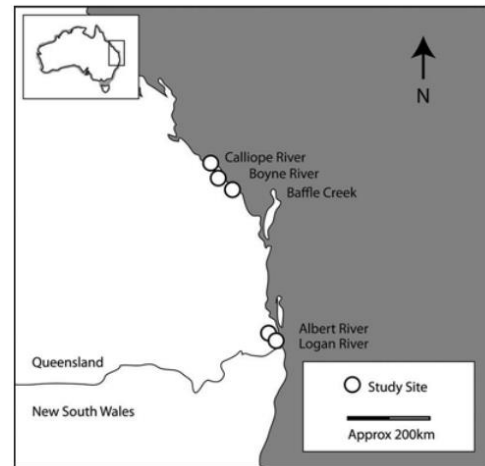


Figure 14. Map of the studied locations on the Australian coast; extracted from Huey *et al.* (2013)

D) Mexico

Article № 8 (Table 3) written by Colín *et al.* (2019) hypothesises about possible philopatric behavior of *Mugil cephalus* in 11 locations of Gulf of Mexico (GOM) and 2 in the Mexican Pacific (MP) (Figure 15). For the research, the authors used mtDNA, COI and control region, and 10 microsatellite (Mce3, Mce4, Mce6, Mce7, Mce8, Mce10, Mce11, Mce14, Mce25, Mce27) by Shen *et al.* (2010).

Results from the COI analysis indicated two distinct genetic groups: the first one with all the locations in the GOM and the second one with the entirety of MP. The first group showed signs of panmixia, using control region and microsatellites, with high gene flow between locations, which could obscure markers of philopatric behavior. However, the second one displayed two distinct genetic groups (north and south) using microsatellites, which could be influenced by a barrier during the spawning season, like the Tehuanos winds in the Gulf of Tehuantepec (GT) (Figure 15). As consequence, it is possible that this genetic structure is not a consequence of philopatry.

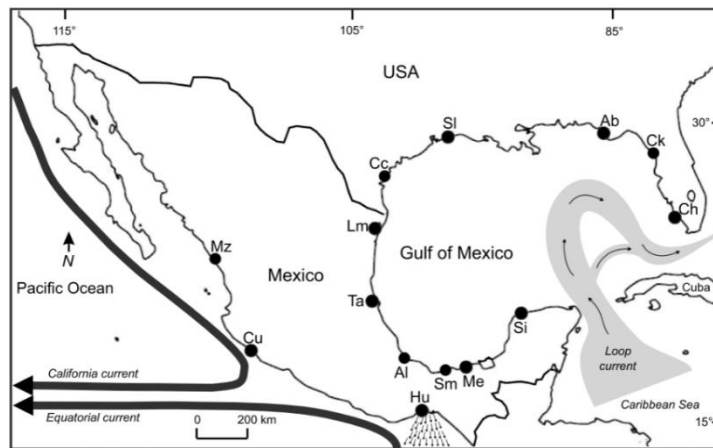


Figure 15. Map of the studied locations, with abbreviations: Charlotte Harbor (Ch), Cedar Key (Ck), Apalachicola Bay (Ab), Sabine Lake (Sl), Corpus Christi (Cc), Madre Lagoon (Lm), Tamiahua Lagoon (Ta), Alvarado Lagoon (Al), Sánchez Magallanes (Sm), Paraíso (Me), Sisal (Si), Mazatlán (Mz), Cuyutlán Lagoon (Cu) and Huave Lagoon System (Hu); shaded zone and black arrows correspond to main currents and the fine arrows represent the zone of influence of the Tehuanos; extracted from Colín *et al.* (2019).

Further, the historical genetic flow between the GOM and MP regions suggests a previously existent connection through either the Isthmus of Panama, the narrowest strip, or interconnection of rivers during the Pleistocene era. There is also an asymmetric migration pattern, with significant migration from the GOM to the MP but not vice versa. These findings support the found panmixia in Gulf of Mexico.

As the authors conclude in their discussion, to close up the gaps of the study, a more consistent study should be done with a sampling of the Pacific slope to learn if the genetic differentiation includes the entire southern zone or only in the GT. In addition, tagging studies or otolith chemistry analysis could help to understand better the movements of the *Mugil cephalus* in the area.

As it is important to understand the limitations and gaps of the studied information, to delve deeper in the topic it is needed to highlight that SNPs were not used in all of the studies, which could be an idea for the future researches. In addition, there could be more cryptic species around the world under the name of *Mugil cephalus*, like *Mugil japonicas* mentioned by Bae *et al.* (2020). To find an answer to that, it would be needed to apply differentiated phylogenetic and population studies.

In addition, it is important to know the geographic distribution of the species to draw the conclusions. *Mugil cephalus* is a highly distributed species around the world. Its individuals were found in coastal waters of all tropical and temperate seas. It includes all the Pacific Ocean, Western Indian Ocean from India to South Africa, Atlantic Ocean, except the Bahamas and Caribbean, but including the Mediterranean and Black Seas, and also the Sea of Okhotsk between Kamchatka and Sakhalin in Russia (Froese and Pauly, 2024). In this work, four regions were studied, covering some parts of Atlantic and Pacific Oceans. More studies should be done in other areas, like the Indian Ocean or Sea of Okhotsk since the species is of a high importance around the world.

4.4 Genetic studies of *Mugil incilis*

The last article is under № 7 (Table 3) by Mendoza-Ureche *et al.* (2019), which studied the *Mugil incilis* populations in six locations of Colombian Caribbean: three with open access to fishing (CVIR, CCAI and BCIS) and three coastal lagoons from National Natural Parks of Colombia (SFFF, CGSSM and SFFC) (Figure 16).

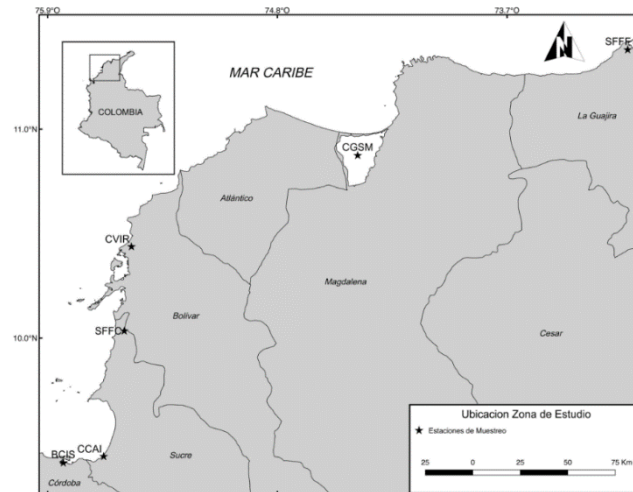


Figure 16. Map of the studied locations: La Virgen Swamp (CVIR), La Caimanera Swamp (CCAI), Cispatá Bay (BCIS), Flora and Fauna Sanctuaries Los Flamencos (SFFF), Grande de Santa Marta Swamp (CGSM) and El Corchal (SFFC); extracted from Mendoza-Ureche *et al.* (2019)

To do so, seven microsatellite loci were used: Mce-15 AM, by Miggiano *et al.* (2005), Mce-2, Mce-3, Mce-7, Mce-11, by Shen *et al.* (2010) and Mce-55 and Mce-80, by Xu *et al.* (2010); which are the same microsatellites as *M. cephalus*.

The authors detected three different populations: the first one in the area from La Guajira (SFFF) to the Sucre (SFFC), the second one in BCIS and the third one in CCAI. That differentiation is probably caused by migratory behavior of the species. In addition, low genetic diversity and recent bottleneck in some locations were found, which indicated that the area is too small for species conservation.

This study suggests that the processes involved in the level of fishing exploitation, in the reproductive cycle and in the oceanographic conditions of the South Caribbean region determine the genetic variability and structure of *M. incilis*. Finally, the authors propose recommendations for the management and conservation of *M. incilis*, like establishing a temporary closing during the period of the species reproductive migration, establishing management units according the populations and generating spaces and institutions for the fishing communities to ensure the appropriate measures for the sustainable fishing of the species.

Since *Mugil incilis* individuals are typically found in the Western Atlantic Ocean, from the coast of Cuba to Brazil (Froese and Pauly, 2024), it is important to highlight how Mendoza-Ureche *et al.* (2019) studied only one country from the entire coast that is a native area for the species. Therefore, the studied area needs to be expanded since the studied one is too small for the conservation. In addition, more studies in the area studied by Mendoza-Ureche *et al.* (2019) should definitely be done, so the management and conservation of *Mugil incilis* could be as effective as possible. Finally, the authors only used microsatellites for the study, so expanding with SNPs could be a great addition for the future studies.

Conclusions

The Boolean search using WOS and SCOPUS resulted to be useful and functional for the search of the articles. In the filtered list of fifteen articles, only four species of the genus *Mugil* were studied from a total of 17 existing species. The most studied one is also the most cosmopolitan one, *Mugil cephalus*. The majority of the articles used microsatellites designed by Miggiano *et al.* (2005) and by Shen *et al.* (2010). Few of them, specifically Krück *et al.* (2013) developed their own microsatellites or, as Avila-Herrera *et al.* (2022), used only SNPs.

In general, the analysed studies were successful in their aims. Regarding *Mugil liza*, there were some limitations, specifically in the article by Mai *et al.* (2014). More studies should be done as the number of sampling could be higher, more locations need to be researched, like Florida's Coast or the Bahamas, and more tests should be done to compare the results.

In the case of *Mugil curema*, different populations were found in the Gulf of Mexico and Mexican Pacific, but there is also a need to delimitation of the species, as Avila-Herrera *et al.* (2021) found a possibility of existence of cryptic species *M. curema* "T2" in Atlantic and *Mugil sp. O* in the Pacific. Yet, later, Avila-Herrera *et al.* (2022) wrote that there is only one species, and another one in one of the studied locations, Celestun. So, additional studies are needed to resolve these discrepancies.

In addition, *Mugil cephalus* was studied in four regions, Mediterranean, Australia, Pacific and Mexico. Since it's a species found almost everywhere around the world, more places should be analysed. In addition, genetic structure of the species needs to be thoroughly studied since there are possibilities of existence of *Mugil japonicus* as said by Bae *et al.* (2020) and other undescribed species under *M. cephalus*.

Finally, as for *Mugil incilis*, only one study, by Mendoza-Ureche *et al.* (2019) was found. It is highly important to study further populations of the species in Colombian Caribbean as the found article did to compare the results, and to study other areas where the species can be found.

As only four species of genus *Mugil* were studied and no population analysis of other species has been found, it is recommended that efforts be directed at carrying out studies using microsatellites and SNPs in other *Mugil* species, and at deepening actual knowledge of the four studied species using SNPs, since it is yet not commonly used like microsatellites.

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