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Population Genetics of Chilean Jack Mackerel, *Trachurus murphyi* Nichols, 1920, (Pisces, Carangidae), in Waters of the South Pacific Ocean

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Abstract: Estimating genetic diversity and population structure with polymorphic markers might provide information for the better management of fish that have economic importance. We used the Chilean jack mackerel, *Trachurus murphyi*, a pelagic species distributed in the south Pacific Ocean, to test the population genetic structure across its distribution. A total of 522 samples were collected from 11 locations in 2008, to be analyzed using six loci microsatellites. We conducted traditional genetic analyses to describe the genetic diversity of *T. murphyi* and whether it shows spatial genetic structure. The results showed a high genetic diversity across locations (Ho = 0.551 to 0.980; He = 0.676 to 0.959). Estimates for the population structure showed a low and non-significant pairwise F_{ST} in all comparisons. We supported the non-genetic differentiation previously reported with the used microsatellite panel. Further comparative temporal studies should be conducted to identify the stability of this pattern. Overall, this study reinforces the hypothesis that, in the Pacific Ocean, Chilean jack mackerel correspond to a large single population.

Keywords: species-specific microsatellites; heterologous loci; Chile; marine resources; SPRFMO

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1. Introduction

New data providing estimations of genetic diversity and population structure in marine fishes may contribute to appropriate fishery management (e.g., [1–3]). Understanding stock structure is important for identifying differentiated reproductive groups (i.e., evolutionarily significant units or genetic stocks) and is the first task for their management [4]. For migratory fishes, which several countries exploit as a resource, it is important to estimate their number because overharvesting can decrease the genetic diversity and, hence, the evolutionary potential of these species [5]. Additionally, habitat destruction, pollution, and climate change have led to a global decline in marine fish biodiversity [6].

The Chilean jack mackerel, *Trachurus murphyi*, is a highly migratory pelagic species that inhabits the South Pacific Ocean [7]. Specifically, *T. murphyi* is distributed off the coast of south Ecuador (1°38′ N) and the south of Chile (55° S); it crosses the Pacific Ocean along the West Drift current, reaching as far as New Zealand and Tasmania [7–9]. In the open ocean, its distribution exceeds 200 nm of the Peruvian Exclusive Economic Zone (EEZ), while, concerning Chile, it exceeds 1000 nm [10]. It is economically important for the countries where it is distributed and also for the European Union and Asia. In the SPPRFMO (South Pacific Regional Fisheries Management Organization) area, for instance, the Chilean jack mackerel catches over the 2013–2022 period progressively increased, with the maximum reached in 2022, in which 928,852 tons were fished [11]. The Chilean jack mackerel is an indeterminate batch spawner [12], where females have asynchronous ovarian development [13] and are able to spawn along their entire distribution [14]. Two main

spawning areas have been proposed as the population structure of *T. murphyi* [7,9,15]; however, this is not fully supported by other methodologies.

Several studies have been conducted to resolve the population structure, which include studies of parasites [16,17], life-history traits [7,18], morphometry and meristic traits [7], otolith microchemistry [19,20], oceanographic modelling [19], and genetics [2,21]. Some of these support the inference of more than one population, while others support the inference of just one population [2,7,16,21]. Despite the complex scenario of population structure in the South Pacific Ocean, Gerlotto et al. [10] refuted independent, discrete self-recruiting populations.

Population genetics studies published on *T. murphyi* have included several molecular markers. Chronologically, in a technical report, Galleguillos and Torres [22] identified polymorphic enzyme loci in samples from Chile (Chiloé, Talcahuano, Juan Fernández, Iquique), Perú, and one oceanic area (39°24′ S; 76°45′ W), while not detecting significant differences between them. Later, using 23 enzymatic loci for samples from Chile, no differences were identified [23]. Using PCR-RFLP in the Internal Transcribed Spacer (ITS2) amplicon and restricted to the *MspI* enzyme, and analyzing samples from Chile (Isla Mocha, Iquique, Juan Fernández), New Zealand, and Australia, showed no significant genetic differences among the samples, while patterns of genetic homogeneity were observed in the study area for these genetic markers [24]. Cárdenas et al. [21], analyzing mitochondrial DNA sequences (control region 772 bp) and nuclear DNA (four heterologous microsatellite loci) for samples from Chile (Iquique, San Antonio, and Concepción), one off the Chilean coast and another around New Zealand, indicated low genetic variability for both types of molecular marker, with no significant genetic differentiation among localities. Later, Canales-Aguirre et al. [25] isolated and characterized eight species-specific polymorphic loci for *T. murphyi*. Galleguillos et al. [2], using three distant locations in the South Pacific Ocean, also did not find any genetic differences. Despite there having been great efforts made to use genetic markers to identify changes in allelic frequencies, no studies have used a combination of heterologous and species-specific microsatellite loci to estimate the genetic diversity and population structure in Chilean jack mackerel. Additionally, the geographic coverage of studies has not always incorporated samples from the peripheral geographic distribution, as well as the use of species-specific markers. For instance, Cárdenas et al. [21] did not include samples from Perú, and for microsatellites, used only heterologous loci.

In this study, we used microsatellite loci to test the hypothesis of no genetic differentiation in the South Pacific Ocean in *T. murphyi*. More specifically, we screened six microsatellite loci across collections from 11 locations distributed across the whole geographical range. We used traditional population genetic parameters, in order to compare with results from previous research. Finally, we discuss our results in a biological context and regarding the expansion of this species to New Zealand.

2. Materials and Methods

2.1. Study Area and Sample Collection

Samples from adult specimens (n = 522) of Chilean jack mackerel were collected across the Southern Pacific Ocean (Figure 1) during 2008 as part of the project FIPA 2007-27 of the Chilean government. Samples were obtained from three locations from Perú (i.e., Paita (n = 34), Punta Lobos de Afuera (n = 34), and Paracas (n = 54)), one location from New Zealand (i.e., west coast South Island; (n = 50)), and seven locations from Chile (i.e., Iquique (n = 46), Caldera (n = 51), Coquimbo (n = 56), coastal Talcahuano (n = 43), oceanic Talcahuano (n = 51), coastal Calbuco (n = 54), oceanic Calbuco (n = 49)). A small piece of muscle tissue was excised from each specimen and stored at 4 °C in absolute ethanol.

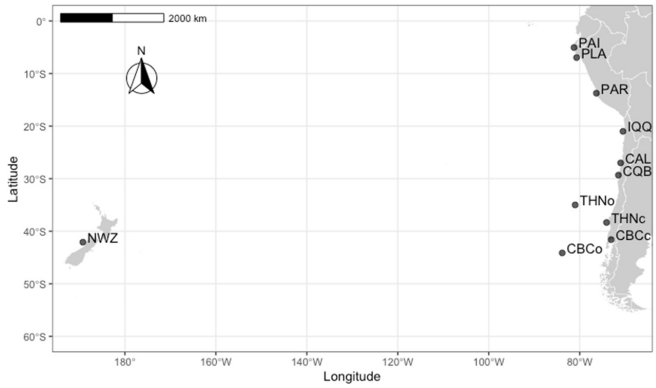

Figure 1. Sampling locations for *T. murphyi* across its whole South Pacific Ocean distribution. PAI: Paita, PLA: Punta Lobos Afuera; PAR: Paracas; IQQ: Iquique; CAL: Caldera; CQB: Coquimbo; THNc: costal Talcahuano; THNo: oceanic Talcahuano; CBCc: costal Calbuco; CBCo: oceanic Calbuco; NWZ: New Zealand.

2.2. DNA Purification and PCR Procedures

Genomic DNA was extracted from muscle tissue samples using proteinase K digestion, followed by a standard phenol–chloroform method and precipitation in ethanol, as described in Grijalva-Chon et al. [26]. DNA was subsequently resuspended in 100 µL of ultrapure water. The quality and quantity of each sample was measured with an Eppendorf biophotometer, and the template DNA was diluted to 20 ng for the PCR amplifications.

We used seven microsatellite loci to study the genetic structure of *T. murphyi*: four heterologous loci developed for *T. trachurus* by Kasapidis and Magoulas [27] (i.e., Tt29, Tt48, Tt62 and Tt133) and three species-specific loci developed by Canales-Aguirre et al. [25] (i.e., TmurA101, TmurA104, and TmurA115). Heterologous loci were amplified in 10 µL reactions containing 1X PCR buffer, 1.5 mM $MgCl_2$, 0.2 mM dNTPs, 0.4 µM of each primer, and 0.1 U/µL Taq DNA polymerase. Thermal cycler parameters were 94 °C for 5 min, followed by 35 cycles of 94 °C for 30 s, 55–57 °C for 45 s, 72 °C for 45 s, and a final extension at 75 °C for 5 min. Species-specific loci were amplified in 10 µL reactions containing 1X PCR buffer, 2 mM $MgCl_2$, 0.2 µM of each primer, 200 mM dNTPs, and 0.03 U/ µL Taq DNA polymerase. The thermal cycler parameters were 94 °C for 3 min, followed by 35 cycles of 94 °C for 40 s, 57 °C for 30 s, and 72 °C for 30 s, with a final extension at 72 °C for 5 min. For all reactions, we used Taq DNA polymerase (Invitrogen), forward primers were fluorescently labeled with a dye (6-FAM, VIC, NED, or PET) and 20 ng of genomic DNA template. PCR amplifications were performed in a PTC-200 thermocycler (MJ Research). The fragments were visualized on an ABI PRISM 3730xl capillary DNA sequencer using GS500 as the internal size standard. The assignment of allele size was carried out using a Peak Scanner v1.0 (Applied Biosystems).

2.3. Microsatellite Data Analysis

We conducted an exploratory analysis to detect genotyping errors and check for the presence of null alleles. Short-allele dominance and the scoring of stutter peaks were tested in Micro-Checker v2.2.3 [28]. The frequency of the null alleles was estimated using the Brookfield algorithm [29] using Genepop on the Web (https://genepop.curtin.edu.au/ (accessed on 13 September 2022).) and using the inbreeding coefficient (F_{IS}) as an estimator of excess homozygosity. We excluded microsatellite loci that showed an average higher than 15% missing data and excess of homozygosity (F_{IS}), and at least 30% of the locations showed null allele frequencies larger than 10%. All loci that met these criteria were excluded from the data set and further analyses.

As a summary statistic of genetic diversity, we estimated the effective sample size (N), number of alleles (N_A), the observed (H_O) and expected (H_E) heterozygosity, inbreeding coefficient (F_{IS}), and departure from Hardy–Weinberg equilibrium (HW) using GENALEX v6 [30]. To detect significant differences from the Hardy–Weinberg equilibrium, we fol-

lowed the procedure of Hedrick [31] implemented in GENALEX, which included a test for conformity with HWE expectations by calculating X^2.

To identify the population structure across the locations surveyed, we used a pairwise F_{ST}, an analysis of molecular variance (AMOVA), and principal component analysis (PCA). We estimated a pairwise F_{ST} comparison between sampling locations in ARLEQUIN v3.5 [32], where the *p*-value was obtained after 10,100 permutations, and sequential Bonferroni correction [33] for multiple comparisons was applied when necessary. We estimated the proportions of genetic variation among sampling locations using an AMOVA implemented in ARLEQUIN. Specifically, we evaluated the following hypotheses: (a) panmixia and (b) the presence of genetic differentiation for the most distant localities (Perú vs. Chile vs. New Zealand). We subjected the multilocus microsatellite data to principal component analyses in ADEGENET [34,35], thus comparing the relationships among individuals from sampling locations.

3. Results

The exploratory analysis showed no genotyping errors such as short allele dominance or stutter bands; nonetheless, locus Tt48 did not meet the criterion tested (Table S1). Overall, locus Tt48 showed an average of 20% missing data (5 of 11 locations higher than 0.15), with an average homozygote excess of 0.18. Checking by null allele presence, locus Tt48 showed that 4 of 11 locations (36%) had a null allele frequency higher than 0.10. Hence, data from this locus were excluded from the analyses (Table S1).

Summary statistics of genetic diversity showed distinct values across locations (Table S2). The number of alleles ranged from 9 (PAI) to 35 (IQQ), the observed heterozygosity ranged from 0.551 (CBCo) to 0.980 (CAL), the expected heterozygosity ranged from 0.676 (CBCo) to 0.959 (NWZ), and the inbreeding coefficient ranged from 0.676 (CBCo) to 0.959 (NWZ) (Table S2).

The pairwise F_{ST} values for all of the loci surveyed ranged from 0 to 0.005, and none of the combinations showed significant differences ($p > 0.05$; Table 1). The analysis of molecular variance showed an F_{ST} of 0.00011 ($p = 0.682$) to test the hypothesis of panmixia, with an F_{ST} of 0.00016 ($p = 0.665$) and F_{CT} of 0.00011 ($p = 0.419$) for far localities (Perú vs. Chile vs. New Zealand) (Table 2). Principal component analyses (PCA) showed a low amount of variation (1.3 and 1.2%), explained by the first and second principal components (Figure 2). Individuals formed a big cloud showing that the population was not differentiated. Two individuals were identified as outliers, one from Paracas and the other from New Zealand. Overall, pairwise F_{ST}, AMOVA, and PCA showed concurring results.

Table 1. Pairwise F_{ST} values calculated for microsatellite dataset of *T. murphyi* across its South Pacific Ocean distribution.

	PAI	**PLA**	**PAR**	**IQQ**	**CAL**	**CQB**	**THNc**	**THNo**	**CBCc**	**CBCo**	**NWZ**
PAI	*										
PLA	0.002	*									
PAR	0.000	−0.006	*								
IQQ	−0.003	−0.004	0.000	*							
CAL	0.002	−0.005	−0.002	−0.002	*						
CQB	0.000	−0.005	0.001	0.001	0.001	*					
THNc	0.003	0.001	0.000	0.000	0.000	−0.004	*				
THNo	0.001	−0.003	−0.001	0.002	0.000	−0.001	0.001	*			
CBCc	0.000	−0.005	0.001	0.001	0.000	0.000	−0.001	0.002	*		
CBCo	0.001	0.000	0.001	0.005	0.001	0.003	0.001	0.000	0.002	*	
NWZ	0.002	−0.003	0.002	0.005	−0.001	0.002	0.001	0.000	0.002	−0.001	*

* Indicates empty cells. PAI: Paita, PLA: Punta Lobos Afuera; PAR: Paracas; IQQ: Iquique; CAL: Caldera; CQB: Coquimbo; THNc: costal Talcahuano; THNo: oceanic Talcahuano; CBCc: costal Calbuco; CBCo: oceanic Calbuco; NWZ: New Zealand.

Table 2. Analysis of molecular variance (AMOVA) for *T. murphyi* samples to evaluate the hypothesis of panmixia and the most distant localities (Perú vs. Chile vs. New Zealand). All *p*-values are based on 10,000 permutations.

Groups	F_{ST}	*p*-Value	F_{SC}	*p*-Value	F_{CT}	*p*-Value
Perú vs. Chile vs. New Zealand	0.00016	0.665	0.00005	0.597	0.00011	0.419
Panmixia	0.00011	0.682				

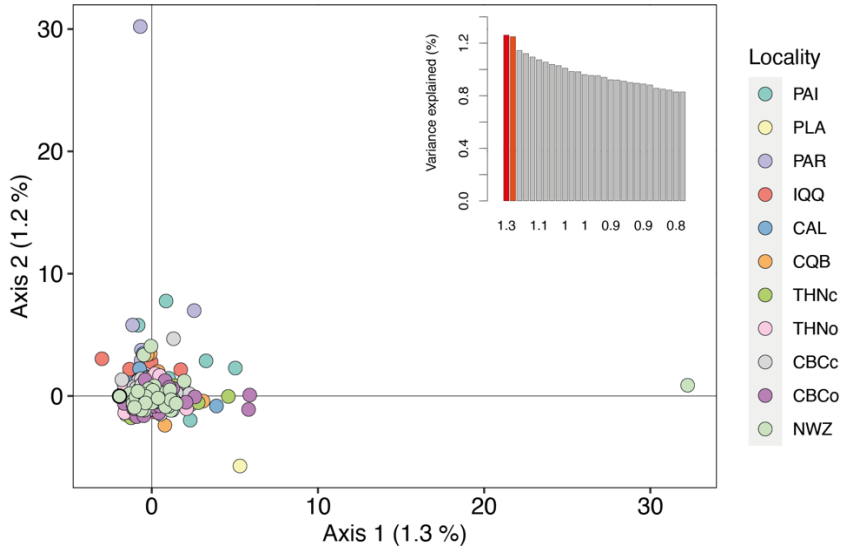

Figure 2. Individual-based principal component analysis for *Trachurus murphyi* localities across the South Pacific Ocean using six microsatellite loci. Barplots above represent the eigenvalues for the PCA, while the red and orange bars show the eigenvalues for axis 1 and axis 2. PAI: Paita, PLA: Punta Lobos Afuera; PAR: Paracas; IQQ: Iquique; CAL: Caldera; CQB: Coquimbo; THNc: costal Talcahuano; THNo: oceanic Talcahuano; CBCc: costal Calbuco; CBCo: oceanic Calbuco; NWZ: New Zealand.

4. Discussion

This study aimed to evaluate the genetic diversity across the geographic distribution of Chilean jack mackerel (*Trachurus murphyi*) using nuclear heterologous and species-specific microsatellite loci as a source of information. We screened six microsatellites in collections from 11 locations through its Pacific Ocean distribution, to estimate how the genetic diversity was distributed spatially. We did not find any genetic differentiation among locations using these loci. Overall, our results reinforce the idea that *T. murphyi* in its geographic distribution corresponds to a large single population.

Genetic Diversity and Population Structure

The six microsatellite loci analyzed for *T. murphyi* across its geographic distribution were highly variable. We found that the average number of alleles showed values of 21.1 (heterologous) and 27.5 alleles per locus (specific), while the observed heterozygosity was 0.787 for heterologous and 0.882 for specific loci. For marine fishes, the genetic variability in microsatellites is, on average, 20.4 alleles per locus and 0.790 heterozygosity [36]. Our values of genetic diversity were qualitatively higher than those for marine species estimated by DeWoody and Avise [36].

The population differentiation analyses showed that *T. murphyi* does not have a genetic structure through its geographical distribution. We estimated a low and non-significant F_{ST} index (pairwise and AMOVA), agreeing with Ward et al. [37], which highlights that marine fish show low genetic differentiation (with values of $F_{ST} < 0.01$) compared to freshwater and anadromous fishes. The non-genetic differentiation obtained here over the geographical area seems to be common for other taxa. For instance, *Dissostichus eleginoides* showed no

differences in its geographic distribution from northern Perú to the Falkland Islands [38]. In the Chilean exclusive economic zone, the marine fishes *Genypterus blacodes*, *Sprattus fuegensis*, and *Engraulis ringens* [1,3,39]; the crustaceans *Jasus frontalis* and *Metacarcinus edwardsii* [40,41]; the Echinodermata *Centrostephanus sylviae* [42]; and the mollusks *Concholepas concholepas* [43] showed the same genetic population pattern. Specifically for *T. murphyi*, several studies have been conducted using a variety of molecular markers. Using allozymes [22,23], PCR-RFLP for ITS marker [24], only heterologous microsatellites and mtDNA [21], and specific microsatellites [2], no significant genetic differentiation has been detected. Although some of these studies were limited by the number of locations, coverage surveyed, sample size, and the polymorphisms of the marker used, they all converged in terms of results.

Geographically, distant *T. murphyi* localities were surveyed in this study (Punta Lobos Afuera (~6° S–81° W), Oceanic Calbuco (44°08′ S–83°51′ W) and New Zealand (47° S–176° W)), in which no genetic differences were found. Ward [44] in his work *Genetics in Fisheries Management*, states "If no genetic differences are detected, then either there is a single stock or there are two stocks which could not be resolved by the test". Otherwise, the null hypothesis of "panmixia" can be rejected if differences are found, but if it cannot be rejected, this does not mean that it is true. Taking into account that gene flow rates of 1% and 5% can homogenize the gene pool of a population, no differences would be found even if they existed in nature, i.e., the species has a population structure, but it is not detected.

If we take into account that the null hypothesis is "panmixia" (a single, randomly mating population), what happens to individuals that are located in distant locations (e.g., New Zealand versus Punta Lobos Afuera or Oceanic Calbuco)? It is plausible, that these individuals do not "congregate" in a common area to breed and therefore do not share the same probability of random mating. For the localities of the southeastern Pacific Ocean (Perú and Chile), the homogeneity found can be explained by biological aspects of the species; for example, (a) the main concentrations of its abundance, in Perú, are located mainly in the northern and central zone, while in Chile, from Arica to Coquimbo (18–30° S) and from Valparaíso to south of Talcahuano (33–37° S); the distribution of these main zones of abundance can change seasonally; (b) it can spawn throughout its distribution [45], in Perú mainly to the south (16–18°30′ S) and in Chile from the northern limit to Corral (40° S); as well as the abundance, reproductive aggregations can vary seasonally; (c) it presents extremely large population sizes (billions of individuals); (d) eggs and larvae are pelagic; (e) juveniles and adults present seasonal movements (trophic-reproductive); (f) they can live in different biotopes, feeding in coastal waters and reproducing in offshore waters [7,19]; (g) the occurrence of the El Niño phenomenon, a phenomenon that produces spatial shifts in abundance and therefore increases the possibility of mixing; (h) the expanded distribution of Chilean jack mackerel due to its increased abundance also causes the limits of the populations to become confused and is therefore another mechanism that makes mixing possible.

For New Zealand, *T. murphyi* was recorded in the subtropical convergence zone above Chatam Rise less than four decades ago [46,47]. This demonstrated that *T. murphyi* has a transoceanic distribution. One explanation for this distribution is that the species expanded its range westward, colonizing new areas due to intra-population pressures [7,48,49]. According to the latter author, Chilean jack mackerel is an invasive species in New Zealand waters. Cárdenas et al. [21] estimated a recent expansion of the distribution range of *T. murphyi*. The low variability found in individuals from New Zealand, the absence of private alleles, and negative values in the demographic analyses (Tajima's D and Fu's Fs) account for this population expansion [21]. Taking into account that, in order to differentiate one population from another, it is necessary to ensure reproductive isolation (10–100 generations; [50]), so far, it is not clear whether *T. murphyi* is continuing to migrate through the subtropical convergence between Chile and New Zealand; if so, a difference at the genetic level would not be expected. Considering that the group of fish that arrived in New Zealand has no interchange of individuals with those present in Chile, little time has

passed for them to accumulate genetic differences that would allow them to be identified as separate groups; furthermore, there must have been millions and not just a few migrant individuals, which means that the genetic drift would not have significant effects. The age of first maturity is close to three years and, considering that *T. murphyi* was reported in New Zealand only four decades ago, there must have been fewer than 15 generations, which are too few to accumulate differences in genetic terms.

In summary, finding no significant differences in the distribution of *T. murphyi* with the three heterologous and three species-specific microsatellite loci does not mean that there are not different stocks of Chilean jack mackerel in the wild. We recognize that we are only using a small panel of loci and that the genome size of genus *Trachurus* is large (801 Mb for the congeneric Atlantic jack mackerel *T. trachurus* [51]). Nonetheless, our results are consistent with those of previous research. Studies using larger panels of specific loci should be carried out to ensure a much more robust approach. Using species-specific microsatellites might open the possibility of differences being found, given that these markers present different repeat and polymorphism motifs, and it is possible that some of these loci may shed new light on the population structure of Chilean jack mackerel. Future studies should focus on temporal comparisons in the whole distribution, mainly comparing samples from spawning and no-spawning seasons. Otherwise, an approach that reduced the complexity of the genome (e.g., ddRAD, RADseq, DARTseq) could provide a large amount of data to identify differences previously not resolved, increasing the power to resolve a lack of population structure in fishes with gene flow [52,53]. Additionally, using genomic approaches, it is possible to access adaptive information that cannot be detected using neutral microsatellites, and the results can uncover hidden, fine-scale population structure and adaptation, despite considerable gene flow (e.g., [54]).

Overall, this study reinforces the hypothesis that, in the Pacific Ocean, Chilean jack mackerel correspond to a large single population.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/fishes8030162/s1, Table S1: Criteria used to exclude loci in heterologous microsatellites by locus and locality; Table S2: Summary statistics of genetic diversity for *Trachurus murphyi* in South Pacific Ocean.

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Informed Consent Statement: Not applicable.

Data Availability Statement: The data presented in this study are available in https://github.com/Canales-AguirreCB/Ferrada-Fuentes_etal_2023_Fishes (accessed on 20 December 2022).

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