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ORIGINAL PAPER

Understanding the population connectivity of *Octopus mimus* in Northern Chile: implications for fisheries management

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Abstract

Understanding the connectivity among populations of benthic marine organisms is essential for defining the stocks of commercially fished species. Such information allows for better management of commercial species' populations. The cephalopod *Octopus mimus* Gould, 1852 is an economically important species exploited by artisanal fishing in northern Chile. To investigate the genetic structure and connectivity of *O. mimus* populations, we analyzed 6,573 SNPs from 88 octopus samples from the Arica to the Atacama Regions of northern Chile (18°S to 27°S). The results showed an absence of significant population structure, suggesting the existence of a single stock in the studied area. Based on our findings, we conclude that a particular region stands out as pivotal for fishing landings. This area aligns with its status as the primary source of migrants within the survey area. Thus, prioritizing management efforts in this zone is crucial for the sustainability of the octopus fisheries in this region.

Keywords Population genetics · Cephalopoda · Landing · Artisanal fishing · Gene flow

Introduction

Knowledge concerning the number of populations or stocks and the levels of gene flow between populations is essential for fisheries management. This knowledge, coupled with parameters such as fishing effort, can be used to improve management plans designed to ensure the sustainability of the fishery resources. Thus, identifying stocks and their patterns of gene flow is crucial for conducting an adequate assessment and implementing proper fishery management (Begg et al. 1999).

Among commercially important marine species, the global exploitation of cephalopods has increased from 0.6 million tons in 1950 to 4.8 million tons in 2014 (FAO 2000). Cephalopod fishing occurs worldwide, with higher extraction volumes in the central-western Pacific and southwestern Atlantic (González and Pierce 2021). Sustainable exploitation of these resources poses significant challenges, considering that the cephalopod life history is characterized by a short life cycle, a high natural mortality rate, and a complex population structure (Arkhipkin et al. 2021). In Chile, cephalopods are harvested along the entire coast. Some species, such as the Jumbo Squid (*Dosidicus gigas* (A. d'Orbigny, 1835) (Arkhipkin et al. 2021; Sernapesca 2023)) and octopuses, are extracted by both industrial and artisanal fleets, but most of these species comes from artisanal fishing, with approximately 99,000 tons landed during 2022 (Sernapesca 2023).

In this context, studying the population structure of marine cephalopods facilitates the delineation of stocks (Sabolić et al. 2021), thereby improving fisheries management by focusing fishing efforts and conservation measures according to the characteristics of each population.

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In Chile, *Octopus mimus* is an economically important species for artisanal fishing. This octopus inhabits intertidal and subtidal rocky areas from northern Peru to central Chile (Zuñiga et al. 2011). However, recent studies indicate that this species is also present off the coasts of Ecuador, Colombia, and Mexico (Pliego-Cárdenas et al. 2016). *O. mimus* is an opportunistic predator in coastal ecosystems (Cortez et al. 1995). The female invests 10% of her body weight in reproduction, while somatic growth during maturation depends on the season, ranging from 26 to 63% of total body growth in weight (Cortez et al. 1999). This species spawns year-round, and the condition of the female deteriorates during parental care of the eggs (Cortez et al. 1995). The fecundity of *O. mimus* has been estimated to be between 60,000 and 400,000 eggs (Castro et al. 2002), similar to other octopuses with planktonic paralarvae (van Heukelem 1983). Embryonic development lasts between 38 and 68 days at 16 and 20 °C, respectively (Castro et al. 2002).

The exploitation of *O. mimus* began in the 1980s when it became a resource of economic and social relevance for Chile and Peru. Due to its coastal habitat, the species is susceptible to commercial exploitation (Ibáñez et al. 2009) and is easily caught using hooks (in the intertidal zone) and semi-autonomous diving (in the subtidal zone), making *O. mimus* highly vulnerable to increases in fishing effort (Defeo and Castilla 1998). Fishing of *O. mimus* has led to a reduction in the population size, putting sustainable exploitation at risk (Olivares et al. 1996). In commercial catches, there is often a higher proportion of females (56%); this can be explained by the maternal care of egg clutches, increasing their vulnerability to fishing (SUBPESCA 2011). Female mortality leaves unprotected clutches, thus fishing poses risks to the population (SUBPESCA 2011). Considering this potential problem, the Chilean government has established several protection measures. A minimum extraction weight of 1 kg was set, and fishing is banned from November to March and June to July to protect the reproductive period (Cardoso et al. 2004).

The present study used SNPs to examine the population structure and gene flow in *O. mimus* in Chile. Additionally, the estimated level of gene flow was related to the catches of each study area to determine the importance of each geographical region to overall gene flow. Therefore, the information obtained herein will be important for *O. mimus* management and conservation plans.

Materials and methods

Study area

A total of 89 samples were collected from seven sites along the fishing zone of *O. mimus*. These sites were Arica ($n = 22$), Caldera ($n = 14$), Caramucho ($n = 10$), Chañaral ($n = 7$), Juan López ($n = 13$), La Chimba ($n = 8$), and San Marcos ($n = 15$) (Fig. 1). A small piece of tentacle from each octopus was stored in 95% ethanol for genetic analysis. All samples were obtained directly from fishermen used for commercial purposes.

Genomic data

Tissue samples were sent to Diversity Arrays Technology Pty., Ltd. (DArT; Canberra, Australia) for DNA extraction and massive sequencing. DNA was digested with the restriction enzymes SbfI and PstI following (Kilian et al. 2012) and fragments > 200 bp were ligated with an 8-base pair barcode and amplified by PCR. The PCR products were standardized and sequenced on a HiSeq 2500 (Illumina Inc, San Diego, USA). The sequences generated were processed using proprietary DArT PL analytical pipelines. After sequencing, a series of quality filters were applied to the raw data using the dartR package (Gruber et al. 2018; Mijangos et al. 2022) in the R software (R Core Team 2024). The filter criteria were as follows: (a) only one SNP was retained in reads containing two or more SNPs; (b) SNPs covered by between 5 and 200 reads were retained; (c) SNPs with a reproducibility > 99% were retained; (d) monomorphic SNPs were removed; (e) SNPs with > 10% of missing data were removed; (f) individuals with > 15% of missing data were excluded, and (g) SNPs with a Minimum Allele Frequency < 1% were removed to avoid the effect of sequencing errors or artifacts in data analysis. All SNPs showing signals of selection (outlier SNPs) were removed to obtain a set of neutral data. These loci were detected using the gl.outflank function implemented in the dartR package. SNPs that deviated significantly from Hardy-Weinberg equilibrium were also removed using the dartR package. Finally, one SNP from pairs with a linkage disequilibrium value > 0.5 was removed using PLINK 2.0 software (Chang et al. 2015). The presence of randomly related individuals in the sample was checked using the gl.grm function of the dartR library. If siblings or half-siblings were detected, one was removed.

Fig. 1 Sampling sites of *O. mimus*. Localities and their sampling size are on the map. The size of the blue circle corresponds to the number of samples per locality. Data from the following sites were combined to estimate gene flow: San Marco with Caramucho, Juan López with La Chimba, and Chañaral with Caldera

Genetic diversity and population structure

To describe the genetic diversity of each sampling site, the observed heterozygosity (*Ho*), the expected heterozygosity (*He*), and the inbreeding coefficient (F_{IS}) were estimated using functions from the dartR package.

Two methods were used to estimate population genetic structure: a Principal Coordinate Analysis (PCoA) implemented in the adegenet library (Jombart and Ahmed 2011) of the R software was used to visualize the distribution of individuals in a multivariate space. b) STRUCTURE software (Pritchard et al. 2010) was used to estimate the most probable number of genetic clusters (K). The latter analysis used an admixture model and correlated allele frequencies. Three runs were performed for each value of K from K = 1 to K = 8, with a burn-in and an after-burn-in of 200,000 iterations. The probability of each K was estimated using the formula described in the STRUCTURE manual (Pritchard et al. 2010) that computed the posterior probabilities of each K.

To detect an effect of the geographical distance in the genetic structure, we test for possible isolation by distance (IBD) using a Mantel test considering pairwise F_{ST} values (obtained with the dartR library) and the geographical distance between the sampled sites measured using Google Earth (https://earth.google.com). This test was performed with the function mantel.rtest of the library ade4 (Dray and Dufour 2007) implemented in the R software and the statistical significance was assessed with 1,000 permutations.

Gene flow of*O. mimus*in the sampling area.

The Estimating Effective Migration Surfaces (EEMS) (Petkova et al. 2016) was used to visualize the pattern of gene flow between sampling sites. This program estimates migration rates under an idealized stepping-stone model and visually represents genetic variation across geographical space, highlighting regions with gene flow rates above and below the average. EEMS was executed using 500 demes and three independent chains of five million MCMC iterations, with a burn-in of one million and sampling every 9999 iterations. Variances were adjusted considering an acceptance rate range between 10 and 40%. The results were plotted using the rEEMSplots R package (Petkova et al. 2016).

The BAYESASS3-SNPs software (Wilson and Rannala 2003; Mussmann et al. 2019) was used to assess the current level of gene flow. For simplicity of the analysis, sites were grouped by political regions as follows from north to south: (i) Arica (Region XV), (ii) Caramucho-San Marcos (Region I), (iii) Juan López-La Chimba (Region II), and (iv) Caldera-Chañaral (Region III). The analysis was conducted using a burn-in of 300,000 iterations followed by 3,000,000 iterations after the burn-in, sampling every 100 iterations. Mixing parameters, i.e., migration rates, allele frequencies, and inbreeding coefficients, were assigned values of 0.15, 0.35, and 0.05, respectively. Five independent runs were performed to assess consistency, each starting with different random seeds.

The clustering of the study sites enables an association of migrant rates with landings across the political regions where *O. mimus* fisheries operate in Chile. Thus, to identify the most important region in the system, the contribution percentages to gene flow were compared with the biomass of *O. mimus* landed from each political region in Chile (Regions XV, I, II, and III). The values for the tons of landed octopus from each political region were obtained from the website of the National Fisheries Service, which contains information from 2018 to 2022 (Sernapesca 2023).

Results

A total of 89 individuals were collected, and 52,369 SNPs were obtained. A pair of individuals collected in Arica showed a high level of relatedness; thus, one individual from this pair was excluded from the analyses. The filter did not identify any loci with significant deviations from Hardy-Weinberg equilibrium, and two pairs of loci showed significant linkage disequilibrium. The gl.outflank function of the dartR package detected two putative loci under selection. A Blast search did not detect similar sequences in GenBank, making it impossible to associate them with a specific cellular function. After quality filtering and removing outlier SNPs, 88 individuals and 6,573 SNPs were retained.

Genetic diversity and population genetic structure

The observed heterozygosity (Ho) ranged from 0.060 (Juan López) to 0.083 (Arica), and the values were generally similar to the expected heterozygosity values. Similarity was also observed in the inbreeding coefficient (F_{IS}) values among the sites, with the Arica locality having the lowest value (Table 1). The presence of a pair of related individuals in the same locality does not affect the estimation of Fis, as one of these individuals was removed before performing genetic diversity analysis.

All methods suggested a lack of population structure in the studied area. The PCoA revealed an overlap of the individuals from all sapling sites within the multivariate space, with Principal Components 1 and 2 accounting for 1.8% and 1.7% of the variance, respectively (Fig. 2a). The results obtained with the STRUCTURE software showed that K = 2

Table 1 Summary of SNPs data of *O. mimus* including sampling sites, sample size before and after filtering, allelic richness (AR), observed heterozygosity (HO), expected heterozygosity (HE) and FIS at each study site

Sampling site	*N* before filter	*N* after filter	AR	Ho	He	FIS
Arica	22	21	1.35	0.083	0.087	0.069
Caramucho	10	10	1.30	0.064	0.083	0.262
San Marcos	15	15	1.32	0.068	0.083	0.205
La Chimba	8	8	1.27	0.063	0.074	0.194
Juan López	13	13	1.28	0.060	0.071	0.183
Chañaral	7	7	1.29	0.078	0.082	0.113
Caldera	14	14	1.32	0.068	0.081	0.194

was the most probable number of genetic clusters. However, the ancestry plot (see Fig. 2b) indicated that these two genetic groups were distributed equally across all localities, suggesting that there is indeed only one genetic cluster. Further, the Mantel test found no relationship between geographic distance and the F_{ST} values ($p = 0.125$; Fig. 3), suggesting no isolation by distance.

Gene flow

The migration rates estimated with EEMS had log(m) values > 0 for the sites of Caramucho, San Marcos, La Chimba, Juan López, and Caldera, suggesting a level of gene flow higher than the average among these sites (Fig. 4). The log(m) values for Chañaral and Arica were < 0, indicating that effective migration is lower than the average. For Chañaral, this result was likely due to the low number of sampled individuals rather than the presence of a migratory barrier, as connectivity was observed between sites both north and south of Chañaral.

Finally, the analysis of current gene flow revealed the exchange of individuals among all regions. Each region received a significant proportion of individuals from self-recruitment (> 85%), followed by immigrants from Region II (from 1 to 9% of immigrants) (Fig. 5). To complement this unequal migrant exchange among regions and associate it with a fishing parameter, we used the available information on landings in the Chilean political regions where the fishery of *O. mimus* is conducted. From 2018 to 2022, Region II had the highest landings per year (1,213 tons on average per year), followed by Region I with an average of 397.8 tons per year. In this context, Region II has the highest landings of *O. mimus* per year and is also the region that exports the most migrants to other regions (Fig. 5).

Discussion

Cephalopods have a unique life history with rapid growth and a short lifespan (Clarke 1996; Moltschaniwskyj 2004). However, this makes them sensitive to ecological disturbances caused by fishing activity or environmental changes, as these can trigger rapid interannual fluctuations in their population sizes (Boyle and Boletzy 1996). Therefore, knowledge of the connectivity and population structure of this species is vital for understanding population dynamics, designing conservation strategies, and developing sustainable management practices. The results obtained for *Octopus mimus* in the northern zone of Chile show an absence of population structure and the presence of high connectivity among individuals from different locations where the species is fished.

While several Octopus species, for example *Octopus insularis* Leite & Haimovici, 2008 (Bein et al. 2023), *Octopus berrima* Stranks & Norman, 1992 (Hua et al. 2023), *Octopus bimaculoides* (Domínguez-Contreras et al. 2018) and *Octopus pallidus* Hoyle, 1885 (Hua et al. 2023) show clear population structure, the absence of genetic differentiation and the high connectivity found in *O. mimus* is common to other merobenthic cephalopod species, for example the squid *Dosidicus gigas* (Sanchez et al. 2016), the octopus *Octopus vulgaris* Cuvier, 1797 in the Mediterranean (Luca et al. 2016), *Octopus hubbsorum* (Berry, 1953) on the western coast of Mexico (Dueñas-Romero et al. 2021) and the squid *Doryteuthis opalescens* (S. S. Berry, 1911) off the US Pacific Coast (Cheng et al. 2021). Further, SNPs heterocigosities of *O. mimus* are similar to other cephalopod species, for example *Hapalochlaena maculosa* (Morse et al. 2018) and *Doryteuthis opalescens* (Cheng et al. 2021).

Octopuses present active swim paralarvae (Fernández-Gago et al. 2019) that could explain the large geographical distribution of *O. mimus* population in this study (950 km of linear distance), described with SNPs in the present study and mtDNA by Pardo-Gandarillas et al. (2018). The lack of genetic structure can be explained by the high mobility of adults in some species in this part of Chile, for example, in *Docidiscus gigas* (Sanchez et al. 2016), and by the long time that their paralarvae spend in the plankton. The paralarvae of *Octopus vulgaris* last for 60 days (Villanueva et al. 1997), and those of *Robsonella fontaniana* (A. d'Orbigny, 1835) live for 70 days in the plankton (Uriarte et al. 2010). In the specific case of *O. mimus*, the paralarvae transition to juveniles after approximately two months of planktonic life (Castro et al. 2002).

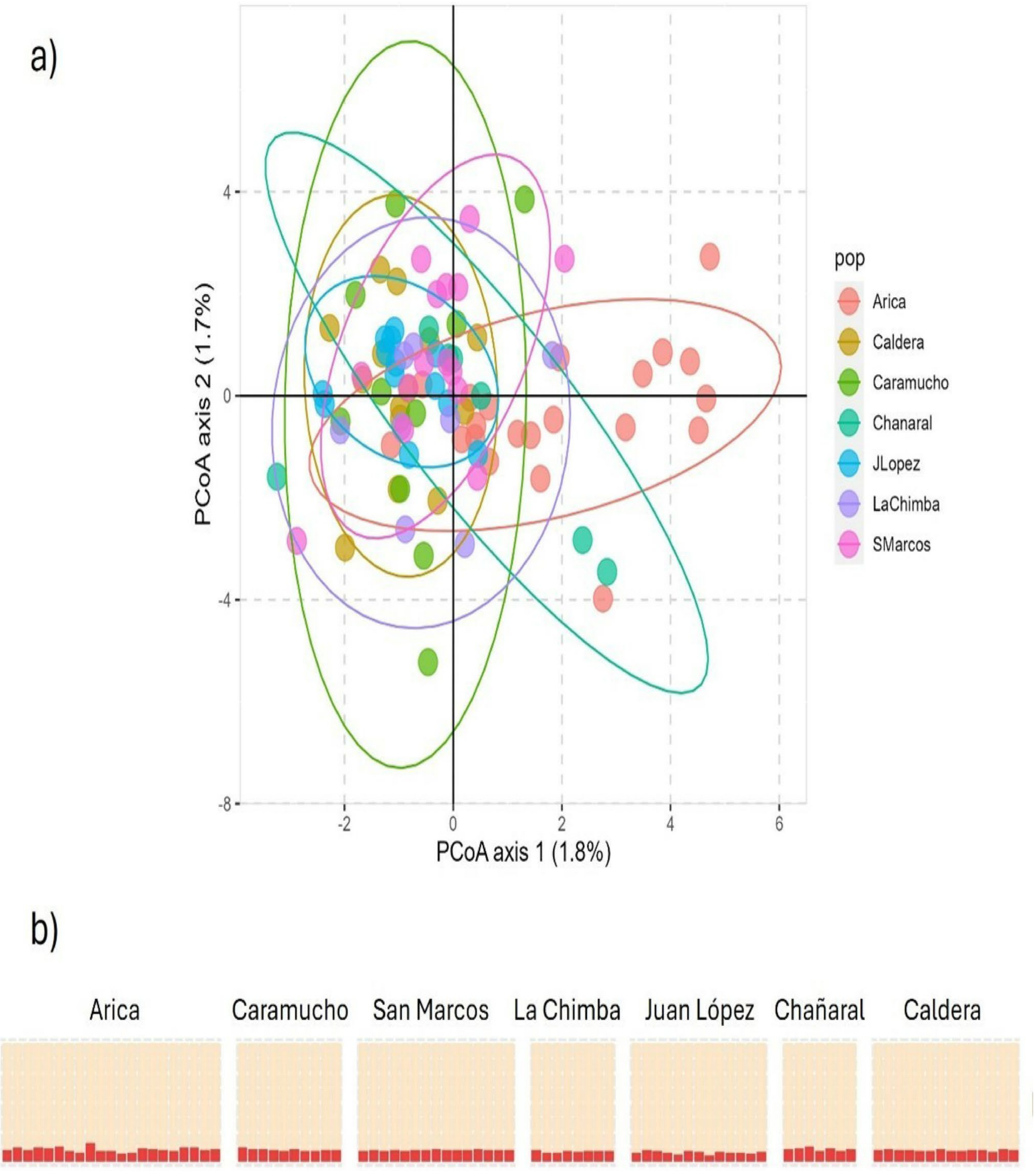

Fig. 2 (**a**) Principal coordinate analysis (PCoA) performed with 6,573 SNPs in 88 individuals of *O. mimus*. The first and second Principal Components (x-axis and y-axis, respectively) capture 3.5% of the total variance. (**b**) Population structure of *O. mimus* inferred using the software STRUCTURE for K = 2 of the 88 individuals from the seven sampling sites along the fishery area in Chile. A vertical bar represents each individual, and each color represents the probability of belonging to one of the K genetic clusters

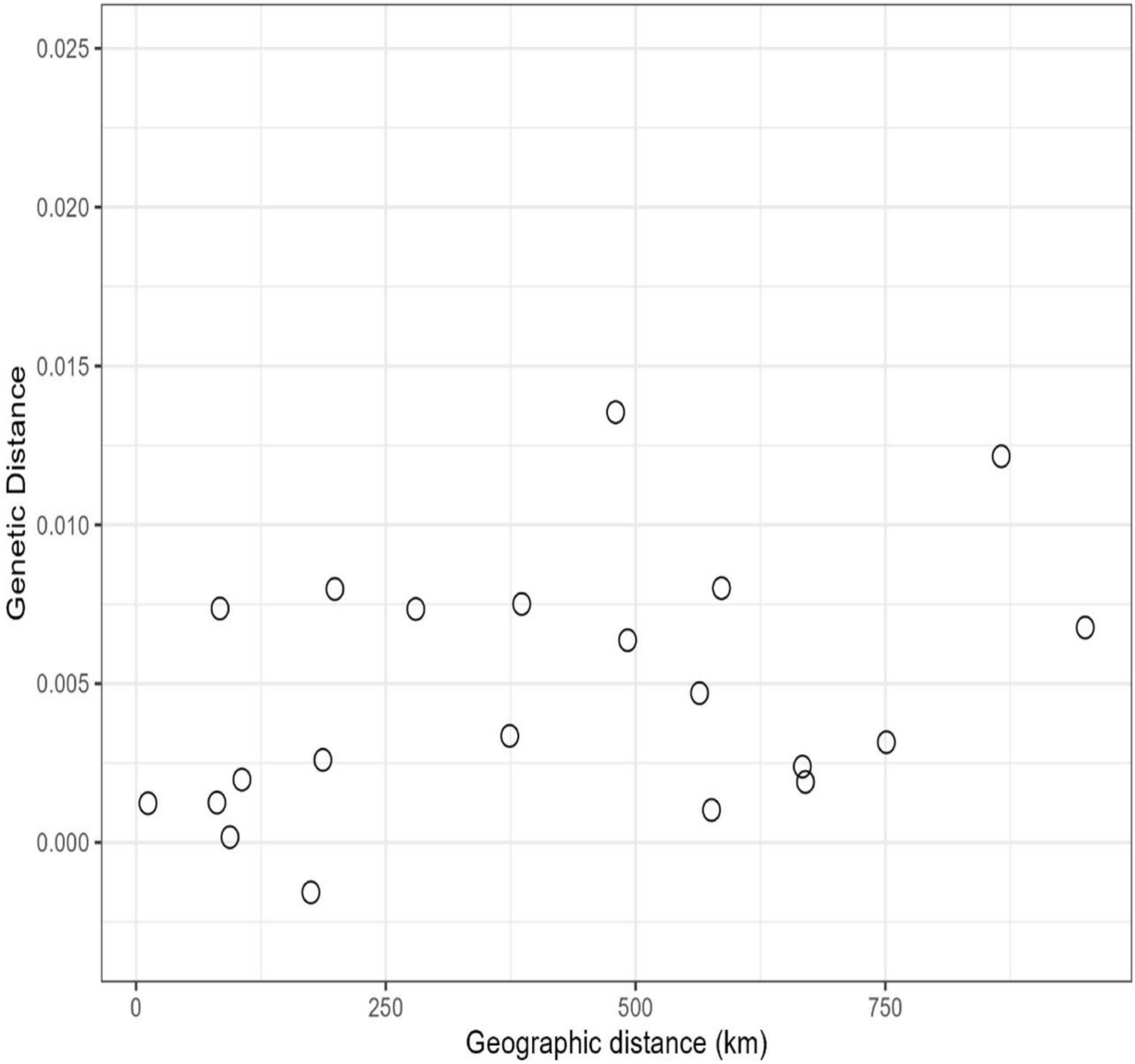

Fig. 3 The relationship between geographic distance and FST among pairs of sampling sites of *O. mimus*. The Mantel test did not detect a significant association between geographic distance and F_{ST} ($p = 0.125$)

The studied area in Chile is not interrupted by biogeographical breaks, however, it is described that the displacement of the paralarvae could be interrupted by breaks. In this context, (Pliego-Cárdenas et al. 2016) described two genetic populations of *O. mimus* separated by the beak located at the 2°11' latitude. Overall, data suggest that paralarvae freely displace in the absence of biogeographic breaks.

The Chilean coast has no apparent barriers to the movement of benthic marine organisms with a planktonic dispersal stage, and there are examples of species with planktonic larvae lasting more than two months exhibiting high connectivity among populations. These include the commercially important gastropod *Concholepas concholepas* (Cárdenas et al. 2016) and the crab *Metacarcinus edwardsii*(Rojas-Hernandez et al. 2016; Veliz et al. 2022). In the case of cephalopods, Sandoval-Castellanos et al. (2010) detected a single large population of *Dosidicus gigas* in the southern Pacific, with little evidence of genetic structure in the two hemispheres. This observed dynamic for other invertebrates with planktonic dispersal stages also appears to apply to *O. mimus*, according to the results of the present and previous studies (Pardo-Gandarillas et al. 2018).

In contrast, it is interesting that there is a positive correlation between gene flow and the biomass of *O. mimus* caught

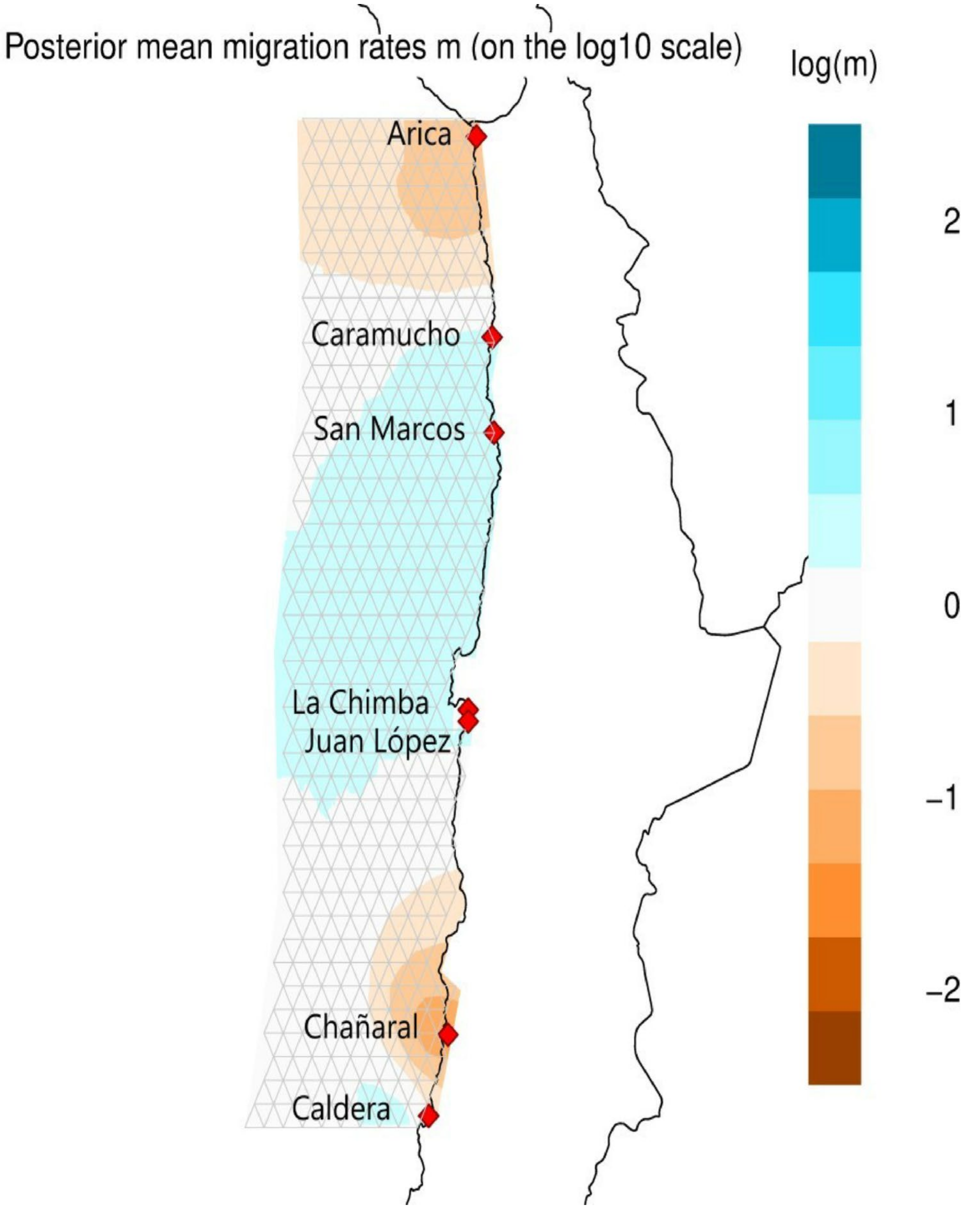

Fig. 4 Visual representation of the estimated effective migration rate using the EMMS software. Log(m) corresponds to the effective migration rate on a logarithmic scale base 10 relative to total migration across the habitat. Blue colors represent areas where the effective migration is higher than average, while brown colors represent areas where the effective migration is lower than average

in different regions. The results revealed an asymmetry in gene flow, with a greater flow from Region II to other areas, indicating that Region II is a source of migrants to other regions. Additionally, fishing effort is unevenly distributed across Chile. In this context, we note that over 60% of the biomass was caught in Region II (where the sampling sites La Chimba - Juan López were located), which, as previously mentioned, is also the region that exports the highest number of migrants to other regions. While our study suggests a relationship between both variables (migrants and landing), it is important to note that landing could have variations or bias due to the sampling methods and access to the fishing coves (Gleadall et al. 2024).

To our knowledge, there is currently no information concerning this relationship for other species. However, there may be unmeasured variables that could provide further insights into the generation of this pattern. The higher fishing activity in Region II may be due to the abundance of *O. mimus* populations in that area. This high abundance may be attributed to the upwelling in this area that enhances nutrient concentration and primary productivity (Marin et al. 1993; Kämpf and Chapman 2016). Therefore, it is essential to continue exploring the relationship between migrants and landings and its implications for the sustainable management of marine resources.

This study provides crucial information for developing a sustainable management scheme for the *O. mimus* fishery in Chile. Understanding the genetic structure and migratory patterns is a fundamental preliminary step for cephalopod stock assessment, as it addresses uncertainties concerning

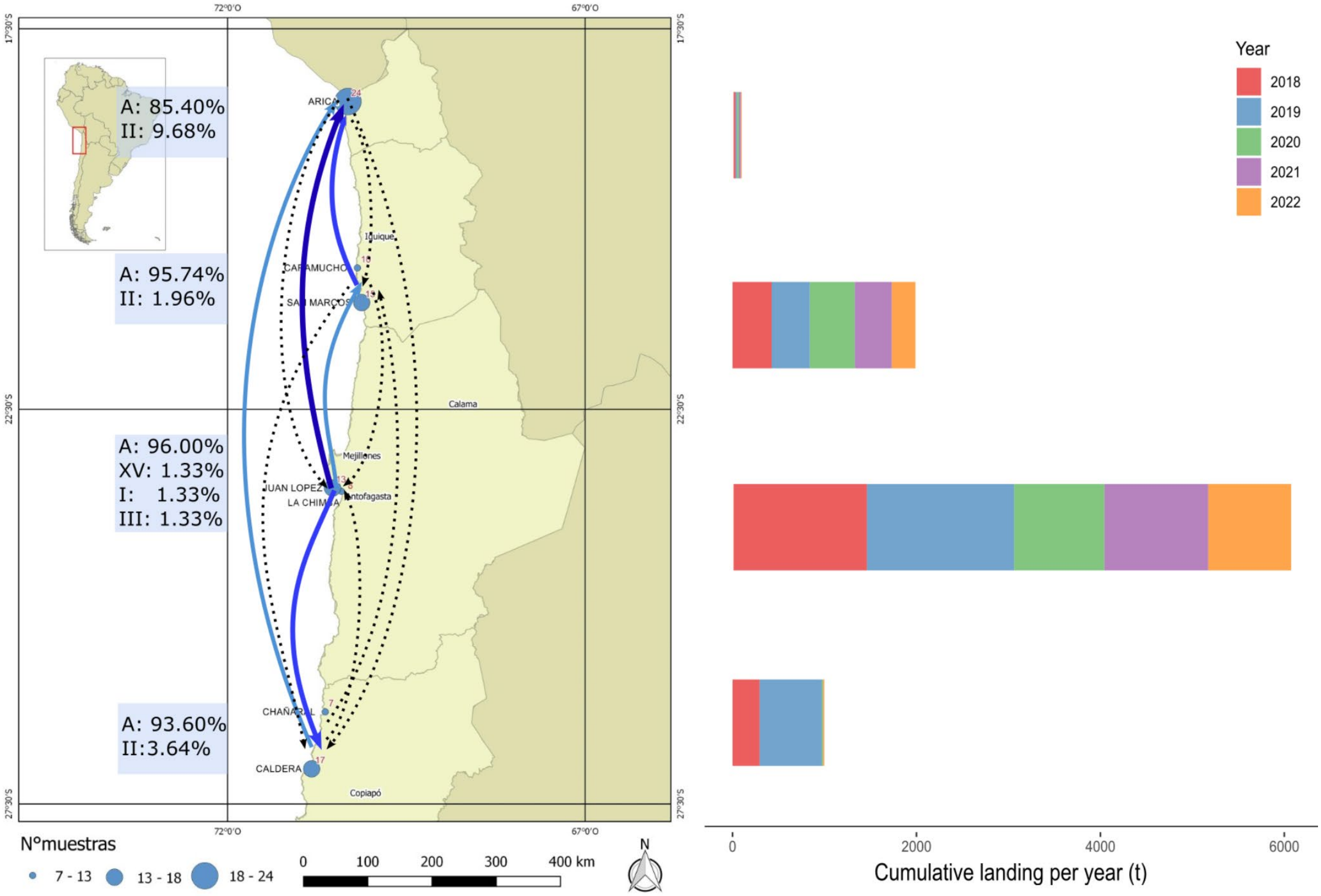

Fig. 5 Comparison between migration rates and landing levels of *O. mimus*. Left: Reciprocal migration between pairs of political regions. The dark blue arrow represents a value of 9% immigrants, blue arrows represent values of > 4% and < 9% immigrants, light blue arrows represent values of > 1% and < 4% immigrants, and dashed arrows represent values of < 1% immigrants. For each sampling site, the figure shows the self-recruitment rate (A) and the site ranked first contributing with immigrants (XV: Arica; I: Caramucho–San Marcos; II: La Chimba–Juan Lopez; III: Caldera-Chañaral). Right: Annual extraction (in tons) of *O. mimus* from each political region (XV, I, II, and III). The Region II ranked first both in immigration rate and in tons of *O. mimus* landed

whether changes in stock size are fishing due to mortality or migratory effects (Arkhipkin et al. 2021). Accurate assessment of the population structure of fishery resources significantly improves the performance of stock assessment models, while neglecting this aspect can lead to incorrect perceptions of stock status and, consequently, failures in fishery management (Cadrin et al. 2014). Additionally, these studies must be accompanied by other genetic studies that allow for traceability of their catches and help prevent illegal fishing.

In this context, monitoring biological and fishing indicators combined with modeling to estimate the stock status at each site, measurements of genetic structure and migration patterns, and adjusting fishing regulations accordingly can help maintain a balance between conservation and resource utilization. Recommendations should focus on implementing measures that ensure the maintenance of genetic variability and facilitate genetic exchange across the species' geographical distribution. Overall, understanding the impact of gene flow and fishing pressure on *O. mimus* populations, especially in Region II, will be crucial for the long-term sustainability of this valuable resource in Chile.

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Data availability a SNPs data dataset of *Octopus vulgaris* in Structure format is available at https://doi.org/10.34691/UCHILE/YWAXF7.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

Ethical standards The study utilized samples directly obtained from fishermen, sourced from individuals used for commercial purposes. Permit Number 24831–FCS–UCH (Universidad de Chile) for sample manipulations.

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