

Research Article

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Integrating genetic and biophysical approaches to estimate connectivity in an isolated, insular system: case of the culturally important marine gastropod *Monetaria caputdraconis*

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Abstract

Population connectivity has a fundamental role in metapopulation dynamics with important implications for population persistence in space and time. Oceanic islands, such as Easter Island (EI) and the Salas & Gómez Island (SG), are ideal for the study of population connectivity because they are separated by 415 km and isolated from other islands in the Pacific Ocean by >2000 km. Considering that the dispersal process could play a critical role in the persistence of their populations, we evaluated the connectivity pattern of the endemic gastropod *Monetaria caputdraconis* between EI and SG using population genetics and biophysical modelling. Eleven microsatellite loci did not show differences in the allelic frequency of individuals located in EI and SG, suggesting the presence of one genetic population. Historical reciprocal migration implies that 0.49% of the recruits in EI come from SG and 0.37% in SG come from EI. Considering year-round larval release and a larval development of 2 weeks in the plankton, a Lagrangian experiment based on a regional oceanic simulation indicated a weak population connectivity with a high rate of self-recruitment. Interestingly, self-recruitment showed both monthly and interannual variation ranging from 1 to 45% of returned larvae, with lower values estimated in SG compared to EI. The results suggest that few larvae/individuals arrive at each other's island, possibly due to stochastic events, such as rafting. Overall, our results indicate that both islands maintain population connectivity despite their distance; these findings have implications for designing conservation strategies in this region.

Introduction

Marine population connectivity, understood as the exchange of individuals among geographically separated groups (Cowen *et al.*, 2007; Pineda *et al.*, 2007; Cowen and Sponaugle, 2009) or discrete populations (Lowe and Allendorf, 2010), plays a fundamental role in the spatial configuration of species, their persistence over time, maintenance of genetic diversity, and, finally, in determining their evolutionary fates (Lowe and Allendorf, 2010). Despite the importance of knowledge regarding marine species connectivity, it is difficult to assess connectivity in species with benthic adults and planktonic larvae as the main dispersal element. For these species having planktonic larval development, a large number of produced larvae per individual during reproductive events and the small larval size make it almost impossible to directly survey larval movement between populations (Levin, 2006; Cowen *et al.*, 2007; McQuaid, 2010).

Different approaches have been developed to quantify this process, including the use of genetic variability (Palumbi, 2003; Hellberg, 2009; Lowe and Allendorf, 2010; Gagnaire *et al.*, 2015; Veliz *et al.*, 2021, 2022) and biophysical modelling (Lett *et al.*, 2008). The use of genetic markers allows to describe the extent of the marine populations (Cowen and Sponaugle, 2009), the dispersal potential of the species (Kinlan and Gaines, 2003), and the asymmetry of the migrant interaction between pairs of groups (e.g., Meerhoff *et al.*, 2018). Biophysical modelling studies estimate the number of larvae exchanged among populations based on the trajectories inferred from the model velocity field (e.g., Endo *et al.*, 2019), the importance of populations in releasing and receiving larvae (e.g., Crochelet *et al.*, 2020), and also enable an estimation of auto-recruitment (e.g., Santos *et al.*, 2018).

Due to their isolation, oceanic islands and their endemic fauna are interesting models for quantifying connectivity (Andrade and Feng, 2018). First, it is possible to obtain samples for the entire geographical range of these species; thus, the noise produced by unsampled populations (see Excoffier and Heckel, 2006) is reduced to zero, although recirculation patterns at the fine scale (sub to mesoscale) nearby the island can be influenced by the island itself (i.e., island mass effect) (Barton, 2001).



The easternmost islands in Polynesia are composed of Eastern Island (EI) and Salas & Gomez (SG), the first inhabited and the second not inhabited by humans. The Chilean government created Motu Motiro Hiva Marine Park (150,000 km²) close to SG, representing the largest fishing exclusion zone in the Americas (Friedlander *et al.*, 2013). These islands are separated by 415 km from each other (Zylich *et al.*, 2014); the next closest islands are the Desventuradas (2000 km east) and Pitcairn (2600 km west) Islands. Both islands share most marine fauna, comprising 30–34% of endemic species (Fernandez *et al.*, 2014; Swearer *et al.*, 2019); in the case of molluscs, 42% of the species have been found to be endemic to these two islands (Rehder, 1980), and the oceanographic patterns of the area show circulation corresponding to the anticyclonic rotation of the South Pacific, conditioned by a system of flows-counterflows and the average geostrophic current in the zone (Pollock, 1992; Rivera and Mujica, 2004). Near the coast of EI, the geostrophic flow includes vertical and horizontal shears, which, combined with the vertical migration behaviour of fishes larvae, promote larval retention (Meerhoff *et al.*, 2017).

These islands are inhabited by the endemic cowry gastropod *Monetaria caputdraconis* (Melville, 1888), which has cultural and economic importance, referred to as 'pure' by the islanders. This species is abundant in shallow areas, where it has ecological significance as a herbivore (Osorio *et al.*, 1993). *M. caputdraconis* is a dioecious species with internal fertilisation; eggs are deposited in capsules attached to rocks, and planktonic veliger larvae then develop after 7 days of incubation (Osorio and Gallardo, 1992); these planktonic larvae last approximately two weeks in the plankton (Osorio, personal communication). *M. caputdraconis* has historically been under exploitation both as a food resource and as an ornamental object (Seaver, 1986), leading to a significant decrease in its abundance (Rivera, 2003; Aburto *et al.*, 2015).

Considering that *M. caputdraconis* is exploited on EI but not in SG Island where the Motu Motiro Hiva Marine Park is located, it is important to know about the degree of connectivity by migrants between these islands and the importance of this park in the species conservation. Here, the connectivity of *M. caputdraconis* between EI and SG was estimated using both genetic and biophysical modelling approaches. Whereas the variability of 11 microsatellite loci was used to infer the population structure and historical reciprocal migration between islands, a biophysical modelling procedure was employed to model larval transport between the two islands using biological and oceanographic information. Both genetic and biophysical modelling data are useful for determining the connectivity of *M. caputdraconis* populations in the entire geographical distribution of the species.

Materials AND Methods

Sampling, DNA extraction and microsatellite loci amplification

Seventy-seven specimens of *M. caputdraconis* were obtained from the intertidal zone by hand from EI (27°7'S; 109°22'W), and twenty-eight individuals of *M. caputdraconis* were collected in SG Island (SG, 26°28'S; 105°28'W) (Figure 1). Samples were stored in 95% ethanol, and a small piece of the muscular foot (approximately 1 mg) was used for DNA extraction with the Wizard Genomic DNA Purification Kit (Promega). DNA quantities were measured with a Nanodrop Spectrophotometer (Thermo Fisher). Eleven polymorphic microsatellite loci described for this species were amplified following the procedure of Vega-Retter *et al.* (2016). Briefly, cycling conditions for all loci consisted of an initial denaturing step of 2 min at 95°C, followed by 35 cycles of 30 s at 95°C, 1 min at 55°C, 1 min at 72°C, and a final elongation step at 72°C for 3 min. We used three multiplexes to amplify the microsatellite loci with primers containing different

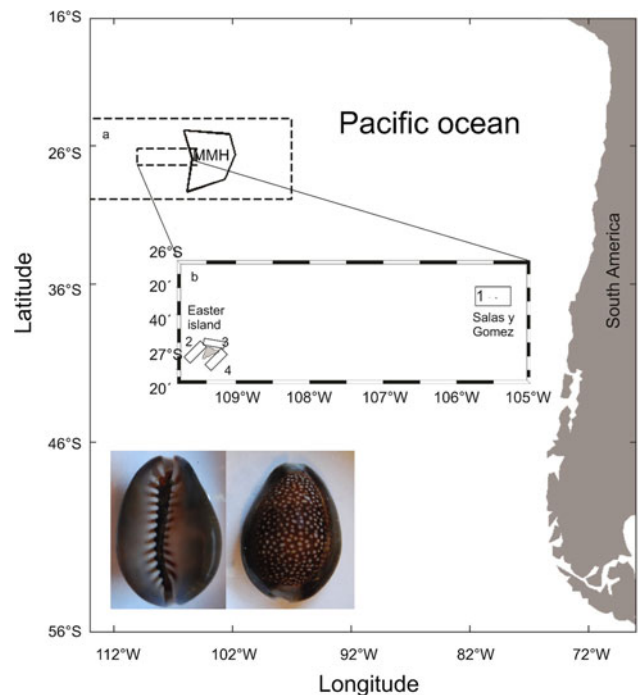


Figure 1. Location of Easter Island (EI) and Salas & Gómez (SG) Island where *Monetaria caputdraconis* inhabits. Rectangles located in EI and SG correspond to larval release/recruitment areas (1–4) for coupled simulations of the regional oceanic circulation system (ROMS). MMH: Motu Motiro Hiva Marine Park. The figure includes ventral and dorsal views of a specimen of *Monetaria caputdraconis* from Rapa Nui. Length size = 2.46 cm.

fluorescent dyes (NED, FAM, VIC, or PET). The first plate amplified the following microsatellites: Pure7 (NED), Pure45 (NED), Pure18 (FAM), and Pure34 (FAM), the second plate: Pure33 (NED), Pure46 (NED), Pure31 (PET), Pure48 (PET), Pure47 (VIC), and Pure28 (FAM); and the third plate: Pure1 (FAM), Pure50 (FAM), Pure3 (VIC), Pure19 (VIC), Pure42 (PET), and Pure15 (NED). The polymerase chain reaction contained 2 µl template DNA (100 ng), 1 µl of each primer, and 10 ml of Type-it Microsatellite PCR Kit (Qiagen, Canada). PCR products were genotyped in the sequencing core at the Pontificia Universidad Católica, Chile, using the internal size standard LIZ 500 (Applied Biosystems) and with the reverse primers of each microsatellite locus marked with a fluorescent dye.

Population genetic structure

The number of alleles per locus and the expected (HE) and observed (HO) heterozygosity were estimated using Genetix software (Belkhir *et al.*, 2000); the allelic richness and genetic diversity with FSTAT software (Goudet, 1995). Using Genetix, linkage disequilibrium was tested using 5000 permutations on monolocus genotypes and departures from Hardy Weinberg Equilibrium (HWE) using 5000 allele permutations. To avoid related individuals in the population genetic analysis, we used the Identix software (Belkhir *et al.*, 2002) to estimate the r_{xy} relatedness index described by Queller and Goodnight (1989).

Testing for a possible population genetic structure between the two islands was carried out using three approximations. First, the F_{ST} index (Weir and Cockerham, 1984) was calculated with GENETIX (Belkhir *et al.*, 2000) with a statistical significance estimated with 10,000 permutations. Second, the G''_{ST} index was calculated using GenAEx 6.5 software (Peakall and Smouse, 2012), and the statistical significance was estimated using 9999 permutations. This last estimator is not influenced by the heterozygosity of

the samples and is not biased when the number of populations is low (Meirmans and Hedricks, 2011). Third, STRUCTURE software (Pritchard *et al.*, 2000) was used to estimate the most probable number of populations or clusters within the universe of samples. This analysis was performed using both admixture and correlated allele frequency models. The procedure was run five times for each K estimation (from $K = 1$ to $K = 3$) with a burn-in of 100,000 and then 200,000 MCMC each. Finally, a principal coordinate analysis (PCoA) was performed to summarise the variation within the data set using the package adegenet (Jombart and Ahmed, 2011) in R software (R Core Team, 2021).

Estimating the reciprocal migration rate

To estimate the migration pattern of *M. caputdraconis* between EI and SG, the historical migration rate (M_H) was assessed using Migrate software (Beerli and Felsenstein, 2001). This software employs a coalescent approach to estimate mutation-scaled migration rates (M) for each group over the last $4N_E$ generations. The default settings were used except for the following run options: (i) the Bayesian inference module using the Brownian motion mutation model; (ii) one single long run utilising heating with temperatures of 1.0, 1.5, 3.0, and 10,000 [see Beerli (2008) for more information about temperatures]; (iii) sampling ten replicates from each set of 400,000 at intervals of 100; and (iv) discarding the first 100,000 visits. The uniform prior distributions ranging from 0 to 100 with a delta of 10 were used for both mutations scaled by population size for theta (Θ) and M . The historical migration rate was calculated as $M_H = M \times \mu$, where M = the historical gene flow rate scaled by the mutation rate and μ = the mutation rate. For this analysis, a mutation rate of $\mu = 2 \times 10^{-3}$ was used, as in other gastropods (Gow *et al.*, 2005). The analysis was replicated four times and the effective number of migrants (N_m) was estimated as $N_m = (\Theta \times M)/4$. Migration analyses were performed at the National Center for High Performance Computing (NHLPC) of the Facultad de Ingeniería, Universidad de Chile.

Biophysical model for larval connectivity

The larval connectivity or exchange of individuals among islands was studied through a spatially explicit individual-based model (IBM) of larval transport that was coupled to the hydrodynamic output of a 3-D interannual configuration of the regional oceanic modelling system (ROMS) for the period 2011–2014 and at approximately 3 km resolution across the study area. The ocean model simulation setup is detailed in Meerhoff *et al.* (2018), who also analysed the connectivity between the two islands based on an IBM approach. The IBM was implemented with the Ichthyop code (Lett *et al.*, 2008), and the larval connectivity between and within islands was calculated for larvae that successfully reached a recruitment area. The following features were used for the analysis:

- Release/recruitment areas. Four areas were defined: three zones at EI following the morphology of the coast and one at SG (Figure 1). We used three areas in EI following the morphology of the island expecting different current circulation among these areas. We do not define different release areas in SG due to the size of the island.
- Number of virtual larvae released. Due to computational limitations, a total of 250,000 virtual larvae were released from the release areas in each simulation.
- Timing of larval release. Considering that the reproductive activity of *M. caputdraconis* occurs year round, with increased activity during spring and summer (Osorio and Gallardo,

1992), the analysis considered 250,000 virtual larvae liberated each month for three years: 2011, 2012, and 2013.

- Depth of larval release. Because most species from the Family Cypraeaidae inhabit waters less than 30 m in depth (Kay, 1985), the release areas were defined at 0–50 m following information regarding the adults' distribution.
- Planktonic larval duration: there is no published information about the pelagic larval duration of *M. caputdraconis*; hence, the model was evaluated for 14 days, following field observation performed by Osorio (personal communication).

For the analysis, a passive horizontal transport (forward Euler method, with a time step of 0.75 h) was implemented to run the model. A successful larva reached (or was found within) the 'recruitment area' at the end of its planktonic larval duration. Recruitment areas coincided with adult spawning areas (release areas).

Results

Population genetic analysis

The 11 loci were polymorphic at both islands; the allelic richness per locus varied from 1.92 (locus Pure50) to 11.86 (Pure18) at EI and from 1.62 (locus Pure 50) to 11.59 (locus Pure18) at SG (Supplementary Information S1). Genetic diversity (EI = 0.701, SG = 0.665) and allelic richness (EI = 7.213, SG = 6.974) were similar in both islands. Significant departures from HWE were detected consistently in one locus (Pure19); therefore, this microsatellite was not used in most of the analysis (Supplementary Information S1). Further, relatedness analysis performed with Identix software not detected related individuals (full or half-sibs) in the samples.

The three methods employed to determine the population structure suggested that *M. caputdraconis* of EI and SG belong to the same genetic population. The F_{ST} and G''_{ST} indexes ($F_{ST} = 0.004$, $P = 0.128$ and $G''_{ST} = 0.078$, $P = 0.101$) did not detect a significant difference between EI and SG. The values of $\ln(K)$ obtained from STRUCTURE showed a maximum likelihood value at $K = 1$ (Figure 2). The PCoA results demonstrated that most individuals shared the same space in the three main principal coordinates axis (Figure 3).

Measures of convergence and robustness of the four runs of Migrate software showed similar values (Supplementary Material S2); the effective sample sizes were in order of thousands as expected for robust analyses (see Beerli *et al.*, 2019). Further,



Figure 2. Population structure of *M. caputdraconis* inferred using the software STRUCTURE for $K = 1$ to $K = 3$ of the 105 individuals analyzed with ten microsatellites loci. A vertical bar represents each individual, and each colour represents the probability of belonging to one of the K genetic clusters.

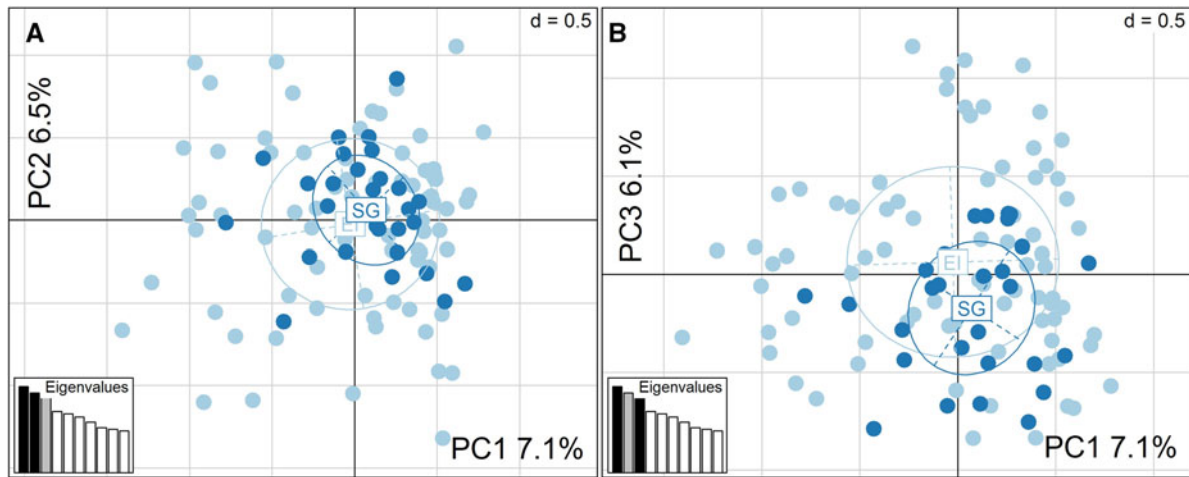


Figure 3. PCoA plot for *Monetaria caputdraconis* samples using ten microsatellites. (a) PC1 vs PC2, (b) PC1 vs PC3. Individuals were coloured by their sampling locality; circles represent 95% of the variance from the centroid. PCoA axes are labelled with the variance that they represent; scree plots of eigenvalues represent variation explained by additional axes.

histograms of Θ showed a unimodal distribution (Supplementary Material S3), describing a correct runtime used for the analyses. The results of the four independent runs of the Migrate software are in Table 1. The mean mutation-scaled historical migration rates (M) were $MSG \rightarrow EI = 2.441$ ($SD = 0.927$) and $MEI \rightarrow SG = 1.837$ ($SD = 0.163$); the estimates of Θ were 9.68 ($SD = 1.842$) for EI and 3.826 ($SD = 0.393$) for SG. Using a mutation rate of 2×10^{-3} , the migration rates between localities were $M_{HSG \rightarrow EI} = 0.49\%$ and $M_{HEI \rightarrow SG} = 0.37\%$. The mean for self-recruitment (estimated as $1 -$ the total immigration rate) was 99.51% at EI and 99.63% at SG. The estimated Nm were $Nm_{SG \rightarrow EI} = 5.91$ and $Nm_{EI \rightarrow SG} = 1.76$ per generation.

Population connectivity according to the biophysical model

No larval connectivity or transport between islands was detected through the biophysical model for the 14 days of evaluated planktonic larval development (see Figure 4). The results were consistent for larvae released every month for 3 years. However, it is interesting to highlight that 1–45% of the total released larvae were self-recruited in EI (Figure 5). The maximum self-recruitment observed in EI was for larvae released in July 2012. However, self-recruitment was lower in SG and only occurred during some months (April and May 2012, Figure 5).

Table 1. Result of the migration analysis performed with Migrate software. Mean and standard deviation were calculated using data of each independent run

	Mutation-scaled migration rate M (individuals per generation)		Mutation-scaled effective population size Θ (number of individuals)	
	MSG→EI	MEI→SG	Θ EI	Θ SG
Run 1	1.262	2.009	8.052	3.265
Run 2	3.321	1.921	9.317	4.184
Run 3	2.195	1.782	12.321	3.939
Run 4	2.985	1.636	9.031	3.917
Mean	2.441	1.837	9.680	3.826
SD	0.927	0.163	1.842	0.393

Discussion

The results of the genetic variability and biophysical model obtained for the gastropod *M. caputdraconis* showed a clear pattern of low connectivity between EI and SG. Whereas the number of migrant estimations obtained with genetic data showed an exchange of <1% between the islands, the biophysical model did not detect particles that moved between the islands at both monthly and annual timescales. These observations suggest that the length of pelagic larval duration and/or movement of the water would not allow a continuous flow of larvae between the islands.

It is known that the time of permanence of larvae in the water column is one of the best predictors of genetic connectivity of marine benthic organisms (Shanks, 2009; Modica et al., 2017). Empirical data confirmed that the longer the pelagic larval duration, the higher the probability of reaching remote zones and, thus, of having a distant connectivity. For example, *Melarhaphes neritoides* presents a pelagic development of 4–8 weeks

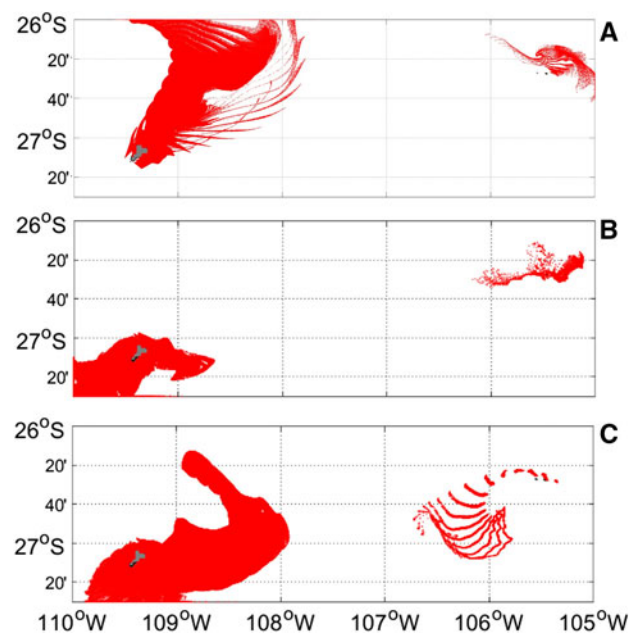


Figure 4. Particle trajectories obtained for particle released in (a) 2011, (b) 2012, and (c) 2013. The figure shows the final position after 14 days of simulations.

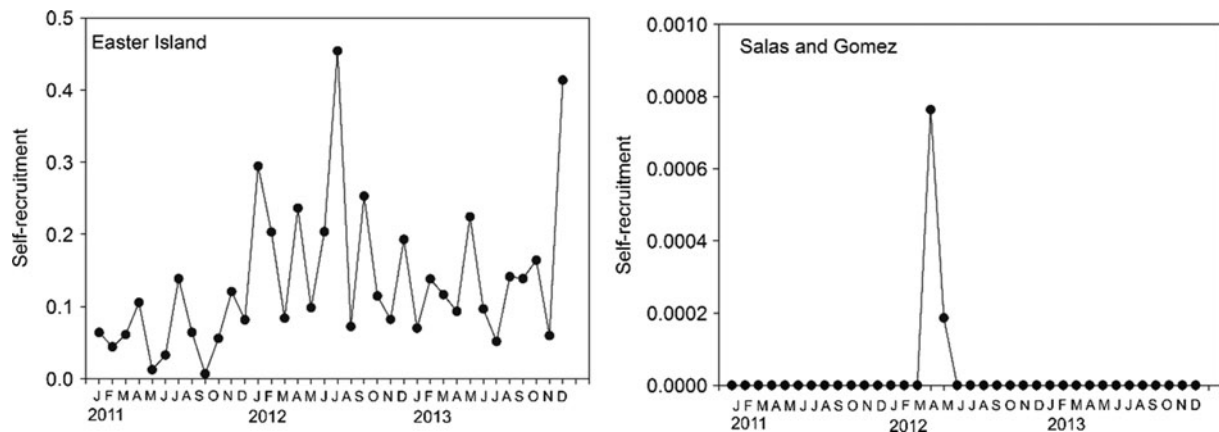


Figure 5. Time series of *M. caputdraconis* self-recruitment in both islands (monthly mean from three replicates is presented).

(Johannesson, 1992), and its populations have a large geographic extension in Europe (Fourdrilis and Backeljau, 2019). In Chile, the muricid *Concholepas concholepas* has a planktonic larval development of up to 3 months (Disalvo, 1988) and shows genetic populations with large geographic extensions (>500 km) (Cárdenas *et al.*, 2016). However, gastropod species with shorter larval development have shown a smaller distance of connectivity between populations. For example, *Patella ferruginea* presented genetic differences in populations separated by more than 100 km in the island of Sardinia (Casu *et al.*, 2006). *P. ferruginea* has a larval development with a similar length to *M. caputdraconis*, suggesting that the planktonic larval duration of *M. caputdraconis* is not sufficient to regularly connect EI and SG. Overall, gastropod species with short larval dispersal are candidates for low connectivity and endemism (Meyer, 2003; Meyer *et al.*, 2005).

Among the physical factors that could influence the larval movement between populations, the wind velocity (Bertness *et al.*, 1996), internal waves (Shanks, 1986), mean direction of currents (Ellien *et al.*, 2004), eddies (Adams and Flierl, 2010), upwelling zones (Roughgarden *et al.*, 1988), and other mesoscale processes (Wing *et al.*, 1998; Shulzitski *et al.*, 2018) are the main drivers. Perhaps, the most documented are the geographic breaks produced by changes in the oceanic currents flow, which prevent the passage of larvae from one region to another. Some breaks have been described in California (Pelc *et al.*, 2009) and Chile (Haye *et al.*, 2014). In the case of the EI and SG system, there are no geographic breaks, and the mean surface currents are $<6 \text{ cm s}^{-1}$ between both islands (Chaigneau and Pizarro, 2005; Meerhoff *et al.*, 2018), which considering an approximate distance between the island of 400 km yields an average transit time of ~ 77 days at such speed (6 cm s^{-1}). EI and SG are located in the east-central South Pacific gyre (von Dassow and Collado-Fabbri, 2014), a typical gyre that circles around large areas of essentially stationary, calm water (Constantin and Johnson, 2017). Hence, the mean water flow between the islands is relatively weak compared to other zones in the south-oriental Pacific Ocean. For example, surface currents measured between Juan Fernández and Desventuradas islands (Chaigneau and Pizarro, 2005) and surface geostrophic velocities in the coast off Chile are up to 20 cm s^{-1} (Letelier *et al.*, 2009). Overall, water currents between EI and SG may be too slow to promote larval movement between these islands. In addition, eddy activity around EI is relatively marked (Dewitte *et al.*, 2021; their Figure 3b) and, thus, may act as a barrier for the connectivity through producing chaotic mesoscale recirculations.

The few migrants detected for *M. caputdraconis* through genetic data, but the lack of migrants obtained through the biophysical model shows that an alternative mechanism could be involved in the connectivity between the islands. One such mechanism

might be the movement of adults through rafting. It is known that some gastropods can perform rafting to cross oceans. For example, it is suggested that *Diloma nigerrima* crossed the Pacific Ocean, from New Zealand to Chile, using macroalgae that drift with the currents (Donald *et al.*, 2011). This mechanism has also been suggested for other gastropod species that do not have free-swimming larvae but present populations with large geographic extensions (González-Wevar *et al.*, 2018). It is possible that the rafting is involved in the movement of the juvenile or adult *M. caputdraconis*, as suggested by Valencia *et al.* (2021) for the fish *K. sandwicensis* between the same islands. Additionally, Rech *et al.* (2020) found that molluscs are frequently rafting taxa in anthropogenic debris in this area. However, it is important to consider that genetic analyses may be influenced by the limited number of loci employed to estimate population genetic structure, as well as the use of the same mutation rate for all microsatellites in the Migrate software. This limitation could impact the accuracy of the reciprocal migration rates calculation, as it may lead to an under or overestimation of the effective number of migrants between the islands. Overall, it is necessary to perform more studies to understand the importance of the number of loci used, debris, and the water circulation between the islands in the population connectivity of marine benthic species.

The self-recruitment of modelled *M. caputdraconis* larvae was higher in EI and presented interannual and monthly variability in both islands. It has been postulated that near the coast of EI, the geostrophic flow includes vertical and horizontal shears, which, combined with the vertical migration behaviour of the larvae, promote larval retention (Meerhoff *et al.*, 2017). In addition, this hydrodynamic pattern that promotes larval retention is consistent with the high abundance of ichthyoplankton and insular ichthyoplankton species reported for the south coast off EI (Castro and Landaeta, 2002; Landaeta *et al.*, 2003). Meanwhile, for the SG islands, more studies are required to understand the factors that explain the restricted periods of self-recruitment to a few months of the year.

What do we know from the EI and SG system until now?

These two islands share most of the endemic species (Friedlander *et al.*, 2013). Hence, some degree of connectivity between their populations is expected. Although there are few species studied in the system, previous studies showed a similar pattern, with no genetic differentiation between the groups inhabiting both islands but with a low level of connectivity. In the case of the endemic lobster *Panulirus pascuensis*, a low but asymmetric connectivity, with considerably more flow from SG to EI, between the islands with both the genetic data and the biophysical model was detected (Meerhoff *et al.*, 2018). This species presents a larva that

exceeds 10 months of planktonic life, which could explain the connectivity detected. On the other hand, for the rudderfish *Kyphosus sandwicensis* which has a larval stage of 1 month, it was not possible to detect particles migrating between both islands, but a historical migration rate of 0.15% from EI to SG and 0.2% from SG to EI was found (Valencia et al., 2021). The authors suggested that stochastic processes such as rafting could be involved in the connectivity of *K. sandwicensis* between these islands.

Thus, the distance between the islands, the relatively weak currents between the islands, and the larval development length would explain the low connectivity of *M. caputdraconis*. In this context, the Motu Motiro Hiva Marine Park located at SG Island could be a reservoir of *M. caputdraconis* conservation; however, larval export may not enough to replenish Easter Island population in the case of overexploitation. Other evidence also showing low connectivity has been reported between marine protected areas (MPAs) from Brazil and compromises the conservation of reef fishes by these MPAs (Endo et al., 2019). These elements are important for understanding how populations of the species remain connected; therefore, they must be considered in the conservation plans proposed for different species with conservation goals.

Finally, in a global warming context, it is expected that there will be an overall increase in south-easterly trade winds of the South-eastern Pacific that are likely to increase the connectivity pattern between Juan Fernandez and Desventuradas islands and along the SG ridge, through increasing wind-driven mean ocean currents (Dewitte et al., 2021). However, in addition to changes in wind, it should be considered that plankton communities of the South Pacific sub-tropical gyre are also threatened by ocean acidification (Doney et al., 2012), and larvae of marine gastropods are particularly vulnerable to this process (Bogan et al., 2019), with possible impacts on larval survival and connectivity.

Supplementary material. The supplementary material for this article can be found at <https://doi.org/10.1017/S0025315423000437>

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Conflict of interest. The authors declare no conflict of interest.

Ethical standards. All analyses were conducted in Chile and complied with its existing laws.

Data availability. The data that support the findings of this study are available from the corresponding author upon request.

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