Limitaciones para la conectividad poblacional del pez *Harpagifer antarcticus*, en las regiones de la Península Antártica e Isla Georgia del Sur

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RESÚMEN BIOGRÁFICO

Desde pequeña tuve mucho interés por el mundo marino y sus habitantes. Siempre me ha gustado estar en el agua o en contacto con el mar. Hasta el día de hoy me fascino y paso mucho tiempo en las pozas, buscando animales o algo interesante que mirar, cada vez que voy a la playa.

Es así que, cuando llegó el momento de elegir una carrera entré a Biología Marina en la Universidad de Valparaíso. Aquí me formé y descubrí las miles de preguntas que podría hacerle al mar. Tuve la suerte de conocer al Dr. Mauricio Landaeta, quien me formó en mis primeras etapas como científica y me mostró lo increíble que es el mundo de los peces. En su laboratorio trabajamos en ecología de larvas de peces, estudiamos sus cambios de forma, como se alimentan y como interactúan con las condiciones ambientales en donde se desarrollan. Fue la primera vez que formé parte de un grupo de investigación, conocí grandes colegas y amigos que hasta el día de hoy me acompañan, y me di cuenta de que quería ser investigadora e ictióloga. Además, entendí lo importante que eran los primeros estadios de vida en la ecología de las especies.

En el 2018 decidí entrar al Doctorado en Ciencias, con mención Ecología y Biología Evolutiva, de la Universidad de Chile. Conocí al Dr. Elie Poulin, quien sería mi guía en esta nueva etapa. Llegué a su laboratorio sin haber trabajado antes con herramientas moleculares, pero con todas las ganas de aprender y crecer como profesional. El camino no fue fácil, pero conté también con el apoyo del Dr. Nicolás Segovia (mi co-tutor), quien me ayudó a navegar lo que a ratos eran las turbias aguas de la genómica del paisaje marino. En el laboratorio de Ecología Molecular conocí nuevos colegas y tremendas personas, además tuve la oportunidad de formar parte de grandes proyectos de investigación. Siempre tuve claro que quería seguir trabajando con peces, pero lo que no esperaba era que mi entusiasmo me llevaría hasta Antártica. Gracias al incentivo y apoyo de mis tutores comencé mi trabajo en estudios de conectividad en ambientes marinos, enfocado principalmente en peces (obvio). Lideré mi propio proyecto y campañas de terreno antárticas, lo cual fue todo un desafío emocional y físico, pero la experiencia me permitió crecer más de lo que esperaba y generar nuevas redes que me entusiasman para el futuro.

Quién imaginaría que una pequeña Valentina, que podía pasar horas en la playa buscando vida y comenzando a hacer preguntas, iniciaría un camino en la ciencia que la llevaría hasta Antártica…

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El camino del doctorado no ha sido fácil, por diferentes motivos, pandémica incluida, a ratos fue un desafío profesional y emocional que sentí que me superaba. Obtener el doctorado nació de mi entusiasmo por la ciencia y por seguir una carrera como investigadora. Me embarqué en esta aventura con ganas de aprender todo lo que pudiera y de crecer. En el transcurso me puse a prueba y no lo habría logrado sin el apoyo de muchas personas que fueron fundamentales.

Me gustaría partir agradeciendo a mi familia y amigues. Mis padres José Antonio Bernal y Alicia Durán, a mis hermanas Bárbara, Daniela y María José y a mis sobrinos Mateo y Benjamín, que junto con mis cuñados Patricio y Tomislav forman parte de un clan medio loco, pero lleno de amor que es mi núcleo familiar. Por acompañarme en este proceso, sin a veces entender muy bien lo que estaba haciendo, pero apoyando mis decisiones y cada uno de los pequeños y grandes logros que he tenido en mi corta pero intensa carrera en la ciencia. Dentro de mi familia también tengo la suerte de incluir a mi compañero de vida Nicolás, un biólogo apasionado por las criaturas y los procesos del pasado, que me toma de la mano para recorrer juntos esta aventura de la vida. Gracias por sostenerme, levantarme, escucharme y apapacharme cuando creí que no lo lograría. Gracias por las risas, las tonterías, el amor y la dedicación que me entregas cada día y que hizo de estos últimos años de doctorado un proceso más llevadero.

Además de mi familia biológica y mi pareja, tengo la fortuna de contar con una tribu, mi familia escogida, mis amigas más cercanas. Agradezco a la vida por habernos encontrado, Fran, Maca, Kharly, Andre y Lauris, mi sexteto poderoso. Por ser mis confidentes, por deconstruirnos y volvernos a armar juntas, por esos podcast que se arman en el grupo de whatsapp. Porque la biología marina nos juntó, pero hoy nuestra loca forma de ver la vida y el amor que nos tenemos nos mantiene unidas. Su apoyo ha sido fundamental para que no me rinda, pero cuando quise llorar y patalear también estuvieron ahí. Especialmente tengo que agradecer a la Fran, que más encima me acompañó en mi primer viaje a Antártica. No estuvo exento de problemas, a ratos fue muy extremo, pero también increíble. Gracias amiga por el apañe infinito, imagino que será una experiencia que nos acompañará toda la vida y que recordaremos en nuestras conversaciones de viejitas.

Siempre he pensado que he tenido suerte en los laboratorios de los que he formado parte, a veces no es fácil encontrarse con grupos humanos cálidos y dispuestos a enseñarte y acompañarte en tu formación. Agradezco a mis tutores Elie Poulin y Nicolás Segovia, por creer en mí, por incentivarme a seguir una carrera en la ciencia, por la paciencia y la confianza que me han tenido. Por darse el tiempo de discutir ideas, de sentarnos a revisar todo lo que fuera necesario, de re analizar, por todas esas conversaciones que me motivaron a seguir y terminar

esta tesis de doctorado. Quiero agradecer también el apañe de mis compañeros del Laboratorio de Ecología Molecular, Fran, Clau, Seba, Guillaume, con quienes tuve tantas buenas conversaciones en “la isla”, donde nos sentábamos a comer alguna cosita e imaginar nuevas investigaciones. Especialmente quiero agradecer a Francisca, si otra Fran que me acompañó a Antártica, por dejarme convencerte de que los peces son geniales y por ser una tremenda compañera de terreno. Además, tengo que agradecer al SpongeTeam, nuestro grupito de bioinformáticos en formación. Cómo olvidar tantas tardes de sufrimiento aprendiendo programación con el Chelo y las terapias de shock de Nico.

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CAPITULO I

LISTA DE ABREVIATURAS

ACC: Corriente Circumpolar Antártica (o Antarctic Circumpolar Current)

AEM: Asymmetric Eigenvector Maps

AIS: Isla Adelaida (o Adelaide Island)

ANOVA: Análisis de Varianza

APCC: Corriente Costera de la Península Antártica (o Antarctic Peninsula Coastal Current)

BF Bayes Factor

BIC: Bayesian Information Criterion

BST: Estrecho de Bransfield (o Bransfield Strait)

CAP: Central parto f the Western Antarctic Peninsula

CHB: Bahía Chile (o Chile Bay)

DAPC: Discriminant Analysis of Principal Components

dbMEM: distance-based Moran's Eigenvector Maps

DIS: Isla Decepción (o Deception Island)

DOI: Isla Doumer (o Doumer Island)

FHA: Foyn Harbour

FIB: Bahía Fildes (o Fildes Bay)

F_{ST}: Índice de fijación, medida de diferenciación poblacional debido a la estructura genética

GBS: Genotyping-by-Sequencing

GEA: Genotype-Environment Association

GRE: Green Reef

H_e: Expected heterozygosity

H_o: Observed heterozygosity

HOS: Horseshoe Island

HWE: Hardy–Weinberg equilibrium

LFMM: Latent Factor Mixed Modelling

MCMC: Markov Chain Monte Carlo

MIN: Zona interior de Bahía Margarita (o inshore Marguerite Bay)

MMRR: Multiple Matrix Regression with Randomization Analysis

MOT: Zona exterior de Bahía Margarita (u offshore Marguerite Bay)

MPA: Área Marina Protegida (o Marine Protected Area)

NGS: Next Generation Sequencing

NKG: Zona norte de la Isla Rey Jorge (o North King George Island)

OA: Océano Austral

PC: Principal Component

PCA: Principal Component Analysis

PDA: Population Differentiation Analyses

PLD: Duración Pelágica Larval (o Pelagic Larval Duration)

PLO: Port Lockroy

RDA: Redundancy Analysis

SACCF: South limit of the Southern ACC Front

SAP: Southern part of the Western Antarctic Peninsula

SGE: Isla Georgia del Sur

SIG: Isla Signy (o Signy Island)

SNP: Single-nucleotide polymorphism

SO: Southern Ocean

sPCA: Spatial Principal Component Analysis

SSH: Islas Shetland del Sur

SST: Sea surface temperature

TSM: Temperatura superficial del mar

WAP: Zona Oeste de la Península Antártica (o Western Antarctic Peninsula)

RESUMEN

La conectividad es uno de los procesos más importantes en la dinámica de poblaciones en ecosistemas marinos. Los estudios de conectividad son fundamentales para determinar procesos que limitan el crecimiento y la resiliencia de las especies. El intercambio de individuos puede estar limitado por varios factores, tales como: los rasgos de historia de vida de las especies, la distancia geográfica, la variabilidad en las condiciones oceanográficas y gradientes ambientales. Dentro de los estudios de conectividad existen dos grandes aproximaciones: los modelos biofísicos que simulan trayectorias de transporte larval para estimar conectividad potencial y las herramientas genómicas, que permiten estimar la conectividad efectiva entre poblaciones locales de una misma especie. Además, usando genómica del paisaje marino se puede estimar el efecto de la distancia geográfica, las corrientes oceanográficas y la variabilidad ambiental en los patrones de diferenciación genética observados.

En el primer capítulo, se combinaron aproximaciones para determinar conectividad de *H. antarcticus* dentro de la Península Antártica Oeste (WAP, por sus siglas en inglés). Se utilizó un modelo biofísico para estimar la conectividad potencial, y genómica de poblaciones para determinar conectividad efectiva. Además, se estimó el efecto de la distancia geográfica entre localidades y de las corrientes oceanográficas en la diferenciación poblacional, utilizando métodos de genómica del paisaje marino. Los resultados del modelo biofísico y de los análisis

genómicos mostraron patrones congruentes. Ambas aproximaciones determinaron la existencia de cuatro grupos genéticos dentro de la Península Antártica, con baja (o nula) conectividad potencial: (1) Islas Shetland del Sur, (2) El estrecho de Bransfield, (3) la zona central de WAP y (4) la zona sur de WAP (Bahía Margarita). Estos grupos genéticamente diferenciados mostraron flujo genético limitado entre ellos, lo cual coincide con las condiciones oceanográficas locales. Al observar ambas metodologías por separado, los patrones eran muy coincidentes, pero los resultados mostraron que la distancia geográfica tendría mayor efecto sobre la variabilidad genética que las corrientes oceanográficas.

En el capítulo dos se amplió la escala geográfica, para comparar las poblaciones locales de *H. antarcticus* de la Península Antártica Oeste y la Isla Georgia del Sur. Esto con el propósito de abarcar una marcada variabilidad espacial y ambiental, que pueda generar patrones de mayor diferenciación genética y adaptación local. Se comparó la estructura genética neutral y adaptativa y se estimó el efecto de la distancia geográfica y de 32 variables ambientales. La estructura neutral mostró clara diferenciación poblacional entre la península y Georgia del Sur. Además, los loci neutrales mostraron un efecto importante de la distancia geográfica, pero también de la productividad primaria y la cobertura de hielo, que estarían limitando la conectividad entre ambas regiones. Sin embargo, para los loci putativamente bajo selección, no se encontró asociación significativa con ninguna variable, por lo que no existe evidencia suficiente para determinar adaptación local.

ABSTRACT

Connectivity is one of the most important processes in population dynamics in marine ecosystems. Connectivity studies are essential to determine population's growth and resilience. The exchange of individuals may be limited by different factors, such as: life history traits of species, geographic distance, variations in oceanographic conditions, and environmental gradients between local populations. To study connectivity patterns there are two main approaches. First, the biophysical models, which simulate larval transport trajectories to estimate potential connectivity and second, the genomic methods, which allow effective connectivity estimations. In addition, using seascape genomics, the effect of geographic distance, ocean currents, and environmental variation on the genetic differentiation can be estimated.

In the first chapter, two approaches were combined to determine the connectivity of *H. antarcticus* within the Western Antarctic Peninsula (WAP). A biophysical model was used to estimate potential connectivity, and population genomics to determine effective connectivity. In addition, we estimate the effect of geographic distance between locations and oceanographic currents on population differentiation using seascape genomics methods. The results of the biophysical model and the genomic analyzes showed congruent patterns. Both approaches determined the existence of four groups within the Western Antarctic Peninsula, with low (or null) potential connectivity: (1) South Shetland Islands, (2) Bransfield

Strait, (3) the central area of WAP and (4) the southern area of WAP (or Marguerite Bay). These genetic groups showed limited gene flow between them, consistent with local oceanographic conditions. Looking the results of both methodologies separately, the patterns were very similar, but the final associations showed that geographic distance have higher effect on genetic structure than oceanographic currents.

In chapter two, we extended the geographic scale to compare local populations of *H. antarcticus* of the Western Antarctic Peninsula and South Georgia Island, with the purpose of comparing greater spatial and environmental variation, which could generate patterns of marked genetic differentiation and local adaptation. The neutral and adaptive genetic structure was compared, and the effect of geographic distance and 32 environmental variables was estimated. The neutral structure showed a marked population differentiation between the Western Antarctic Peninsula and South Georgia Island. In addition, the neutral loci showed a significant relationship with geographic distance, but also with primary productivity and ice cover, which could represent limitations to connectivity between both regions. However, for the loci putatively under selection, no significant association was found with any variable, so there is no sufficient evidence to determine local adaptation.

INTRODUCCIÓN GENERAL

Conectividad en ambientes marinos

La conectividad, definida como el intercambio de individuos entre poblaciones locales geográficamente separadas (Pineda et al. 2007), constituye uno de los procesos más importantes de la dinámica de poblaciones en sistemas marinos (Cowen et al. 2000, Cowen & Sponaugle 2009). Este intercambio puede ocurrir en las diferentes etapas de la historia de vida de los organismos (larvas, juveniles y/o adultos), y cuando los individuos migrantes se reproducen de manera exitosa, la conectividad demográfica se traduce en conectividad genética (Manel et al. 2019). El término general incluye un continuo desde la ausencia de conectividad o aislamiento (todas las poblaciones resultan de auto-reclutamiento) a la alta conectividad (la mayor parte del reclutamiento proviene de larvas o juveniles de otras poblaciones) (Jones et al. 2009). Entender los patrones de conectividad es fundamental para determinar procesos naturales que limitan el crecimiento de las poblaciones y cómo estas responden a perturbaciones, ya sean naturales o antropogénicas (Cowen et al. 2000, Warner & Cowen 2002, Kritzer & Sale 2004, Sale et al. 2005, Almany et al. 2007). Por lo tanto, tiene gran relevancia en establecer cómo las especies pueden ser conservadas y definir una escala apropiada de manejo (Krueck et al. 2017, Manel et al. 2019).

En organismos marinos con ciclos de vida complejos, la dispersión depende en su mayor parte de la etapa larval pelágica, ya que en el estado adulto la movilidad tiende a ser reducida (Kritzer & Sale 2004, Johnson et al. 2018). Por lo tanto, el transporte y retorno de larvas hacia ambientes donde puedan asentarse es fundamental para la dinámica poblacional y por consecuencia para la conectividad de las poblaciones locales (Sponaugle et al. 2002, Warner & Cowen 2002). La dispersión larval y las condiciones ambientales e hidrográficas en las que se desarrollan las larvas, son factores fundamentales para la conectividad. Esto, debido a que no sólo determinan el transporte de individuos, sino que también influyen en la demografía local y la diversidad genética de las poblaciones (Diehl et al. 2007, Gaines et al. 2010, Johnson et al. 2018). Por esto es importante que los estudios de conectividad poblacional en sistemas marinos consideren las primeras etapas de la historia de vida de los organismos, los diferentes procesos que las afectan y su potencial de conectar poblaciones locales (Cowen & Sponaugle 2009).

Uno de los factores importantes que podría producir patrones de retención, en vez de altos niveles de conectividad, es la adaptación local (Marshall et al. 2010, Savolainen et al. 2013). El ajuste de las poblaciones a su entorno puede contrarrestar el efecto de homogenización del flujo génico (Marshall et al. 2010, Sanford & Kelly 2011, Savolainen et al. 2013). Cuando las condiciones ambientales son variables (dentro del rango de distribución de una especie), esto tiene el potencial de conducir a procesos de adaptación, debido a que el entorno

local puede determinar que algunos rasgos fenotípicos se vean favorecidos a través de la selección natural (Savolainen et al. 2013, Hoban et al. 2016, Manel et al. 2016). La adaptación local puede provocar diferencias entre la conectividad potencial y efectiva, ya que puede reducir el reclutamiento o establecimiento de individuos inmigrantes y su adecuación biológica, dando como resultado genotipos residentes (locales) con mejor adecuación biológica en su hábitat nativo que genotipos foráneos, provenientes de otras poblaciones (Kisdi 2002, Kawecki & Ebert 2004, Marshall et al. 2010, Sanford & Kelly 2011, Savolainen et al. 2013, Rellstab et al. 2017). Este acoplamiento entre ambiente y fenotipo ocurre de manera más frecuente en organismos con estados adultos sedentarios o de movilidad reducida, por lo que sería esperable encontrar más señales de adaptación local en especies costeras o bentónicas que en especies pelágicas donde el adulto puede tener mayor capacidad dispersiva (Marshall et al. 2010).

Se debe considerar que el efecto homogeneizador del flujo genético no afectaría de manera uniforme a todo el genoma, si no que sería de importancia en zonas del genoma que son neutrales (no sujetas a procesos de selección) y no aplicable a loci bajo selección (Conover et al. 2006, Marshall et al. 2010, Sanford & Kelly 2011). Es importante tener en cuenta que loci potencialmente bajo selección, pueden mostrar patrones de diferenciación poblacional, incluso si existe un flujo genético importante. De esta manera, las poblaciones que aparecen conectadas en base al estudio de marcadores neutrales, podrían mostrar patrones de estructuración y adaptación local al incluir loci sujetos a selección (Conover et al.

2006, Tigano & Friesen 2016). Por lo tanto, para estudiar procesos de adaptación local por efecto de la heterogeneidad ambiental, se deben incluir marcadores potencialmente sujetos a selección, ya estos procesos podrían limitar el flujo génico efectivo (o conectividad efectiva) entre ambientes contrastantes (Kawecki & Ebert 2004, Sanford & Kelly 2011, Tigano & Friesen 2016).

Con el creciente desarrollo de la genómica, y la posibilidad de acceder a sitios del genoma putativamente bajo selección, en la última década ha aumentado la evidencia de patrones de adaptación local en ambientes marinos (Selkoe et al., 2014; Nielsen et al., 2020). Diversos estudios, desarrollados para diferentes especies, han descrito estructuración poblacional asociada a variabilidad ambiental y la presencia de señales de selección en el genoma (e.g. Benestan et al., 2016; Bernatchez et al., 2019; Nielsen et al., 2020; Pertierra et al., 2020, Benestan et al., 2023). Es así que, a medida que se lleva a cabo más investigación al respecto, se acumula evidencia para considerar que la variabilidad ambiental puede representar una barrera para la conectividad. Considerando también los efectos del cambio climático en los ecosistemas marinos, se hace fundamental determinar de qué manera las condiciones ambientales influyen en la estructura genética y la existencia de posible adaptación local, en miras de cumplir con objetivos de conservación (Narum et al., 2013; Razgour et al., 2018; Nielsen et al., 2020; Benestan et al., 2023).

Estimaciones de conectividad en ambientes complejos: métodos indirectos

Debido a los desafíos logísticos que significa la estimación directa de conectividad poblacional en ecosistemas marinos, y particularmente en el Océano Austral, las aproximaciones indirectas han sido ampliamente utilizadas para abordar esta problemática.

Dentro de los estudios de conectividad en ambientes marinos se pueden encontrar diferentes aproximaciones (Calò et al. 2013, Kool et al. 2013, Bryan-Brown et al. 2017, Manel et al. 2019). Por un lado, se encuentra la **conectividad potencial**, la cual hace referencia al potencial o la capacidad que tienen las larvas de llegar de un lugar a otro. Estos estudios incorporan modelos biofísicos para simular las trayectorias de dispersión larval, los cuales han aumentado su complejidad con los años, incorporando diferentes variables que los hacen más realistas (Treml et al. 2008, Gallego et al. 2017, Manel et al. 2019). Por otro lado, está la **conectividad efectiva**, que se refiere a cuando ocurre dispersión (transporte de individuos) y además los individuos migrantes son capaces de reproducirse exitosamente en la población a la cual llegan (Marshall et al. 2010, Manel et al 2019). Estos estudios utilizan herramientas genéticas para estimar estructuración y flujo genético (Beerli & Felsenstein 2001, Leblois et al. 2004, Manel et al. 2019).

Los modelos biofísicos se han convertido actualmente en una de las principales

herramientas indirectas para estudiar la conectividad potencial en sistemas marinos, ya que permiten entender la variabilidad espacio temporal de las poblaciones (Werner et al. 2007, Paterno et al. 2017). Estos modelos entregan la posibilidad de conocer el grado de homogeneización y estructuración poblacional que se genera producto de factores físicos y biológicos, acoplando modelos biológicos a modelos hidrodinámicos de circulación oceánica (Griffin et al. 2001, Butler 2003, Xue et al. 2008). Debido a las dificultades que representa rastrear directamente algunos organismos marinos o estadios de vida de estos (que representan la etapa dispersiva), por el pequeño tamaño de sus huevos y/o larvas, su baja concentración en océano abierto y las grandes distancias que puede implicar, los modelos numéricos se han transformado en una gran herramienta para la investigación de la conectividad potencial (Young et al. 2015, Paterno et al. 2017, Jahnke & Jonsson 2022). Generalmente, estas herramientas combinan modelos de seguimiento de partículas Lagrangianas con información de un modelo físico de circulación oceánica para predecir el movimiento de los individuos (Paris et al. 2007). Estos modelos son herramientas eficientes que permiten simular trayectorias de dispersión larval y estimar la probabilidad de dispersión entre poblaciones, con las cuales se pueden generar matrices de conectividad potencial, que posteriormente también podrían sustentar estudios de genética del paisaje marino (Galindo et al. 2006, Benestan et al. 2016, Manel et al. 2019). En el Océano Austral, estas técnicas de modelamiento biofísico han sido previamente utilizadas para describir la influencia del flujo oceanográfico y la variabilidad en estadios de vida temprana. Diversos estudios se han realizado

para evaluar la conectividad entre poblaciones de krill en Antártica, tanto a escala local como circumpolar (e.g. Murphy et al. 2004, Thorpe et al. 2004, Piñones et al. 2013). Además, distintos modelos bio-físicos se han utilizado para estudiar la influencia del flujo oceánico en la dispersión y retención en especies del suborden Notothenioidei en la zona de Antártica Marítima y contrastarla con datos de estructura genética, e incluso para estimar el impacto de los cambios de temperatura en la conectividad potencial, bajo un escenario de cambio climático (e.g. Young et al. 2015 y 2018, La Mesa et al. 2015).

Otro de los métodos más importantes en estimaciones indirectas de conectividad, son las herramientas de la genética de poblaciones. Estas han sido ampliamente utilizadas para caracterizar la conectividad efectiva entre poblaciones de especies marinas, o para determinar la escala espacial relevante de estructuración poblacional (Kool et al. 2013, Manel & Holderegger 2013). Gracias al avance de las técnicas de secuenciación masiva, hoy en día es posible realizar escaneos de genomas a un costo relativamente bajo, lo que ha facilitado el crecimiento del área de la genómica de poblaciones, generando un gran avance en los estudios de conectividad. Además de estimaciones de estructuración y flujo genético, el escaneo de genomas permite evaluar señales de selección dispersas por el genoma, lo cual ha despertado un creciente interés de los investigadores por estudiar cómo la variabilidad ambiental influye en la diversidad genética (neutral y selectiva) de las poblaciones, generando adaptación local (Riginos et al. 2016, Selkoe et al. 2016, Grummer et al. 2019). En este contexto,

la genómica del paisaje, definida como una disciplina que utiliza la composición y configuración del paisaje para determinar la influencia del ambiente en los patrones de la genómica de poblaciones (Riginos et al. 2016), ofrece herramientas para identificar diferentes factores ambientales que pueden actuar como agentes selectivos y de esta manera se han convertido en aproximaciones de gran importancia dentro los estudios de conectividad (Benestan et al. 2016, Manel et al. 2019, Grummer et al. 2019).

Tanto los modelos biofísicos cómo la genómica del paisaje marino han tenido grandes avances durante los últimos años (Jahnke & Jonsson 2022). Estas herramientas se pueden complementar en los estudios de conectividad, lo que permite tener un escenario más realista de lo que ocurre con el intercambio de individuos en ambientes marinos (Baltazar-Soares 2018, Jahnke & Jonsson 2022).

Características oceanográficas de la zona de estudio

Este estudio se enmarca en dos regiones del Océano Austral (OA): La zona oeste de la Península Antártica (WAP, por sus siglas en inglés) y la Isla Georgia del Sur (SGE, por sus siglas en inglés). WAP se extiende aproximadamente desde los 61ºS en el norte hasta 75ºS en el sur, mientras que SGE, considerando tanto la plataforma como la zona oceánica, se extiende entre los 53-56ºS y los 34-44°O (Murphy et al., 2013).

La zona oeste de la Península Antártica está influenciada por distintas corrientes y masas de agua, lo que genera una compleja dinámica oceanográfica. Considerando las características hidrográficas, WAP se puede dividir en dos regiones distintas, el Estrecho de Bransfield y la región central (Moffat & Meredith 2018). El Estrecho de Bransfield forma una cuenca alargada orientada de forma paralela a la costa (con profundidades que superan los 2000 m), que limita con la península al sureste, con las islas Shetland del Sur al noroeste y con el Estrecho de Boyd al sur (Gordon & Nowlin 1978, Moffat & Meredith 2018). Mientras que la región central, se encuentra entre las islas Low (límite norte) y Alexander (límite sur), con profundidades típicas de 400 m, posee una serie de canales que atraviesan la plataforma y que se profundizan hacia la costa (Moffat & Meredith 2018). Se ha descrito que el intercambio entre estas dos regiones podría estar inhibido por diferencias en la batimetría (fuertemente inclinada en Bransfield y poco profunda en el límite con la zona central) y en el forzamiento del viento, que va en dirección norte en Bransfield y hacia el sur en la zona central de la península (van Lipzig et al. 2004, van Wessem et al. 2015, Moffat & Meredith 2018).

La fuerte influencia de las aguas del Mar de Weddell en el estrecho de Bransfield y de la Corriente Circumpolar Antártica (ACC, por sus siglas en inglés) en la zona central de la Península Antártica, sumada a la variabilidad en la batimetría que presentan estos dos sectores, provocan un fuerte gradiente en las propiedades

hidrográficas a lo largo de la costa en esta región (Moffat & Meredith 2018).

En el estrecho de Bransfield dominan aguas más frías a lo largo de la costa del continente (provenientes del Mar de Weddell), que fluyen en dirección suroeste (Sangrà et al. 2011, 2017, Moffat & Meredith 2018). Cuando la corriente de Bransfield alcanza el borde sur de las Islas Shetland del Sur, la corriente de toma dirección hacia el noreste, y cuando llega al extremo noreste de este grupo de islas, recircula alrededor de un remolino anticiclónico, ubicado entre la Isla Rey Jorge y la Isla Elefante (Sangrà et al. 2017, Moffat & Meredith 2018). Luego, la corriente fluye hacia el sur, bordeando la plataforma norte de las islas Shetland, generando una circulación en sentido contra reloj alrededor de este grupo de islas (Sangrà et al. 2017, Moffat & Meredith 2018). Además, en el Estrecho de Bransfield se han descrito dos frentes: uno más profundo a lo largo del talud de las Islas Shetland del Sur, llamado Frente de Bransfield, y otro poco profundo, más cercano a la península, llamado Frente de la Península, que separa el Agua Zonal de Transición con influencia de Bellingshausen y el Agua Zonal de Transición con influencia del Mar de Weddell. Estudios recientes sugieren que este último (Frente de la Península) podría constituir una barrera para la dispersión de algunas especies que habitan esta zona (Leiva et al. 2018, 2019).

En la región central de la Península Antártica, la circulación superficial depende de dos corrientes principales. En el talud y la plataforma exterior, la circulación está dominada por la Corriente Circumpolar Antártica, que fluye hacia el noreste

(Moffat & Meredith 2018). Mientras que, cerca de la costa, el sistema está dominado por la Corriente Costera de la Península Antártica, que en esta área tiene un flujo predominante hacia el suroeste (Moffat et al. 2008, Moffat & Meredith 2018).

La región de la Isla Georgia del Sur se encuentra en el camino de la ACC, por lo tanto, las condiciones oceanográficas locales están fuertemente influenciadas por dicha corriente (Murphy et al. 2013). Cuando la ACC se encuentra la plataforma suroeste de esta isla, se genera una zona de divergencia, donde el flujo de la corriente se separa. Entonces, una parte de la ACC fluye hacia el noroeste de SGE y otra continua en dirección hacia el este (Murphy et al. 2013). Se ha descrito que la plataforma de la Isla Georgia del Sur está influenciada por afloramientos y hundimiento de aguas profundas, que interactúan con la batimetría local y generan dinámicas de circulación complejas a pequeña escala (Murphy et al. 2013).

Variabilidad ambiental de la zona de estudio

Entre WAP y SGE, se ha descrito una marcada estacionalidad en las condiciones ambientales, también relacionada a las diferencias de latitud entre estas regiones.

Uno de los ejemplos más claros de variabilidad ambiental son los patrones

estacionales de la temperatura superficial del mar (TSM). En WAP, durante el verano, la TSM suele estar por encima de 0º, con valores máximos alrededor de 1 ºC (Murphy et al. 2013). En esta misma estación, en SGE la TSM máxima ronda los 3,5 ºC e incluso puede superar los 4 ºC (Murphy et al. 2013). Bajo condiciones de otoño-invierno se produce la mayor diferencia, ya que la TSM en WAP suele rondar los -1 ºC y gran parte de esta región está cubierta por hielo (generalmente entre junio y noviembre). Mientras que, durante la misma temporada en SGE, el rango de TSM es de alrededor de 2 ºC y no hay avance y retroceso del hielo marino, ya que SGE se encuentra sobre el límite geográfico de formación (Murphy et al. 2013).

Además de la temperatura y la cobertura de hielo, otra variable ambiental importante en WAP y SGE es la productividad primaria (o niveles de clorofila). La zona costera de ambas regiones ha sido descrita como un área de alta productividad primaria y clorofila a, debido a la ocurrencia de surgencia y al enriquecimiento de hierro (Atkinson et al. 2004, Arrigo et al. 2008, Murphy et al. 2013). Durante la primavera y el verano, se producen extensas floraciones de fitoplancton tanto en WAP como en SGE, que pueden alcanzar concentraciones de clorofila a ~30 mg m^{-3} (Vernet et al. 2012), también asociados al derretimiento de las masas de hielo (Whitehouse et al. 1996, Whitehouse et al. 2000, Garibotti et al. 2003, Korb & Whitehouse 2004, Murphy et al. 2013). En contraste, durante condiciones de invierno, los niveles de productividad primaria son bajos en ambas regiones, con valores mínimos de clorofila a ~0,2 mg m^{-3} (Vernet et al.

2012), asociados a tormentas, baja luminosidad y presencia de hielo. El último particularmente para WAP, donde el período de baja productividad primaria es de 2 a 3 meses más largo que en SGE (Atkinson et al. 2001, Stammerjohn et al. 2008).

En términos generales, se han descrito dos patrones en cuanto a la concentración de fitoplancton en la península antártica. Primero, las aguas costeras presentan mayor biomasa de fitoplancton y productividad que las regiones de océano abierto. Segundo, dentro de las aguas costeras existe gradiente de norte a sur en los aumentos de concentración de fitoplancton, los blooms partirían más temprano de norte hacia el sur, siguiendo el retroceso del hielo marino (Arrigo et al. 1998, Smith et al. 1998 y Garibotti et al. 2003).

Harpagifer antarcticus como especie modelo

En el presente estudio, se trabajó con individuos del género *Harpagifer* de WAP y SGE, incluyendo individuos de *H. antarcticus* de WAP e islas adyacentes e individuos recolectados en SGE, previamente descritos como *H. georgianus*. Para el desarrollo de esta investigación *H. antarcticus* y *H. georgianus* se consideran como una sola unidad evolutiva, debido a reciente evidencia proporcionada por nuevos análisis genéticos con marcadores moleculares tradicionales (COI, D-loop e ITS) y single-nucleotide polymorphism o SNPs (Fig. 1, Segovia et al. en preparación). Debido a la falta de evidencia de divergencia

de linajes entre *H. antarcticus* y *H. georgianus*, y para propósitos de esta tesis, de aquí en adelante nos referiremos a esta unidad evolutiva como *H. antarcticus*.

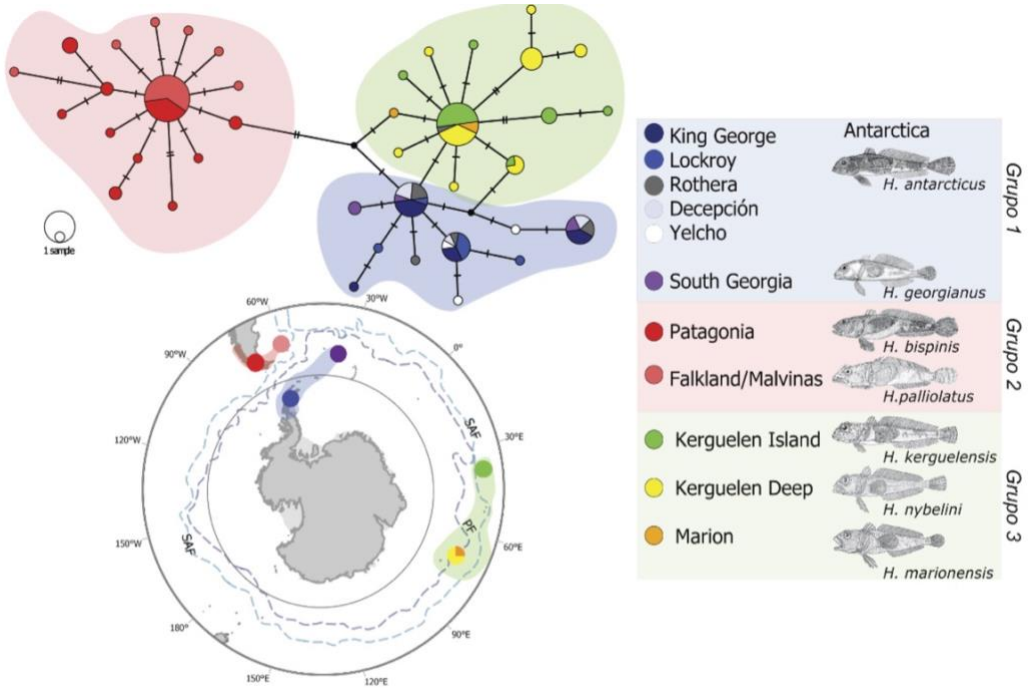

Figura 1. Segovia et al. (en preparación) muestra una red de haplotipos de COI para el género *Harpagifer* en Patagonia/Malvinas (rojo), Antártica (azul) y sub-Antártica (verde).

La especie *H. antacticus* pertenece al Suborden Notothenioidei, familia Harpagiferidae. Los adultos habitan aguas costeras someras y pozas intermareales, desde la región oeste de la Península Antártica hasta las islas Orcadas del Sur y Sandwich del Sur (Hureau 1990). Es una especie de crecimiento lento (4-10 mm por año) que alcanza una edad máxima de 9 años a una talla de 95 mm (Daniels 1983).

Esta especie posee un ciclo de vida complejo, con una etapa adulta bentónica, (de baja capacidad natatoria) y una etapa larval pelágica. Se ha descrito que esta especie tiene una baja fecundidad, ya que cada hembra desova entre 300 y 1500 huevos (White & Burren 1992). Estos huevos son puestos en un solo nido que tanto la hembra como el macho cuidan durante el período de desarrollo embrionario (Daniels 1978, 1979), que dura entre 105 y 150 días (White & Burren 1992), por lo que los huevos no constituirían una etapa de dispersión. Las larvas plantónicas se han encontrado principalmente en aguas someras cercanas a la costa, <1 km (White & Burren 1992, Piacentino et al. 2018). Después de la eclosión, las larvas de *H. antarcticus* tienden a abandonar rápidamente el nido y nadar hacia la superficie, donde podrían ir a la deriva con las corrientes oceánicas y dispersarse (Daniels, 1978; La Mesa et al. 2017).

Se ha descrito que los períodos de incubación de los huevos y eclosión larval podrían variar entre localidades y también de forma interanual, ya que se han encontrado larvas con saco vitelino en diferentes periodos del año (entre octubre y enero) en distintas zonas (Daniels 1978, Kellermann 1990, White & Burren 1992). Algunos autores sugieren que esto tendría relación con las condiciones ambientales locales, debido a que el momento de la eclosión larval estaría acoplado con períodos de aumento en la intensidad del viento y de las concentraciones de fitoplancton, lo cual garantizaría que las larvas de *H. antarcticus* se liberen en el momento más adecuado para la alimentación temprana (Daniels 1978, White & Burren 1992, La Mesa et al. 2017). Las larvas

de esta especie poseen una dieta omnívora, dentro de la cual la diatomea *Thalassiosira minuscula*, los huevos de eufáusidos y copepoditos aparecen como los ítems presa más importantes (Landaeta et al. 2017). Se estima que la metamorfosis, y por lo tanto el asentamiento de los juveniles en el fondo, ocurre a un tamaño de 23-27 mm de longitud (White & Burren 1992), después de una duración larval pelágica de entre tres y cuatro meses, lo que generalmente ocurre antes del primer invierno (La Mesa et al. 2017). Esta duración pelágica está entre las menores dentro del suborden Notothenioidei (Kellermann 1990, North 1991), y es similar a algunas especies para las que se ha descrito estructuración poblacional y limitaciones al flujo genético (e.g. Young et al., 2015, 2018).

La baja capacidad natatoria de los adultos, junto con una baja fecundidad y la postura de huevos bentónicos con cuidado parental en zonas costeras podrían generar baja conectividad entre las poblaciones locales de *H. antarcticus*, a lo largo de su distribución. A esto se le suma la reciente evidencia de estructuración genética y limitaciones al flujo genético entre poblaciones distantes del congénere *H. bispinis*, en la Provincia Magallánica (Segovia et al. 2022).

Implicancias para la conservación en Antártica

En peces antárticos, la conectividad entre las poblaciones varía dependiendo de la especie y de la zona de estudio. Se ha descrito alto flujo genético entre poblaciones para algunas especies y fuerte estructuración para otras, lo cual

estaría asociado a diferencias en los rasgos de historia de vida, como por ejemplo si los huevos son pelágicos o bentónicos, si existe cuidado parental de los nidos y si existen variaciones latitudinales en los periodos de desove incubación y eclosión (e.g. Damerau et al. 2012, 2014, Young et al. 2015, 2018, Caccavo et al. 2018). Para la zona oeste de la Península Antártica, Leiva et al. (2019) describieron alto flujo genético y conectividad entre poblaciones locales de la esponja *Dendrilla antarctica* y lograron detectar señales de adaptación local en el genoma, promovidas por selección divergente que estaría asociada a variaciones en la duración de la capa de hielo marino en distintas localidades de la Península Antártica. Se debe tener en cuenta que esta especie posee larvas lecitotróficas de larga duración pelágica (Koutsouveli et al. 2018), lo cual favorecería su dispersión (Leiva et al. 2019).

Desde el año 2011 la Comisión para la Conservación de los Recursos Vivos Marinos Antárticos (CCAMLR, por sus siglas en inglés) ha identificado 11 áreas prioritarias para establecer AMPs en el continente antártico, una de ellas corresponde a la zona oeste de la Península Antártica y el mar de Escocia (donde se encuentra la Isla Georgia del Sur). Sin embargo, hasta la fecha aún no se declarado esta zona como AMP, pese a que existe una propuesta de los gobiernos de Chile y Argentina. Es importante que este tipo de propuestas tengan respaldo de estudios científicos que aborden los patrones de conectividad para que el diseño de medidas de conservación cumpla con dicho objetivo (Smith & Metaxas 2018). Establecer la escala espacial de la conectividad y el efecto de la

variabilidad ambiental en los patrones de diferenciación poblacional, es crucial para el entendimiento de la dinámica de las poblaciones, estructura genética y biogeografía de los organismos marinos y en consecuencia, para el diseño de áreas marinas protegidas (Manel et al. 2019).

Existen algunos estudios de conectividad poblacional realizados en la Península Antártica y el Mar de Escocia que muestran que los patrones observados dependen en gran medida de los rasgos de historia de vida de las especies (Young et al. 2015, Galaska et al. 2016, Young et al. 2018, Leiva et al. 2019). Por lo tanto, es necesario generar información de especies con historias de vida contrastantes que permitan tener un escenario completo de cómo es el intercambio de individuos dentro y entre estas zonas y cómo este proceso interactúa con las condiciones oceanográficas y la variabilidad espacial y ambiental.

En este contexto, se espera que los resultados descritos en esta investigación sean un aporte de información relevante para la propuesta de AMPs en la Península Antártica, generando conocimiento de cómo los rasgos de historia de vida, las dinámicas oceanográficas locales y la variabilidad ambiental pueden afectar los patrones de conectividad en esta región.

Hipótesis de trabajo

Hipótesis 1

La conectividad entre poblaciones locales de *Harpagifer antarcticus* a lo largo de la zona oeste de la Península Antártica (WAP, siglas en inglés) es limitada, debido a características biológicas de la especie y a la variabilidad de las condiciones oceanográficas locales.

- Objetivo general: Determinar los patrones de conectividad entre las poblaciones locales de *H. antarcticus* a lo largo de WAP, combinando aproximaciones para estimar conectividad potencial y efectiva.
- Objetivos específicos:
    1. Determinar la dispersión potencial de *H. antarcticus*, utilizando modelamiento bio-oceanográfico de partículas lagrangianas para simular el transporte larval.
    2. Determinar la estructura genética de las poblaciones de *H. antarcticus* en la Península Antártica, identificando SNPs dispersos por el genoma usando Genotyping-by-Sequencing (GBS).
    3. Inferir los patrones de conectividad efectiva contemporáneos entre poblaciones de *H. antarcticus*, a través de estimaciones de flujo genético.
    4. Estimar la influencia de la distancia geográfica y de las corrientes oceanográficas en la estructuración genética de *H. antarcticus*, utilizando métodos de genómica del paisaje marino.

Hipótesis 2

Existe una marcada diferenciación genética entre las poblaciones locales de *H. antarcticus* a lo largo de las regiones de la zona oeste de la Península Antártica (WAP) y la Isla Georgia del Sur (SGE), asociada a un efecto significativo de la distancia geográfica y la variabilidad ambiental entre estas dos zonas, que representan barreras para el intercambio de individuos y generan adaptación local.

- Objetivo general: Estimar estructuración genética neutral y adaptativa de *H. antarcticus* entre las poblaciones de las regiones WAP y SGE, y el efecto de la variabilidad espacial y ambiental en los patrones observados.
- Objetivos específicos:
    1. Buscar marcadores putativamente bajo selección natural utilizando métodos de Análisis de Diferenciación Poblacional (PDA, siglas en inglés) y de Análisis de Asociación Genotipo-Ambiente (GEA, siglas en inglés), considerando variables ambientales de importancia biológica que muestren un gradiente (como temperatura, cobertura de hielo, entre otras) a lo largo de las regiones de WAP y SGE.
    2. Comparar la estructura genética neutral y adaptativa entre las poblaciones de *H. antarcticus* a lo largo de WAP y SGE.
    3. Estimar el efecto de la variabilidad espacial y ambiental entre WAP y SGE en la diferenciación poblacional de *H. antarcticus* e identificar patrones de adaptación local, utilizando herramientas de genómica

del paisaje marino.

CAPÍTULO I

Dispersal barriers inside the Antarctic Peninsula? Population structure and the influence of sub-regional oceanographic conditions on connectivity patterns in an Antarctic fish

1. Introduction

Connectivity, i.e. the exchange of individuals among populations, is a pivotal process driving population dynamics and resilience of marine species (Cowen et al., 2000; Cowen and Sponaugle, 2009). Understanding the patterns of connectivity is essential to determine population demography, survival, recovery and adaptation to changing conditions at both ecological and evolutionary time scales (Cowen et al., 2000; Cowen and Sponaugle, 2009; Gary et al., 2020). For marine organisms with bentho-pelagic life cycles, connectivity depends mostly - or exclusively - on the pelagic larval stage (Johnson et al., 2018). Therefore, the transport or retention of larvae through ocean currents critically influence population dynamics and consequently population connectivity (Sponaugle et al., 2002, Warner and Cowen, 2002). Given the logistical challenges posed by directly estimating connectivity in marine ecosystems, researchers have extensively relied on indirect approaches to tackle this issue. On the one hand, populations are connected through drifting larvae and biophysical models are efficient tools to simulate larval dispersal trajectories and inform on potential connectivity between locations (Treml et al., 2008; Manel et al., 2019). On the other hand, population

genomics studies use genetic markers to estimate the effective genetic connectivity or gene flow (Manel et al., 2019). Yet, this genetic connectivity is a result of both historical and contemporary events, while studies of larval connectivity focus only on contemporary time. Furthermore, genetic connectivity occurs beyond larval connectivity, when migrant individuals settle and reproduce successfully (Marshall et al., 2010; Manel et al., 2019). Incorporating both approaches, population genomics and biophysical models, are now widely used to assess connectivity of marine populations and determine the drivers of population structuring (Kool et al., 2013; Manel and Holderegger, 2013; Riginos et al., 2016; Liggins et al., 2020).

Comparing and combining the outputs of biophysical models and genomic approaches could improve the understanding of connectivity patterns, the influence of larval dispersal on genetic differentiation and facilitate the interpretation of population structure (Selkoe et al., 2010; Schiavina et al., 2014; Jahnke and Jonsson, 2022). Using both approaches in synergy, valuable and reliable information for conservation planning and monitoring can be obtained such as the delineation of evolutionary significant units to protect in priority (Andrello et al., 2022; Jahnke and Jonsson, 2022; Nielsen et al., 2022). Therefore, these are powerful tools to study connectivity in fragile areas with high conservation interest as Antarctic ecosystems. Especially the Western Antarctic Peninsula, which is one of the most affected regions by climate change worldwide (Moffat and Meredith, 2018; Henley et al., 2019). Besides, there are very few

studies that combine biophysical models and genomic approaches in polar regions, making these areas underrepresented in seascape genomics (Jahnke & Jonsson 2022).

The Western Antarctic Peninsula (WAP) is characterized by complex oceanographic dynamics, influenced by different currents and water masses. From a hydrographic view, Moffat and Meredith (2018) divided the WAP in two main regions: (1) Bransfield Strait, limited by the Peninsula to the southeast, the South Shetland Islands (SSH) to the northwest and by Boyd Strait to the south; and (2) the central WAP, extended from Low Island (in the north) to Alexander Island (in the south). The Bransfield Strait has a strong influence of water masses from the Weddell Sea that flow southward from the tip of the Peninsula (Sangrà et al., 2011, 2017; Moffat and Meredith, 2018). Along the southern continental slope of the SSH, ocean circulation is bounded by the Bransfield current that flows to the northeast and when reaches the northeast tip of the SSH it recirculates around as an anticyclonic eddy (Sangrà et al., 2017). Afterward, along the northern continental shelf of the SSH, the current flows to the southwest, generating an anticlockwise recirculation of the Bransfield current around the SSH (Sangrà et al., 2017; Moffat and Meredith, 2018). In the central WAP, at the slope and outer shelf, the surface circulation is dominated by a north eastward flow, associated with the Antarctic Circumpolar Current (ACC). Nearshore, the circulation is characterized by a flow towards the southwest, associated with the Antarctic Peninsula Coastal Current (APCC) (Moffat et al., 2008; Moffat and

Meredith et al., 2018). Nevertheless, some studies suggest the APCC in Gerlache Strait flows towards the Bransfield Strait, but this circulation pattern may vary seasonally (Niiler et al., 1991; Zhou et al., 2002; Moffat and Meredith, 2018). The along-shore exchange between the Bransfield Strait and the central WAP could be inhibited by differences in the bathymetry (steeply inclined in Bransfield and relatively shallow in the border with the central region) and also by differences in the wind forcing, northward in Bransfield and southward in the central WAP (van Lipzig et al., 2004; van Wessem et al., 2015; Moffat and Meredith, 2018). Due to the complex oceanographic dynamics described for WAP, this is an interesting area to combine approaches (biophysical modeling and population genomics) to estimate connectivity, considering the interaction of the organisms with the local ocean currents and hydrographic conditions.

The notothenioid fish *Harpagifer antarcticus* Nybelin, 1947, is a benthic demersal species with a complex life cycle (i.e., benthic eggs and pelagic larvae), that inhabits the western side of the Antarctic Peninsula, the South Shetland, South Orkney and the South Sandwich Islands (Hureau, 1990). The adults are commonly found in coastal rocky habitats, from intertidal pools to around 100 m deep, in protected coves (White and Burren, 1992). Compared to other notothenioids, the adults of the genus *Harpagifer* have been considered as fishes with relatively low buoyancy and swim capabilities (Fernández et al., 2012). Each female spawns about 300-1500 eggs (White and Burren, 1992), which are laid in a single nest guarded by both male and female during the embryonic development

of around 150 days (Daniels, 1978, 1979; White and Burren, 1992). Due to this nesting behavior, the eggs are not considered as a dispersal stage. The planktonic larvae of *H. antarcticus* inhabit mainly inshore waters, at 15-20 m depth (White and Burren, 1992; Piacentino et al., 2018). Their newly hatched larvae tend to rapidly leave the nest and swim towards the sea surface, where they could drift with the ocean currents and be dispersed (Daniels, 1978; La Mesa et al. 2017). The pelagic larval duration (PLD) for *H. antarcticus* has been estimated between three and four months (La Mesa et al., 2017). The poor swim capabilities of the adults, in addition with the low fecundity and egg laying in coastal waters, could limit the potential dispersal, generating low levels of gene flow and affecting connectivity among *H. antarcticus* populations (La Mesa et al., 2017).

In this study, the notothenioid fish *Harpagifer antarcticus* was used as model species to assess connectivity along the Western Antarctic Peninsula and determine the seascape drivers that influence the observed patterns, by combining complementary approaches to estimate physical and genetic connectivity.

2. Materials and methods

2.1 Sampling design and molecular techniques

For genomic analyses, 143 individuals of *H. antarcticus* were collected by hand, from intertidal zone (on rubble bottom habitats) and through SCUBA diving in

shallow waters of 11 localities along the Western Antarctic Peninsula (WAP), between 60.72ºS 45.66ºW and 67.89ºS 67.40ºW (Fig. 1; Supplementary material, Table S1), during austral summer conditions from 2004 to 2021. All specimens were sacrificed following a bioethical protocol, prior preservation in 95% ethanol. DNA extractions were done using the DNeasy Blood® and Tissue Kit (QIAGEN®, USA). The quantity and integrity of DNA were measured using Qubit 4 (Thermo, USA). The Genotyping-by-Sequencing (GBS) method was used, at the Biotechnology Center of the University of Wisconsin, using (after optimization) the ApeKI restriction enzyme. After enzyme digestion, each DNA fragment was linked to a barcode adaptor to recognize it *in silico*. Libraries were prepared using a HiSeq2000 (Illumina, USA) platform.

2.2 Biophysical model

An implementation of the Regional Ocean Modeling System (ROMS; Haidvogel et al. 2008) was used to simulate ocean circulation along the western Antarctic Peninsula. To estimate the potential role of the ocean as an advective mechanism, Lagrangian particle tracking simulations were implemented to determine the potential dispersal of *H. antarcticus* larvae. The implementation of ROMS for the western Antarctic Peninsula (Hudson et al., 2021) has 1.5 km horizontal resolution and 24 vertical sigma layers. It includes a dynamic sea ice model (Budgell, 2005) and the interaction between floating ice shelves and the ocean (Holland and Jenkins, 1999; Dinniman et al., 2011). Atmospheric forcing is

from archived forecasts from the Antarctic Mesoscale Prediction System (Powers et al., 2012), tidal forcing was added at the model lateral boundaries using tidal sea surface height and velocity from the CATS2008 regional Antarctic tidal model (Padman et al., 2002).

The model was run from November 2008 to May 2009, this period was selected because it is a date near the middle of the total sampling campaigns and it is the oldest period included in the biophysical model. A total of 1000 neutrally buoyant particles (100 per site) were released every 10 days, on 10 sites along the model domain (Fig. 1), starting from November 15, 2008 until February 15, 2009 (giving a total of 10 runs of the model). A total of 10,000 particles were released and tracked during 100 days (estimated pelagic larval duration for *H. antarcticus*, La Mesa et al., 2017). This means that any particle that entered a release grid cell of any site at day 100 was considered as a potential successful settled individual. There is no information about larval behavior for *H. antarcticus*, such as swimming capability or vertical migration patterns, therefore simulated larvae drifted as passive particles. These particles were released at 0, 20, 40 and 60 m depth, and they were advected by the model circulation at every model time step (50 s) using the full 3D velocity fields (at the time and position of each particle) plus a random walk in the vertical direction, which is a function of the parameterized model vertical diffusion (Hunter et al., 1993; Visser, 1997). Particle positions were saved hourly. The vertical random walk was included for all particle releases, except for surface releases.

With the output of the Lagrangian simulations, three matrices were created. First, the mean trajectory matrix T, which provides information about the path traveled by the particles. The cell T_{ij} shows the number of particles released from site *i* (origin, at x axis) that passed through (but not necessarily settled) in site *j*. It is a mean value of every day of the simulation to estimate the route the particles follow from their origin point during the 100 days of simulation. This matrix was made for each of the 10 runs of the model, then the 10 matrices were averaged to obtain the mean trajectory matrix. The second was a dispersal matrix D, considering all 10 release points. The cell D_{ij} shows the number of particles that were released from site *i* (origin, at x axis) and potentially settled in site *j* (destination, at y axis) at day 100. The diagonal of this matrix (D_{ii}) represents local retention (self-recruitment), particles released from site *i* that return to site *i* (or their origin point). The D matrix was constructed for each of the 10 runs of the model, obtaining 10 matrices, which were averaged to construct the final dispersal matrix. Then, this final dispersal matrix was transformed to a connectivity matrix C, where C_{ij} shows the proportion of total particles that potentially settled in site *j* that originated from site *i*. This C matrix showed the results of potential dispersal of *H. antarcticus* larvae.

A total of 10 release points were selected for the Lagrangian simulations, 7 of them corresponded to localities from which there were also available samples, used for genomic analyses: Fildes Bay (FIB), Chile Bay (CHB), Deception Island

(DIS), Bransfield Strait (BST), Foyn Harbour (FHA), Doumer Island (DOI) and Adelaide Island (AIS). The other 3 points, North King George Island (NKG), inshore and offshore Marguerite Bay (MIN and MOT respectively) were selected as potential habitats for *H. antarcticus* and to test possible stepping-stone connectivity with the biophysical model. The T matrix provides information about the particle's trajectory during the 100 days of simulation. While the C matrix represents the final scenario at day 100, the potentially settled individuals after being transported to another location or retained at the origin.

The results of this biophysical model were visually compared to genetic structure output and then used to estimate the effect of larval dispersal on genetic variation through a regression analysis. For the latter, only the connectivity matrix (C) was used, considering the 7 locations that have both genomic and biophysic data.

2.3 SNP calling

For quality checks, reads were visualized in FastQC 0.10.1. SNP-calling was carried out with the pipeline Universal Network-Enabled Analysis Kit (UNEAK) in Tassel v. 3 software (Lu et al., 2013). The SNPs were filtered using a site minimum call rate of 0.75, a minimum proportion of sites present of 0.7 and a minor allele frequency of 0.01 as recommended by Benestan et al. (2016). After these filters, deviations from Hardy–Weinberg equilibrium (HWE) were tested, per locus and per population, using 10,000 permutations in Arlequin 3.5.2.2 (Excoffier and

Lischer, 2010). The p-values were corrected using a false discovery rate correction (q-value = 0.05). The SNPs considered in HWE disequilibrium in at least 60% of the populations were removed from the final dataset.

SNPs potentially under diversifying selection (hereafter outliers) were detected using population differentiation analyzes. Two approaches were used. First, was the pcadapt (Luu et al., 2016) R package. This approach uses a Principal Component Analysis (PCA) to detect population structure, then each SNP is regressed at the principal components (PCs) retained. Here 10 PCs were retained based on their eigenvalues according to Cattell's recommendation. Then, a statistical test is applied to the PCA when regressing SNPs with the PCs and a cut-off of q-values = 0.05 was selected to assign the outliers. Because pcadapt does not require grouping individuals into populations, this package is not impacted by admixed individuals (Luu et al., 2016). The second was the software BayeScan 2.1, which implements a F_{ST} outlier approach to detect loci highly differentiated that exacerbate the genetic structure (Foll and Gaggiotti, 2008). BayeScan uses a Bayesian method to estimate the probability of each locus to be under the effect of selection. This method assumes that allele frequencies follow a Dirichlet distribution and uses locus-specific and population information from F_{ST} coefficients. Although BayeScan is impacted by the presence of admixed individuals (Luu et al., 2016), it does not assume equal differentiation between pairs of populations. It has been described that BayeScan is robust when dealing with complex demographic scenarios for neutral genetic differentiation. To

perform Bayescan run, 500,000 iterations, 10% burn-in period and a prior odd of 1,000 were used. To avoid the occurrence of false positives on outlier loci detection, using both pcadapt and BayeScan, a false discovery rate correction of q-values = 0.05 was used. The outliers detected by both approaches were eliminated from our final dataset that aims to highlight demographic isolation and assess connectivity patterns. After filtering, a final data set of 20,778 neutral SNPs genotyped at 143 individuals was obtained.

2.4 Genetic diversity, population structure and gene Flow

The genetic diversity estimations were made by sampling locations. Expected (H_e) and observed heterozygosity (H_o) and allele frequencies were estimated with Genodive v.3.05 (Meirmans, 2020). Using HP-rare 1.0 software (Kalinowski, 2005), private alleles among genetic clusters were calculated.

Population structure was inferred using different approaches. First, pairwise F_{ST} comparisons among localities were calculated using Genodive v.3.05 (Meirmans, 2020), significance levels were estimated using 10,000 permutations. For F_{ST} calculations, the SIG and GRE localities were eliminated from the dataset, due to the low number of individuals. Supervised discriminant analysis of principal components (DAPC) was performed in adegenet R package (Jombart et al., 2010), using the information of the geographical origin of each individual, to identify genetic clusters. The function optim.a.score() was used to estimate the

optimal number of PCs to retain for the DAPC, here 14 PCs were retained. To select the optimal number of clusters, the function find.cluster() was used to estimate k-means with the Bayesian information criterion (BIC). To evaluate the probability of assignment of an individual to a genetic cluster, Structure 2.3.4 software was used (Pritchard et al., 2000). This program is based on a Bayesian clustering approach to both identify populations from the dataset and assign individuals to one or more of these populations. This analysis begins by randomly assigning individuals to a preset number of clusters (or population), then the program estimates allele frequencies for each group to base on those estimations and make a re-assignment of the individuals. Specifically, 10 replicates were run in parallel using Strauto (Chatre and Emerson, 2017), with 200,000 MCMC and 10% burn-in. The optimal k values for Structure were estimated using Evanno's method (Evanno et al., 2005) and ln(Pr(X|K) values, to identify the k for which Pr(K=k) is highest (Pritchard et al., 2000). Different k values (e.g. different clustering results), with a biological meaning were considered to discuss (Porras-Hurtado et al., 2013; Meirmans, 2015). Then, conStruct R package (Bradburd et al., 2018) was used to test the effect of isolation by distance on genetic variation. This analysis incorporates the spatial location of each individual and the geographical distance between them to test isolation by distance patterns. With conStruct it is possible to estimate both discrete (nonspatial assignment model, like Structure) and continuous (including spatial information) patterns of population structure (Bradburd et al., 2018). Three independent chains with three layers and 10,000 iterations were run. The contribution of each layer was

calculated using cross-validation runs. The function compare.two.runs() was used to compare the runs of the three independent analyses.

The results of the population structure analyses and a geographical criteria were used to identify genetic clusters and test gene flow among them. Using BA3-SNPs (Mussman et al., 2019), a modified version of BayesAss 3.04 (Wilson and Rannala, 2003) for next-generation sequence data, contemporary migration rates between clusters were estimated. Bayesass implements a Bayesian method to assign individuals to populations (or genetic clusters) and identify migrants. With fewer assumptions than long-term gene flow estimations, this analysis can be applied to populations that are not in genetic equilibrium. This program allows the relaxation of the assumption that genotypes are in Hardy-Weinberg equilibrium within populations (Wilson and Rannala, 2003). The recent migration rates between clusters were estimated using 500,000 iterations and 10% burn-in period. The default values of mixing parameters, i.e., migration rate, allele frequencies and inbreeding coefficients, were used for the BA3-SNPs run. Additionally, HP-rare 1.0 software (Kalinowski, 2005) was used to detect private alleles among genetic clusters.

2.6 Influence of distance and larval dispersal on genetic variation

2.6.1 Geographic distance

The geographic distance between pairs of sampling sites were converted to distance-based Moran's eigenvector maps (dbMEM). First the latitude and longitude data were transformed into cartesian coordinates with the SoDA R package (Chambers, 2008). From this, a Euclidean distance matrix was generated using the function dist() from vegan R package (Oksanen et al., 2020). Using this matrix, the dbMEM vectors were created with the function dbmem() from adespatial R package (Dray et al., 2006; Legrendre and Legendre, 2012).

2.6.2 Larval dispersal

To quantify larval dispersal, as described above, a biophysical model was used. From the connectivity matrix, the probability of connectivity between locations (through larval dispersal) was calculated for each pair of sampling sites. These proportions of migrant individuals were converted to Asymmetric Eigenvector Maps (AEM). The AEM vectors are similar to dbMEM vectors, but this method considers the directionality of some spatial processes that can influence species distribution at different scales, such as larval dispersal modulated by ocean currents (Blanchet et al., 2008). Pairwise dispersal probabilities were converted into a site-by-edge binary matrix, where two sites were considered connected when the dispersal probability value was > 0 (Boulanger et al., 2021). From this matrix, the AEM vectors were calculated using the function aem() from adespatial R package (Dray et al., 2006; Legendre and Legendre, 2012).

2.6.3 Contribution of the variables to genetic structure

To determine the contribution of the geographical distance (dbMEM) and the larval dispersal (AEM) to the neutral genetic structure, a Redundancy Analysis (RDA) was performed in the vegan 2.5-7 R package (Oksanen et al., 2020). For this analysis, genotype data were standardized using the function decostand(), Hellinger's method, from vegan. Starting with all variables (all dbMEM and AEM vectors), ordistep() function was used in vegan, to determine the optimal model, using a forward selection procedure. Significance for each variable was evaluated with a marginal ANOVA test with 10,000 permutations. All the selected variables after this step were tested in a full RDA model.

Finally, two partial Mantel test were performed in the vegan 2.5-7 R package (Oksanen et al., 2020): (1) between genetic distance and geographical distance, using larval dispersal as covariate and (2) between genetic distance and larval dispersal, using geographical distance as a covariate. The genetic distance corresponded to the F_{ST} matrix (described above). The geographical distance was calculated from the coordinates of each sampling site, transformed to a Euclidean distance matrix. For the larval dispersal, the AEMs vectors were transformed to a Euclidean distance matrix. To estimate the relationship between these matrices (genetic distance, geographic distance and larval dispersal) all values were first standardized using the function (x-mean(x)/SD(x)). After the partial Mantel test, a Multiple Matrix Regression with Randomization Analysis or MMRR (Wang, 2013)

was performed in the package PopGenReport (Adamack and Gruber, 2014; Gruber and Adamack, 2015), to estimate the relative contribution of geographic distance and larval dispersal to genetic differentiation. Then, a regular Mantel test was conducted between the genetic distance and the joint effect of geographic distance and larval dispersal.

Both for RDA and partial Mantel tests, only seven localities were considered: FIB, CHB, DIS, BST, FHA, DOI and AIS, because all of them were included both in genomic analysis and biophysical modeling.

3. Results

3.1 Potential connectivity from the biophysical model

The mean trajectory matrix shows that the particles released in South Shetland Islands (SSH) seem to be transported mainly to the north. On average, the path traveled by the particles released in this area revealed that they are not transported to other regions of the WAP (Fig. 2a). No particles originated in the SSH have the potential to settle in other regions of the WAP (Fig. 2b). Nevertheless, according to the biophysical model, this area would not be completely isolated from the rest of the peninsula. A small proportion of particles from BST, FHA and DOI showed mean trajectories that include the SSH (Fig. 2a) and could have the potential to settle there (0.1-0.7%, Fig. 2b). For BST it

highlights that no particles from other localities passed through this area during the 100 days of simulation (Fig. 2a). Only a few particles released here spend time in their origin point, but none settle. On the other hand, this locality could be a source of individuals for other areas, such as SSH, FHA and even DOI in small proportion (Fig. 2b). At the central part of the WAP, FHA and DOI localities showed high values of particles that remain in their origin point and the highest levels of self-recruitment of this study (Fig. 2a and b). However, in the connectivity matrix FHA and DOI showed a potential exchange of individuals, with a predominant northern flow, 3% of the particles from DOI potentially settle at FHA. In the case of the southern region of the WAP (AIS, MOT and MIN localities), at Marguerite Bay, an isolation pattern was observed. The particles released here showed mean trajectories including only AIS, MOT and MIN, no potential transport was detected from any of the other localities (Fig. 2a). Also, the particles released in these three localities would not have the potential to disperse northward. Nevertheless, within Marguerite Bay, the highest levels of potential dispersal were registered, from AIS to MIN (8.7%) and from MIN to MOT (3.5%, Fig. 2b).

3.2 Effective connectivity from population genomics

After a successful SNP calling, 22,529 SNP were obtained for *H. antarcticus* from the Antarctic Peninsula. A total of 515 SNPs were considered in HWE disequilibrium and then removed from the dataset. Using the population

differentiation analyses, a total of 1,236 SNPs were identified as candidates for local adaptation (1,231 with pcadapt and 304 with Bayescan, 299 were shared) and therefore, they were removed from the dataset. A total of 20,778 neutral SNPs were used to estimate population structure and contemporary gene flow.

3.2.1 Population diversity and structure

Similar levels of genetic diversity were observed among sampling locations, the expected heterozygosity ranged from 0.280 (SIG) to 0.294 (BST) and the allele richness ranged from 1.328 (SIG) to 1.463 (BST) (Table 1). The pairwise F_{ST} ranged from -0.0001 to 0.011, all values were significantly different from zero, except for the comparisons between CHB-DIS, FHA-DOI and AIS-HOS (Fig. 3a). The dendrogram based on pairwise F_{ST} distances showed four clusters (Fig. 3b), one corresponds to South Shetlands Islands (FIB, CHB and DIS), BST alone, the central part (FHA, PLO and DOI) and the southern Antarctic Peninsula (AIS and HOS).

The DAPC showed the presence of three main genetic groups (Fig. 4a). The first one corresponded to the South Shetland Islands (FIB, CHB and DIS) and could include the locality of Bransfield Strait (BST). A second group including GRE, FHA, PLO and DOI at the central part of the Antarctic Peninsula. The third group corresponds to the southern localities, AIS and HOS.

Structure results were not in total agreement with DAPC, since this analysis detected the optimal number of groups could be around k=2 (Evanno's) and k=3 (ln(Pr(X|K)). The k=2, showed the predominance of one genetic group and a lack of admixture for the localities of BST, GRE and FHA, forming one homogenous cluster. At the south WAP, AIS appears as another location showing a lack of admixture and where a different genetic group predominates (Fig. 4b). On the other hand, considering an optimal k=3, the observed patterns are more likely DAPC results. It highlights the presence of genetic differentiation of BST and AIS, both with low levels of admixture (predominance of blue and red color, respectively, Fig. 4b). In addition, a third cluster, formed by localities at the central region of the WAP (including GRE, FHA, PLO y DOI) appears with the highest contribution of a third genetic group (in orange). The conStruct results, similarly, to Structure, showed the genetic differentiation of BST, the predominance of a genetic group in AIS (in red) and in the central region (in orange) (Fig. 4c). Both in Structure and conStruct, the results showed similar patterns of admixture for AIS and SIG, dominated by the same genetic group (Figs. 4b and 4c), but this result should be taken with caution, because of the low number of individuals for SIG locality.

3.2.2 Gene flow

Considering the results of the different genetic structure analyzes and a geographic criteria, for gene flow estimations the dataset was subdivided in five

clusters: Signy Island alone (SIG), one with all the South Shetland locations (SSH), another with only Bransfield Strait (BST), a group for the central region (CAP), with GRE, FHA, PLO and DOI, and finally a cluster for the southern region (SAP), grouping AIS and HOS locations. Low levels of contemporary gene flow between these groups were determined by BayesAss (Fig. 4c). Nevertheless, no private alleles were detected using HP-rare, either by comparison of genetic groups or sampling locations. The SIG may be a location that receives at least a 4% of immigrants from all other sampling locations (Fig. 4c).

3.3 Spatial and oceanographic drivers of connectivity

For the final RDA model four Moran Eigenvector Maps vectors were retained (dbMEM1, dbMEM2, dbMEM3 and dbMEM6), which reflect spatial influence, and two larval dispersal vectors (AEM2 and AEM5), which reflect ocean current, based on the selection procedure. The dbMEM6 and AEM2 showed no significant contribution in the full RDA model (Table 2). Nevertheless, the full RDA was globally significant ($p < 0.001$), the included variables explained 6.5% of genetic variation. The first two RDA axes were significant ($p < 0.001$), accounting for 1.86% (RDA1) and 1.24% (RDA2) of the overall genetic variation (Fig. 5). The two AEM vectors and dbMEM2 are related to the separation of DOI (at the central AP, Fig. 5), while dbMEM3 is associated with the differentiation of CHB along the first and second RDA axes (Fig. 5).

The partial Mantel test between genetic distance and geographic distance, controlled by larval dispersal, was highly significant ($R = 0.622$, $p < 0.05$; Fig. 6a). To estimate the effect of larval dispersal, only the AEM5 vector was used for the partial Mantel test, because it was the only one showing significant contribution to the full RDA model (Table 2). However, the analysis using larval dispersal as a response variable, controlling by geographic distance, did not show significant relationship ($R = 0.085$, $p = 0.312$; Fig. 6b). The AEM5 vector was included for the MMRR analysis to determine the joint effect with geographic distance on population differentiation. Nevertheless, the regular Mantel test, using the weighted effect of geographic distance and larval dispersal (through MMRR) as one variable, showed that the addition of the latter did not have a great impact on the model fit ($R = 0.633$, $p < 0.05$; Fig. 6c).

4. Discussion

This study shows some congruent results between biophysical modeling and population genomics. Lagrangian simulations highlighted the presence of dispersal barriers for *H. antarcticus* larvae, which could be generating the observed population structure and a lack of connectivity between different regions inside the Western Antarctic Peninsula. The observed connectivity patterns could be explained considering local oceanographic conditions. Previous studies reported that the complex circulation patterns and the local hydrographic conditions inside the WAP promote retention at the inner shelf and limit

connectivity (Piñones et al., 2011, 2013). Furthermore, in a recent study, Gallagher et al. (2023) indicated that ocean currents may play a key role limiting inter-region connectivity at the WAP, isolating krill populations between Low Island and Bransfield Strait. Also, Parker et al. (2015) described changes in faunal composition and shift in dominant taxa, associated with different hydrographic regimes along the WAP shelf. These authors separate the WAP in four regions, according to oceanographic conditions and fauna: (I) the northern peninsula, including the South Shetland Islands and the Bransfield Strait, (II) the northern middle peninsula (Palmer-Renaud) community, (III) the southern middle peninsula community including the Marguerite Bay system and (IV) the southern peninsula (Charcot Island) community, from Lazarev Bay on the north and to the south of Charcot Island. Regions I to III in Parker et al., (2015) coincide with the three major groups detected here for *H. antarcticus*.

The genomic analyses showed the differentiation of at least three groups for *H. antarcitus* along the WAP. The first corresponds to the SSH (FIB, CHB and DIS) and BST, grouped in the DAPC but separated in F_{ST} and structure analyses. A potential larval transport from BST to SSH, but not in the opposite direction, was observed in the biophysical model. This is consistent with the circulation patterns described for the Bransfield Strait, where the Bansfield current flows southward and reaches the southern slope of the SSH, then the current change direction and flow to the northeast and the waters are recirculated around the SSH (Sangrá et al., 2017, Moffat and Meredith, 2018). Yet possible, the BayesAss results showed

low levels of contemporary gene flow from BST to SSH (1%, not shown in Fig. 3). A small proportion of particles originated in BST potentially settle in SSH, even so, gene flow is insufficient to avoid population differentiation. The anticlockwise recirculation of water around SSH could explain why the particles released there showed mean trajectories and potentially settle only inside this group of islands.

A second genetic group, the central part of the WAP (GRE, FHA, PLO and DOI), was identified by F_{ST}, DAPC and structure (k = 3) analyses. In the biophysical model output, particles released in FHA and DOI showed mean trajectories predominantly in their origin location and one of the highest proportions of potential dispersal was observed from DOI to FHA. Possible explanation for high levels of self-recruitment and low levels of gene flow between the central WAP and the rest of the peninsula may be the presence of shallow areas with weak circulation near Anvers Islands. Moffat and Meredith (2018) suggested that these shallow areas could act as retention areas with long residence times. Between Anvers and Adelaide Islands at least four large submarine banks have been described, promoting the existence of possible retention areas that may impede high levels of larval exchange (Moffat and Meredith, 2018). Nevertheless, a small proportion of particle connectivity was detected by the biophysical model from localities at central WAP (FHA and DOI) to SSH. This potential transport could be possible through the Gerlache Strait where the APCC flows towards the southern Bransfield Strait, then the particles could be advected to the SSH (Niiler et al., 1991; Zhou et al., 2002; Moffat and Meredith, 2018). But again, this potential larval transport is insufficient to maintain genetic connectivity between the central WAP

and the SSH, which is reflected in the low contemporary gene flow between these two areas (< 1%, not shown at Fig. 3).

The third genetic group observed (SAP), corresponds to AIS and HOS localities at Marguerite Bay. The Marguerite Bay system is characterized by a cyclonic circulation, where the APCC flows southward along the coast (Piñones et al., 2011; Moffat and Meredith, 2018). It has been described that the Laubeuf Fjord, located south of Adelaide Island (inside Marguerite Bay) is relatively isolated (Piñones et al., 2011). Studies of Lagrangian particles tracking revealed that this is an area of local retention, with long residence times (Piñones et al., 2011). These characteristics may explain why particles, representing *H. antarcticus* larvae, released at Adelaide Island and the inner part of Marguerite Bay (MIN) showed mean trajectories only inside this region. The potential larval transport follows the predominant current direction to the south, generating the highest proportion of connectivity between AIS and MIN. However, the SAP region may not be completely isolated. It is interesting that the same dominant genetic group is present in AIS and SIG, which could be caused by a weak but existing outflow northward along the southeast bank of Marguerite Trough (Moffat and Meredith, 2018). According to regional models this outflow originates near MOT location (in present study) and could reach the Southern ACC Boundary (Dinniman and Klinck, 2004; Piñones et al., 2010; Moffat and Meredith., 2018). This could explain the lower particle exchange between MOT and the other localities inshore Marguerite Bay (AIS and MIT). Reaching the ACC, potential larval migration from

Marguerite Bay to the north could facilitate the transport of *H. antarcticus* larvae offshore, to SIG. Nevertheless, although possible, these results have to be taken with caution, considering the low number of individuals of SIG sampled in this study. This requires further investigation.

This is one of the few studies giving evidence of neutral population structure and limited levels of gene flow inside the WAP. Previous reports of population differentiation were made in other Antarctic fishes with similar or longer PLDs, but mostly between WAP (as a group) and other localities in the eastern Antarctic Peninsula, and the islands in the Scotia Sea (South Orkney Islands, South Sandwich Islands and South Georgia, e.g. Young et al., 2015, 2018). Agostini et al. (2015) discarded panmixia and detected significant genetic differentiation between the south-western and the northern tip of WAP in *Pleuragramma antarctica* using microsatellites. These authors also attributed the low levels of gene flow between these two regions of the WAP to local oceanographic conditions in Marguerite Bay and the presence of gyres that would favor the local retention of planktonic organisms (Piñones et al., 2011 Agostini et al., 2015). The results of the present study highlight the importance of combining different approaches to determine connectivity in the WAP and contrasting patterns for different species. The limited connectivity between regions inside WAP and the identification of source/sink contributions, associated to shelf dynamics or isolated localities, are important features for establishing conservation priorities with implications for the Marine Protected Areas proposed for the Antarctic Peninsula

in the last decade.

Although the estimated effect of the oceanographic currents (AEM vectors) on the observed population structure was low, the RDA showed a significant relationship. The local oceanographic conditions of different regions inside WAP seems to influence clustering in *H. antarcticus* populations. The relationship is more evident when visually comparing the biophysical and population genomics outputs (e.g. as DAPC), and contrasting the results with the available evidence of hydrography in WAP. The low percentage of variance explained by larval dispersal, in the RDA, could be explained because not all the localities included in the present study have available information for both biophysical and genomics analyses. Thus, the influence of local oceanographic conditions on genetic variation could be underrepresented. In addition, it must be considered that the pelagic larval duration for *H. antarcticus* is not entirely clear. Different authors described PLDs from three to four months (e.g. White and Burren, 1992; La Mesa et al., 2017). Here a 100 days period was established to estimate larval dispersal among localities. This assessment was made considering that metamorphosis and consequently the settlement occur around 23-27 days post hatching (White and Burren, 1992), after a relatively short PLD (La Mesa et al., 2017). Changing the PLD could also affect the adjustment of the biophysical model to the genetic structure observed.

Apparently, considering the partial Mantel test results, the geographic distance

has a greater effect on the population structure of *H. antarcticus*. The genetic differentiation (represented by F_{ST} values) is higher as distance between localities increases. In this case, the incorporation of dispersal vectors in the partial Mantel test had no significant effect. Therefore, the gene flow could be spatially limited for *H. antarcticus*, confirming an isolation by distance pattern for this species inside the WAP. However, it should be considered that the local oceanographic conditions vary following latitude. As described above, predominant ocean currents flow differently at the northern, central and southern parts of the WAP. In consequence, it is difficult to separate completely the effect of geographic distance and local oceanographic conditions on genetic differentiation in this area. Besides, the dispersal vectors (AEM vectors) used in partial Mantel were the same used in the RDA and therefore could be subject to the same adjustment problems.

Finally, our results are similar to what has been described previously for conspecifics. Genetic structure and limitations for contemporary gene flow has been reported for *Harpagifer bispinis* at the Magellan Province (Segovia et al., 2022). This consistent pattern of population differentiation and restrictions to connectivity may also be associated with the biology and ecology of Harpagiferidae. Benthic adults with poor swim capabilities with low buoyancy (Fernández et al., 2012), low fecundity and benthic eggs, and a shorter larval pelagic period (compared to other Notothenioids, see Kellermann, 1989; North, 1991) may decrease individual exchange (Segovia et al., 2022). The

characteristics of *Harpagifer* spp. and the complex ecosystems they inhabit would allow patterns of genetic structure and limited gene flow.

Figures

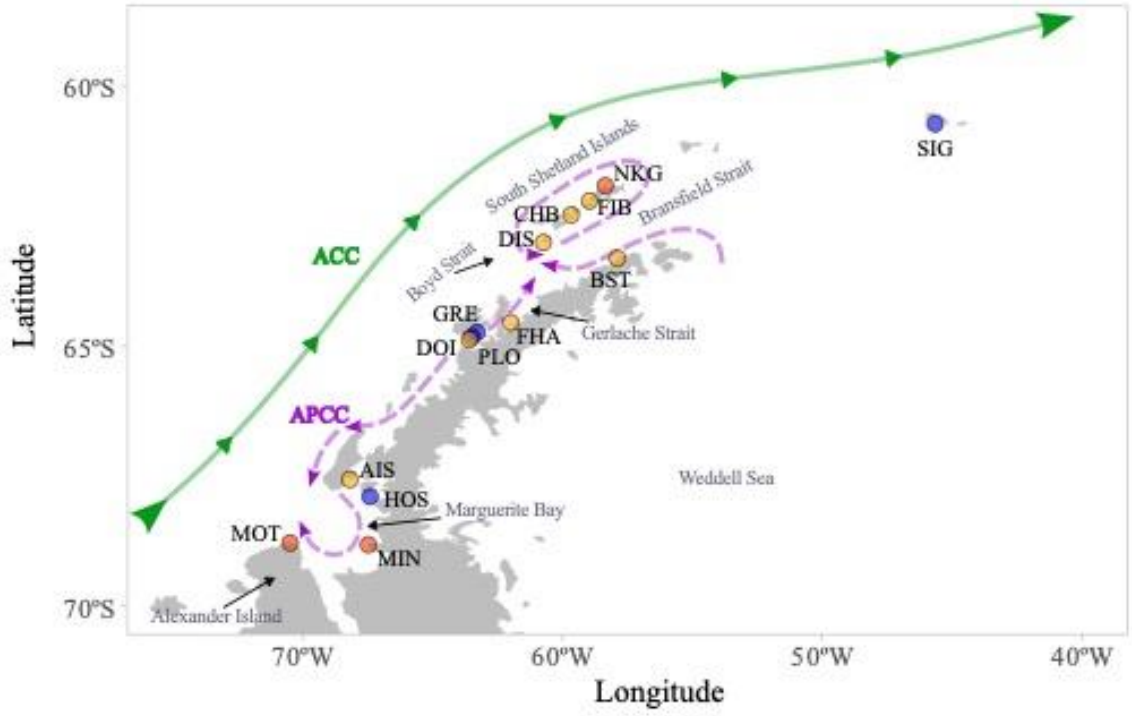

Figure 1. Sampling sites for *H. antarcticus* along the Antarctic Peninsula. Where SIG: Signy Island, NKG: North area of King George Island, FIB: Fildes Bay, CHB: Chile Bay, DIS: Deception Island, BST: Bransfield Strait, GRE: Green Reef, FHA: Foyn Harbour, PLO: Port Lockroy, DOI: Doumer Island, AIS: Adelaide Island, HOS: Horseshoe Island, MOT: offshore Marguerite Bay and MIN: inshore Marguerite Bay. Yellow circles represent localities with genetic data that were included in the biophysical model. Blue circles are localities with only genetic information. Red circles are localities that were included in the biophysical model to simulate possible stepping-stone connectivity, but for which there is no genetic information.

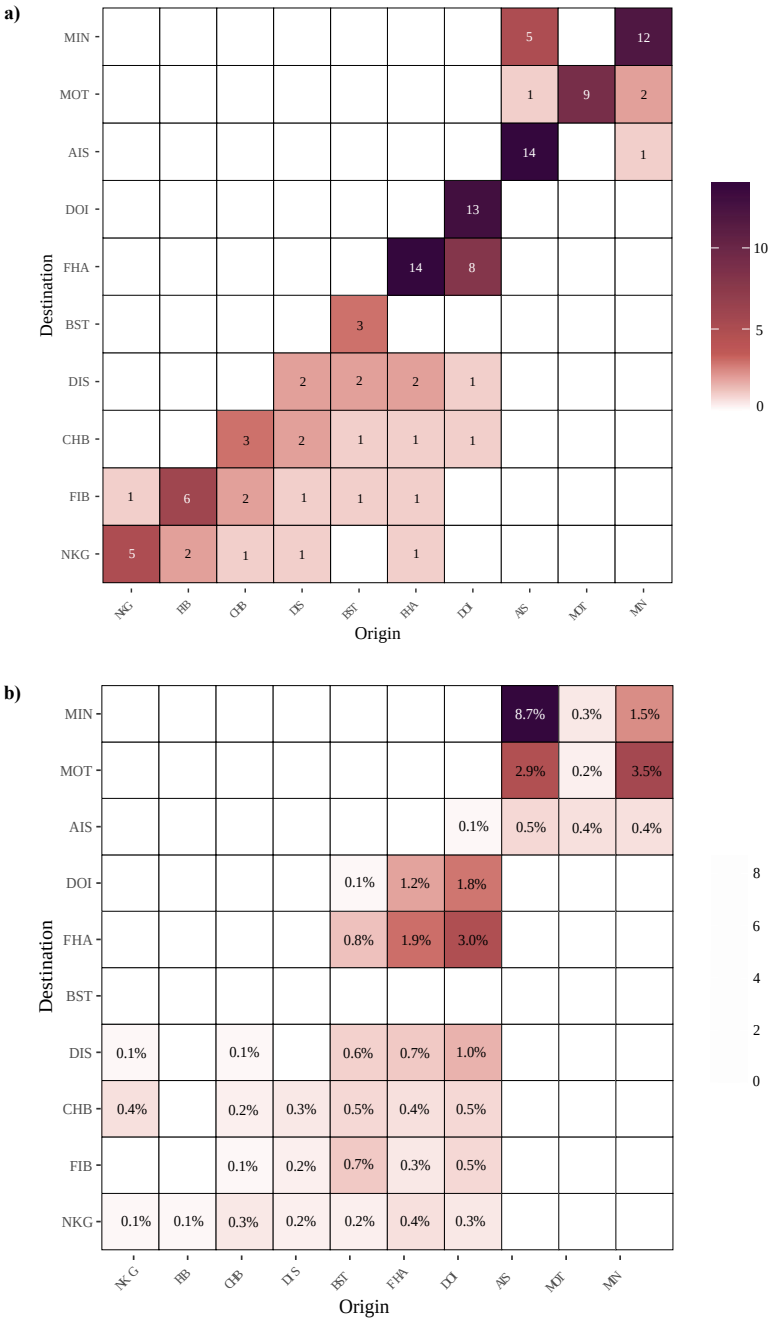

Figure 2. Biophysical model results, where (a) corresponds to the mean trajectory matrix (T), representing the trajectory that the particles traveled during 100 days in 10 releases (10 runs of the model), and (b) corresponds to the connectivity matrix (C), the final scenario at day 100, from biophysical modeling of *H. antarcticus* larval dispersal.

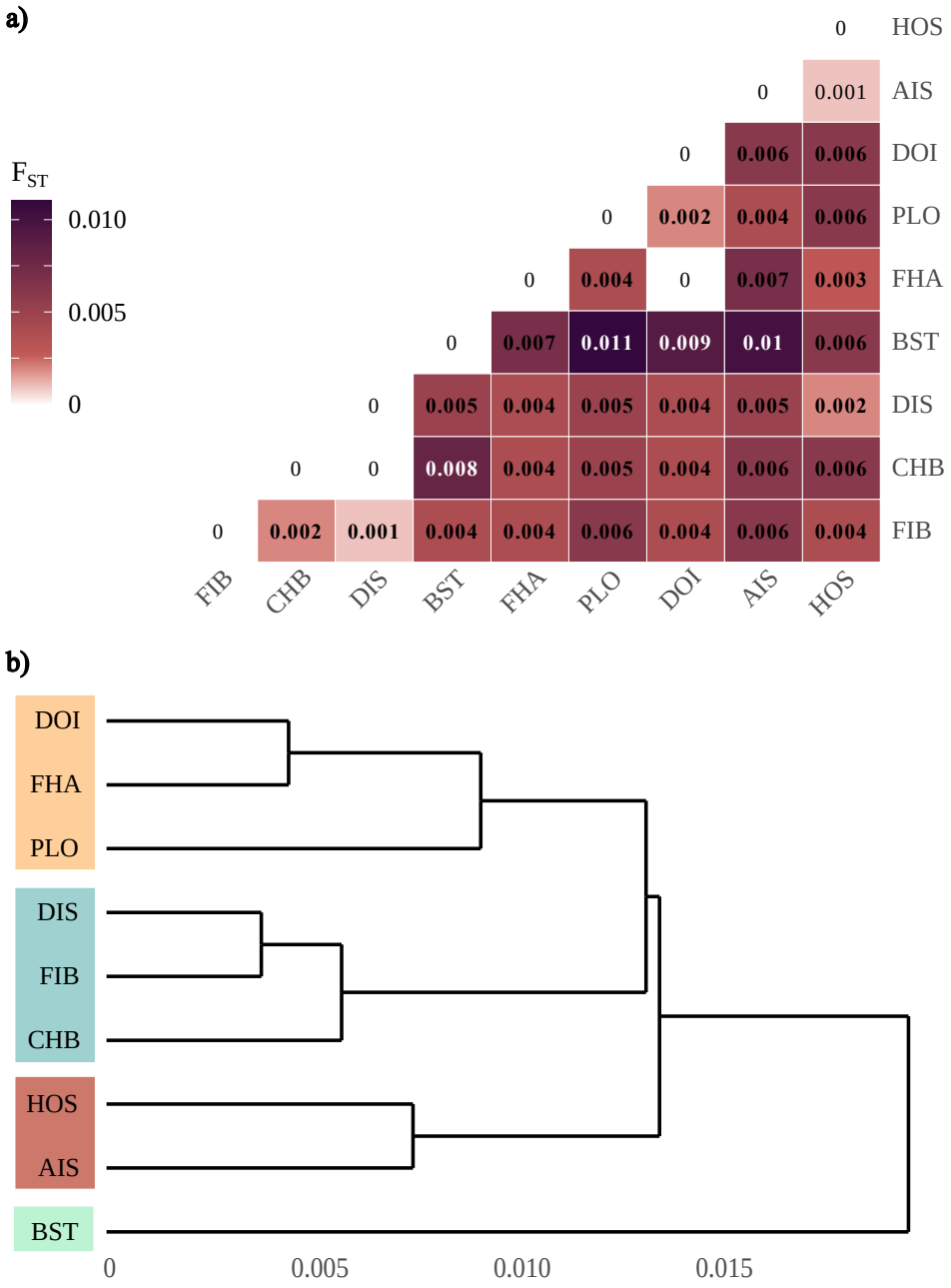

Figure 3. Pairwise F_{ST} comparisons among localities, based on 20,778 neutral SNPs, where (a) corresponds to the F_{ST} matrix and (b) corresponds to a dendrogram based on pairwise F_{ST} distances. Significant values are shown in bold.

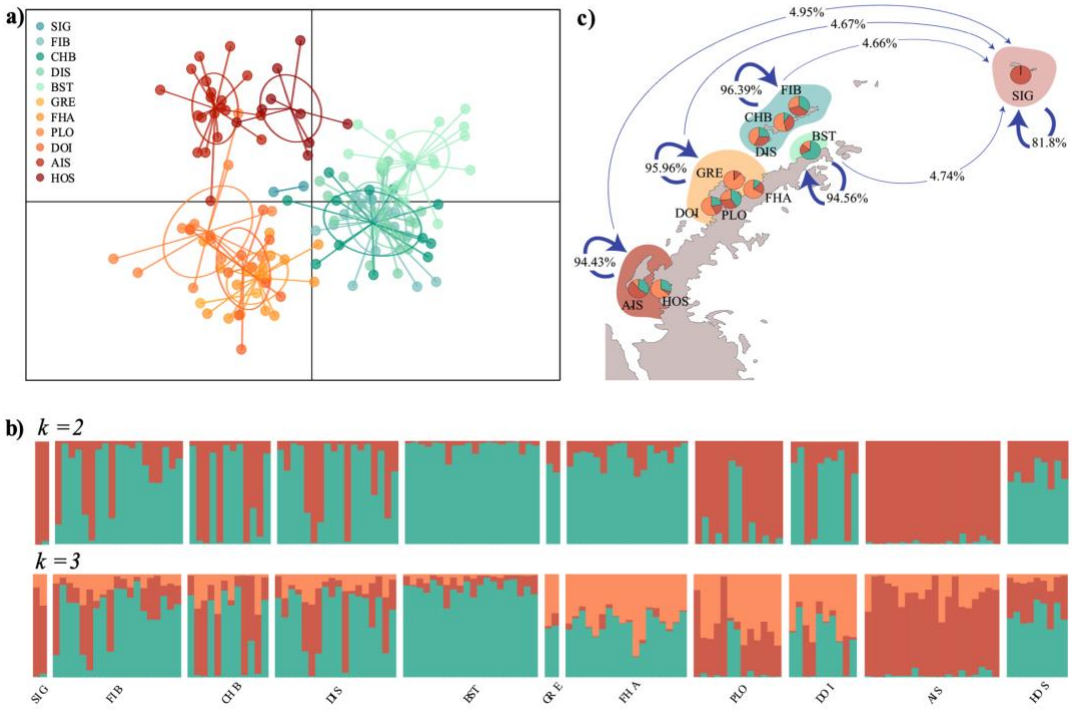

Figure 4. Genetic structure of *H. antarcticus* along the Antarctic Peninsula. Where (a) corresponds to the scatter plot of DAPC showing the first two axes, (b) the Structure results with optimal k = 2 and k = 3, and (c) shows pies with the average admixture proportions in each location from conStruct results and the gene flow estimations from BayesAss, considering five clusters (values below 4% are not shown). Arrow directions show asymmetrical migration and their thickness represent the proportion of migrants individuals.

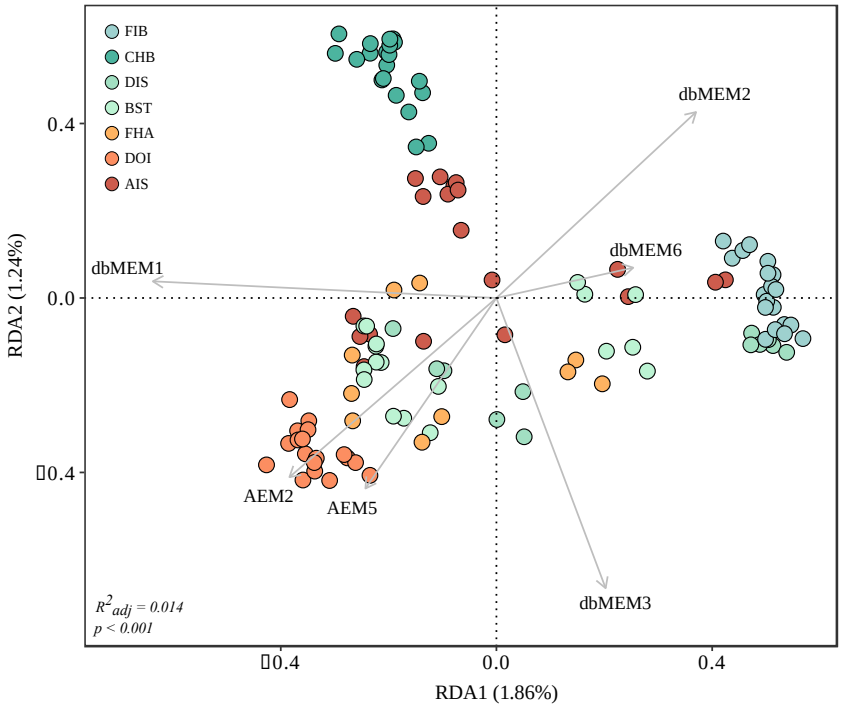

Figure 5. Redundancy analysis (RDA) biplot for neutral loci of *H. antarcticus*. Where dbMEM are distance-based Moran Eigenvector Maps representing geographical isolation and AEM are Asymmetric Eigenvector Maps representing isolation by potential larval dispersal. Arrows represent these selected variables (after model optimization) that drive the observed genetic variation.

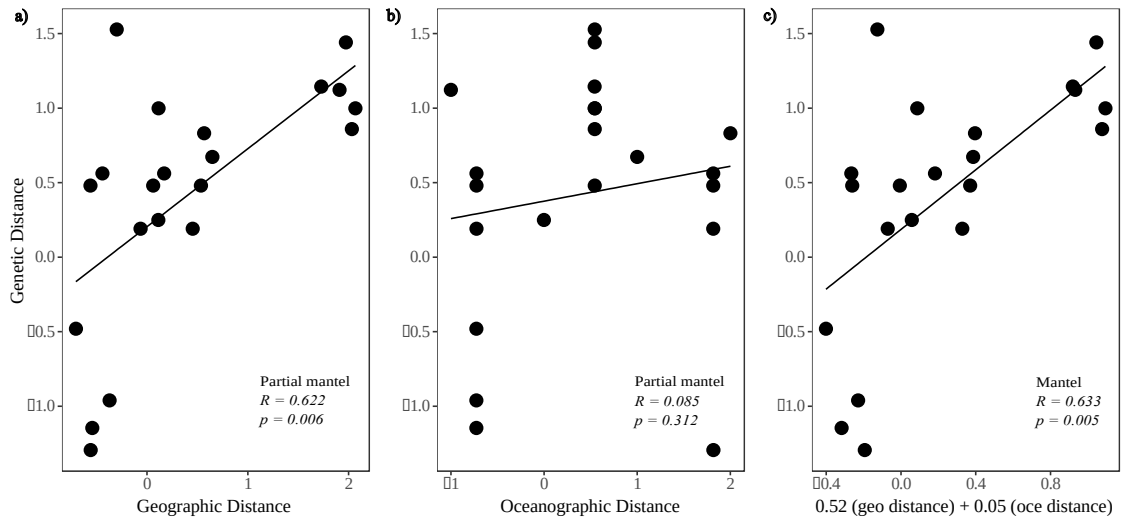

Figure 6. Scatter plots showing (a) partial mantel test between genetic distance and geographic distance (using oceanographic distance as covariate), (b) partial mantel test between genetic distance and oceanographic distance (using geographic distance as covariate) and (c) the joint effect of geographic and oceanographic distance, based on the results of a Multiple Matrix Regression with Randomization analysis (MMRR).

Tables

Table 1. Genetic Diversity for SNP-GBS of *H. antarcticus*, showing the acronyms for each locality (POP), number of individuals (N), effective number of alleles (Al), observed (Ho) and expected (He) heterozygosity and inbreeding coefficient (Gis).

POP	N	Al	Ho	He	Gis
SIG	2	1.328	0.165	0.280	0.413
FIB	9	1.430	0.166	0.288	0.424
CHB	12	1.437	0.164	0.287	0.428
DIS	18	1.449	0.184	0.289	0.364
BST	20	1.463	0.246	0.294	0.164
GRE	2	1.347	0.195	0.291	0.330
FHA	18	1.445	0.167	0.288	0.419
PLO	13	1.437	0.167	0.285	0.416
DOI	10	1.437	0.184	0.289	0.362
AIS	20	1.446	0.169	0.285	0.406
HOS	9	1.450	0.240	0.293	0.183

Table 2. Results of Redundancy Analysis (RDA), showing the contribution of each geographical distance (dbMEMs) and larval dispersal (AEMs) variables included in the full model. Significant values are shown in bold.

Variable	Variance	F	p-value
dbMEM1	0.00979	1.7722	**0.001**
dbMEM2	0.00760	1.3757	**0.001**
dbMEM3	0.00763	1.3816	**0.001**
dbMEM6	0.00587	1.0624	0.061
AEM2	0.00570	1.0314	0.135
AEM5	0.00591	1.0704	**0.043**
Residuals	0.60756		

Supplementary material

Table S1. Sampling sites of *H. antarcticus*, along the Western Antarctic Peninsula.

Site	**Longitude**	**Latitude**
SIG	-45.6610	-60.7273
FIB	-58.9537	-62.2094
CHB	-59.6708	-62.4788
DIS	-60.7357	-63.0073
BST	-57.8855	-63.3091
GRE	-63.2821	-64.7349
FHA	-61.9900	-64.5467
PLO	-63.4955	-64.8252
DOI	-63.5836	-64.8759
AIS	-68.1853	-67.5642
HOS	-67.4048	-67.8924

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CAPÍTULO II

Contrasting the influence of geographic distance and environmental variation on the population structure of *Harpagifer antarcticus* in the Western Antarctic Peninsula and South Georgia

1. Introduction

In the last decade evidence of population structure and local adaptation has increased for many marine species (Selkoe et al., 2014; Nielsen et al., 2020). The establishment of environmental variation representing a barrier to gene flow is gaining support in different marine systems and organism (Benestan et al., 2016; Bernatchez et al., 2019; Nielsen et al., 2020; Pertierra et al., 2020, Benestan et al., 2022). Determining the influence of environmental conditions on the genetic structure and possible local adaptation patterns is essential for species conservation, also considering the global change effects in marine ecosystems (Narum et al., 2013; Razgour et al., 2018; Nielsen et al., 2020; Benestan et al., 2022).

The advances in Next Generation Sequencing (NGS) and genomic tools have allowed the expansion of seascape genomics field (Gagnaire and Gaggiotti, 2016; Selkoe et al., 2016; Nielsen et al., 2020), which has among of its main goals (and advantages) the differentiation of putatively neutral and adaptive variation (Balkenhol et al., 2019, Nielsen et al., 2020). Using NGS methods, it is possible to identify candidate loci that differ significantly over environmental gradients by

looking for associations between allele frequencies with environmental variables (Rellstab et al., 2015 Riginos et al., 2016; Forester et al., 2018; Nielsen et al., 2020). This outlier loci could provide information on the adaptive populations structure and local adaptation processes (Capblancq et al., 2020; Rellstab et al., 2015; Schoville et al., 2012). The seascape tools allow us to determine the influence of environmental variation on specie's genomic patterns (Boulanger et al., 2021), in different ways, such as: environmental gradients acting as barriers that reduce gene flow (e.g. Stanlet et al., 2018), local environmental conditions generating selective pressures and local adaptation (Manel and Holderegger, 2013; Dayan, 2018) and environmental differences that impede gene flow and colonization of new habitats (Manel et al., 2020; Boulanger et al., 2021). The better understanding of the different processes that shape the genetic variation of marine species is fundamental to delimit relevant conservation units, their adaptative potential and therefore how vulnerable they are in face of climate change (Gagnaire et al., 2015; Benestan et al., 2019; Capblancq et al., 2020; Boulanger et al., 2021).

The Southern Ocean (SO) ecosystems are among the most susceptible to be affected by climate change (Schofield et al., 2010; Constable et al., 2014; Henley et al., 2020). It is expected that the SO experiments a series of different oceanographic and environmental changes in the next decades, that will affect de ecology of the organisms inhabit here (Constable et al., 2014; Rogers et al., 2020). Therefore, it is relevant to know how species of SO interact with current

climatic conditions and the habitat that surrounds them, to improve our understanding for their conservation and how they could be affected by variations in the future.

At the Southern Ocean, the Western Antarctic Peninsula (WAP) and the South Georgia Island (SGE) are the most studied regions in terms of ecosystems dynamics. There is vast information of oceanographic and ecologic processes occurring in these areas, which allows comparison studies at different levels (Murphy et al., 2013). The WAP extends from about 61ºS at the north to 75ºS at the south and the SGE region, considering shelf and oceanic areas, extends from around 53-56ºS and 34-44°W (Murphy et al., 2013). The major physical differences between WAP and SGE are related to large-scale process in the Southern Ocean (Murphy et al., 2013). Even though both lie below the polar front, the Antarctic Circumpolar Current (ACC) impacts differently. At the WAP, the ACC flows along the shelf break, while at SGE the ACC flows around the island. This means that WAP is located south of the Southern ACC Front (SACCF) and SGE at the north of the SACCF (Murphy et al., 2013). The topography and bathymetry of both regions also differ. Along WAP there are zones deeper than SGE that connect inshore to oceanic waters and allow intrusions of deep waters, but also several island occurring along the coast may restrict the exchange offshore in other areas (Murphy et al., 2013 and references there in). While at SGE, the northward deviation of the ACC generates upwelling areas and mesoscale eddies, the flow disperses materials to the north, affecting the physical, chemical

and biological dynamics (Murphy et al., 2013 and reference there in).

There is marked seasonality differences of the environmental conditions, linked to latitude differences between these WAP and SGE regions. One example is the seasonal patterns of sea surface temperature (SST). In the WAP, during summer conditions, the SST is usually above 0º, with a peak in February around 1 ºC (which ranged from − 1.5 to 2.5 ºC) (Murphy et al., 2013). During the same month (February), at SGE the mean maximum SST is around 3.5 ºC and can exceed 4 ºC (Murphy et al., 2013). A marked difference occurs in late autumn and winter conditions, when the SST at WAP is usually around -1 ºC and a great portion of this region is covered by ice (generally between June and November). While, during the same season, the SST range is around 2 ºC at SGE, with a monthly minimum mean of 0.2 ºC (Murphy et al., 2013). There is no seasonal advance and retreat of sea ice at SGE, because SGE is located north of the limit of the sea ice zone (Murphy et al., 2013).

Both regions have been described as areas of enhanced primary productivity and chlorophyll a, due to the upwelling occurrence and iron enrichment (Atkinson et al., 2004; Arrigo et al., 2008; Murphy et al., 2013). During spring and summer, extensive phytoplankton blooms dominated by diatoms, have been described for both WAP and SGE (Whitehouse et al., 1996a; Whitehouse et al., 2000; Garibotti et al., 2003; Korb and Whitehouse, 2004; Murphy et al., 2013). In contrast, low levels of primary productivity predominate during winter conditions in both

regions, associated to storms, low light levels and the presence of ice cover. The last one particularly for WAP, where the low primary productivity period is longer than in SGE (for 2 to 3 months) (Atkinson et al., 2001; Stammerjohn et al., 2008).

Although WAP and SGE have been described as part of a large-scale continuum ecosystem, there is consistent evidence of environmental variation. The marked seasonality (associated to latitude differences) generates a gradient from colder, more ice covered and shorter periods of high primary productivity areas (WAP), to warmer open waters, free of sea ice and longer periods of phytoplankton blooms (SGE) (Murphy et al., 2013). Considering this information and the large extension of the WAP-SGE system (> 2000 km), this an interesting area to study population structure and the effect of spatial and environmental variability on these patterns.

There are previous reports of marked genetic structure between the WAP and SGE regions. Significant population differentiation patterns have been described for notothenioid fishes, as *Champsocephalus gunnari* (Young et al., 2015, 2018) and *Chaenocephalus aceratus* (Damerau et al., 2014), and invertebrates such as the sea star *Glabraster antarctica* (Moore et al., 2018) and *Nacella concinna* (González-Wevar et al., 2013). Damerau et al. (2014) suggested potential constraints to gene flow due to local adaptation processes occurring in these areas. On the contrary, Young et al. (2015) mention that there is little evidence to support isolation by adaptation. Nevertheless, none of these studies explicitly

includes analyzes to determine local adaptation patterns, leaving open questions of the role of environmental variation in the observed genetic differentiation, and proposing the need of further investigation of locally adapted populations in the WAP-SGE system.

Fishes from the genus *Harpagifer* are small benthic species, commonly found on rubble bottom habitats in intertidal pools and cobble substrate coves (Daniels and Lipps, 1982, White and Burren, 1992). The Harpagiferids are considered as low fecundity fishes that present a well described nesting guard behavior (Daniels, 1978, 1979; White and Burren, 1992). Also, the adults have very poor swim capabilities, due to the low buoyancy (Fernández et al., 2012). Thus, the only way to disperse and connect local population is through their larval planktonic stages. Due to their history life traits, their interaction with the fragmented and complex ecosystems they inhabit, Harpagiferids will be susceptible to limitations of population gene flow which generates genetic structure (Segovia et al., 2022).

In the present study, we worked with *Harpagifer* from WAP and SGE. We include individuals of *H. antarcticus* from WAP and adjacent islands and individuals collected in SGE, previously described as *H. georgianus*. Here we considered *H. antarcticus* and *H. georgianus* as a single evolutionary unit, due to evidence provided by new genetic analyses with tradicional markers (COI, D-loop, ITS) and SNPs scattered throughout the genome (Segovia et al. in prep) With this information, i.e. no evidence of lineage divergence between *H. antarcticus* and *H.*

georgianus, we decided to considered hereafter our samples as only *H. antarcticus*, and we treated them as one species to perform seascape genomic analyses. The presence of the *H. antarcticus* in geographically widely separated locations which present environmental gradients, as WAP and SGE, may allow a significant effect of spatial and environmental variation on population differentiation and possible local adaptation patterns.

Applying seascape genomics approach, the goals of the present study were to (1) determine population differentiation (2) investigate the effect of spatial and environmental variation on genetic structure and (3) identify candidate SNPs potentially involved in local adaptation processes, in *H. antarcticus* along the WAP and SGE regions.

2. Materials and methods

2.1 Sampling

For genomic analyses, 146 individuals of *H. antarcticus* were collected by hand, from intertidal zone (on rubble bottom habitats) and through dives in shallow waters of 9 localities along Western Antarctic Peninsula and South Georgia Island, between 54.24ºS 36.63ºW and 67.89ºS 67.40ºW (Fig. 1), during austral summer conditions. All specimens were sacrificed following a bioethical protocol, prior preservation in 95% ethanol.

2.2 DNA extraction and SNP calling

DNA extractions were done using the DNeasy Blood® and Tissue Kit (QIAGEN®, USA). The quantity and integrity of DNA were measured using Qubit 4 (Thermo, USA). The SNPs were obtained from Genotyping-by-Sequencing (GBS) method at the Biotechnology Center of the University of Wisconsin, using, after optimization, the ApeKI restriction enzyme. After enzyme digestion, each DNA fragment was linked to a barcode adaptor to recognize it in silico. Libraries were prepared using a HiSeq2000 (Illumina, USA) platform. For quality checks, reads were visualized in FastQC 0.10.1. SNP-calling was carried out with the pipeline Universal Network-Enabled Analysis Kit (UNEAK) in Tassel v. 3 software (Lu et al. 2013). The SNPs were filtered using a site minimum call rate of 0.75, a minimum proportion of sites present of 0.7 and a minor allele frequency of 0.01. After these filters, we tested deviations from Hardy–Weinberg equilibrium (HWE), per locus and per population, using 10,000 permutations in Arlequin 3.5.2.2 (Excoffier & Lischer 2010). The p-values were corrected using a false discovery rate correction (q-value = 0.05). The SNPs considered in HWE disequilibrium in at least 60% of the populations were removed from the final dataset. After these filters, we obtained a final data set of 28,769 SNPs genotyped at 146 individuals.

2.3 Defining data sets: Separating neutral and adaptive SNPs

To identify SNPs putatively neutral or under selection (outliers), we used two approaches: (1) Population differentiation analyses (PDA) and (2) genotype-

environment association (GEA).

For the PDA, we used two methods, the first is PCAdapt R package, to identify throught a Principal Component Analysis (PC), markers excessively related to population structure, that will be considered as outlier SNPs (Luu et al. 2016). The second is BayeScan 2.1, which implement a F_{ST} outlier approach to detect loci highly differentiated from what is expected under a neutral distribution that exacerbate the genetic structure (Foll & Gaggiotti 2008). We performed the BayeScan run using 500,000 iterations, 10% burn-in period and a prior odd of 1000. To avoid the occurrence of false positive on outlier loci detection, we used a false discovery rate correction of q-values = 0.05. Then, we generate two datasets: the neutral dataset, where all SNPs detected as outliers (by any of both PDA methods) were removed, and the PDA outlier dataset, composed by the SNPs detected in common by the two analyses (PCAdapt and BayeScan).

The GEA methos are used to estimate possible correlation between the frequency of a particular genotype and environmental variables. First, a total of 32 environmental variables were obtained from Bio-Oracle database (Tyberghein et al., 2012; Assis et al., 2017), including maximum, minimum, mean, and range values of sea surface temperature, salinity, chlorophyll concentration, primary production, ice cover and ice thickness, at each 9 sampling locations (Table 1). Before GEA analyses, all values of matrices were standardized (x−mean(x)/SD(x)). We used three different methods that test for signatures of

local adaptation to increase level of stringency, allowing the identification of candidate outliers using a cross-validation approach and reducing false positives (Lotterhos & Whitlock, 2015; Rellstab et al., 2015). First is Bayenv2 software, which uses allele counts across populations to search for correlation with environmental variables, using Bayesian approach. This method incorporates neutral population structure by employing a covariance matrix of population differentiation, based on the X^TX statistic, which is analogous to F_{ST} (Günther & Coop, 2013). Following the manual of Bayenv2, we used the last printed matrix from the output generated by the covariance matrix estimation step, for further analysis. All 32 environmental variables were included to estimate correlations. We ran Bayenv2 using 100,000 iterations and to consider a SNPs under selection we estimate the Bayes factor (BF). Values of BF >= 3 were considered as substantial evidence of genotype-environment association (Jeffreys 1961).

The second statistical approach to identify outlier loci was Samβada v.0.7, which uses logistic regression between genetic markers and multiple environmental variables (Stucki et al., 2017). With Samβada, population structure proxy can be included in the analysis by treating, one or more, population variables as another variable in the environmental matrix (Duruz et al., 2019). In the current study, before running Samβada, we performed a Discriminant Analysis of Principal Components (DAPC) on the SNPs data (the same genotype matrix for Samβada) using the package adegenet in R (Jombart, 2008) (see section 2.5 for more

details). To account population structure, the two first discriminant functions resulting from this procedure were added as co-variables in the association analysis. For each genotype-environment association, p-values of G-scores (G) and Wald scores (W) were calculated by comparing the spread of G and W from Samβada to a chi-squared distribution (Duruz et al., 2019). Then we corrected the p-values for multiple testing using the q-value package in R (Storey, 2003). Association with $q < 0.05$, for both statistics (G and W) were considered significant. Only the best model, i.e. the lowest q-value of G-score, were retained for each SNP.

As a third method, we used Latent Factor Mixed Modelling (LFMM, Frichot et al., 2013) in the R package LEA (Frichot & François, 2015). This approach introduces population structure using unobserved (latent) variables, while the algorithm estimate association between genetic and environmental variation, the program uses K latent factors to infer levels of population structure (Frichot et al., 2013). To estimate the number of latent factors for the LFMM analysis, we performed a population structure analysis using sNMF (Frichot et al., 2014, 2014), which estimates $K = 2$ as the optimal number of genetic clusters. Then we use the lfmm() function, we ran 5 independent runs of 100,000 iterations each and 10,000 burn-in. Following Frichot and Francois (2015) we combined the z-scores of the 5 replicates, using the Fisher-Stouffer method, median z-score across replicates. To compute adjusted p-values from the combined z-scores, we calculated the

genomic inflation factor (λ), which also provides information about the optimal K. When λ is close to 1, the chosen K is correct, a λ < 1 the test is too conservative and λ > 1 means the test is too liberal (Frichot et al., 2013). The final list of outlier SNPs was obtained using the Benjamini-Hochberg algorithm, with a false discovery rate of q ≤ 0.1 (i.e. 10% of the outlier loci are expected to be false positives).

Finally, for each environmental variable we look for loci that showed significant association, i.e. considered as being under selection, by two or three methods. With this information we obtained the GEA outlier SNPs.

2.4 Neutral and adaptive population structure

To evaluate population structure, we performed two analyses, separately for putative neutral and adaptive SNPs (identified through PDA analyses, see results). First, pairwise population F_{ST} was computed in Genodive v.3.05 (Meirmans 2020), using 10,000 permutations to estimate statistical significance. For F_{ST} comparisons SIG locality was removed due to the low number of individuals (2). The second approach was the Discriminant Analysis of Principal Components (DAPC), performed in adegenet R package (Jombart et al. 2010). For DAPC we used the information of the geographical origin of each individual, to identify genetic groups. The function optim.a.score() was used to estimate the optimal number of principal components to retain for the DAPC (Thia 2022). For

neutral dataset we retained 14 PCs and 13 PCs for outlier dataset. The function find.cluster() was used to estimate k-means with the Bayesian information criterion (BIC) and to select the optimal number of clusters for DAPC.

2.5 Drivers of genetic variation

The influence of geographic location and environmental variation on the putatively neutral and adaptive genetic variation was determined using three approaches: (1) Redundancy Analysis (RDA), (2) partial Mantel test and (3) Spatial Principal Component Analysis (sPCA).

For the RDAs, to estimate the contribution of geographical distance, we used a spatial eigenfunction approach based on distance-based Moran's eigenvector map (dbMEMs). Here, the geographical distances between pairs of sampling sites are decomposed into a new set of independent spatial variables. The latitude and longitude data were transformed into cartesian coordinates, using SoDA R package (Chambers 2008). From this, we generated an Euclidean distance matrix, with the function dist() from vegan R package (Oksanen et al. 2020). Using this matrix, the dbMEM vectors were created in adespatial R package, with the function dbmem() (Dray et al., 2006; Legrendre and Legendre, 2012). These resulting vectors were used as explanatory variables in the two RDAs, separately for neutral (27035) and outliers (346) SNP datasets.

The same 32 environmental variables, obtained from Bio-Oracle database and described above (see section 2.3, GEA description), were used to calculate the contribution of environmental variation on genetic structure. Two independent RDAs were performed, one with the neutral SNPs and a second using the outliers SNPs.

For all RDAs, the procedure was the same. First, we calculate the allele frequencies using PLINK 1.9 software (Purcell et al. 2007), separately for the neutral and the outlier datasets. The allele frequencies were standardized, using Hellinger's method, with the decostand() function in vegan R package (Oksanen et al. 2020). Then, to estimate the optimal model, we started with all explanatory variables (the dbMEMs or environmental variables) and run the function ordistep(), also in vegan. Using an analysis of variance (ANOVA) with 1,000 permutations, we calculated the correlation between genotype (allele frequencies) and each spatial (dbMEM) or environmental variables, one variable at a time. Only variables with a p-value ≤ 0.05 were retained for next step. We performed RDA considering the selected variables, using the rda() function in vegan R package. The significance of each RDA was assessed through an ANOVA with 1,000 permutations.

Partial Mantel test were performed in the vegan 2.5-7 R package (Oksanen et al., 2020): (1) between genetic distance and geographic distance, using environmental variables as covariate, (2) between genetic distance and primary

productivity and (3) between genetic distance and ice cover (selected environmental variables, see results), using geographical distance as a covariate. The genetic distance corresponded to the F_{ST} matrix (described in section 2.5), only for neutral SNPs (no spatial and environmental relationship detected for outlier loci, see results). The geographical distance was calculated using the coordinates of each sampling site as input with the function earth.dist() from frossil R package (Vavrek et al., 2011), then transformed to a Euclidean distance matrix. The selected environmental variables were those that showed significant contribution to the genetic variation in the RDA. Thus, two variables were used to perform separate partial Mantel tests with genetic distance, the primary productivity range (pprange) and the mean values of ice cover (icecovmean) (see results, section 3.3). The values of both environmental variables were transformed to a Euclidean distance matrix. After the partial Mantel test, a Multiple Matrix Regression with Randomization analysis or MMRR (Wang, 2013) was performed in the package PopGenReport (Adamack and Gruber, 2014; Gruber and Adamack, 2015), to estimate the relative contribution of geographic distance, pprange and icecovmean to genetic differentiation. Then, a regular Mantel test was conducted between the genetic distance and the joint effect of geographic distance and the two selected environmental variables.

Finally, we performed a Spatial Principal Component Analysis (sPCA) with adegenet R package (Jombart 2008). This analysis accounted the spatial contribution to genetic patterns and allow us to illustrate how our genetic variation

is associated with environmental gradients, beyond the expected based on sites proximity (Benestan et al., 2016). For the sPCA, we used the neighbourhood-by-distance method, based on latitude and longitude data of our sampling sites, to build the spatial proximity network among localities, following Benestan et al., (2016). Then, we extracted the “lagged scores” from the sPCA run, which accounted for genetic variability linked to spatial structure among sampling sites, and we used them to represent a multi-locus geographic cline (Benestan et al., 2016; Segovia et al., 2020). For the sPCA we used a subset of our putatively neutral loci (filtered by 0.9 site minimum call rate and 0.05 minor allele frequency) of 4582 SNPs. To determine the best predictors of the variation of the neutral structure, we performed linear regressions between multi-locus clines and geographic distance (dbMEMs), and between multi-locus clines and two environmental variables (primary productivity range and mean ice cover), based on the relationship this both showed previously in RDA (see results).

3. Results

3.1 Defining data sets: Separating neutral and adaptive SNPs

To separate putatively neutral and adaptive SNPs, we start using the previously filtered data set (28,769 SNPs). With the PDA, using PCAdapt and BayeScan we identified 1,725 and 355 SNPs under potential selection, respectively. From these, 346 SNPs were shared by both methods and were selected to construct

the PDA outlier data set. A total of 1,734 loci (1,725 PCAdapt and 9 unique from BayeScan) showed signal of selection and were removed to create the putatively neutral data set with 27035 SNPs.

Starting with the same filtered data set (28,769 SNPs), but using the GEA methods, Bayenv2 and LFMM detected a total of 1692 and 1841 candidates SNPs respectively, associated with all 32 environmental variables used (Table 2). Samβada had the most conservative result, with 286 candidate SNPs associated to 10 variables (Table 2). However, no SNPs were detected in association with any environmental variable by more than one method, i.e. there is no shared candidate SNPs, and therefore we did not find sufficient evidence of genotype-environment associations. No further analyses were performed with these data sets. Due to this, outlier SNPs hereafter only refer to those detected by PDA (346 SNPs).

3.2 Neutral and adaptive population structure

The F_{ST} values for the putatively neutral SNPs ranged from 0.001 to 0.031 and all values were significantly different from zero (p-values < 0.05), except for the FIB-DIS and CHB-DIS comparisons (p-values > 0.05). All SGE pairwise comparisons were one order of magnitude higher than any other (Fig. 2a). For the outlier loci the F_{ST} values ranged from 0.007 to 0.581. In this case, despite the SGE comparisons were higher than with the neutral loci (0.029 to 0.365), the pairwise

values for other localities were also high (Fig. 2b), then the pattern of genetic structure is different. Therefore, the exacerbated genetic differentiation of SGE observed with the neutral loci, is masked by the overall higher F_{ST} values of the outlier data (Fig. 2b).

The results from DAPC, using the 27,035 neutral SNPs data set, revealed a congruent pattern of clustering, with a clear separation of SGE locality from the rest of the sites of the WAP. Nevertheless, four genetic clusters were identified using the BIC criteria. A gradient of differentiation was observed inside the WAP, but this is surpassed due to the higher structuration of SGE (Fig. 3a). For the putatively under selection SNPs, 346 detected by PDA methods, the DAPC results were less clear. At the first axis of variation a small separation of SGE was observed, although this separation was much more pronounced in the neutral dataset (Fig. 3b). Additionally, BST appears as another group, more separated from the rest of the WAP localities. Overall, three genetic cluster were detected in this analysis.

3.3 Drivers of genetic variation

For the first RDA, considering neutral genetic (allele frequencies from 27,035 SNPs) and the geographical variation, following ordistep results, we select three spatial vectors (dbMEM1, dbMEM2 and dbMEM8). This model explained 67% of the observed genetic structure and was highly significant (R^2 adj = 0.48, $p < 0.05$).

The dbMEM1 and dbMEM2 were related to the differentiation of SGE from the AP along the RDA2, while the dbMEM8 was associated to the separation of SIG locality along the RDA1 (Fig. 4a). A second RDA was built with the neutral genetic variation and the 32 environmental variables. In this case, based on the ordistep selection procedure, only the range of primary productivity (pprange) and the mean ice cover (icecovmean) were retained for the RDA. The model was also highly significative and explained 51% of genetic variation (R^2 adj = 0.35, $p < 0.05$). Both, the range of primary productivity and the mean ice cover seems to be more related to the differentiation of SGE mainly, but also with the grouping of FIB, CHB and DIS (all localities of the South Shetland Islands) and the separation of this group from the rest of the WAP (Fig. 4b). The SIG locality was also observed as a differentiated group, but not highly associated to any environmental variable. We performed the RDAs following the same procedure for the putatively under selection loci (346 SNPs). We used the same eight dbMEM vectors and the 32 environmental variables to look for association. Nevertheless, when running the ordistep function, no dbMEM vectors or environmental variable showed significant values of correlation with allele frequencies. Thus, no variable was selected to continue with the RDA for this data set.

For the partial Mantel test, the environmental variables used were the range of primary productivity and the mean values of ice cover, because these two variables showed significant contribution to the genetic variation in the previous RDA model. The partial Mantel test between genetic distance and geographic

distance, controlled by environmental variables, was significant and the regression coefficient (R) slightly differing when use primary productivity range (R = 0.65, p = 0.03; Fig. 5a) or the mean ice cover (R = 0.69, p = 0.01; Fig. 5a) as co-variates. To estimate the effect of the two selected environmental variables, we performed two analyses separately for each one, using geographic distance as co-variate. The partial Mantel test between genetic distance and primary productivity range was also significant (R = 0.49, p = 0.02; Fig. 5b).

In the same way, the mean ice cover showed significant relationship with genetic distance, with higher r-value (R = 0.62, p = 0.01; Fig. 5c). Both environmental variables, together with geographic distance, were then included for the MMRR analysis to determine the joint effect of these three factors on the population structure. We used the weighted effect of geographic distance, primary productivity range and mean ice cover (through MMRR, Table 3) as one variable. The results showed that the incorporation of these three increased the model fit (R = 0.85, p = 0.001; Fig. 5d).

The linear regressions performed with the multi-locus clines (lagged scores from sPCA) and (1) the spatial variables (dbMEM1, dbMEM2 and dbMEM8) and (2) the environmental variables (primary productivity range and mean ice cover), indicated that the spatial variables together have the best fit with neutral genetic structure (R^2 adj = 0.97, p < 0.05). From the spatial variables, the dbMEM2 was the one that contributed the most (R^2 adj = 0.59, p =0.0005; Fig. 6c). The linear fit

of the spatial variables with the neutral structure is related to the differentiation of four genetic groups, which showed dissimilar lagged scores among sampling sites. The first and more northeast group is SGE, then we could differentiate SIG locality (between SGE and WAP), a third group with the northern and central WAP localities (FIB, CHB, DIS, BST, FHA and DOI) and finally the southern WAP (AIS locality) (Fig. 6c). Other interesting results is the significant relationship of multi-locus clines with environmental variation (Fig. 6a y b), although the regression fit is lower than spatial variables, the primary productivity range (R^2 adj = 0.30, $p < 0.05$; Fig. 6d) and the mean ice cover (R^2 adj = 0.31, $p < 0.05$; Fig. 6e) showed significant relationship with genetic variation.

4. Discussion

Determine genetic variation patterns and its association with environmental variability, across species distribution, is crucial to improve our understanding of the ecology and the impact of climate change on living organisms (Razgour et al., 2019; Boulanger et al., 2021). In the present study, we describe the putatively neutral and adaptive genetic structure in *H. antarcticus* from two regions of the Southern Ocean (WAP and SGE). We determine the role of spatial location and environmental gradients on the observed patterns of population differentiation and search signals of local adaptation along *H. antarcticus* distribution. We found a marked population differentiation between the SGE and WAP individuals for the neutral loci (less clear when we used the outliers SNP) and significant influence

of geographic distance, primary productivity range and mean ice cover on the observed neutral genetic variation. Our results showed a lack of evidence to determine candidate SNPs associated to different environmental variables (LFMM, Bayenv and Samβada results). In addition, no association was found between outliers SNPs (detected by PDA) and environmental variables tested here, what we considered as absences of local adaptation evidence for *H. antarcticus* populations along WAP and SGE.

Our result of marked genetic structure between WAP and SGE are congruent with other studies conducted on these regions of the Southern Ocean, particularly with patterns described for other notothenioid fishes (e.g. Young et al., 2015, 2018), which could be relate to gene flow limitations associated to species ecology and the complex oceanographic and environmental condition in the study area. Besides, the observed pattern for *H. antarcticus* is consistent with a previous report for the congener *Harpagifer bispinis* in the Magellan Province, for which marked population structure and limited gene flow were described between distant localities (Segovia et al., 2022).

Despite that WAP and SGE could be connected due the main northward flow of the ACC, there seems to be limitations to the transport and establishment of individuals of *H. antarcticus* between these two regions. On the one hand, we have the long distance that separates WAP and SGE. We found significant effect

of geographic distance on the observed genetic structure, population differentiation increases in more distant localities (mantel test results), confirming an isolation-by-distance more than an isolation-by-environment pattern. Besides, previous larval transport simulations suggest weak and intermittent potential dispersal from WAP to SGE in *Champsocephalus gunnari*, which have similar reproduction and life cycles to *H. antarcitus*, with benthic eggs and similar pelagic larval duration (Young et al., 2015, 2018). This could represent biological limitations to dispersal between WAP and SGE, due to the long distance. On the other hand, beyond the effect of geographic distance, we found population structure linked to variations in the primary productivity and the sea ice cover. Our results suggest that the gradient of both environmental variables have significant effect on the genetic differentiation between WAP and SGE individuals. The RDA analysis based on neutral SNPs, showed a relationship between SGE separation and the variations in sea ice cover mean and the range of primary productivity. This could be related to the seasonality and latitudinal gradient that both variables present in the study area. A marked differences between WAP and SGE is that the last one is located above the limit for sea ice formation and has a larger period of enhanced primary productivity (Murphy et al., 2013), which could explain the observed patterns. The environmental variation could be acting as a barrier for the gene flow and generating population structure.

Along our study area, previous investigations have identified a gradient in the phytoplankton biomass, high biomass in the northern area have been registered

earlier in the productive season, which advances southward as the sea ice retreats in the same direction (Smith et al., 1998; Garibotti et al., 2003). With an exception in the southern part of the Antarctic Peninsula, in Margarite Bay (Marrari et al., 2008). This means that phytoplankton blooms occurred earlier in some areas, which could be an important factor to consider thinking in larval hatching periods and survival. Phytoplankton blooms in SGE and WAP sustain important zooplankton communities, which in turn are the main source of food for fish larvae (Murphy et al., 2013; Burrow et al., 2011). Cushing (1975) proposed for the first time the match/mismatch hypothesis, suggesting that larval growth and survival depend on the availability of food and therefore with the matching of spawning or hatching periods with high food availability periods (James et al., 2003; Burrow et al., 2011). Landaeta et al., (2017), described the presence of both, phyto and zooplankton as important prey items in *H. antarcticus* larvae diet. Across the WAP and SGE region, the seasonality has great impact on phyto and zooplankton communities (Ward et al., 2012; Murphy et al., 2013). At the southern areas, primary and secondary production generally occurs later in the productive season, due to their interaction mainly with upwelling, ice cover formation and melting and nutrient conditions (Prézelin et al., 2004; Whitehouse et al., 2008a; Ardelan et al., 2010; Murphy et al., 2013). This could be an explanation of the significant influence of both primary productivity and ice cover on genetic variation. With longer productive periods, the northern areas (as SGE) could reach higher productivity and would have more extended food availability periods to enhance the successful feeding of *H. antarcticus* larvae. Besides, moving southward,

localities are more impacted for the sea ice formation and melting, which in turn are associated to phyto and zooplankton blooms. Thus, it would be expected that *H. antarcticus* larvae also present variations in their hatching periods between localities, associated to a coupling with the productive season. We have no accurate information of how hatching or spawning periods variate across *H. antarcticus* distribution; therefore, more investigation is needed as a complement of life history traits that could affect population dynamics and genetic variation in this species.

Our main finding, the marked neutral genetic structure between WAP and SGE, linked to geographic and environmental variation in *H. antarcticus*, could have important conservation impact. It seems to be several limitations to individual exchange between these two regions and the present study accumulate evidence in this regard. The long distance could represent a barrier to dispersal from WAP to SGE. Despite the predominant currents flow in that direction, it seems that could also be biological limitations for connectivity, i.e. pelagic larval duration not enough for individuals to reach SGE. The oceanographic condition also impedes the potential dispersal in the opposite direction (from SGE to WAP), due to the main water flows in the Scotia Sea that would transport individuals to the northeast (Murphy et al., 2013; Young et al., 2015, 2018). This means that there is a lack of population connectivity between WAP and SGE, revealed as population structure in *H. antarcticus* (and other organisms), which, in a scenario of local extinction in SGE, would means that is very difficult (if possible) to individuals from WAP to

recolonize that distant location. Besides, this population differentiation could be exacerbated under climate change conditions. An increase in sea temperature is predicted to reduce planktonic duration and increase mortality of fish larvae in the Southern Ocean, generating more limitations to connectivity (Young et al., 2018). In addition, changes in the environmental conditions could have consequences in the primary and secondary productivity, resulting in changes in the food availability and the survival of larvae and adult individuals. The WAP and SGE ecosystems are among the ecosystems most affected by climate change. Particularly WAP is one of the most rapidly warming regions worldwide, showing significant changes in temperature and sea ice seasonality, since the mid-twentieth century (Stammerjohn et al. 2012, Henley et al. 2019). Therefore, it is necessary to continue studying population dynamics and how there are related to the environmental conditions.

Figures

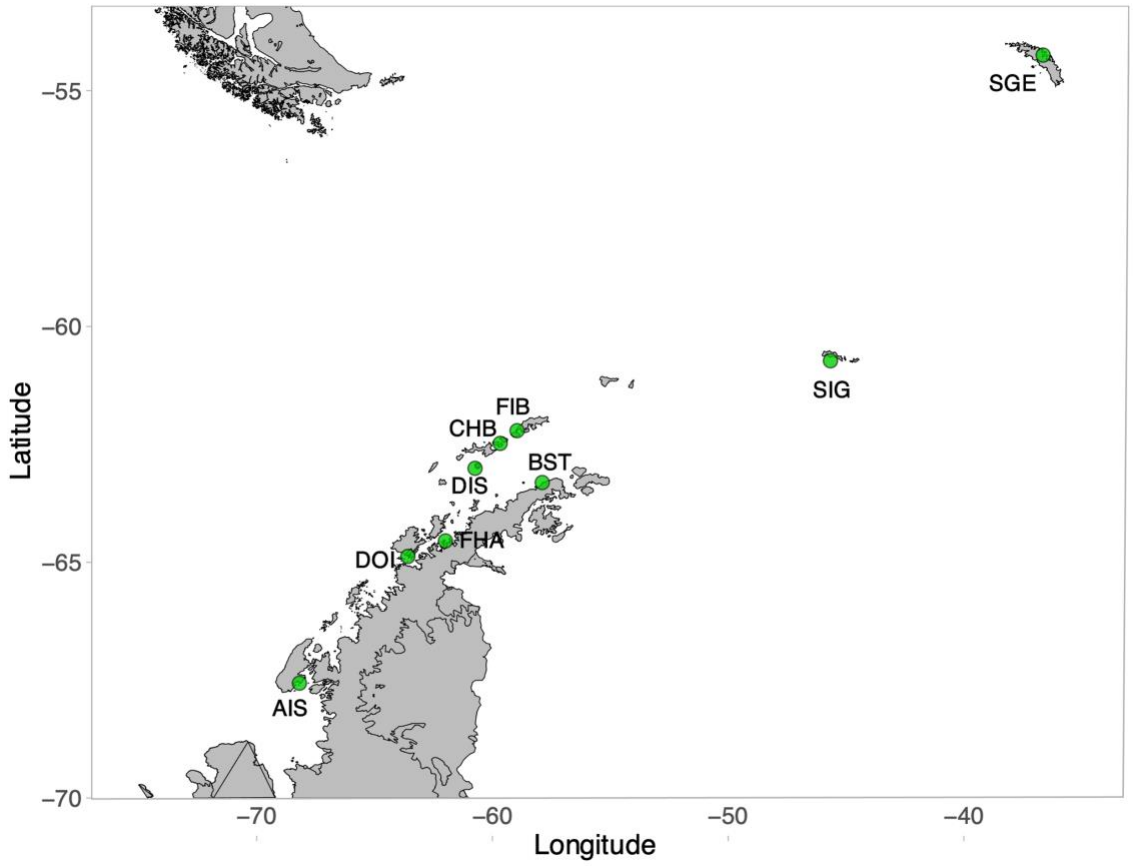

Figure 1. Sampling sites for *H. antarcticus* along Western Antarctic Peninsula and South Georgia regions. Where SGE: South Georgia Island, SIG: Signy Island, FIB: Fildes Bay, CHB: Chile Bay, DIS: Deception Island, BST: Bransfield Strait, FHA: Foyn Harbour, DOI: Doumer Island and AIS: Adelaide Island.

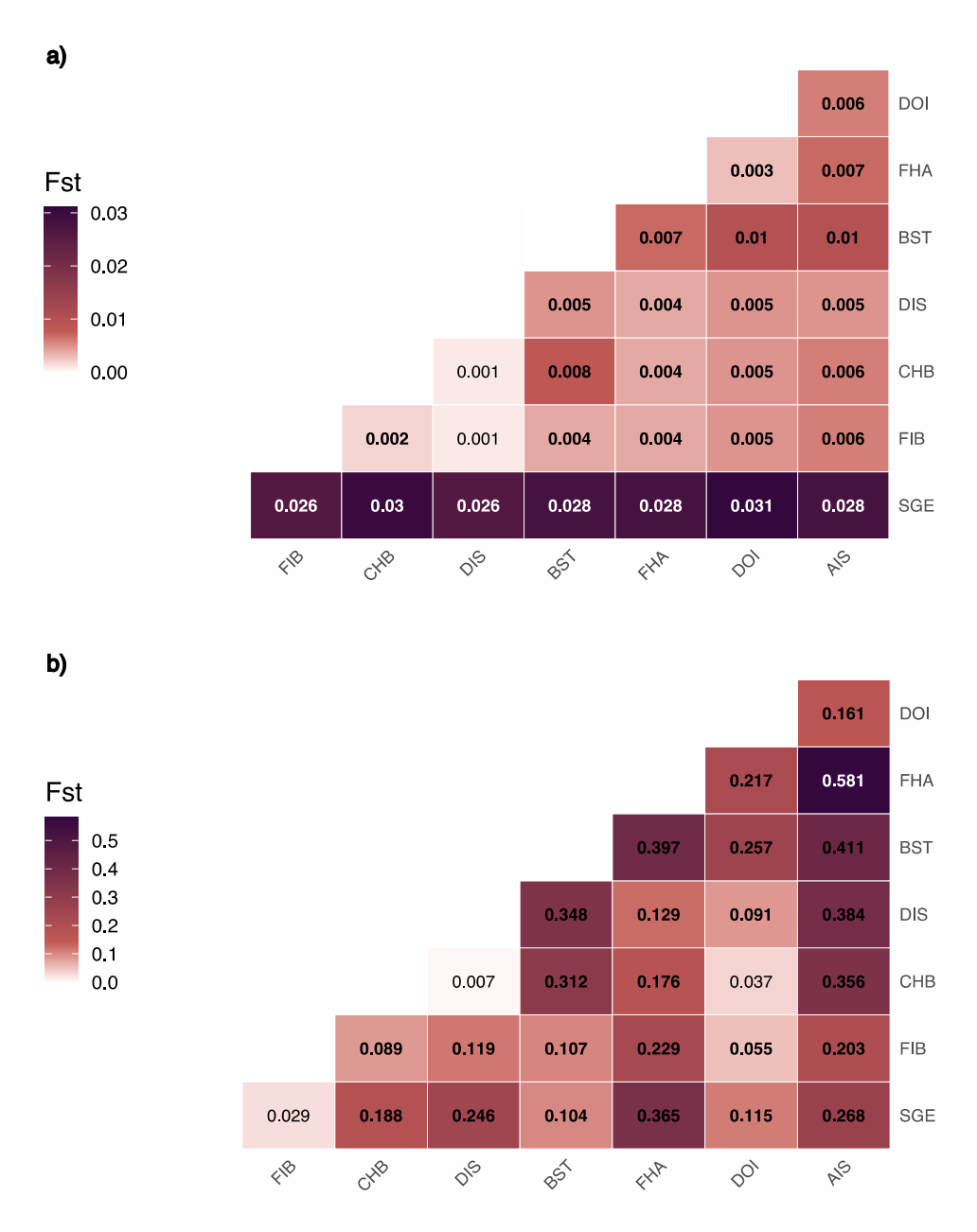

Figure 2. Pairwise F_{ST} comparisons among localities. Where (a) corresponds to pairwise comparisons for putatively neutral (27,035 SNPs) and (b) under selection loci (346 SNPs). Significant values are shown in bold.

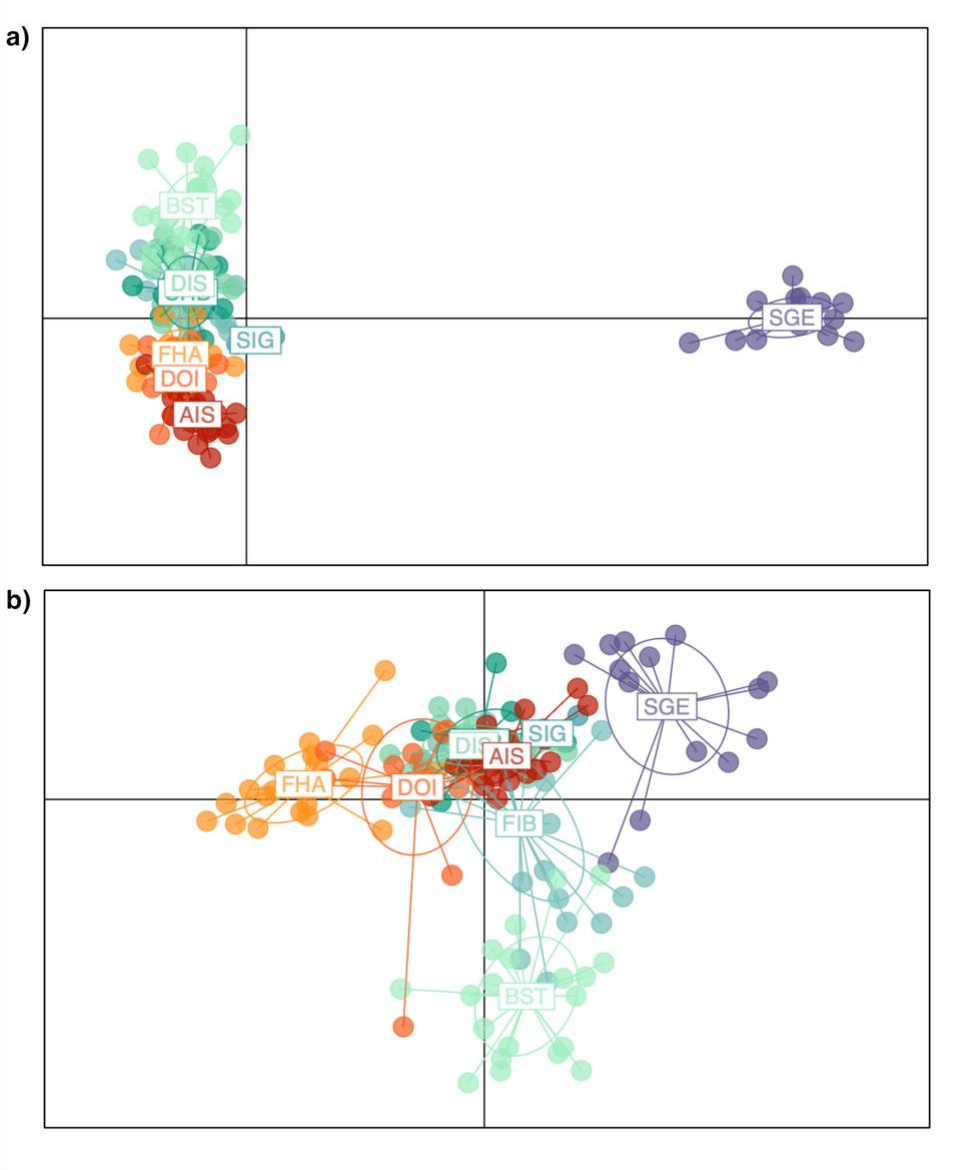

Figure 3. Scatter plot of Discriminant Analysis of Principal Components (DAPC), showing the first two axes, representing the genetic structure of *H. antarcticus* along Maritime Antarctica. Where (a) corresponds to the scatter plot of DAPC for putatively neutral (27,035 SNPs) and (b) under selection (346 SNPs).

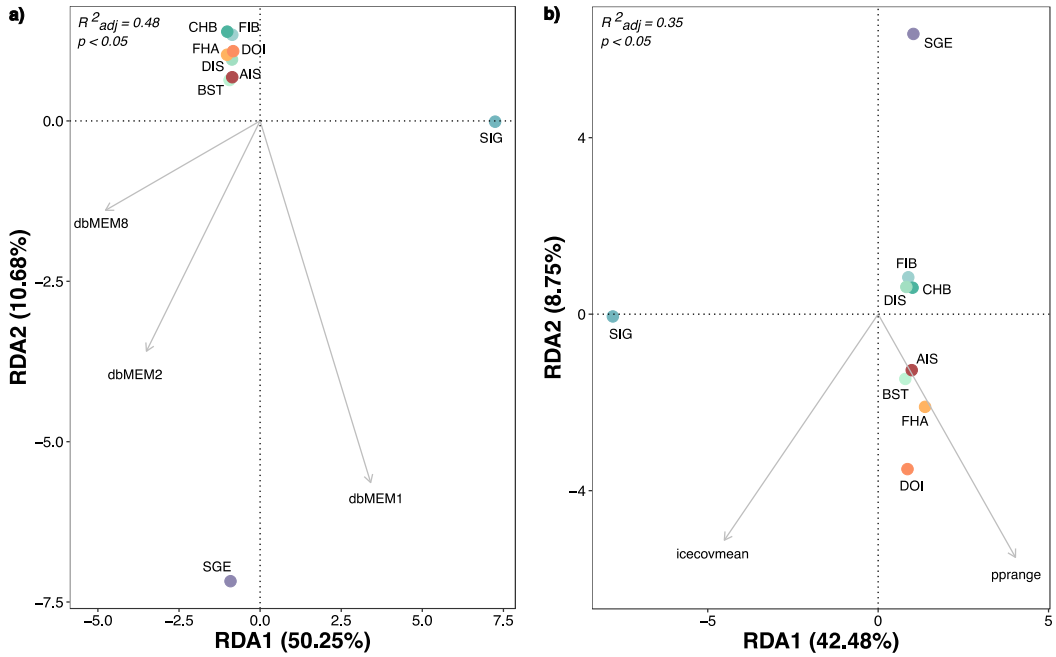

Figure 4. Redundancy analysis (RDA) results for putatively neutral loci (27,035 SNPs). Where dbMEM are distance-based Moran's Eigenvector Maps (representing geographical distance), icecovmean corresponded to the mean value of ice cover and pprange corresponded to the range of primary productivity. Arrows represent these selected variables (after model optimization) that drive the observed genetic variation.

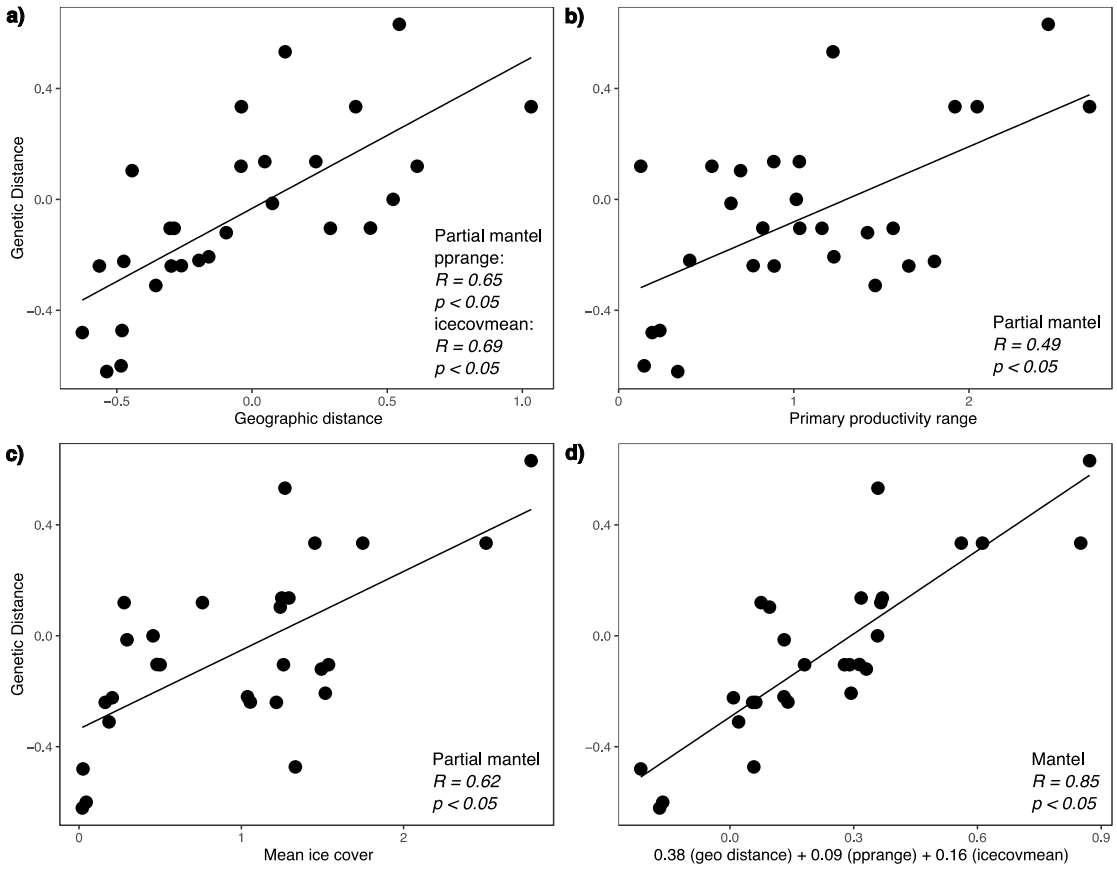

Figure 5. Scatter plots showing (a) partial mantel test between genetic distance and geographic distance (using environmental variables as covariate), (b) partial mantel test between genetic distance and primary productivity range (using geographic distance as covariate), (c) partial mantel test between genetic distance and mean ice cover (using geographic distance as covariate) and (d) the joint effect of geographic and environmental variables (primary productivity and ice cover), based on the results of a Multiple Matrix Regression with Randomization analysis (MMRR).

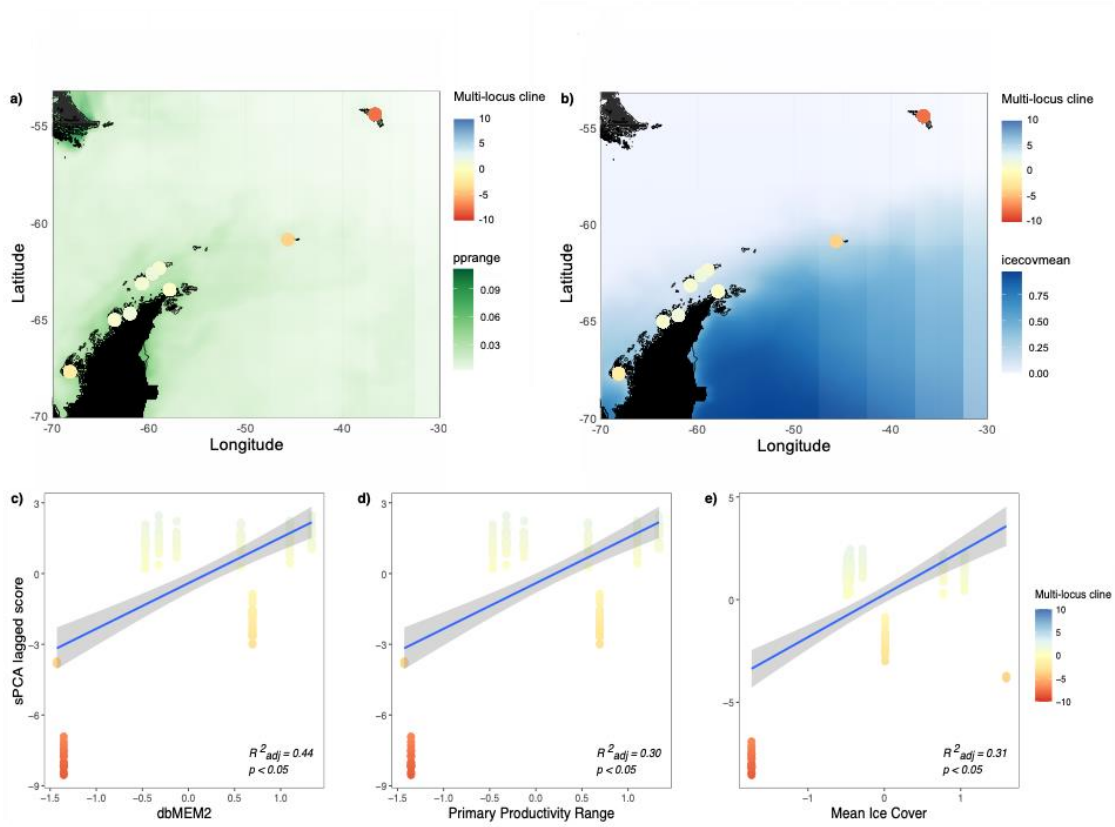

Figure 6. Spatial genetic variation of putatively neutral loci subset (4582 SNPs) in the 9 sites studied in *H. antarcticus*. Where (a) and (b) are representations of the spatial structure of the range of primary productivity (pprange) and the mean ice cover (icecovmean), respectively, along our study area. Panels below corresponds to scatter plots of linear regression between multi-locus clines (determined by lagged scores from sPCA) and (c) dbMEM2, (d) primary productivity range and (e) mean ice cover values of each locality.

Tables

Table 1. Values of environmental variables extracted from Bio-Oracle for each sampling location: South Georgia Island (SGE), Signy Island (SIG), Fildes Bay (FIB), Chile Bay (CHB), Deception Island (DIS), Bransfield Strait (BST), Foyn Harbour (FHA), Doumer Island (DOI) and Adelaide Island (AIS).

Environmental variable	SGE	SIG	FIB	CHB	DIS	BST	FHA	DOI	AIS
chlorophyll									
Lt max	0,800	1,165	2,103	2,057	2,141	2,450	3,251	2,366	2,436
Lt min	0,432	0,124	0,187	0,184	0,159	0,134	0,137	0,111	0,080
max	0,892	1,480	2,345	2,268	2,439	2,900	3,527	2,833	3,113
mean	0,624	0,426	0,851	0,895	0,832	0,945	1,355	0,985	0,905
min	0,382	0,097	0,125	0,108	0,109	0,097	0,087	0,088	0,066
range	0,510	1,383	2,219	2,160	2,330	2,803	3,440	2,745	3,047
Ice cover									
Lt max	0,000	0,833	0,503	0,499	0,423	0,643	0,421	0,717	0,439
max	0,002	0,918	0,777	0,725	0,754	0,812	0,818	0,893	0,655
mean	0,000	0,273	0,106	0,104	0,102	0,206	0,119	0,229	0,143
range	0,002	0,918	0,777	0,725	0,754	0,812	0,818	0,893	0,655
Ice thickness									
Lt max	0,005	0,672	0,500	0,497	0,499	0,652	0,572	0,694	0,645
max	0,018	0,876	0,701	0,639	0,632	1,043	0,667	0,966	0,730
mean	0,001	0,227	0,138	0,145	0,153	0,267	0,242	0,306	0,344
range	0,018	0,876	0,701	0,639	0,632	1,043	0,667	0,966	0,730
Primary productivity									
Lt max	0,013	0,010	0,023	0,025	0,023	0,034	0,044	0,035	0,034
Lt min	0,002	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000
max	0,016	0,013	0,027	0,030	0,025	0,039	0,049	0,046	0,040
mean	0,007	0,003	0,008	0,009	0,008	0,011	0,015	0,009	0,009
min	0,001	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000
range	0,014	0,013	0,027	0,030	0,025	0,039	0,049	0,046	0,040
Salinity									
Lt max	33,871	34,137	34,328	34,328	34,306	34,335	34,390	34,035	33,569
Lt min	33,666	33,193	33,672	33,578	33,357	32,932	33,189	31,757	31,310
max	33,918	34,350	34,518	34,535	34,569	34,523	34,609	34,381	34,101
mean	33,767	33,793	34,037	34,009	33,898	33,829	33,912	33,157	32,685
min	33,544	32,356	33,230	33,040	32,483	32,006	32,570	30,190	29,128
range	0,374	1,995	1,288	1,494	2,086	2,517	2,039	4,191	4,972
Sea surface temperature									
Lt max	3,586	0,422	1,166	1,201	1,306	-0,281	1,484	0,870	0,909
Lt min	0,269	-1,804	-1,650	-1,663	-1,692	-1,846	-1,591	-1,665	-1,820
max	4,540	1,155	1,574	1,589	1,740	0,135	1,912	1,390	1,720
mean	1,818	-0,963	-0,475	-0,458	-0,464	-1,300	-0,514	-0,637	-1,035
min	0,023	-1,929	-1,864	-1,887	-1,882	-1,933	-1,775	-1,820	-1,880
range	4,517	3,084	3,438	3,476	3,622	2,068	3,687	3,210	3,600

Table 2. Number of putatively adaptive loci detected for *H.antarcticus*, using genotype-environment associations. The table shows candidate SNPs associated to 32 environmental variables, with Latent Factor Mixed Modelling (LFMM), Bayenv2 and Samβada methos, and the outliers detected for more than one (joint). Where Lt corresponds to the average of the maximum and minimum records per year (e.g., temperature of the warmest month, on average).

Environmental variable	**LFMM**	**Bayenv**	**Samβada**	**Joint**
chlorophyll				
Lt max	51	57	0	0
Lt min	47	61	2	0
max	51	59	7	0
mean	16	44	2	0
min	71	55	0	0
range	55	56	2	0
Ice cover				
Lt max	25	62	0	0
max	51	58	0	0
mean	4	65	0	0
range	50	58	1	0
Ice thickness				
Lt max	42	63	0	0
max	54	54	0	0
mean	14	62	133	0
range	54	54	0	0
Primary productivity				
Lt max	14	56	0	0
Lt min	76	63	0	0
max	4	51	0	0
mean	56	58	0	0
min	74	57	0	0
range	5	58	0	0
Salinity				
Lt max	7	55	8	0
Lt min	5	51	0	0
max	11	55	20	0
mean	8	59	36	0
min	5	53	0	0
range	5	56	0	0

Sea surface temperature				
Lt max	128	63	0	0
Lt min	84	58	0	0
max	141	67	0	0
mean	97	49	75	0
min	72	56	0	0
range	315	68	0	0

Table 3. Multiple Matrix Regression with Randomization analysis (MMRR) results. Where, geo dist: geographic distance, icecovmean: mean ice cover and pprange: primary productivity range.

Layer	**Coefficient**	**tstatistic**	**tpvalue**	**Fstat**	**Fpvalue**	**R^2**
Intercept	-0.2931	-4.0291	0.0050	20.6992	0.0003	0.7212
geodist	0.3765	4.2859	0.0345			
icecovmean	0.1643	2.9068	0.0543			
pprange	0.0852	1.3945	0.3029			

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CONCLUSIONES GENERALES

En este trabajo, hemos estudiado los patrones de conectividad poblacional del del pez *Harpagifer antarcticus* y el efecto de distintos factores que pueden influir en el intercambio de individuos en dos regiones del Océano Austral, la zona oeste de la Península Antártica y la Isla Georgia del Sur, en el arco de Escocia.

H. antarcticus es una especie que posee características biológicas que lo hacen un modelo destacado para estimar estructuración poblacional y limitaciones al flujo genético. Estudios previos, realizados en el congénere *H. bispinis* determinaron la presencia de una marcada diferenciación poblacional entre localidades distantes. Lo cual se confirmó también para *H. antarcticus*. Los rasgos de historia de vida, comunes a las distintas especies del género *Harpagifer*, y su interacción con la distancia geográfica, las condiciones oceanográficas y la variabilidad ambiental, generan limitaciones para el flujo genético y estructuración poblacional.

Al ser una especie con ciclo de vida complejo, la etapa larval de *H. antarcticus*, representa la etapa dispersiva y, por lo tanto, sería fundamental en la conectividad poblacional. En este estudio se demostró que la conectividad potencial, es decir, es transporte larval entre localidades de la zona oeste de la Península Antártica, es consistente con la conectividad efectiva, y por lo tanto tiene un efecto significativo en la diferenciación genética. Las simulaciones de

trayectorias de dispersión de larvas mostraron que, dentro de esta región, el flujo de las corrientes y la presencia de áreas de retención representan barreras para la conectividad de *H. antarcticus*.

Tanto los resultados de las estimaciones de conectividad potencial (modelamiento biofísico), como de conectividad efectiva (genómica de poblaciones), mostraron la presencia de distintos grupos genéticos dentro de la Península Antártica, cuyos límites estarían relacionados con cambios en las condiciones oceanográficas locales. Este es uno de los pocos estudios que ha detectado estructuración poblacional y flujo genético limitado dentro de esta región. Por lo tanto, es de gran relevancia para el conocimiento de patrones de conectividad a escala fina en esta área, pensando además en el aporte que puede representar para propuestas de Áreas Marinas Protegidas.

A mayor escala, cuando comparamos las regiones de la zona oeste de la Península Antártica con la Isla Georgia del Sur, se detectó una marcada diferenciación genética de esta última. Tanto así, que la estructuración a escala fina, dentro de la península, queda en segundo plano. Ampliar nuestra escala de estudio nos permitió probar el efecto de la distancia geográfica (> 1200 km) y de la variabilidad ambiental que presentan estas dos regiones, en la estructura poblacional. En este contexto, se determinó que la distancia geográfica es el factor con mayor efecto en la diferenciación genética, más que los potenciales efectos y barreras ambientales, detectándose un patrón de aislamiento por

distancia para *H. antarcticus*. No obstante, las herramientas de la genómica del paisaje marino mostraron escasa presencia de loci candidatos a adaptación local, y por lo tanto de un efecto significativo de la variación ambiental o potenciales procesos selectivos como principales forzantes de la diversidad y estructura genética. Hubo dos variables ambientales, sin embargo, que mostraron relación significativa con la estructura genética: la productividad primaria y la cobertura de hielo. Lo interesante es que ambas presentan una marcada variabilidad estacional en las regiones de la Península Antártica y la Isla Georgia del Sur. Aumentos en la productividad primaria se dan de manera sucesiva de norte a sur en la época de primavera-verano, siguiendo el retroceso y derretimiento de las capas de hielo. En otoño-invierno, grandes regiones de la Península Antártica quedan cubiertas de hielo marino, mientras que la Isla Georgia del Sur se ubica sobre el límite de formación de capa de hielo. Estas fluctuaciones en la época de alta productividad y la presencia de hielo marino estarían actuando como barreras para la conectividad entre ambas zonas. Aunque, como se mencionó anteriormente, este efecto es mucho menor al que promueve la distancia geográfica para explicar la diversidad y estructura genética de *Harpagifer antarcticus* en el área de estudio.

Nuestros resultados confirman la importancia de las primeras etapas de desarrollo en la dinámica poblacional de *H. antarcticus*. El transporte larval, en conjunto con la dinámica oceanográfica, es un factor importante en la estructuración poblacional dentro de la Península. Además, pese a un potencial

transporte desde la península hacia Georgia del Sur, la llegada de individuos estaría limitada por la duración de la etapa larval, que no sería suficiente para cubrir la separación geográfica de ambas zonas. Un acople entre los periodos de eclosión larval y las condiciones ambientales podría explicar el efecto significativo de la productividad primaria y la cobertura de hielo. Esto debido a que se ha descrito en general para larvas de peces, que los periodos de eclosión estarían acoplados a periodos de alta productividad (para asegura la alimentación y sobrevivencia) y, como ya se mencionó para nuestra zona de estudio, la productividad y la cobertura de hielo están íntimamente relacionadas. Esto último requiere de más estudios, por lo que se considera relevante desarrollar más investigación de la etapa larval de *H. antarcticus* y de cómo esta varía entre localidades para mejorar nuestro entendimiento de cómo algunos rasgos de historia de vida están relacionados a la variabilidad ambiental local y podrían limitar la conectividad.

La presencia de estructura poblacional y flujo genético limitado entre poblaciones locales de *H. antarcticus* de la Península Antártica e Isla Georgia del Sur, se suma a la creciente evidencia de baja conectividad para estas dos regiones. Esto es importante considerando que ambas son zonas prioritarias de conservación y se espera que sean de las más afectadas por el cambio climático. Los resultados sugieren que, en un escenario de extinción local, sería difícil (si no imposible) el repoblamiento por individuos de distintas regiones. Por lo tanto, medidas de conservación que se tomen en una región podrían no tener efectos significativos

en la otra.

Finalmente, los resultados de este estudio demuestran lo relevante de combinar aproximaciones para estudiar conectividad en ecosistemas marinos. Las estimaciones indirectas de conectividad son herramientas eficientes que nos permiten abordar el intercambio de individuos desde distintas perspectivas y considerando diferentes etapas de vida de las especies. Además, el crecimiento y desarrollo de metodologías de la genómica del paisaje marino nos permiten relacionar de manera más directa la influencia de distintos factores que afectan el intercambio de individuos, como la distancia geográfica, las corrientes oceanográficas y la heterogeneidad ambiental. Se sugiere el desarrollo de más estudios de conectividad que aborden la problemática desde esta amplia perspectiva, en distintas especies, para representar de mejor manera lo que ocurre en el Océano Austral. Sobre todo, considerando que este es un ecosistema frágil, muy susceptible a efectos negativos del cambio climático.

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