



Universidad de Concepción  
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Programa de Doctorado en Oceanografía

**Conectividad de huevos y larvas de merluza de cola  
entre el sistema estuarino y zona oceánica adyacente,  
en la Patagonia Chilena**

**(Connectivity of Patagonian grenadier eggs and larvae  
between the estuarine system and adjacent oceanic  
zone, in Chilean Patagonia)**

Tesis para optar al grado de Doctor en Oceanografía

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La Tesis de “*Doctorado en Oceanografía*” titulada “*Conectividad de huevos y larvas de merluza de cola entre el sistema estuarino y zona oceánica adyacente, en la Patagonia Chilena*” y realizada bajo la Facultad de Ciencias Naturales y Oceanográficas, Universidad de Concepción, ha sido aprobada por la siguiente Comisión de Evaluación:

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Dedicada a mi familia,  
por regalarme su tiempo y apoyo incondicional para alcanzar esta meta.

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## RESUMEN

La dinámica oceanográfica del Sistema Estuarino Patagónico y su zona oceánica adyacente está modulada por la circulación estuarina (masas de agua oceánicas y aportes de agua dulce), mareas y el viento. Esta dinámica es influida por factores forzantes de escalas temporales y espaciales diferentes, tales como cambios en la intensidad de la deriva del viento del oeste (WWD) o la corriente del Pacífico Sur (SPC), la oscilación decadal del Pacífico (PDO), la oscilación del sur de El Niño (ENSO), el modo anular del sur (SAM), oscilación Madden Julian (MDO). Además, durante las últimas décadas, los cambios en las descargas de agua dulce producto de las precipitaciones y el derretimiento del hielo glacial demuestran que el cambio climático global también está afectando el ambiente de la Patagonia. Aún se desconoce si estos procesos afectan potencialmente las áreas de desove y la distribución de las primeras etapas de vida de especies de peces como *M. magellanicus* que se distribuyen entre el sistema estuarino y la zona oceánica adyacente en la Patagonia chilena. La merluza de cola (*Macruronus magellanicus*) presenta una amplia distribución en la zona austral de América del sur, que incluye el Océano Atlántico suroeste y el Pacífico sureste entre los  $\sim 33^{\circ}\text{S}$  y  $\sim 56^{\circ}\text{S}$ . En el Atlántico suroeste no se han reportado áreas de desove importantes para merluza de cola, además, se ha encontrado una disminución del stock de los adultos en invierno, lo cual, sugiere que esta especie realizaría migraciones inter-oceánicas para reproducirse junto al stock del Pacífico. En el Pacífico sureste el stock desovante se concentra entre los  $\sim 43^{\circ}\text{S}$  y  $\sim 48^{\circ}\text{S}$ , asociados a los cañones submarinos en el quiebre de la plataforma continental (mar exterior). En el Sistema Estuarino Patagónico (SEP, mar interior) y la zona oceánica adyacente (mar exterior) de la Patagonia chilena se han encontrado huevos y larvas de merluza de cola, lo que ha permitido postularlas como potenciales zona de desove y crianza de esta especie, sin embargo, su persistencia espacial y temporal aún no ha sido demostrada, ni se han descrito

sus características ambientales. Por otra parte, se desconoce si los huevos y larvas presentes en el mar interior provienen del área principal de desove en el mar exterior, o si el desove ocurre tanto en el mar exterior como interior.

El objetivo general de esta tesis fue evaluar los procesos bio-oceanográficos que influyen en la conectividad de los estadios tempranos de vida de merluza de cola entre el Sistema Estuarino Patagónico y la zona oceánica adyacente en la Patagonia Chilena, planteándose como hipótesis que existe conectividad de huevos y larvas de *M. magellanicus* entre estas dos zonas. Para cumplir con el objetivo, se analizaron muestras estratificadas de ictioplancton, zooplancton y data hidrográfica de 26 cruceros oceanográficos realizados en primavera e invierno, en el Sistema Estuarino Patagónico y su zona oceánica adyacente en el periodo 1995-2019. Se cuantificaron los huevos y larvas de merluza de cola, se clasificaron las larvas por talla y se presentó la abundancia estandarizada de huevos y larvas en cada uno de los cruceros realizados. Se exploró la variabilidad espacial (mar interior-exterior), estacional (invierno-primavera) e interanual (1995-2019) de la abundancia de huevos y larvas de merluza de cola, así como de las características bio-oceanográficas (temperatura, salinidad, potenciales predadores (medusas) y presas (copépodos)) en la zona de estudio. Para dos años del periodo de estudio se obtuvieron mediciones de velocidades residuales horizontales estratificadas en tres canales con orientación este-oeste (costa-océano) de la Patagonia norte chilena mediante ADCP, en primavera e invierno. Las velocidades residuales se asociaron a la distribución y abundancia vertical de huevos y larvas para determinar flujos netos de individuos e inferir transporte (conectividad) entre el mar exterior-interior.

Los resultados muestran que el mar interior y exterior de la Patagonia norte chilena son importantes áreas de desove y crianza para merluza de cola, sin embargo, la abundancia de huevos y larvas disminuyó hasta el último año

muestreado en casi todas las zonas analizadas, lo que se asoció a una disminución del stock desovante y/o a un retraso en la época de desove de esta especie. Los huevos fueron más abundantes en invierno que en primavera y se ubicaron en los estratos más profundos muestreados (>50 m) lo que favorecería su ingreso al mar interior desde la plataforma continental debido al patrón de circulación estuarina. Los flujos netos estimados en invierno sugirieron que los huevos dentro del mar interior de la Patagonia norte chilena ingresarían desde la plataforma continental adyacente, y posteriormente larvas desarrolladas serían exportadas de regreso a la plataforma continental, sin embargo, no se descartó un desove secundario en el mar interior. Hacia el sur de la Patagonia, las menores abundancias de huevos y larvas encontrados provendrían de un desove secundario dentro del mar interior, lo cual, se deduce de una menor conectividad y/o transporte de los estadios tempranos de vida de merluza de cola entre el mar interior-exterior. El ingreso y/o retención de los estadios iniciales de vida en el mar interior y la posterior exportación de larvas desarrolladas al océano facilitaría una alimentación adecuada a los estadios de desarrollo de esta especie, además de una menor probabilidad de ser depredada en las etapas de vida más vulnerables. Los modelos aditivos generales (GAM's) mostraron un efecto lineal significativo entre los huevos y la salinidad, un efecto no lineal entre la abundancia de larvas y la temperatura, mayores abundancias larvales asociadas a una menor abundancia de depredadores (medusas) y a una mayor abundancia de presas (copépodos).

Los cambios ontogenéticos en la distribución de *M. magellanicus* asociados a las características bio-oceanográficas de la zona de estudio respaldan la hipótesis de conectividad en sus estadios tempranos de vida entre el Sistema Patagónico Estuarino y la zona oceánica adyacente en la Patagonia norte, lo que formaría parte de su estrategia reproductiva para otorgar mayores probabilidades de sobrevivencia a su descendencia.

## ABSTRACT

The oceanographic dynamics of the Patagonian Estuarine System and its adjacent oceanic zone is modulated by estuarine circulation (oceanic water masses and freshwater inputs), tides and wind. These dynamics are influenced by forcing factors of different temporal and spatial scales, such as changes in the intensity of the westerly wind drift (WWD) or the South Pacific Current (SPC), the Pacific Decadal Oscillation (PDO), the El Niño Southern Oscillation (ENSO), the Southern Annular Mode (SAM), Madden Julian Oscillation (MJO). In addition, over the last few decades, changes in freshwater discharge from precipitation and glacial ice melt demonstrate that global climate change is also affecting the Patagonian environment. It is still unknown whether these processes potentially affect the spawning areas and early life stage distribution of fish species such as *Macruronus magellanicus* that are distributed between the estuarine system and the adjacent oceanic zone in Chilean Patagonia. Patagonian grenadier (*Macruronus magellanicus*) has a wide distribution in the southern part of South America, which includes the southwestern Atlantic Ocean and the southeastern Pacific Ocean between  $\sim 33^{\circ}\text{S}$  and  $\sim 56^{\circ}\text{S}$ . In the southwest Atlantic, no important spawning areas have been reported for Patagonian grenadier, and a decrease in the adult stock in winter has been found, suggesting that this species would make inter-oceanic migrations to reproduce with the Pacific stock. In the southeastern Pacific, the spawning stock is concentrated between  $\sim 43^{\circ}\text{S}$  and  $\sim 48^{\circ}\text{S}$ , associated with submarine canyons at the break of the continental shelf (outer sea). In the Patagonian Estuarine System (SEP, inner sea) and the adjacent oceanic zone (outer sea) of Chilean Patagonia, eggs and larvae of Patagonian grenadier have been found, which has allowed postulating them as potential spawning and rearing areas for this species, however, their spatial and temporal persistence has not yet been demonstrated, nor have their environmental characteristics been described. On the other hand, it is not known if the eggs and



larvae present in the inner sea come from the main spawning area in the outer sea, or if spawning occurs in both the outer and inner sea.

The general objective of this thesis was to evaluate the bio-oceanographic processes that influence the connectivity of the early life stages of Patagonian grenadier between the Patagonian Estuarine System and the adjacent oceanic zone in Chilean Patagonia, hypothesizing that exist connectivity of eggs and larvae of *M. magellanicus* between these two zones. To fulfill the objective, stratified samples of ichthyoplankton, zooplankton and hydrographic data from 26 oceanographic cruises conducted in spring and winter in the Patagonian Estuarine System and its adjacent oceanic zone in the period 1995-2019 were analyzed. Eggs and larvae of Patagonian grenadier were quantified, larvae were classified by size, and the standardized abundance of eggs and larvae was presented for each of the cruises conducted. The spatial (inshore-offshore), seasonal (winter-spring) and interannual (1995-2019) variability of the abundance of hake eggs and larvae, as well as bio-oceanographic characteristics (temperature, salinity, potential predators (medusae) and prey (copepods)) in the study area were explored. For two years of the study period, measurements of stratified horizontal residual velocities were obtained in three east-west oriented channels (coast-ocean) of northern Chilean Patagonia using ADCP, in spring and winter. Residual velocities were associated with the distribution and vertical abundance of eggs and larvae to determine net fluxes of individuals and infer transport (connectivity) between the outer and inner sea.

The results show that the inner and outer sea of northern Chilean Patagonia are important spawning and nursery areas for Patagonian grenadier, however, the abundance of eggs and larvae decreased until the last year sampled in almost all the areas analyzed, which was associated with a decrease in the spawning stock and/or a delay in the spawning season of this species. Eggs were more abundant

in winter than in spring and were located in the deepest strata sampled (>50 m) which would favor their entry into the inner sea from the continental shelf due to the estuarine circulation pattern. Estimated net fluxes in winter suggested that eggs within the inner sea of northern Chilean Patagonia would enter from the adjacent continental shelf, and subsequently developed larvae would be exported back to the continental shelf, however, secondary spawning in the inner sea was not ruled out. To the south of Patagonia, the lower abundances of eggs and larvae found would come from a secondary spawning within the inner sea, which is deduced from a lower connectivity and/or transport of the early life stages of Patagonian grenadier between the inland-outer sea. The entry and/or retention of early life stages in the inland sea and the subsequent export of developed larvae to the ocean would facilitate an adequate diet for the developmental stages of this species, in addition to a lower probability of being predated in the most vulnerable life stages. General additive models (GAM's) showed a significant linear effect between eggs and salinity, a non-linear effect between larval abundance and temperature, higher larval abundances associated with lower abundance of predators (medusae) and higher abundance of prey (copepods).

The ontogenetic changes in the distribution of *M. magellanicus* associated with the bio-oceanographic characteristics of the study area support the hypothesis of connectivity in its early life stages between the Patagonian Estuarine System and the adjacent oceanic zone in northern Patagonia, which would be part of its reproductive strategy to provide greater probabilities of survival to its offspring.

## 1. INTRODUCCIÓN

### 1.1. Dinámica oceanográfica del Sistema Estuarino Patagónico (SEP) y la zona oceánica adyacente

La dinámica oceanográfica del SEP y la zona oceánica adyacente está modulada por los aportes de agua dulce de los ríos locales, precipitación, escorrentía superficial, aguas subterráneas y glaciares, por las masas de agua; subantártica (SAAW), ecuatorial subsuperficial (ESSW), intermedia antártica (AAIW), subantártica modificada (MSAAW) y estuarina (EW), así como por la Corriente del Pacífico Sur, la circulación estuarina, las mareas y el viento. Esta dinámica, se encuentra influida por factores de forzamiento a escala temporal y espacial diferentes, tales como cambios en la intensidad de la deriva del viento del oeste (WWD) o la corriente del Pacífico Sur (SPC), la oscilación decadal del Pacífico (PDO), la oscilación del sur de El Niño (ENSO), el modo anular del sur (SAM), oscilación Madden Julian (MDO), entre otros (Iriarte et al., 2014; Narváez et al., 2019; Strub et al., 2019). Además, durante las últimas décadas, los cambios en las descargas de agua dulce producto de las precipitaciones y el derretimiento del hielo glacial demuestran que el cambio climático global también está afectando el ambiente de la Patagonia (Van Wyk de Vries et al., 2023). Aún se desconoce si estos procesos afectan potencialmente las áreas de desove y la distribución de las primeras etapas de vida de especies de peces como *M. magellanicus* en alta mar y en la costa de la Patagonia chilena (Niklitscheck et al. al., 2014; Ozorio-Zuñiga et al., 2018).

En la zona oceánica adyacente al SEP (aproximadamente entre los 40°S y 50°S) se bifurca la Corriente del Pacífico Sur (SPC) o corriente de deriva de los vientos del oeste (WWD) originando dos corrientes principales; al norte, la corriente de Humboldt y al sur, la Corriente del Cabo de Hornos (CHC). La extensión latitudinal

de estas corrientes es modificada por la variabilidad estacional de la WWD, cuya latitud norte de aproximación al continente cambia de entre 35-40°S en el invierno a ~46°S en el verano. El flujo principal de la Corriente de Humboldt (HC) avanza hacia el ecuador y se une a la Corriente Ecuatorial Sur (SEC). Este flujo principal está ubicado hacia el océano (~75–85°W) de flujos costeros más estrechos que se extienden aproximadamente hasta los 40°S. Debajo de estos se encuentra la corriente sub-superficial Perú-Chile (PCUC) que fluye hacia el polo y es continua desde el norte de Perú hasta aproximadamente 50°S (Fig. 1.1) (Linford et al., 2023; Strub et al., 2019; Thiel et al., 2007).

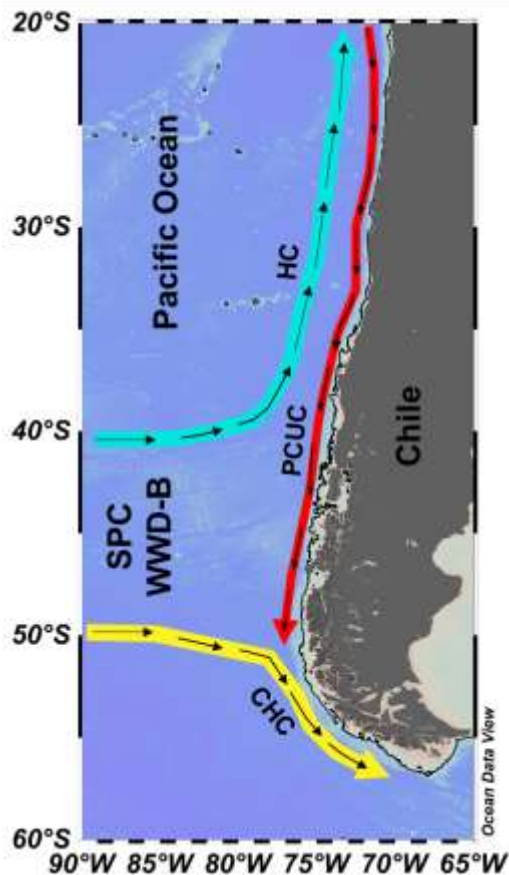


Fig. 1.1. Principales corrientes en el Pacífico Sur oriental que influyen en el centro-sur chileno, mostrando la bifurcación de la Corriente del Pacífico Sur (SPC) o Deriva del Viento del Oeste (WWD), la corriente de Humboldt (HC), la corriente Cabo de Hornos y la corriente sub-superficial Perú-Chile (PCUC).

## **1.2. La importancia del Sistema Estuarino Patagónico (SEP) y la zona oceánica adyacente como zonas de desove y crianza de organismos marinos**

El Sistema Estuarino Patagónico (SEP) y la zona oceánica adyacente desde el fiordo de Reloncaví (41°S) hasta el Cabo de Hornos (56°S), se caracterizan por la presencia de un complejo sistema de fiordos, canales, golfos, bahías, cañones submarinos y constricciones batimétricas (Fig. 1.2). Tanto el SEP como la zona oceánica adyacente han sido identificadas como áreas de desove y crianza para diversas especies de importancia ecológica e interés comercial, que incluyen; merluzas (*Macruronus magellanicus*, *Merluccius australis*, *Micromesistius australis*), crustáceos (*Munida gregaria*), pequeños pelágicos (*Sprattus fueguensis*, *Engraulis ringens*), entre muchos otros. Incluso se sugiere que especies como; *Dissostichus eleginoides*, *Merluccius australis*, *Micromesistius australis* y *Macruronus magellanicus* realizan migraciones inter-oceánicas para desovar en estas áreas. Como zona de crianza de la merluza de cola el SEP contribuye con 10 a 35% del reclutamiento de esta especie en la Patagonia Chilena, mientras que la zona oceánica adyacente contribuiría con el mayor porcentaje, entre 64-85%. Estos datos resaltan la importancia del SEP y la zona oceánica adyacente como zonas de desove y crianza de organismos marinos y particularmente de *M. magellanicus* (Ozorio-Zuñiga et al., 2018; Niklitschek et al., 2014; Leal et al., 2011; Bustos et al., 2008; Bustos et al., 2007; Arkhipkin et al., 2008; León et al., 2008).

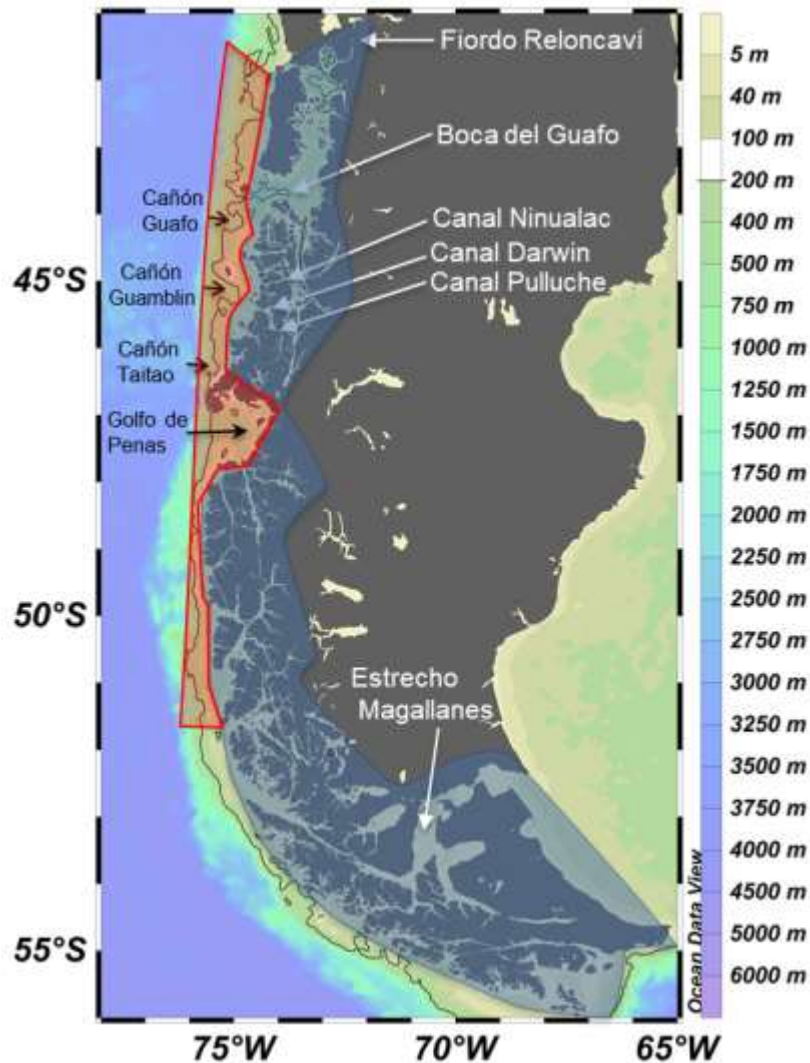


Fig. 1.2. Sistema Estuarino Patagonico (SEP) (sombreado azul; mar interior) y zona oceánica adyacente (sombreado rojo; mar exterior). La línea negra indica el quiebre de la plataforma continental.

A pesar de que el SEP y la zona oceánica adyacente han sido relativamente bien estudiados por separado, la dinámica y conectividad entre estos sistemas aún sigue estando poco conocida, al igual que ocurre en muchas otras zonas del planeta. Más investigaciones de conectividad entre sistemas se han realizado principalmente en la costa atlántica de América del Norte, Europa (Höffle et al.,

2014; Guillam et al., 2020; Guerreiro et al., 2021) y sólo recientemente se han comenzado a llevar a cabo en larvas de crustáceos y peces en los fiordos de la Patagonia Chilena (León et al., 2008; Meerhoff et al., 2014; Flores et al., 2020). La presencia de huevos, larvas y/o juveniles de una misma especie en el SEP y la zona oceánica adyacente, ha conllevado a proponer hipótesis de transporte y/o conectividad de estadios tempranos de vida entre estas zonas. Sin embargo, son pocas las investigaciones realizadas evaluando ambas zonas simultáneamente, y, además, muestran resultados contrastantes entre especies. Para *Merluccius australis* se determinó baja conectividad del mar exterior con el mar interior en invierno, mientras que para *Munida gregaria* se obtuvo ingreso y exportación entre el mar interior y exterior (León et al., 2008; Meerhoff et al., 2014; Flores et al., 2020). Estos resultados revelan la necesidad de ampliar el conocimiento acerca de cómo las especies utilizan la dinámica entre estos ecosistemas, para sus estrategias reproductivas.

### **1.3. Merluza de cola**

La merluza de cola *Macruronus magellanicus* (Lonnberg, 1907) se distribuye en el extremo sur de América del Sur, entre Valparaíso (~33°S) y el Cabo de Hornos (~56°S) en el Pacífico sureste, y en el Atlántico suroeste entre ~35° y ~56°S (Fig. 1.3). Es el recurso demersal más abundante en la Patagonia chilena y el segundo del total de desembarques anuales en Argentina. Sin embargo, el stock de esta especie en Chile ha ido declinando desde 1999 y su estado de explotación actual es "Agotado". Es una especie Gadiforme euribática, localizada en la plataforma y talud continental a profundidades entre 20 y 800 m. Juveniles y adultos de esta especie se encuentran segregados, mientras que los juveniles son pelágicos, los adultos cambian a un hábitat demersal. En el Atlántico sudoccidental, los juveniles sólo se encuentran en Agua de Plataforma y los adultos en Agua Costera y de Plataforma. En el Pacífico sureste, los juveniles se encuentran en

el Agua Subantártica (SAAW) y los adultos se encuentran en el SAAW y en el Agua Ecuatorial Subsuperficial (ESSW) (Machinandiarena et al., 1999; Niklitschek et al., 2014; Giussi et al., 2016; Castillo-Jordan et al., 2019; Álvarez et al., 2022; SSPA, 2023).

Las zonas de desove, crianza y estacionalidad del desove de *M. magellanicus* no están claramente identificadas. Algunas hipótesis señalan que, desde la primavera austral hasta el otoño, los adultos de *M. magellanicus* se dispersan por sus zonas de alimentación en la plataforma patagónica oriental y el sur de Chile, y durante el invierno austral, parte del stock migra a áreas de desove más al norte a lo largo de la Patagonia chilena. Dado que no se han encontrado áreas de desove importantes en el Atlántico, se ha propuesto que el stock del Atlántico migraría para reproducirse en el Pacífico sureste. La mayor parte de la información disponible actualmente sugiere que la reproducción ocurre entre el invierno y la primavera y que las mayores agregaciones de desove conocidas ocurren entre 43-48°S en cañones submarinos ubicados en la plataforma occidental de la Patagonia chilena (Niklitschek et al., 2014; Mckeown et al., 2015; Giussi et al., 2016; Payá, 2020; Gorini et al., 2021).



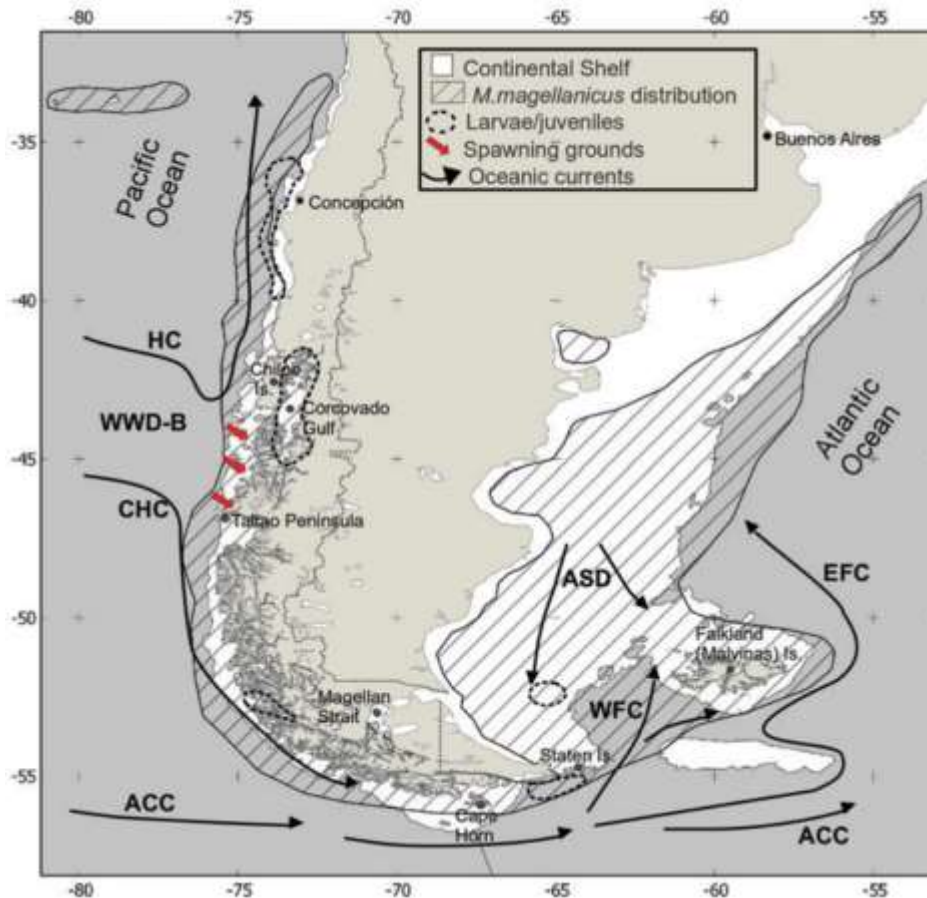


Fig. 1.3. Distribución de merluza de cola (*Macrurus magellanicus*) en Sudamérica, plataforma continental (área en color blanco), principales corrientes oceánicas y deriva de los vientos Oeste con acrónimos en inglés. HC = Humboldt Current, WWD-B = Western Wind Drift or CPS bifurcation, CHC = Cape Horn Current, ACC = Antarctic Circumpolar Current, EFC = Eastern Branch of Falkland Current, WFC = Western Branch of Falkland Current, ASD = Argentinian Shelf Drift (Tomado de Niklitschek et al., 2014).

Históricamente, se han propuesto otras potenciales áreas de desove de esta especie que han sido inferidas a partir de la presencia de huevos, larvas e incluso algunos ejemplares adultos maduros. Entre estas áreas se incluyen canales de aguas interiores de la Patagonia Chilena, la plataforma continental y Patagonia Argentina, entre otras (Giussi et al., 2016; Ernst et al., 2005). Sin embargo, su

persistencia espacial y temporal no ha sido confirmada. Por otra parte, se desconoce si los huevos y larvas encontrados en el mar interior de la Patagonia chilena provienen de un desove dentro del mar interior o si provendrían del área principal de desove en el mar exterior. Las investigaciones realizadas se han enfocado principalmente en estudiar la composición y abundancia de las larvas de peces en los fiordos de la Patagonia, o en las aguas adyacentes del Océano Pacífico sureste. Estas son importantes áreas de desove y crianza de muchas especies, y en particular de *M. magellanicus*, sin embargo, ningún estudio ha realizado análisis de la distribución de estadios tempranos de desarrollo de esta especie incluyendo ambas zonas simultáneamente y analizando el patrón de flujos y los procesos de conectividad entre éstas dos zonas (Gorini et al., 2021; Payá 2020; Osorio-Zúñiga et al., 2018; Giussi et al., 2016; Landaeta et al., 2012; Machinandiarena and Ehrlich, 1999).

Esta compleja dinámica oceanográfica entre el SEP y la zona oceánica adyacente podría causar grandes variaciones estacionales, interanuales y decadales en el transporte de huevos y larvas, sin embargo, se desconoce qué tipo de influencia puedan tener estos procesos físicos y su variabilidad sobre la distribución espacial de los estadios tempranos de vida de las especies en estas zonas y consecuentemente sobre sus estrategias reproductivas y su sobrevivencia.

#### **1.4. Estrategias reproductivas de los peces entre sistemas estuarinos y oceánicos**

Los peces han desarrollado numerosas estrategias reproductivas que incluyen tácticas como la selección de zonas de desove y periodos reproductivos, así como la utilización de flujos y corrientes que, combinados con cambios en la distribución vertical en sus estadios tempranos de vida, les permiten ingresar,

retenerse o exportarse entre los estuarios y las zonas oceánicas adyacentes. Estas tácticas son empleadas para sobrellevar aspectos críticos de su ontogenia, tales como facilitar la primera alimentación, regular el encuentro con predadores y presas, así como la distancia y dirección de su transporte hacia o desde las zonas de crianza, aumentando de este modo, las probabilidades de sobrevivencia de su descendencia. Conocer cómo las especies utilizan este conjunto de tácticas es esencial para comprender la dinámica poblacional, así como para desarrollar y mejorar modelos numéricos que incluyen procesos físicos y biológicos, los cuales son herramientas poderosas para contribuir al manejo de las pesquerías y para la protección y conservación de especies. De igual forma, permitiría visualizar potenciales cambios dentro de las estrategias reproductivas o incluso inferir la capacidad adaptativa de las especies ante las variaciones climáticas (Lough and Potter, 1993; Lowerre-Barbieri et al., 2011; Hurst et al., 2009; Keckeis et al., 2017; Ospina-Alvarez et al., 2018; Guerreiro et al., 2021; Zhang et al., 2022).

El transporte de huevos y larvas entre ambientes estuarinos y la zona oceánica adyacente, como parte de las estrategias reproductivas de las especies, es un tema de estudio complejo, debido a los componentes bióticos y abióticos que deben ser analizados. Entre estos ecosistemas deben considerarse los flujos horizontales y verticales influidos por la morfología de la costa, características batimétricas asociadas a la plataforma continental, la circulación estuarina y la variabilidad de las corrientes oceánicas, entre otros componentes abióticos. Por otra parte, están los aspectos del componente biótico tales como la boyantes de los huevos, la duración de la fase larval, el comportamiento larval y la migración y/o transporte activo de las larvas. Cabe señalar que los antiguos paradigmas de dispersión pasiva en los estadios tempranos de vida de los peces han sido desafiados por hallazgos que muestran la capacidad de las larvas para orientarse

y moverse en dirección a los criaderos, así como para distribuirse distintivamente en la columna de agua (Pineda et al., 2007; Keckeis et al., 2017).

Las estrategias reproductivas dependen de cada especie y pueden variar incluso entre especies filogenéticamente cercanas. Por ejemplo, en el océano Pacífico sur oriental *Merluccius gayi* desova en el quiebre de la plataforma continental y sus huevos y larvas son transportados sub-superficialmente hacia la costa, a las áreas de crianza. El transporte de huevos y larvas desde la zona oceánica hacia la costa ha sido reportado también para *Macruronus novaezelandiae* en sus dos áreas principales de desove en Nueva Zelanda. Sin embargo, para *Merluccius australis* cuyo desove principal ocurre en el quiebre de la plataforma continental chilena (zona oceánica), y se determinó que sus huevos y lavas (con saco vitelino) no son transportados a la costa (mar interior). Las diferencias en el transporte costa-océano de los estadios tempranos de vida de las especies hacen necesario su estudio detallado para construir modelos biofísicos basados en los individuos (IBM's), los cuales son útiles para hacer inferencias acerca de las estrategias reproductivas de las especies y en cómo estas podrían adaptarse (o no) a los cambios ambientales (Flores et al., 2020; Landaeta y Castro, 2012; Zeldis et al., 1998).

Los antecedentes expuestos muestran la necesidad de realizar estudios acerca del transporte y/o conectividad en estadios tempranos de vida de especies marinas entre sistemas estuarinos y oceánicos, los cuales permitirían comprender su dinámica poblacional, estrategias reproductivas y contribuir al desarrollo y mejoras de modelos biofísicos. El análisis de la dinámica poblacional, estrategias reproductivas y modelos biofísicos son herramientas fundamentales para el manejo de las pesquerías, protección ambiental, ecología de restauración y predicción de adaptación antes cambios ambientales. En este sentido, se ha trazado como **objetivo general** del presente estudio "Evaluar los procesos bio-

oceanográficos que influyen en la conectividad de los estadios tempranos de vida de la merluza de cola (*Macruronus magellanicus*) entre el Sistema Patagónico Estuarino (SEP) y la zona oceánica adyacente en la Patagonia Chilena”. Para cumplir este objetivo se propusieron las hipótesis y objetivos descritos a continuación.

## **1.5. Hipótesis y objetivos específicos**

### **Hipótesis 1**

Existe conectividad en los estadios tempranos de vida de *Macruronus magellanicus* entre el sistema estuarino patagónico y la zona oceánica adyacente en la Patagonia chilena.

### **Objetivos específicos:**

- Determinar la variabilidad espacio temporal de las características bio-oceanográficas en las zonas de desove y crianza de merluza de cola (*Macruronus magellanicus*), en el sistema estuarino patagónico y zona oceánica adyacente en la Patagonia Chilena, Pacífico sudeste.
- Determinar la conectividad de huevos y larvas de merluza de cola (*Macruronus magellanicus*) entre el sistema estuarino patagónico y zona oceánica adyacente en la Patagonia Chilena, Pacífico sudeste.

Cada uno de estos objetivos es abordado como un capítulo en el desarrollo de esta tesis, los que además se constituyeron en dos manuscritos. El objetivo 1, conforma el capítulo 1, cuyo resultado fue el manuscrito titulado: “Efectos de las condiciones bio-oceanográficas en la distribución de estadios tempranos de vida

de merluza de cola (*Macruronus magellanicus*) entre el Sistema Estuarino Patagónico y la plataforma continental adyacente en la Patagonia Chilena”, el cual está siendo sometido a revisión por la revista Estuaries, Coastal and Shelf Science desde el 21/12/2023. El objetivo 2, capítulo 2, resultó en el manuscrito titulado: “Transporte inferido de estadíos tempranos de vida de merluza de cola (*Macruronus magellanicus*) entre los canales del norte de la Patagonia y la plataforma continental”, el cual fue publicado en la revista “Continental Shelf Research”.

## **2. MATERIALES Y MÉTODOS**

En esta sección se describe brevemente la metodología empleada para la obtención de los resultados de los dos capítulos de la tesis. La descripción detallada de la metodología empleada para abordar cada objetivo es descrita en cada uno de los capítulos (manuscritos).

### **2.1. Área de estudio**

El área de estudio abarca el Sistema Estuarino Patagónico occidental (O. Pacífico), desde aproximadamente los 41°S hasta los 56°S, y la zona oceánica adyacente a lo largo del quiebre de la plataforma continental (aproximadamente entre los 42°S – 51°S), áreas que se denominaran en lo sucesivo mar interior y exterior respectivamente (Fig. 2.1).

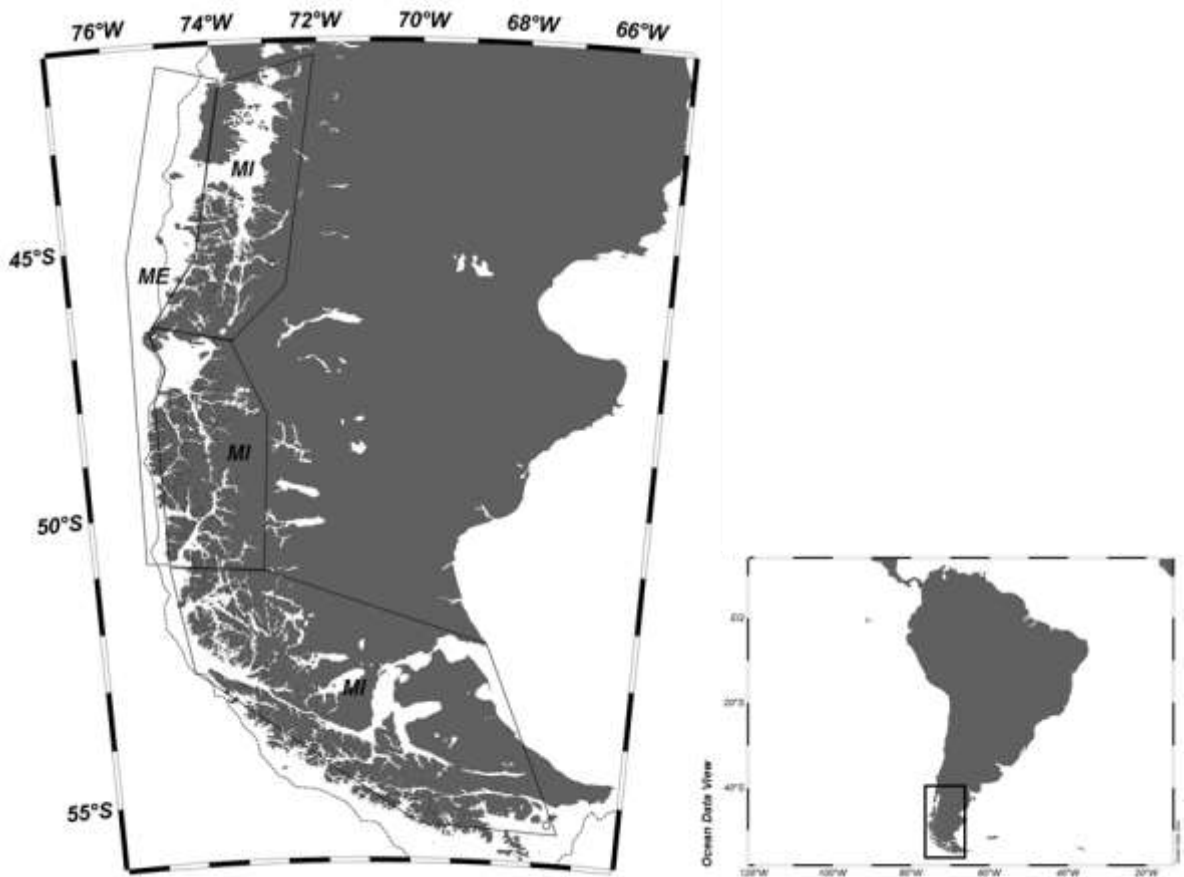


Fig. 2.1. Área de estudio. La línea segmentada indica el quiebre de la plataforma continental. ME = Mar exterior, MI = Mar interior.

## 2.2. Datos bio-oceanográficos

Se analizó información hidrográfica y muestras de zooplancton de los años 1995 al 2019 (primavera e invierno) colectadas en cruceros oceanográficos realizados por el Programa CIMAR-Fiordos en el mar interior, así como de cruceros de evaluación hidroacústica de la merluza austral y de cola llevados a cabo por IFOP, y de la expedición Taitao llevada a cabo por el Centro COPAS Sur Austral realizados en el mar exterior. Las muestras de zooplancton de estos cruceros fueron recolectadas con redes bongo (60 cm de diámetro, 300µm de luz de malla,

muestras integradas) y Tucker trawl (1m<sup>2</sup>, 300µm de luz de malla, muestras estratificadas), ambas redes equipadas con flujómetros para calcular el volumen de agua muestreado y posteriormente estandarizar las abundancias de los organismos encontrados. Esta información se utilizó para identificar y caracterizar las zonas de desove y crianza de *M. magellanicus* y determinar si existió variabilidad zonal (mar interior-exterior), meridional (latitud, longitud), estacional (primavera-invierno), interanual (1995-2019) y a distintos estratos de profundidad.

### **2.3. Identificación de zonas de desove y crianza**

Se identificaron las zonas de desove y crianza de *M. magellanicus* tanto en el mar interior como exterior a partir de las muestras de zooplancton obtenidas en los cruceros. En el laboratorio se identificaron, contaron y midieron los huevos y larvas de *M. magellanicus* de acuerdo a Patchell et al. (1987), Machinandiarena and Ehrlich (1999) and Balbontin et al. (2004). Con esta información se representó la distribución y abundancia estandarizada de huevos y larvas de *M. magellanicus*, en secciones horizontales mediante diagramas de burbuja (Surfer 16).

### **2.4. Distribución vertical de huevos y larvas**

Se elaboraron perfiles verticales estratificados de distribución de huevos y larvas de merluza de cola a partir de promedios de abundancia de las estaciones muestreadas en las que se encontró presencia de huevos y larvas. Los perfiles se graficaron por cada crucero para huevos y larvas por separado. Además, en el caso de las larvas se graficaron perfiles verticales durante el día y la noche, para inferir si las larvas de esta especie presentaban migraciones verticales.



## **2.5. Estimación de cambios en la distribución vertical y horizontal de huevos y larvas**

La estimación de cambios verticales y horizontales en la distribución de huevos y larvas, se realizó mediante el cálculo de centroides (centros de masa) a partir de la relación  $WA = \frac{\sum(N_i Z_i)}{\sum(N_i)}$ , donde: WA = “weighted average” (“promedio ponderado” a profundidad o latitud),  $N_i$  = abundancia de organismos en el estrato o latitud  $i$ ,  $Z_i$  = profundidad media en el estrato o latitud  $i$ .

## **2.6. Caracterización hidrográfica**

La caracterización hidrográfica se realizó con la data de CTD (Seabird 19+ y 25), obtenida en las estaciones oceanográficas de los distintos cruceros. Con esta información se elaboraron secciones verticales de temperatura y salinidad utilizando Ocean Data View V.5.6.3. Además, se obtuvieron promedios de temperatura y salinidad por estrato, estación de muestreo y época del año para asociarlos a la distribución y abundancia de huevos y larvas de merluza de cola.

Por otra parte, para dos años se obtuvo la data de velocidad y dirección de los flujos horizontales en los canales con orientación este-oeste: Darwin (45°30’S), Ninualac (45°05’S) y Pulluche (45°50’S) tomada en el Programa de Investigación CIMAR-Fiordos 8 y 9 durante la primavera de 2002, e invierno y primavera de 2003. La data en cada uno de los canales fue obtenida mediante mediciones de ADCP (Acoustic Doppler Current Profile) (Workhorse RDI 307 KHz), el cual registró datos de velocidad y dirección del flujo cada 30 segundos durante 24 horas, hasta una profundidad máxima de 100 m. Esta data de velocidad y dirección se promedió por estratos (0-20 m, 20-50m, 50-100m, >100m), para que coincidiera con los estratos muestreados de zooplancton en los que se colectó huevos y/o larvas de merluza de cola. A partir de esta información se calcularon

los flujos instantáneo y neto de huevos y larvas en sentido este-oeste (gradiente costa-océano, que permitieron estimar el ingreso y/o exportación de huevos y larvas entre el mar interior y exterior.

## **2.7. Caracterización biológica**

La caracterización biológica del área de estudio comprendió la identificación y cuantificación de potenciales presas de larvas de *M. magellanicus* y de potenciales depredadores de sus huevos y larvas. Como potenciales presas se cuantificó y estandarizó la abundancia total de copépodos (en sus diferentes estadios de vida; nauplios, copepoditos, copépodos adultos), mientras que como potenciales predadores se cuantificó y estandarizó la abundancia total de medusas.

## **2.8. Cambios ontogenéticos en el gradiente costa – océano y en la distribución vertical de *M. magellanicus***

La distribución de huevos y/o larvas en los diferentes grupos de tallas se representó mediante diagramas de burbujas en mapas horizontales en el gradiente costa-océano, con la finalidad de estimar cambios ontogenéticos entre el mar interior y exterior. De manera similar, se elaboraron perfiles verticales de la distribución de huevos y larvas por talla, que permitieron estimar cambios ontogenéticos en su distribución vertical. Esta información se utilizó además para identificar patrones que sugirieron importación y/o exportación de huevos y larvas de merluza de cola entre el mar interior y exterior.

## **2.9. Análisis estadísticos**

Se realizaron pruebas de normalidad a los datos bio-oceanográficos utilizando el test de Shapiro–Wilk, en general los residuales no mostraron distribución normal, por lo cual, se optó por la utilización de estadística no paramétrica que incluyó test de Kruskal-Wallis, pruebas post hoc de Dunn’s, análisis multivariado permutado de la varianza (PERMANOVA) y análisis de porcentajes de similitud (SIMPER). Por otra parte, se emplearon Modelos Aditivos Generalizados (GAM’s) utilizando el software R, para evaluar las relaciones entre las variables bio-oceanográficas (salinidad, temperatura, potenciales predadores y presas) y la ubicación geográfica (latitud y longitud) sobre la abundancia de huevos y larvas de merluza de cola. Con estos modelos además se estimaron los intervalos de temperatura y salinidad en los cuales existió mayor abundancia de huevos y larvas de esta especie.

### 3. RESULTADOS

**3.1 Capítulo 1:** Efectos de las condiciones bio-oceanográficas en la distribución de estadios tempranos de vida de merluza de cola (*Macruronus magellanicus*) entre el Sistema Estuarino Patagónico y la plataforma continental adyacente en la Patagonia Chilena. Manuscrito enviado a la revista Estuarine, Coastal and Shelf Science el 21/12/2023.

#### Resumen

Especies de peces demersales como merluza de cola (*Macruronus magellanicus*) se encuentran ampliamente distribuidas por la zona austral de América del Sur y, dentro de su complejo ciclo de vida, una fracción de su población realiza migraciones inter-oceánicas (Pacífico-Atlántico) para su reproducción y desove. Mientras que en el Atlántico sur no se han identificado áreas importantes de desove de *M. magellanicus*, en la Patagonia Chilena su estrategia reproductiva aparentemente consiste en utilizar un “portafolio” de áreas alternativas y/o secundarias de desove y crianza, ubicadas en la plataforma continental y en el Sistema Estuarino Patagónico. Sin embargo, no se ha confirmado el uso ni la persistencia espacial y temporal de estas áreas de desove y crianza, ni se han descrito sus características ambientales. Con el fin de identificar y describir potenciales áreas de desove y crianza de *M. magellanicus* en la Patagonia chilena, analizamos muestras de zooplancton, ictioplancton y datos hidrográficos obtenidos de 26 cruceros oceanográficos realizados en primavera e invierno, en el Sistema Estuarino Patagónico y su plataforma continental adyacente entre años 1995-2019. Los resultados muestran que la abundancia de huevos y larvas disminuyó hasta nuestro último año muestreado y, también, que ambas zonas de la Patagonia norte chilena son importantes áreas de desove y crianza para esta especie. En invierno, en la Patagonia norte la mayoría de los huevos ingresaron a los canales y fiordos desde la plataforma continental, hacia el sur de la Patagonia, el escaso desove parece ocurrir dentro del mar interior. Los huevos

fueron más abundantes en invierno que en primavera y se ubicaron en los estratos muestreados más profundos (>50 m), mientras que las larvas se distribuyeron heterogéneamente en toda la columna de agua. Los modelos aditivos generales (GAM's) mostraron un efecto lineal significativo entre los huevos y la salinidad con máxima abundancia en salinidades alrededor de (34) y un efecto no lineal entre la abundancia de larvas y la temperatura, siendo más abundantes entre 9-10°C. De igual forma asociaron mayores abundancias larvales a una menor abundancia de depredadores (medusas) y una mayor abundancia de presas (copépodos). La distribución de huevos y larvas de *M. magellanicus* entre el Sistema Estuarino Patagonico y la zona oceánica adyacente parece ser parte de una estrategia reproductiva encaminada a brindar mayores posibilidades de sobrevivencia a su descendencia.

## Estuarine, Coastal and Shelf Science

### Effects of bio-oceanographic conditions on the distribution of *Macrurus magellanicus* early life stages between Patagonian Estuarine System and Continental Shelf.

--Manuscript Draft--

Manuscript Number:	YECSS-D-23-01028
Article Type:	Research Paper
Keywords:	Macrurus magellanicus; Chilean Patagonia; early life stages; alternative nursery areas; inter-oceanic migration; secondary spawning areas.
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Abstract:	Demersal fish species such as the Patagonian grenadier ( <i>Macrurus magellanicus</i> ) are widely distributed around the austral zone of South America and, within their complex life cycle, a fraction of its population carry out inter-oceanic migrations (Pacific-Atlantic) for reproduction and growth. While in the south Atlantic no important spawning areas of <i>M. magellanicus</i> have been identified, in the south Pacific Patagonia their reproductive strategy apparently uses a "portfolio" of alternative or secondary spawning and nursery areas located either on the continental shelf or inshore zones, within the Patagonian Estuarine System. The spatial and temporal persistence use of these alternative spawning areas, though, has not been confirmed nor the environmental characteristics of the spawning and early life stages nursery habitats. In order to identify and describe potential spawning and nursery areas of <i>M. magellanicus</i> in Chilean Patagonia, we analyzed ichthyoplankton, hydrographic data and zooplankton, obtained from 26 oceanographic cruises conducted in spring and winter in the Pacific Patagonian Estuarine System and its adjacent continental shelf between years 1995-2019. The results show that eggs and larval abundances have been decreasing until our last sampled year and also that both zones in the northern Chilean Patagonia are important spawning and nursery areas for this species. In winter, in the northern and central Patagonia, most eggs entered to the channels and fjords from the continental shelf. Towards the south of Patagonia, the scarce spawning seems to occur within the inshore zones. Eggs were more abundant in winter than in spring and located in the deepest sampled strata (>50m) while larvae were heterogeneously distributed throughout the water column. General additive models (GAM's) showed a significant linear effect between eggs and salinity with maximum abundance at salinities around (34) and a non-linear effect between larval abundances and temperature, being larvae more abundant between 9-10 °C, higher larval abundances associated with lower abundance of predators (medusae) and higher abundance of prey (copepods). The distribution of eggs and larvae of <i>M. magellanicus</i> between the Patagonian Estuarine System and Patagonian Pacific Shelf seems to be part of a reproductive strategy aimed at providing greater chances of survival to their offspring.
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	Edwin J. Niklitschek, PhD edwin.niklitschek@ulagos.cl Experience in the study of the factors that influence the abundance, diversity and transport of fish larvae in coastal areas.
	Ian Potter, PhD i.potter@murdoch.edu.au Vast experience in the study of the factors that influence the abundance and diversity of fish larvae in estuaries.
<b>Opposed Reviewers:</b>	

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1 **Effects of bio-oceanographic conditions on the distribution of early life stages**  
2 **of Patagonian grenadier (*Macruronus magellanicus*) between Pacific**  
3 **Patagonian Estuarine System and adjacent Continental Shelf.**

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12 Demersal fish species such as the Patagonian grenadier (*Macruronus magellanicus*)  
13 are widely distributed around the austral zone of South America and, within their  
14 complex life cycle, a fraction of its population carry out inter-oceanic migrations  
15 (Pacific-Atlantic) for reproduction and growth. While in the south Atlantic no  
16 important spawning areas of *M. magellanicus* have been identified, in the south  
17 Pacific Patagonia their reproductive strategy apparently uses a "portfolio" of  
18 alternative or secondary spawning and nursery areas located either on the  
19 continental shelf or inshore zones, within the Patagonian Estuarine System. The  
20 spatial and temporal persistence use of these alternative spawning areas, though,  
21 has not been confirmed nor the environmental characteristics of the spawning and  
22 early life stages nursery habitats. In order to identify and describe potential spawning  
23 and nursery areas of *M. magellanicus* in Chilean Patagonia, we analyzed  
24 ichthyoplankton, hydrographic data and zooplankton, obtained from 26  
25 oceanographic cruises conducted in spring and winter in the Pacific Patagonian  
26 Estuarine System and its adjacent continental shelf between years 1995-2019. The  
27 results show that eggs and larval abundances have been decreasing until our last  
28 sampled year and also that both zones in the northern Chilean Patagonia are  
29 important spawning and nursery areas for this species. In winter, in the northern and  
30 central Patagonia, most eggs entered to the channels and fjords from the continental  
31 shelf. Towards the south of Patagonia, the scarce spawning seems to occur within  
32 the inshore zones. Eggs were more abundant in winter than in spring and located in  
33 the deepest sampled strata (>50m) while larvae were heterogeneously distributed  
34 throughout the water column. General additive models (GAM's) showed a significant  
35 linear effect between eggs and salinity with maximum abundance at salinities around  
36 (34) and a non-linear effect between larval abundances and temperature, being  
37 larvae more abundant between 9-10 °C, higher larval abundances associated with  
38 lower abundance of predators (medusae) and higher abundance of prey (copepods).  
39 The distribution of eggs and larvae of *M. magellanicus* between the Patagonian  
40 Estuarine System and Patagonian Pacific Shelf seems to be part of a reproductive  
41 strategy aimed at providing greater chances of survival to their offspring.

42 **Keywords:** *Macruronus magellanicus*, Chilean Patagonia, early life stages,  
43 alternative nursery areas, inter-oceanic migration, secondary spawning areas.



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#### 44 **Highlights**

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- 46 1. Pacific continental shelf and estuaries are important for spawning and
- 47 nursery.
- 48 2. Eggs and larvae show different vertical distributions and transport.
- 49 3. Eggs and larval abundances decreased during the 24-y studied.
- 50 4. It presents interoceanic (Pacific-Atlantic) migrations for reproduction and
- 51 growth.
- 52 5. The reproductive strategy includes alternative spawning and nursery areas.

## 53 1. Introduction

54

55 The continental shelf and slope along with estuaries are used by many marine fish  
56 species as spawning and nursery areas because the high food abundance, the  
57 refuge that they provide against predators and the favorable habitats for their early  
58 life stages development and survival (Potter et al., 2015; Sponaugle et al., 2002;  
59 Blaber 1985; Cushing 1975). These ecosystems may be utilized simultaneously or  
60 alternatively, according to the needs at each stage of development (Guerreiro et al.,  
61 2021; Boehlert and Mundy, 1988; Pietrafesa and Janowitz, 1988). The selection of  
62 spawning and/or nursery areas depends on the reproductive strategy of each  
63 species and can vary even among phylogenetically close species (Veroes et al.,  
64 2023; Flores et al., 2020; Landaeta and Castro, 2012; León et al., 2008). One of the  
65 most extensive estuarine regions of the world is the Chilean Patagonian Estuarine  
66 System (PES) which along with its adjacent continental shelf (41°S-56°S) is a large  
67 spawning and nursery area for commercially important species such as hakes  
68 (*Macruronus magellanicus*, *Merluccius australis*, *Micromesistius australis*), king  
69 crabs and squat lobster (*Lithodes antarcticus*, *Munida gregaria*) and small pelagic  
70 fishes (*Sprattus fueguensis*, *Engraulis ringens*) (Giussi et al., 2016; Leal et al., 2011;  
71 Arkhipkin et al., 2009; Bustos et al., 2008; León et al., 2008; Bustos et al., 2007).

72

73 *Macruronus magellanicus* Lonnberg, 1907, also known as Patagonian grenadier,  
74 long-tail hake, Patagonian hoki, and Argentine hoki, is distributed around the  
75 southern tip of South America, between Valparaiso (33°S) and Cape Horn (55°58'S)  
76 in the southeastern Pacific and between 35° and 56°S in the southwestern Atlantic.  
77 It is a Gadiform eurybathic species, located on the continental shelf and slope at  
78 depths between 20 and 800 m (Alvarez et al., 2022; Giussi et al., 2016). Juveniles  
79 and adults have different distributions in the water column and water masses, while  
80 juveniles are pelagic, the adults change to a demersal habitat. In the southwestern  
81 Atlantic juveniles are found in Shelf Waters and adults can be found in Coastal and  
82 Shelf Waters. In the southeastern Pacific juveniles are found in Subantarctic Water  
83 (SAAW) and adults are found in the SAAW and Equatorial Subsurface Water

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84 (ESSW). It is the most abundant demersal resource in the Chilean Patagonia and  
85 the second of the total annual landings in Argentina. Due to its role in the ecosystem,  
86 its commercial importance, as well as its wide distribution and abundance, *M.*  
87 *magellanicus* has been the subject of several fisheries studies (Castillo-Jordan et  
88 al., 2019; Giussi et al., 2016; Niklitschek et al., 2014). However, information about  
89 its reproductive ecology, particularly on its spawning and nursery areas, is still scarce  
90 (Ozorio-Zuñiga et al., 2018; Niklitschek et al., 2014).

91

92 The spawning and nursery areas and spawning seasonality of *M. magellanicus* are  
93 not clearly identified. Mckeown et al. (2015) and Giussi et al. (2016) report that from  
94 austral spring to autumn, *M. magellanicus* adult are dispersed throughout their  
95 feeding grounds on the eastern Patagonian shelf (Atlantic) and western Patagonian  
96 shelf (Pacific), and during the austral winter, part of the stock migrates to more  
97 northern spawning areas along the Chilean Patagonia. Since no important spawning  
98 areas have been found in the Atlantic, it has been proposed that the Atlantic stock  
99 would carry out an inter-oceanic migration to reproduce in the southeast Pacific  
100 (Gorini et al., 2021; Payá, 2020; Giussi et al., 2016). Most available information  
101 currently suggests that reproduction occurs between winter and spring and the  
102 largest known spawning aggregations occur between 43°S and 48°S in submarine  
103 canyons located on the western Patagonia shelf. Some spawning has also been  
104 reported on the continental shelf south of the Magellan Strait and also, small  
105 aggregations of spawners and juveniles have been reported in the Gulf of San  
106 Matias (42°S), Gulf of San Jorge (46°S) in the southwest Atlantic (Argentina) and in  
107 others small areas from the Patagonian slope (Gorini et al., 2021; Giussi et al., 2016;  
108 Niklitschek et al., 2014).

109

110 Besides the main spawning area off the northern Chilean Patagonia, and based on  
111 the occasional presence of eggs, larvae and even some mature *M. magellanicus*  
112 adult specimens, spawning and nursery areas have been proposed to occur also in  
113 fjords and channels of the Chilean Patagonia, but their spatial and temporal  
114 persistence have not been confirmed (Veroes et al., 2023; Gorini et al., 2021; Payá

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115 et al., 2020; McKeown et al., 2015). Eggs collected in the inner zone of northern  
116 Patagonian could come also from the adjacent continental shelf. An assessment,  
117 based on otolith elemental composition suggested that the relative contribution of  
118 the inner and offshore zones as nursery grounds to the recruitment of *M.*  
119 *magellanicus* was different, being the inner zone nursery grounds important, but their  
120 contribution less than that of the offshore zone (Veroes et al., 2023; Niklitscheck et  
121 al., 2014).

122  
123 The spawning areas of *M. magellanicus* located in the southeastern Pacific (41°S –  
124 56°S) either in the Pacific shelf break or in the inner zone of Chilean Patagonia,  
125 present variable oceanographic characteristics driven by different time and space  
126 scale forcing factors, such as changes in intensity of the West Wind Drift (WWD) or  
127 South Pacific Current (SPC), local wind components, El Niño Southern Oscillation  
128 (ENSO), Southern Annular Mode (SAM) and the estuarine circulation at the inshore  
129 zone (Narváez et al., 2019; Strub et al., 2019; Ozorio-Zuñiga et al., 2018; Niklitscheck  
130 et al., 2014). During the last decades changes in freshwater discharges products of  
131 rainfall and glacial ice melting demonstrate that global climate change is affecting  
132 the Patagonia environment as well (Van Wyk de Vries et al., 2023; Iriarte et al.,  
133 2014). If these processes potentially affect the spawning areas and distribution of  
134 the early life stages of fish species such as *M. magellanicus* offshore and inshore of  
135 Chilean Patagonia, is still unknown.

136  
137 To be able to determine the way how changing environmental processes modify  
138 aspects of the early life history such as distribution, connectivity between inshore  
139 and offshore zones or the relative abundance of any species, first, a detailed  
140 knowledge on the general spawning and nursery grounds, on their more usual main  
141 locations and on the usual environmental characteristics in these areas is required.  
142 Since the fate of the early life stages may determine the success of recruitment,  
143 knowledge of the spawning and nursery areas of the species, as well as the factors  
144 that affect the distribution of their early life stages are necessary to understand the  
145 population dynamics of any fisheries resource. This information may be used in

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4 146 individual-based models (IBM's), for instance, to visualize alternative pathways  
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6 147 within reproductive strategies or even to infer the adaptive capacity of the species in  
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8 148 face of the climatic variations experienced in the area (Flores et al., 2020; Ospina-  
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10 149 Alvarez et al., 2018; Pineda et al., 2007).

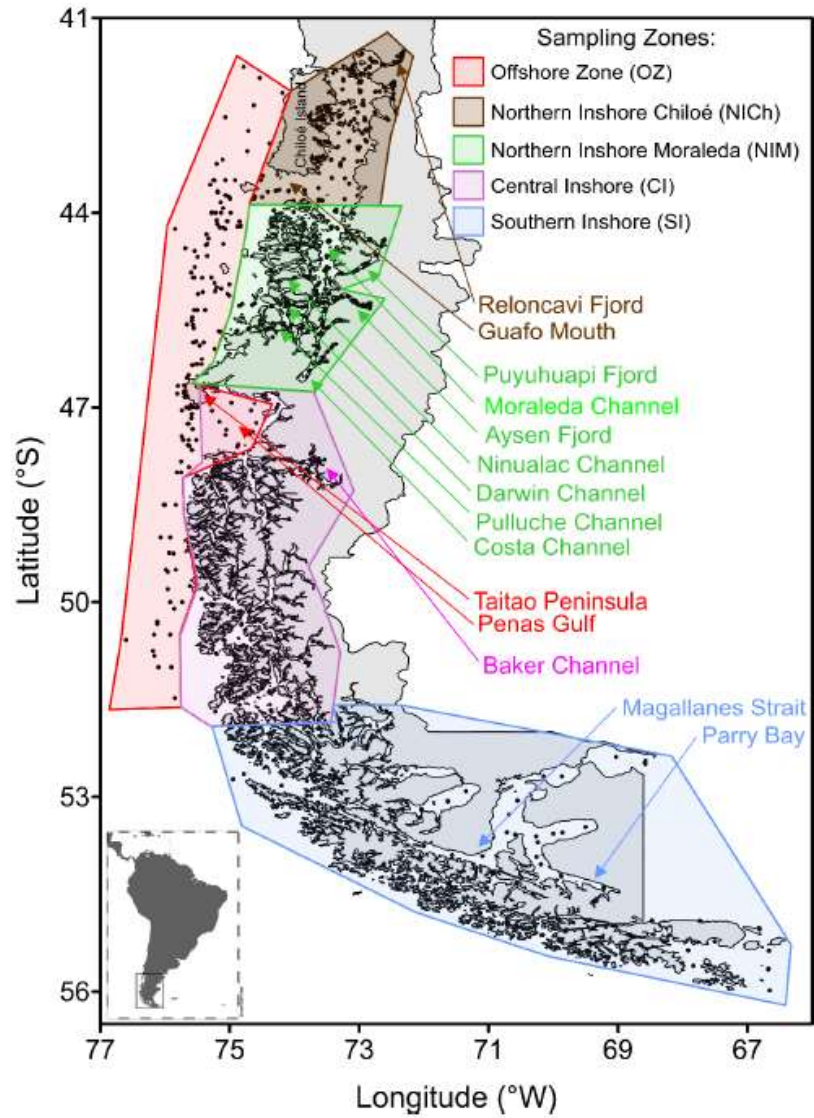
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13 151 This study documents the distribution and abundance of the early life stages of *M.*  
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15 152 *magellanicus* during winter and spring (main spawning season) in the southwestern  
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17 153 Patagonia and describes its spawning and nursery areas utilizing oceanographic  
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19 154 data and ichthyoplankton samples from 26 oceanographic cruises conducted in the  
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21 155 offshore and inner zone of Chilean Patagonian between 1995 and 2019. The general  
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23 156 objective was to determine whether changes in the distribution of eggs and larvae  
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25 157 occurred along with variations in bio-oceanographic characteristics (temperature,  
26  
27 158 salinity and potential predators and prey). Our results show that the offshore zone  
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29 159 along Chilean Patagonia is the main spawning and nursery area for *M. magellanicus*,  
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31 160 and that secondary/alternative spawning and nursery areas occur in inner zones  
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33 161 (fjords and channels). They also reveal that the environmental conditions at these  
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35 162 zones differ between areas and also that they vary during the spawning season and  
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37 163 interannually. These results suggest that the variation in the spawning and nursery  
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39 164 locations could be part of a reproductive strategy aimed at providing greater chances  
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41 165 of survival to their offspring

## 42 166 43 167 **2. Methods**

### 44 168 45 169 **2.1 Fieldwork and samples collection**

46 170  
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48 171 Chilean Patagonia was divided into five main sampling zones: Northern Inshore  
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50 172 Chiloé (NICH), Northern Inshore Moraleda Channel (NIM), Central Inshore (CI),  
51  
52 173 Southern Inshore (SI) and the Offshore Zone (OZ) (OZ; 42°S–52°S). Thus, the term  
53  
54 174 Inshore Zone (IZ) was used to refer to all inshore sea zones (NICH, NIM, CI, SI)  
55  
56 175 together (Fig. 1).





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177 Fig. 1. Study area. Black circles indicate the location of the oceanographic and/or  
 178 zooplankton sampling stations.

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4 179 Hydrographic data and mesozooplankton samples used to analyze *M. magellanicus*  
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6 180 eggs and larvae distributions and their variations were collected in 26 oceanographic  
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8 181 cruises, during winter and spring season from 1995 to 2019, inshore and offshore  
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10 182 the Chilean Patagonia (Table 1) (CIMAR-Fiordos cruises 1–17, acoustic stock  
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12 183 assessment surveys for *M. magellanicus* 2013–2017 and 2019 and the Taitao  
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14 184 Expedition 2018).

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17 186 Stratified mesozooplankton samples were collected by oblique tows using a Tucker  
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19 187 trawl net (1 m<sup>2</sup> mouth, 300- $\mu$ m mesh size) in the IZ and OZ cruises (except during  
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21 188 CIMAR cruises 1, 2, 3 and 4) where a Bongo net (60 cm diameter, 300- $\mu$ m mesh  
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23 189 size) was used. The zooplankton samples were collected from 200 m depth to the  
24  
25 190 surface or from 10 m above the bottom (if the maximum depth did not exceed 210  
26  
27 191 m). The plankton nets were equipped with flowmeters to estimate the volume of the  
28  
29 192 seawater filtered. All samples were preserved onboard in 5% formaldehyde buffered  
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31 193 with sodium borate. At all oceanographic stations temperature and salinity profiles  
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33 194 were obtained from CTD casts (Seabird SBE-25).

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## 36 196 **2.2 Laboratory work**

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39 198 Mesozooplankton samples were sorted into zooplankton groups; *M. magellanicus*  
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41 199 eggs and larvae were identified and counted following Patchell et al. (1987),  
42  
43 200 Machinandiarena and Ehrlich (1999) and Balbontin et al. (2004). Larvae were  
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45 201 measured according to their standard length (SL). Medusae (potential predators on  
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47 202 eggs and larvae) and Copepods (prey for larvae) were also quantified. The  
48  
49 203 abundance of eggs and larvae were expressed as ind./1000m<sup>3</sup>, medusae as  
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51 204 ind./100m<sup>3</sup> and copepods as ind./m<sup>3</sup>.

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## 53 206 **2.3 Data analysis**

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57 208 To describe the hydrographic characteristics of the study area, horizontal maps and  
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59 209 vertical sections of temperature and salinity from data collected *in situ* were prepared  
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210 using Ocean Data View (ODV 5.3.0). In addition, vertical sections of absolute salinity  
211 (SA in g/kg) were prepared and calculated from the Thermodynamic Equation of  
212 Seawater 2010 (TEOS-10) using ODV 5.3.0. The water masses were described  
213 using the salinity criteria (Sievers, 2008; Sievers and Silva, 2008).

214  
215 Horizontal maps of standardized abundances (ind./1000m<sup>3</sup>) of *M. magellanicus* eggs  
216 and larvae were produced using Surfer 13 to visualize potential spawning and  
217 nursery areas. For diagramming the mean vertical distribution of eggs and larvae  
218 per cruise, profiles of the abundance (ind./1000m<sup>3</sup>) of eggs and larvae per sampled  
219 stratum at all stations were averaged among stations in each cruise.

220  
221 To identify potential associations between ichthyoplankton and hydrographic data,  
222 we used the median values of temperature and salinity in each stratum in which eggs  
223 and/or larvae of *M. magellanicus* were found. At the IZ, the strata corresponded to 4  
224 depth ranges: 0-25 m, 25-50 m, 50-100 m and >100 m (depending on the maximum  
225 depth of the area), except in 2008 and 2010 (0-25 m, 25-50 m, 50-200 m) and 2009  
226 (0-50 m; 50-200 m) when zooplankton strata were sampled differently. In the OZ,  
227 the strata sampled were 0-50 m, 50-100 m, 100-200 m and >200 m in winter, and 0-  
228 25 m, 25-50 m, 50-200 m in spring.

229  
230 Data of copepods abundance (considered potential prey for *M. magellanicus* larvae)  
231 and medusae (considered potential predators of *M. magellanicus* eggs and larvae)  
232 at the IZ came from reports conducted in the same study area and seasons,  
233 previously published (Castro et al., 2022; Iriarte et al., 2018; González et al., 2016;  
234 Palma et al., 2014; González et al., 2013; Palma et al., 2011; González et al., 2011;  
235 Bravo et al., 2011; González et al., 2010), as well as from results of our zooplankton  
236 analyses of samples conducted for the present study. Data on potential predators  
237 and prey were only available in the strata 0-25 m and 25-50 m, so only eggs and  
238 larvae in these strata were considered for prey-predator relationship analyses.  
239 Horizontal maps were prepared to visualize possible “match” or “mismatch” between  
240 potentials predators and prey on the OZ-2018 and NICH-2011 cruises (the only



241 cruises in which simultaneous data were obtained from *M. magellanicus* eggs and  
 242 larvae, copepods and medusae).

243

244 Statistical analyses of the bio-oceanographic data included testing for normal  
 245 distribution (Shapiro-Wilk test). Because the data (despite the various  
 246 transformations applied) did not allow the use of parametric methods, Kruskal-Wallis  
 247 tests were applied. If significant differences were found, Dunn's post hoc was  
 248 conducted to determine the groups that likely caused the differences.

249

250 GAM's were utilized to explore potential associations between hydrographic  
 251 (temperature, salinity) and biological factors (prey and predator abundances) and *M.*  
 252 *magellanicus* eggs and larvae following Diaz-Astudillo et al. (2022). First, for the 26  
 253 cruises (using stations with at least one stratum with presence of eggs and/or larvae)  
 254 we modeled the response of *M. magellanicus* egg and larvae ( $\log(X + 1)$ ) to 3  
 255 predictors: latitude-longitude and the environmental factors temperature and salinity.  
 256 And then, for the spring cruises OZ-2018 and NICH-2011, in which eggs and/or  
 257 larvae of *M. magellanicus*, copepods and medusae were collected simultaneously,  
 258 we modeled the response of *M. magellanicus* egg and larvae to 5 predictors: spatial  
 259 (lat, long) and environmental factors (salinity, temperature), predator abundance ( $\log$   
 260 ( $X + 1$ )) and prey abundance ( $\log(X + 1)$ ).

261

262 We used 'mgcv' package (Wood, 2017) and 'gratia' package (Simpson, 2022) under  
 263 R (Core Team, R., 2021) to construct the GAM's models. The general model form  
 264 is:

265

$$Y = g^{-1} + (\beta_0 + fx1 + fx2 + \dots + fxi + \zeta + \epsilon)$$

267

268 Where Y is the response value to be modeled,  $g^{-1}$  is the inverse link function,  $\beta_0$  is  
 269 the intercept,  $f_{xi}$  is the smooth function of the covariates,  $\zeta$  is the random effect of  
 270 the group-specific intercepts, and  $\epsilon$  is the error term. The bests models were

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4 271 selected according to the lowest Akaike Information Criterion (AIC), highest deviance  
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6 272 explained, and all terms being statistically significant.  
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### 10 274 **3. Results**

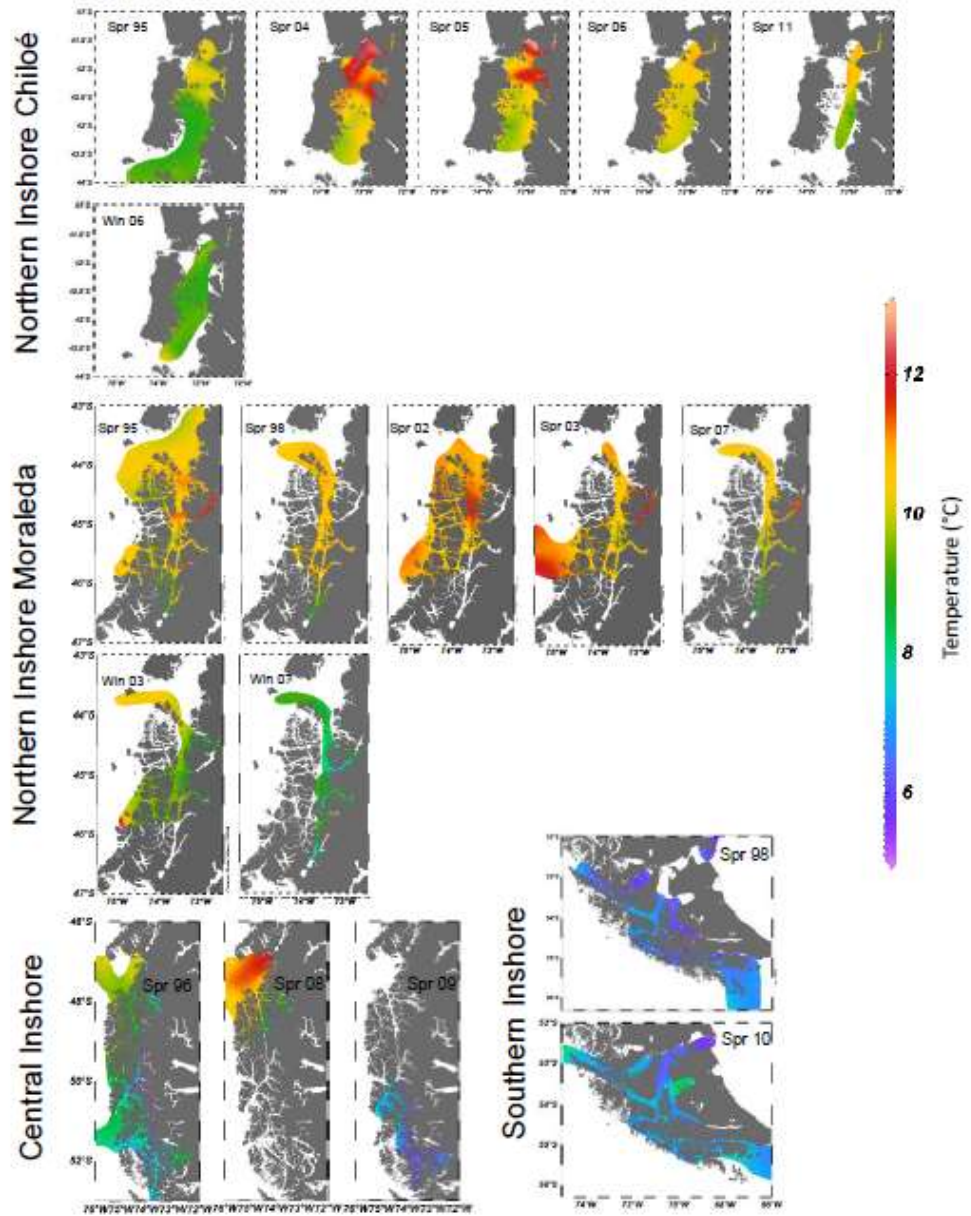
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#### 13 276 **3.1 Oceanographic conditions**

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17 278 In spring and winter a decrease in sea surface temperature (SST) was observed  
18 279 from north to south within each zone analyzed in the inshore (IZ) and offshore zones  
20 280 (OZ) (Fig. 2). This pattern was not observed in spring 1998 in the SI where the  
22 281 gradient was positive, but without significant differences between the northern and  
24 282 southern stations ( $t = +0.2$  °C; Kruskal-Wallis,  $p > 0.05$ , Appendix A.1). The largest  
26 283 difference in SST between the northern and southern stations in each zone was  
28 284 obtained at NICH in 2005 ( $\Delta t = -1.9$  °C; Kruskal-Wallis,  $p = 6.73e^{-7}$ ) and the smallest  
30 285 at SI in 2010 ( $\Delta t = -0.04$  °C; Kruskal-Wallis,  $p > 0.05$ ). In winter, the temperature  
32 286 gradient was narrower than in spring and without significant differences between the  
34 287 northern and southern stations (Kruskal-Wallis,  $p > 0.05$ ). In the west-east oriented  
36 288 channels of the northern Patagonia (NIM; Ninualac, Darwin and Pulluche) and in the  
38 289 southernmost areas (CI and SI) in spring there were also negative temperature  
40 290 gradients between the oceanic-coastal stations.  
41 291

42 292 Interannual variations in SST were observed in each of the zones evaluated in both  
44 293 spring and winter (Fig. 2). SST was higher in spring than winter in all zones and in  
46 294 almost all periods evaluated (Kruskal-Wallis and Dunn's post hoc,  $p < 0.05$ , Appendix  
48 295 A.1-A.3). The warmest periods found were NICH spring 2004 ( $12.8 \pm 0.2$  °C), OZ  
50 296 spring 2018 ( $11.0 \pm 0.1$  °C), NIM spring 2003 ( $10.6 \pm 0.1$  °C), CI spring 2008 ( $9.3 \pm 0.3$   
52 297 °C) and SI spring 2010 ( $7.2 \pm 0.1$  °C). On the other hand, the coldest periods were CI  
54 298 spring 2009 ( $6.4 \pm 0.1$  °C), SI spring 1998 ( $6.5 \pm 0.1$  °C), OZ winter 2015 ( $8.6 \pm 0.3$  °C),  
56 299 NIM winter 2007 ( $8.7 \pm 0.1$ ) and NICH winter 2006 ( $10.2 \pm 0.1$  °C).  
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301 Fig. 2. Sea surface temperature (°C) from the cruises carried out in the inshore zone  
 302 of Chilean Patagonia. White dots represent the station locations.

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303 Surface salinity in all zones of IZ presented similar latitudinal (north-south) and  
304 longitudinal (west-east) gradients in spring and winter, showing greater variability in  
305 spring (Fig. 3). Along the IZ, the lowest salinities tended to occur towards the eastern  
306 sector. In the NICH the lowest salinities were recorded to the northeast (~3; spring  
307 2005; Reloncaví Fjord), while in south-central Patagonia they were to the southeast  
308 (NIM, ~1; spring 1995, Aysén Fjord), CI, ~1; spring 1996, Baker Channel) and SI  
309 ~26; spring 1998, Parry Bay). The highest salinities in the NICH and NIM were found  
310 towards the Guafo mouth (~34), while the highest salinities in the west-east oriented  
311 channels (NIM: Ninualac, Darwin, Pulluche) were towards the oceanic stations in  
312 both spring and winter (Fig. 3).

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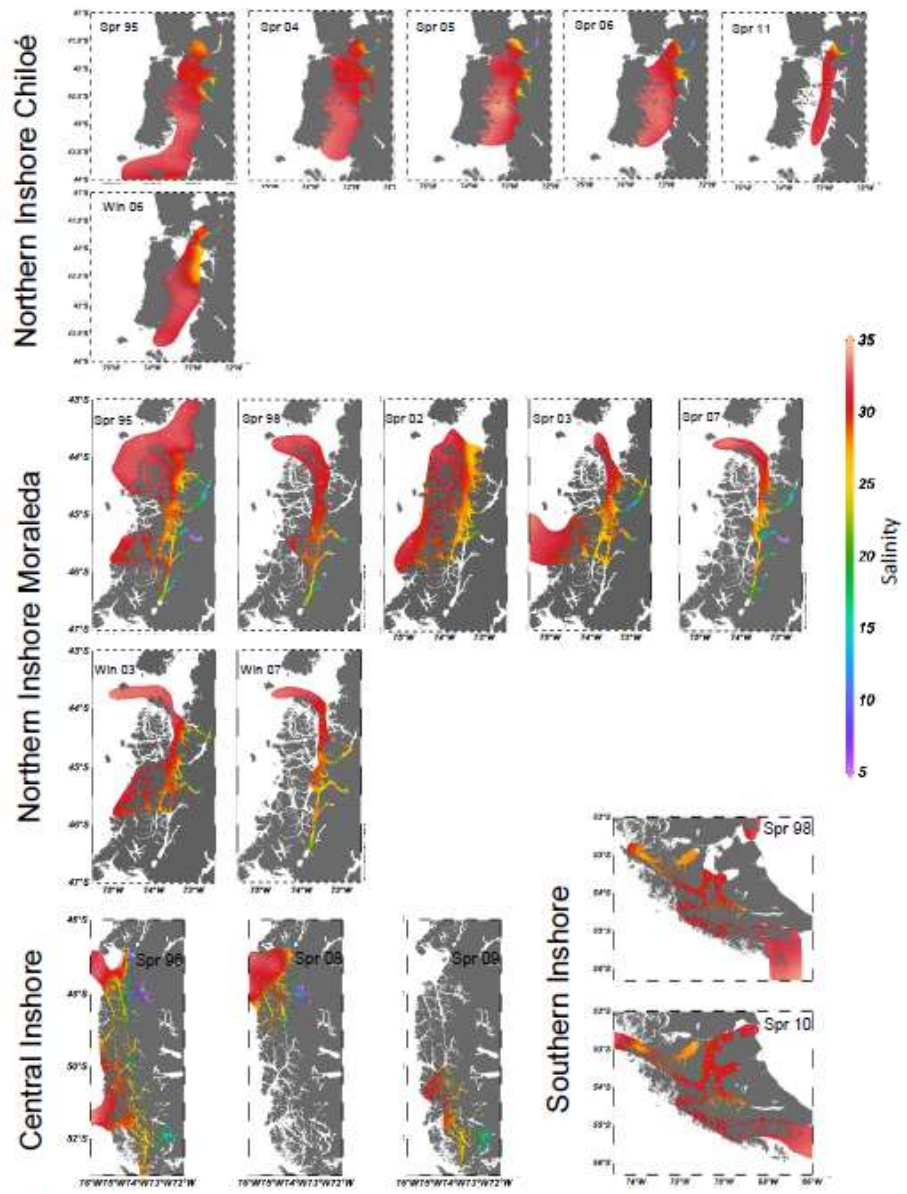
314 In the OZ, surface intrusions of low salinity water are observed in spring and winter,  
315 the depth and extent of which varied between years (Fig. 4). The lowest surface  
316 salinities (30.5) were recorded in the winters of 2015 (between 49-50°S) and 2019  
317 (at 44.3°S), while the maximum surface salinities (~34) were obtained in winter 2016  
318 (between 44-46°S). The latitudinal and longitudinal gradients of temperature and  
319 salinity decreased with increasing depth in the IZ and OZ (Fig. 4).

320

321 The greatest seasonal and interannual difference in salinity ( $\Delta S = -3.4$ ) was obtained  
322 in the NICH between spring 2005 and winter 2006. In the NIM only spring 2007  
323 differed from the rest of the evaluated periods recording the lowest salinity of all the  
324 evaluated zones ( $23.5 \pm 1.4$ ). Finally, in the OZ only winter 2016 was different from  
325 the rest of the evaluated periods finding the highest surface salinity of the evaluated  
326 zones ( $33.6 \pm 0.1$ ) (Kruskal-Wallis and Dunn's post hoc,  $p < 0.05$ , Appendix B.1-B.3),  
327 while in the CI and SI no inter-annual differences in salinity were obtained (Kruskal-  
328 Wallis  $p > 0.05$ ).

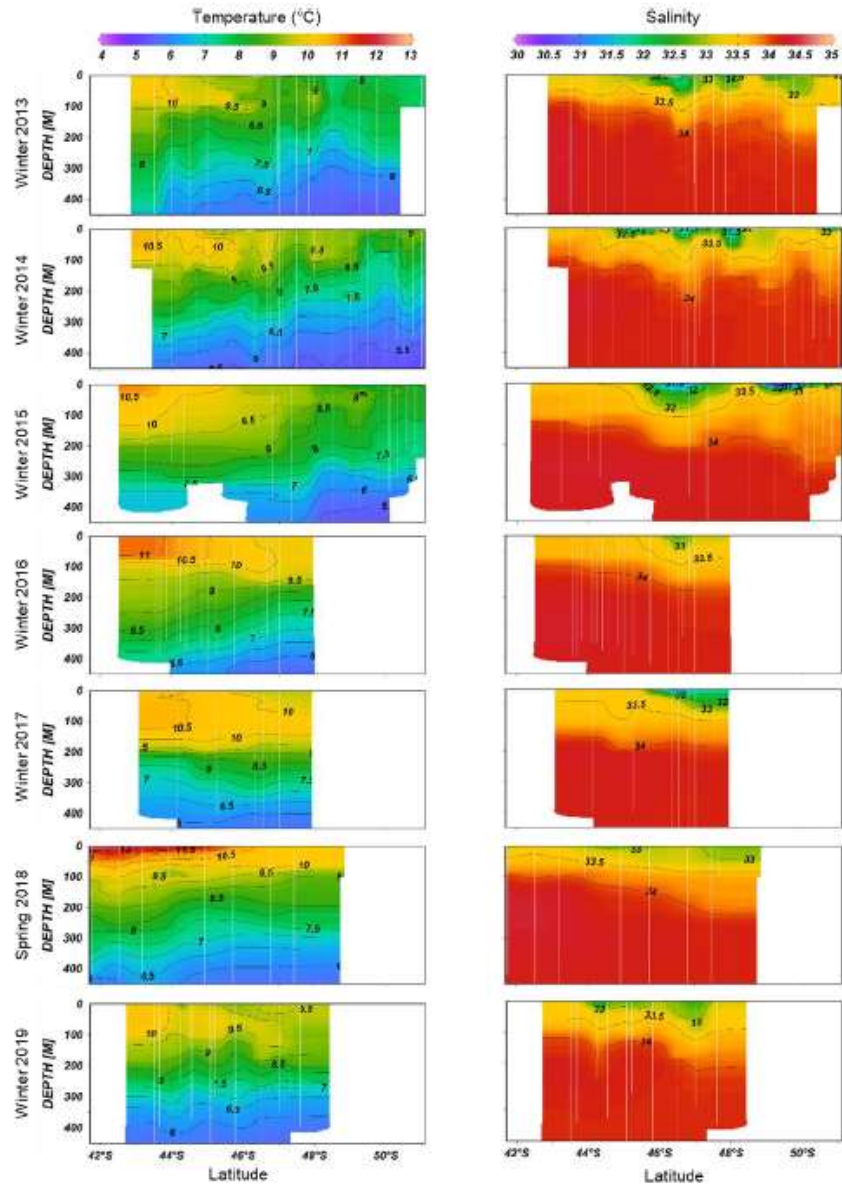
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331 Fig. 3. Sea surface salinity from the cruises carried out in the inshore zone of Chilean  
332 Patagonia  
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335 Fig. 4. Temperature (°C) and salinity vertical sections from the cruises carried out  
 336 along the north-south transect in the offshore zone of Chilean Patagonia. White dots  
 337 represent the station locations.

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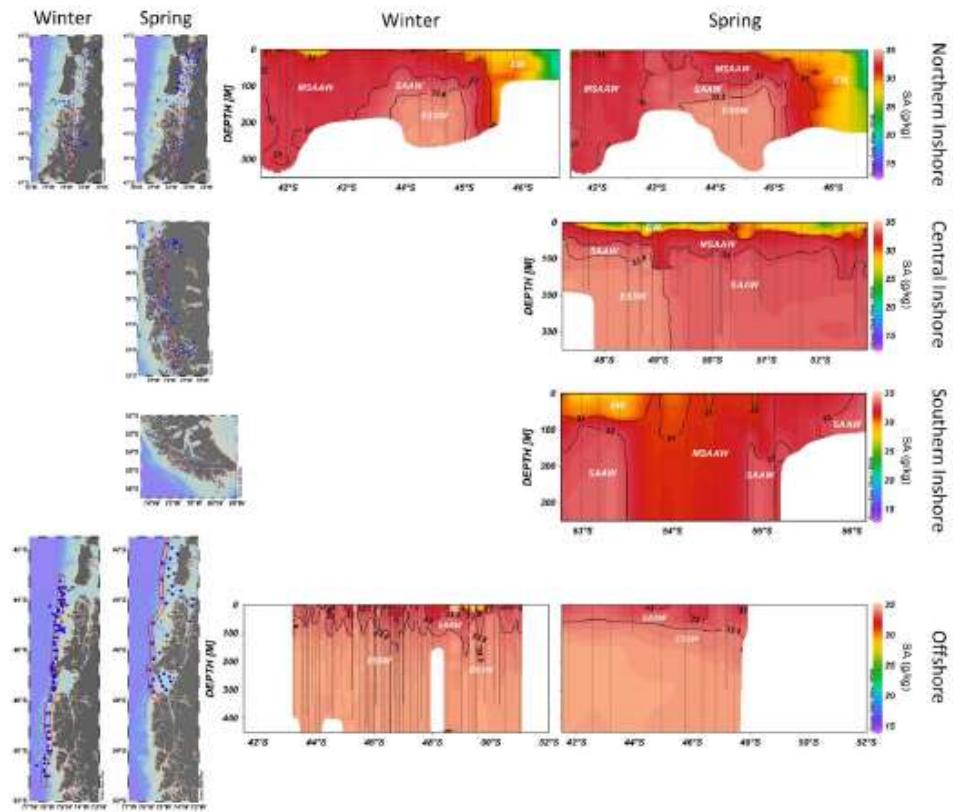
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338 Fig. 5 shows the offshore and inshore hydrographic conditions in the north-  
339 Patagonian area (43.5-46.5°S) in 2013 and 2007, respectively. In OZ the  
340 temperature and salinity gradient between 0 to 100 m was less variable than in the  
341 IZ, with temperatures between 9-10°C and salinities around 33, while in the IZ it  
342 varied between 8-10.5°C and 23-34 respectively. At depths greater than 100 m in  
343 the OZ of northern Chilean Patagonia, temperature decreased with depth, while  
344 salinity was relatively homogeneous and above 34. In the IZ, temperatures below  
345 100 m remained around 10°C while salinities greater than 34 were only found in  
346 deep strata at latitudes between 43.5-45°S. In the IZ, a greater influence of oceanic  
347 waters was observed up to 44.7°S with salinities higher than 32 in deep (>50 m) and  
348 shallow (<50 m) strata higher than 30, while the lowest temperature (~23°C) and  
349 salinity (23) was found towards the inward of the costa channel (46.5°S) (greater  
350 estuarine influence).

351

352 In the OZ the SAAW and ESSE water masses were present, which entered the inner  
353 sea and were found permanently in the NIZ in spring and winter and in the CI in  
354 spring. Similarly, in the NIZ and the CI, the Estuarine Water (EW) and Modified Sub-  
355 Antarctic Water (MSAAW) water masses were found. On the other hand, in the SI in  
356 spring EW, MSAAW and SAAW were also observed, however, ESSW is not found  
357 (Fig. 6).

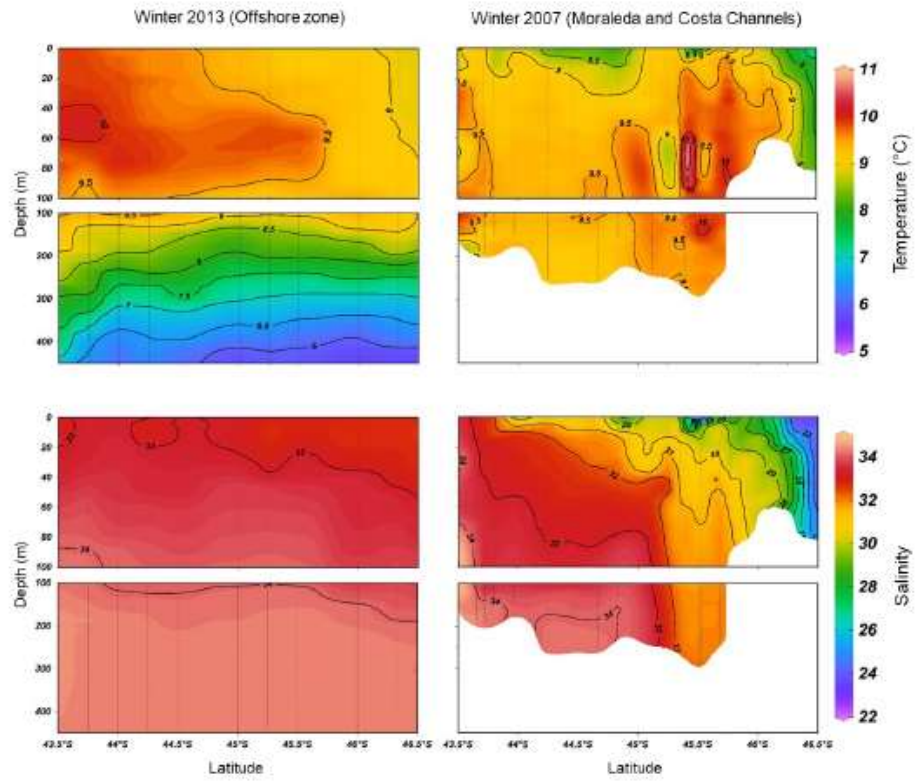
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358  
359 Fig. 5. Absolute salinity vertical sections from the inshore (1995 – 2011) and  
360 offshore (2013 – 2019) cruises during winter and spring season. Black dots  
361 represent the stations locations.



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362  
363 Fig. 6. Temperature (°C) and salinity vertical sections at offshore zone (Winter 2013)  
364 and inshore zone (Winter 2007) in the northern Chilean Patagonia.

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4 365 **3.2 Distribution of *M. magellanicus* eggs and larvae in Chilean Patagonia**

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8 367 ***Horizontal distribution***

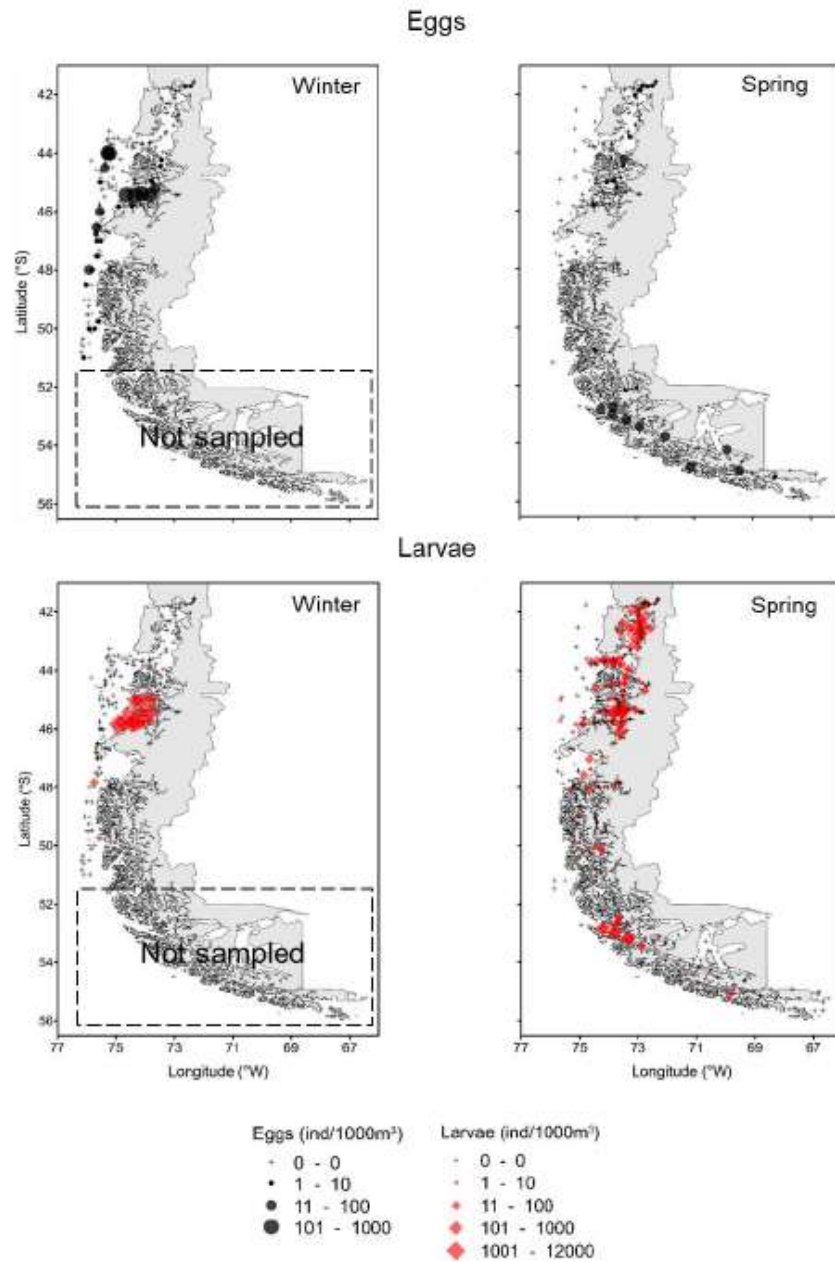
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11 369 The distribution of eggs and larvae showed seasonal, zonal and interannual  
12 changes. Eggs were present throughout the Chilean Patagonia (41-56°S) in the OZ  
13 370 only in winter and in the IZ in spring and winter. Larvae were found in the IZ and OZ,  
14 371 but more abundantly in the IZ in both seasons (Fig. 7). The highest occurrence and  
15 372 abundance of eggs and larvae was found in winter at NIM (2003), while in spring  
16 373 eggs were found mainly at SI (2010) and larvae at NICH (2011), NIM (1998) and SI  
17 374 (1998). However, it is necessary to consider that no samples were obtained from the  
18 375 CI and SI in winter, or at latitudes higher than 52°S in the OZ in spring and winter.  
19 376 The percentage of stations with eggs presence (positive stations) in winter (IZ and  
20 377 OZ pooled) was higher than that of larvae (eggs = 19% vs larvae = 10%), while the  
21 378 opposite occurred in spring (eggs = 10% vs larvae = 33%) (Tables 1, 2). Eggs and  
22 379 larvae were less abundant and with lower percentage of positive stations in IZ in the  
23 380 period 2002-2010 compared to the maximums reached in each zone between 1995-  
24 381 1998 (except in winter 2003 in the NIM and spring 2011 in the NICH, where the  
25 382 historical maximums of abundance were recorded). In the OZ, in winter, this trend of  
26 383 decreasing egg and larval abundance was also observed in the period 2013-2019  
27 384 (Figs. 8 and 9, Tables 1 and 2).  
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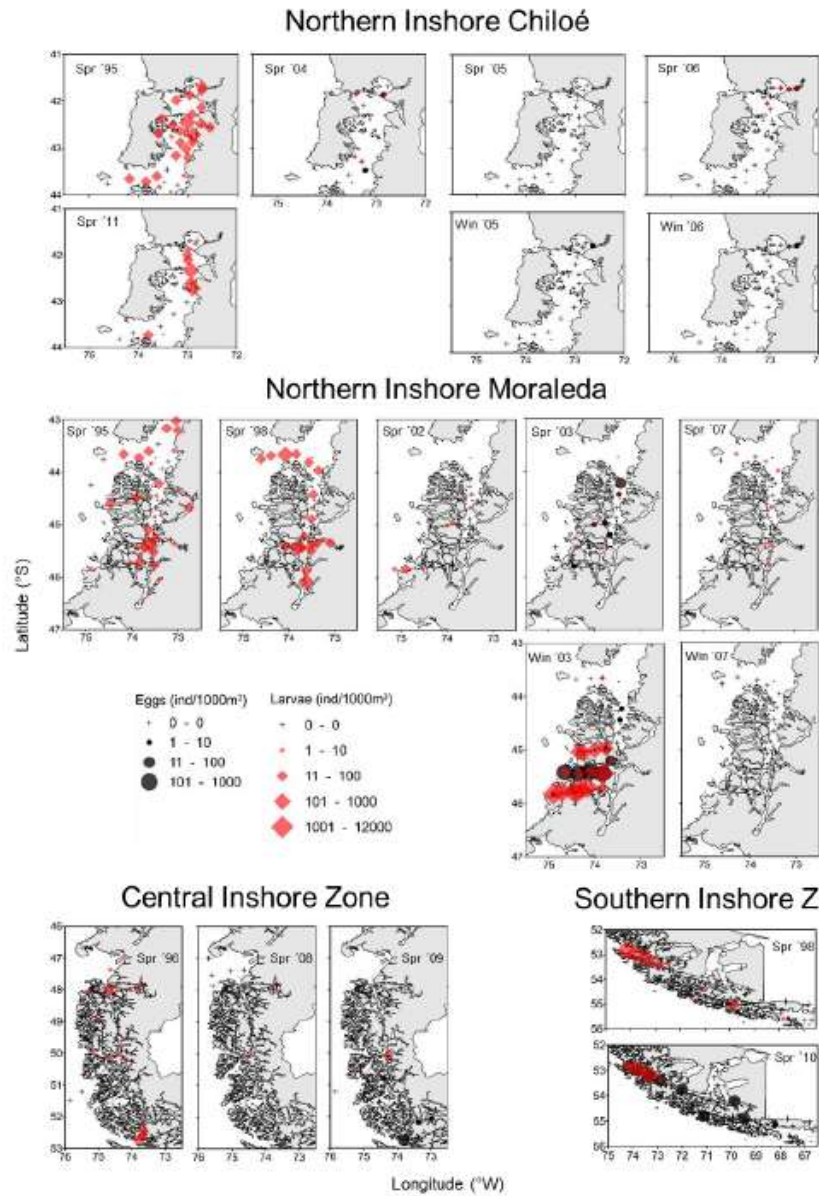
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33 In general, eggs and larvae were more abundant in winter than in spring and at the  
34 388 IZ than the OZ (Fig. 7). In winter (IZ and OZ pooled) the average abundance of eggs  
35 389 was  $12.7 \pm 7.0$  ind/1000m<sup>3</sup> and of larvae was  $158.1 \pm 1103.5$  ind/1000m<sup>3</sup>, higher than  
36 390 in spring ( $1.0 \pm 5.0$  ind/1000m<sup>3</sup> and  $12.4 \pm 53.7$  ind/1000m<sup>3</sup>, respectively). In the IZ  
37 391 (winter and spring pooled) the average abundance of eggs ( $6.2 \pm 56.2$  ind/1000m<sup>3</sup>)  
38 392 and larvae ( $65.3 \pm 652.4$  ind/1000m<sup>3</sup>) was higher than that of eggs ( $5.7 \pm 33.1$   
39 393 ind/1000m<sup>3</sup> and larvae ( $0.6 \pm 3.8$  ind/1000m<sup>3</sup>) at the OZ respectively (Tables 1 and  
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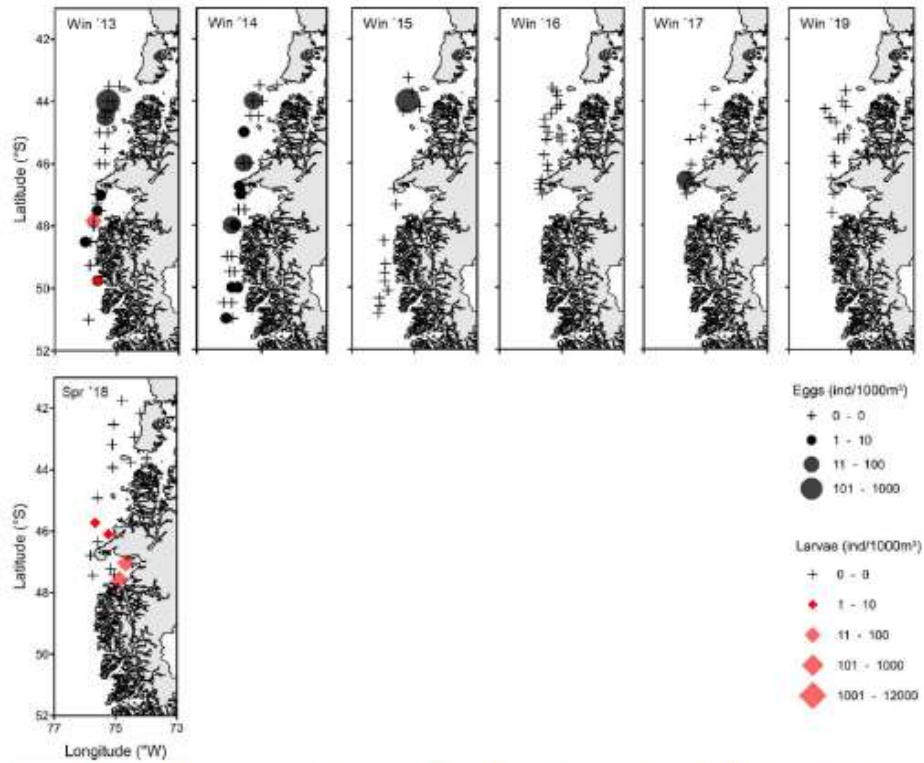
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396 Fig. 7. Distributions of *M. magellanicus* eggs and larvae in all cruises (1995 - 2019)  
397 carried out in winter and spring in the inshore and offshore zone in the Chilean  
398 Patagonia.



399

400 Fig. 8. Distributions of *M. magellanicus* eggs and larvae from cruises carried out in  
401 spring and winter (1995 - 2010) in the inshore zone of Chilean Patagonia.





402

403 Fig. 9. Distributions of *M. magellanicus* eggs and larvae from all cruises carried out  
 404 in winter (2013 – 2017 and 2019) and spring (2018) in the offshore zone of Chilean  
 405 Patagonia.

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407 Table 1. Percentage of occurrence (%O), mean abundance, standard deviations and  
 408 larval length of *M. magellanicus* eggs and larvae from cruises carried out in spring  
 409 (1995 - 2018) in the inshore and offshore zone in the Chilean Patagonia.

410

Zone/ Cruise	Season / Year	Number of sampled station	% O Eggs	% O Larvae	Mean abundance and standard deviations (ind/1000m <sup>3</sup> ) of ALL sampled stations		Larval length (mm)			
					Eggs	Larvae	Mean	Min.	Max.	
<b>Spring (Inshore zone)</b>										
NiCh CIMAR 1	Spring 1995	34	NA	74	NA	28.6±38.4	NA	NA	NA	
NiCh CIMAR 10	Spring 2004	10	20	40	0.6±1.4	2.1±3.0	12.1±13.8	3.5	28.0	
NiCh CIMAR 11-2	Spring 2005	19	0	0	0	0	-	-	-	
NiCh CIMAR 12-2	Spring 2006	19	5	21	0.5±0.9	0.2±0.9	NA	NA	NA	
NiCh CIMAR 17	Spring 2011	17	0	47	0	53.0±147.3	11.7±4.1	3.3	17.2	
NiM CIMAR 1	Spring 1995	55	NA	45	NA	7.3±20.4	NA	NA	NA	
NiM CIMAR 4	Spring 1998	30	NA	67	NA	49.4±59.2	NA	NA	NA	
NiM CIMAR 8	Spring 2002	17	0	41	0	2.2±3.8	16.3±5.9	12.0	23.0	
NiM CIMAR 9-2	Spring 2003	17	35	29	1.4±2.7	0.4±0.7	11.1±7.6	4.0	21.0	
NiM CIMAR 13-2	Spring 2007	21	0	29	0	1.3±2.1	7.4	7.4	7.4	
CI CIMAR 2	Spring 1996	71	NA	27	NA	2.1±5.8	NA	NA	NA	
CI CIMAR 14	Spring 2008	39	0	5	0	0.3±1.5	9.1±3.0	7.3	12.5	
CI CIMAR 15	Spring 2009	32	13	9	0.8±3.0	1.5±7.5	4.1±0.7	3.2	5.2	
SI CIMAR 3	Spring 1998	40	NA	23	NA	38.0±132.5	NA	NA	NA	
SI CIMAR 16	Spring 2010	39	23	10	4.8±11.5	7.5±27.5	3.8±0.3	2.8	4.8	
<b>Mean</b>	<b>Spring</b>	<b>31±16</b>	<b>10±13</b>	<b>31±22</b>	<b>1.2±5.4</b>	<b>13.3±55.8</b>	<b>9.2±6.1</b>	<b>2.8</b>	<b>28.0</b>	
<b>Spring (Offshore zone)</b>										
OZ Taitao 2018	Spring 2018	18	0	22	0	1.9±4.0	7.1±1.8	5.4	10.5	
<b>Mean Spring (Inshore and offshore zone)</b>										
<b>Mean</b>	<b>Spring</b>	<b>31±17</b>	<b>10±13</b>	<b>33±20</b>	<b>1.0±5.0</b>	<b>12.4±53.7</b>	<b>7.5±5.6</b>	<b>2.8</b>	<b>28.0</b>	

411

412 Table 2. Percentage of occurrence (%O), mean abundance, standard deviations and  
 413 larval length of *M. magellanicus* eggs and larvae from cruises carried out in winter  
 414 (2003 - 2019) in the inshore and offshore zones in the Chilean Patagonia and mean  
 415 values in the inshore and offshore zone in spring and winter pooled.

416

Zone/ Cruise	Season / Year	Number of sampled station	% O Eggs	% O Larvae	Mean abundance and standard deviations (ind/1000m <sup>3</sup> ) of ALL sampled stations		Larval length (mm)		
					Eggs	Larvae	Mean	Min.	Max.
<b>Winter (Inshore zone)</b>									
NIM	Winter	24	42	67	69.5±194.7	1230.3±2910.4	3.9±0.2	2.5	5.7
CIMAR 9-1	Winter	20	0	0	0	0	-	-	-
NIM	Winter	20	0	0	0	0	-	-	-
CIMAR 13-1	Winter	19	5	0	0.2±1.0	0	-	-	-
NICH	Winter	19	5	0	0.1±0.4	0	-	-	-
CIMAR 11-1	Winter	19	5	0	0.1±0.4	0	-	-	-
CIMAR 12-1	Winter	19	5	0	0.1±0.4	0	-	-	-
<b>Mean</b>	<b>Winter</b>	<b>21±2</b>	<b>13±19</b>	<b>17±34</b>	<b>20.2±107.9</b>	<b>355.8±1640.4</b>	-	-	-
<b>Winter (Offshore zone)</b>									
OZ	Winter	24	25	8	13.6±53.8	1.7±7.8	NA	NA	NA
Hidroa 2013	Winter	28	36	0	5.4±17.5	0	-	-	-
OZ	Winter	15	7	0	17.8±69.1	0	-	-	-
Hidroa 2014	Winter	15	7	0	17.8±69.1	0	-	-	-
OZ	Winter	20	0	0	0	0	-	-	-
Hidroa 2015	Winter	20	0	0	0	0	-	-	-
OZ	Winter	8	13	0	1.7±4.9	0	-	-	-
Hidroa 2016	Winter	8	13	0	1.7±4.9	0	-	-	-
OZ	Winter	12	0	0	0	0	-	-	-
Hidroa 2017	Winter	12	0	0	0	0	-	-	-
OZ	Winter	12	0	0	0	0	-	-	-
Hidroa 2018	Winter	12	0	0	0	0	-	-	-
<b>Mean</b>	<b>Winter</b>	<b>18±7</b>	<b>14±16</b>	<b>1.0±2.0</b>	<b>6.7±35.8</b>	<b>0.4±3.7</b>	-	-	-
<b>Mean Winter (Inshore and offshore zone)</b>									
<b>Mean</b>	<b>Winter</b>	<b>18±7</b>	<b>19±18</b>	<b>10±25</b>	<b>12.7±77.0</b>	<b>158.1±1103.5</b>	<b>3.9</b>	<b>2.5</b>	<b>5.7</b>
<b>Mean Inshore zone (Spring and Winter)</b>									
<b>Mean</b>	<b>IZ</b>				<b>6.2±56.2</b>	<b>65.3±652.4</b>			
<b>Mean Offshore zone (Spring and Winter)</b>									
<b>Mean</b>	<b>OZ</b>				<b>5.7±33.1</b>	<b>0.6±3.8</b>			

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418 When comparing IZ and OZ during winter (although in different years), the highest  
419 egg abundance was found in the NIM in 2003 ( $69.5 \pm 194.7$  ind/1000m<sup>3</sup>), which was  
420 higher than the  $17.8 \pm 69.1$  ind/1000m<sup>3</sup> in 2015 in the OZ. Spring egg abundance in  
421 the IZ was higher in the SI ( $4.8 \pm 11.5$  ind/1000m<sup>3</sup>) while no eggs were found in the  
422 OZ. The highest abundance of larvae was also obtained in the NIM in winter 2003  
423 with  $1230.3 \pm 2910.4$  ind/1000m<sup>3</sup>, while in the OZ larvae were only found in winter  
424 2013, with an abundance of  $0.1 \pm 0.5$  ind/1000m<sup>3</sup>. In spring, in the IZ, the zone with  
425 the highest larval abundance was the SI ( $22.9 \pm 96.9$  ind/1000m<sup>3</sup>), while in the OZ the  
426 abundance was only  $1.9 \pm 4.0$  ind/1000m<sup>3</sup> (Tables 1 and 2).

427  
428 Interannually, the frequency of occurrence and abundance of eggs and larvae of *M.*  
429 *magellanicus* has tended to be lower after the historical peaks reached in the NIM in  
430 winter 2003 and in spring 1995-1998 in the NIM, CI and SI. In contrast, only in the  
431 NICH there were increases in larval abundance from spring 1995 to 2011 (from  
432  $28.6 \pm 38.4$  ind/1000m<sup>3</sup> to  $53.0 \pm 147.3$  ind/1000m<sup>3</sup>) and also in CI egg abundance  
433 (from 0 ind/1000m<sup>3</sup> in 2008 to  $0.8 \pm 3.0$  ind/1000m<sup>3</sup>) in 2009 (Fig. 8, Tables 1 and 2).  
434 Same as in the IZ, a decrease in the abundance and frequency of occurrence of *M.*  
435 *magellanicus* eggs and larvae was observed at the OZ. The highest egg abundance  
436 in the OZ was obtained in winter 2015 ( $17.8 \pm 69.1$  ind/1000m<sup>3</sup>), while no eggs were  
437 found in winter 2019. On the other hand, larvae were only present in the OZ in winter  
438 2013 and spring 2018 (Fig. 9 Tables 1 and 2).

439  
440 Overall, differences in egg abundance were obtained between winter and spring (IZ  
441 and OZ pooled) (Kruskal-Wallis,  $p = 0.047$ ), between NIM (2003) and OZ (2015) in  
442 winter (maximum egg abundances) (Kruskal-Wallis,  $p = 0.003$ ), between SI and CI  
443 in spring (Kruskal-Wallis and Dunn's post hoc,  $p < 0.05$ , Appendix C.1), as well as  
444 interannually in the OZ between winters 2014 and 2016 (Kruskal-Wallis and Dunn's  
445 post hoc,  $p < 0.05$ , Appendix C.2). In contrast, no differences were found in egg  
446 abundances between the inner and outer sea (spring and winter pooled), nor  
447 interannually in winter and spring in the NICH, as well as no differences were  
448 detected in spring between zones; OZ, CI, NIM (Kruskal-Wallis,  $p > 0.05$ ).



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449 Larval abundance differed between the IZ and OZ (spring and winter pooled,  
450 Kruskal-Wallis,  $p = 3.98e^{-7}$ ), between spring and winter (IZ and OZ pooled, Kruskal-  
451 Wallis,  $p = 1.05e^{-8}$ ), and between the NIM (2003) and OZ (2013) in winter (maximum  
452 larval abundances) (Kruskal-Wallis,  $p = 4.65e^{-2}$ ). In spring, differences in larval  
453 abundance were found between the north (NIM, NICH) and central-south (CI and SI)  
454 zones (Kruskal-Wallis,  $p < 0.05$ , Appendix D.1). In contrast, no differences in larval  
455 abundance were found between the OZ and any of the IZ, nor between the  
456 contiguous zones (NIM and NICH) or (CI and SI) (Kruskal-Wallis,  $p > 0.05$ , Appendix  
457 D.1). Interannually, differences were found in spring in all the IZs evaluated (Kruskal-  
458 Wallis and Dunn's post hoc,  $p < 0.05$ , Appendix D.2 - D.4), except in SI (Kruskal-  
459 Wallis,  $p > 0.05$ ).

460

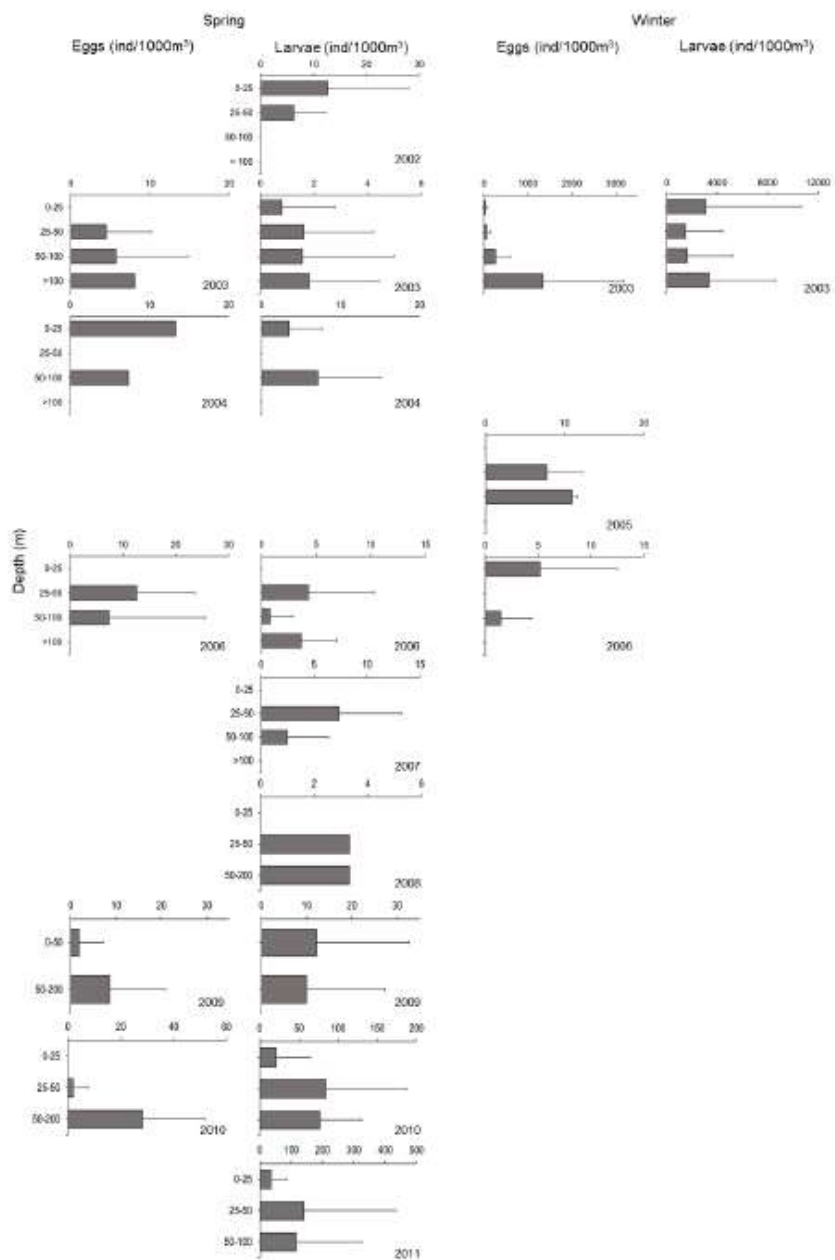
#### 461 ***Vertical distribution***

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463 Eggs and larvae showed differences in their distributions along the water column.  
464 The vertical distribution of eggs in the IZ and OZ in spring and winter tended to be  
465 more abundant at the deepest strata (>50 m) than the shallowest strata (0-50 m)  
466 (except in NICH; 2004 and 2006). On the other hand, larvae did not tend to aggregate  
467 at any specific stratum (Figs. 10 and 11).

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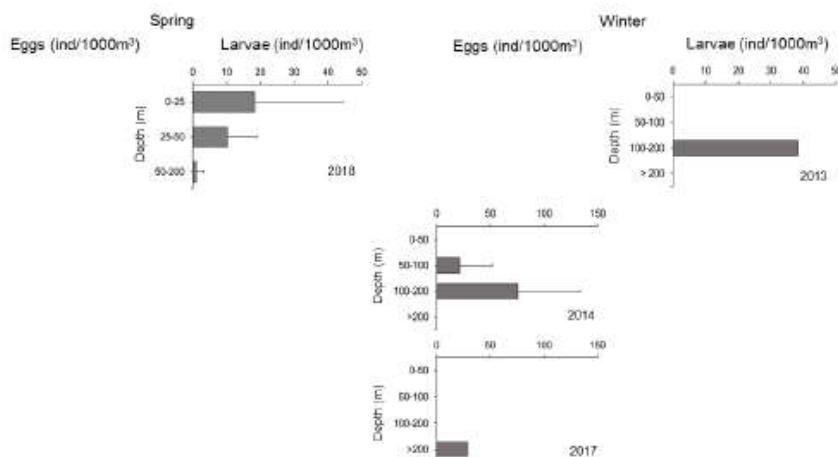
469 The average egg abundance per stratum in the IZ in all spring cruises increased with  
470 depth (0-25 m =  $0.5 \pm 2.6$  ind/1000m<sup>3</sup>, 25-50 m =  $4.0 \pm 6.9$  ind/1000m<sup>3</sup>, 50-100 m =  
471  $6.3 \pm 11.8$  ind/1000m<sup>3</sup> and 100-150 m =  $8.1 \pm 0$  ind/1000m<sup>3</sup>). No eggs were found in  
472 the OZ in spring. Egg abundance in the IZ in winter 2003 (NIM, when the highest  
473 egg abundance occurred) was also higher in the deepest stratum (>100 m;  
474  $1334.3 \pm 1869.0$  ind/1000m<sup>3</sup>) compared with the shallowest one (0-20 m;  $28.2 \pm 57.1$   
475 ind/1000m<sup>3</sup>). Finally, in the OZ in winter the average egg abundance (2014 and 2017  
476 pooled) was higher in the stratum 100-200 m ( $50.3 \pm 60.2$  ind/1000m<sup>3</sup>) and lower in  
477 the 0-50 m (0 ind/1000m<sup>3</sup>).



478

479 Fig. 10. Mean density and standard deviations per depth strata of *M. magellanicus*  
 480 eggs and larvae (ind/1000 m<sup>3</sup>) in Winter and Spring from cruises carried out in the  
 481 Inner Sea of Chilean Patagonia.

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483 Fig. 11. Mean density and standard deviations per depth strata of *M. magellanicus*  
 484 eggs and larvae (ind/1000 m<sup>3</sup>) in winter and spring from cruises carried out in the  
 485 Outer Sea of Chilean Patagonia.

486

487 The average larval abundance in the IZ in spring of all cruises was higher in the 25-  
 488 50 m ( $43.4 \pm 146.0$  ind/1000m<sup>3</sup>) and lower in the >100 m ( $2.4 \pm 2.8$  ind/1000m<sup>3</sup>). In the  
 489 OZ, the only cruise conducted in spring (2018) showed higher larval abundance in  
 490 the 0-25 stratum ( $9.2 \pm 13.1$  ind/1000m<sup>3</sup>) and lower in the 50-200 m layer ( $0.6 \pm 1.1$   
 491 ind/1000m<sup>3</sup>). On the other hand, at the IZ and OZ in winter only larvae were found  
 492 at NIM (2003) and OZ (2013). At the NIM (winter 2003) (zone and period in which  
 493 the highest larval abundance was found) the highest abundances occurred at the >  
 494 100 m stratum ( $3369.7 \pm 5299.1$  ind/1000m<sup>3</sup>) and the lowest at the 25-50 m  
 495 ( $1517.7 \pm 2921.1$  ind/1000m<sup>3</sup>), whereas in the OZ (2013) larvae were only found in  
 496 the 100 - 200 m stratum.

497

498 Differences in egg abundances were found between strata 0-25 and 50-100 in the  
 499 spring cruises in the IZ (all spring cruises in the IZ pooled) and in winter 2003 in the  
 500 NIM (Kruskal-Wallis and Dunn's post hoc,  $p < 0.05$ , Appendix E.1 and E.2), but not  
 501 between strata in the OZ in 2014 and 2017 (both cruises pooled) (Kruskal-Wallis,  $p$

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4 502 > 0.05). No differences in larval abundances were found between strata in the IZ  
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6 503 spring cruises, nor in winter 2003 in the NIM or in spring 2018 in the OZ (Kruskal-  
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8 504 Wallis,  $p > 0.05$ ).  
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### 11 506 **3.3 Larval length**

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15 508 The average larval length in all spring cruises conducted at the IZ was greater than  
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17 509 that found in winter 2003. The range of larval lengths in winter 2003 (NIM) was  
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19 510 between 2.5 and 5.7 mm (mean =  $3.9 \pm 0.2$  mm) while in spring it ranged from 2.8 to  
20  
21 511 28.0 mm (mean =  $9.2 \pm 6.1$  mm). In addition, a decrease in larval length was observed  
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23 512 interannually in spring, larval length at NICH decreased from 12.1 mm (2004) to 11.7  
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25 513 mm (2011), at NIM from 16.3 mm (2002) to 7.4 mm (2007) and at CI from 9.1 mm  
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27 514 (2008) to 4.1 mm (2009) (Tables 1 and 2).  
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30 516 The vertical distribution of larvae by size of all the cruises carried out in the IZ in  
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32 517 spring and winter showed that while the longer larval length was located in the  
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34 518 shallower stratum (0-25 m) and smaller larvae at the deepest (> 50 m), the opposite  
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36 519 occurred in the OZ in spring. The spring larval length in the IZ in the stratum 0-25 m  
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38 520 ( $12.7 \pm 8.2$  mm) was larger than at the strata 50-100 m ( $10.2 \pm 4.1$  mm) and 25-50 m  
39  
40 521 ( $6.3 \pm 4.6$  mm). In winter the larval length at the IZ in the stratum 0-25 m ( $4.1 \pm 0.3$   
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42 522 mm) was longer than in the strata >100 m ( $3.9 \pm 0.3$  mm), 50-100 m ( $4.0 \pm 0.3$  mm)  
43  
44 523 and 25-50 m ( $4.0 \pm 0.3$  mm). In contrast, in the OZ only larvae collected in spring 2018  
45  
46 524 could be measured whose larval length was shorter in stratum 0-25 m ( $7.0 \pm 1.1$  mm)  
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48 525 and longer in stratum 50-200 m ( $7.4 \pm 1.4$  mm).  
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50 526

51 527 Differences in larval length were found between winter and spring (Kruskal-Wallis  $p$   
52 528 =  $4.75e^{-4}$ ), and between 2008 and 2009 in the CI (Kruskal-Wallis  $p$  =  $9.38e^{-3}$ ).  
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54 529 Similarly, differences were found between strata (0-25 m and 25-50 m, 25-50 m and  
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56 530 50-100 m) in the spring cruises at IZ (Kruskal-Wallis and Dunn's post hoc,  $p < 0.05$ ,  
57  
58 531 Appendix F.1) and among all strata in winter 2003 (NIM) (Kruskal-Wallis and Dunn's  
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60 532 post hoc,  $p < 0.05$ , Appendix F.2). No differences in interannual larval length were  
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4 533 detected at NICH or NIM, between strata 0-25 and 50-100 m during spring in the IZ,  
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6 534 nor at any of the strata in spring in the OZ (Kruskal-Wallis,  $p > 0.05$ ).

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10 536 **3.4 Potential preys and predators of *M. magellanicus* eggs and larvae**

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13 538 Potential prey (copepods) of larvae and predators (medusae) of eggs and larvae of  
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15 539 *M. magellanicus* were more abundant in spring than in winter in both zones (IZ and  
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17 540 OZ) of the Chilean Patagonia. On the other hand, the abundance of potential prey  
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19 541 and predators was higher in the OZ in winter and spring compared to the IZ, except  
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21 542 in spring 2006, when the highest abundance of predators was obtained in NICH. In  
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23 543 this same area, a sharp decrease in medusae abundance was found from spring  
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25 544 2006 (2319 ind/100m<sup>3</sup>) to spring 2011 (180 ind/100m<sup>3</sup>) with the latter year being the  
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27 545 lowest value of predators found in this study, coinciding with an increase in copepod  
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29 546 abundance (from  $245.4 \pm 136.5$  ind/m<sup>3</sup> to  $265.4 \pm 237.5$  ind/m<sup>3</sup>) in the same period.  
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31 547 In IZ, the abundance of copepods gradually increased in the southward areas, while  
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33 548 that of medusae decreased (Tables 3 and 4).

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36 550 In the cruises where larvae of *M. magellanicus* and their potential predators and prey  
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38 551 were found simultaneously, the highest larval abundance was located in the NICH,  
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40 552 where the medusae abundance was low or null. Similarly, in the area where the  
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42 553 highest abundance of medusae were found, no larvae occurred. On the other hand,  
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44 554 the highest abundance of copepods was found around the Taitao Peninsula towards  
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46 555 the Golfo de Penas and at the Boca del Guafo, areas in which an intermediate  
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48 556 abundance of *M. magellanicus* larvae was found (Fig. 12).

557 Table 3. Copepods mean abundance (ind/m<sup>3</sup>) between 0-50 m in spring and winter  
 558 in the inner and offshore zone in the Chilean Patagonia.

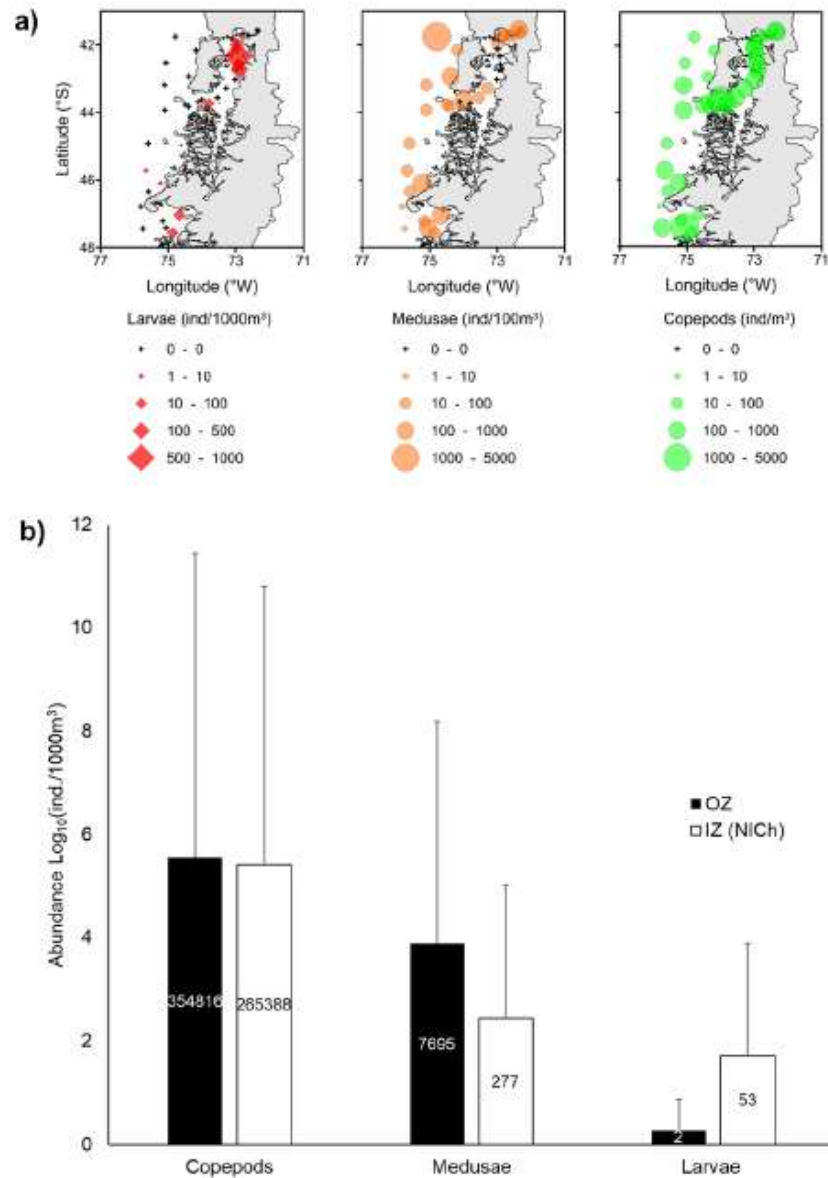
Cruise	Zone	Year	Copepods mean abundance (0-50 m) and standard deviations (ind/m <sup>3</sup> )	
			Winter	Spring
Cimar 12	NICH	2006	8.43 ± 19.1	245.4 ± 136.5
Cimar 13	NIM	2007	24.6 ± 23.2	259.9 ± 468.8
Cimar 15	CI	2009	-	319.0 ± 304.1
Cimar 16	SI	2010	-	361.6 ± 662.3
Cimar 17	NICH	2011	-	265.4 ± 237.5
Taitao	OZ	2018	-	633.5 ± 1549.2
Hidroacústico	OZ	2019	46.3 ± 32.6	-

559

560 Table 4. Medusae abundance (ind/100m<sup>3</sup>) in spring and winter in the inner and  
 561 offshore zone in the Chilean Patagonia.

Cruise	Zone	Year	Medusae (Abundance ind/100m <sup>3</sup> )				Reference
			Winter		Spring		
			Mean	Min – Max	Mean	Min – Max	
Cimar 12	NICH	2006	177	4.5 – 859	2319	372 – 7858	Palma et al., 2011
Cimar 13	NIM	2007	44	1.7 – 163	367	6.8 – 3562	Bravo et al., 2011
Cimar 15	SI	2010	-	-	287	3.7 – 2734	Palma et al., 2014
Cimar 17	NICH	2011	-	-	180	1.0 – 360	This study
Taitao	OZ	2018	-	-	770	2.1 – 7766	This study
Hidroacústico	OZ	2019	101	27 – 183	-	-	This study

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563

564 Fig. 12. (a) Distributions of *M. magellanicus* larvae and their potential predators and  
 565 preys in the offshore and inshore zone of Chilean Patagonia in spring. (b). Mean  
 566 abundance and standard deviation of copepods, medusae and larvae offshore and  
 567 inshore of the Chilean Patagonia in spring.

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4 568 **3.5 Relationship between bio-oceanographic conditions and *M. magellanicus***  
5 569 **eggs and larvae determined through GAM's.**  
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10 571 Different combinations of GAM's were run to statistically evaluate the influence of  
11 572 bio-oceanographic variables on the distribution and abundance of *M. magellanicus*  
12 573 eggs and larvae.  
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17 575 ***Model: Spatial, temperature and salinity***  
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21 577 The best model for eggs explained 43.9% of the deviancy and included the spatial  
22 578 term and salinity as covariates. For larvae the best model included the spatial term  
23 579 and temperature and explained 59.0% (Table 5). In the models separately, the  
24 580 spatial term explained the highest percentage of the deviance (Eggs = 31.0% and  
25 581 Larvae = 42.8%). On the other hand, salinity explained 1.9% of the deviance in the  
26 582 eggs model and temperature 21.6% in the larvae model (Table 5).  
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33 584 In the full model, the spatial model showed a slight latitudinal disaggregation of *M.*  
34 585 *magellanicus* eggs and larvae; while the highest egg abundances were found around  
35 586 45°S, larvae were more abundant towards the north (~43°S) and south (>45°S)  
36 587 (Appendix G). In the salinity model, a non-linear and contrasting effect between eggs  
37 588 and larvae was observed. From salinity 30 and upper values, a positive effect on  
38 589 eggs was observed, with the highest abundances at salinities around 34. Larvae,  
39 590 instead, were more abundant at salinities of 30. In the temperature model, the effect  
40 591 was also non-linear. However, in this case the highest abundances of eggs and  
41 592 larvae were obtained between 9°C and 10°C (Appendix G). Temperature in the egg  
42 593 model and salinity in the larval model were not significant in the total model ( $p >$   
43 594 0.05), so they were excluded from each final model; however, when they were  
44 595 excluded, no changes were observed with respect to the pattern described in the full  
45 596 model (Appendix H, Table 5).  
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50 598 ***Model: Potential predators and preys***  
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600 The best model for larval abundance explained 32.6% of the variance and was  
 601 obtained by the tensor (mixture) of the covariates medusae/copepods, in which the  
 602 highest larval abundance is obtained in the interaction of lower abundance of  
 603 medusae and higher abundance of copepods. When evaluating the separate effect  
 604 of potential predators and prey on larval abundance, a linear effect was observed in  
 605 both cases; negative for predators and positive for prey; however, the individual  
 606 effects were not significant in the model (Appendix I, Table 6).

607

608 Table 5. GAMs results for different tested models in Model: Spatial, temperature  
 609 and salinity.

Life Stage	Model	Terms	Dev. Expl (%)	AIC	$\Delta$ AIC
Eggs	Full model	Lat/Lon, Temp, Sal	46.1	256.43	0.51
	Spatial	Lat/Lon	31.0	267.01	11.09
	Salinity	Sal	1.9	278.54	22.62
	Temperature	Temp	10.3	273.26	17.34
	<b>Final Model</b>	<b>Lat/Lon, Sal</b>	<b>43.9</b>	<b>255.92</b>	<b>0</b>
Larvae	Full model	Lat/Lon, Temp, Sal	60.0	494.11	2.13
	Spatial	Lat/Lon	42.8	539.20	47.22
	Salinity	Sal	14.5	586.30	94.32
	Temperature	Temp	21.6	576.80	84.82
	<b>Final Model</b>	<b>Lat/Lon, Temp</b>	<b>59.0</b>	<b>491.98</b>	<b>0</b>

610

611 Table 6. GAM results for different tested models in Model: Potential predators and  
 612 prey.

Life Stage	Model	Terms	Dev. Expl (%)	AIC	$\Delta$ AIC	P value	
Larvae	Full model	Med + Copep	21.0	71.16	2.12	0.082	
	Predator	Med	10.3	72.48	3.44	0.111	
	Prey	Copep	9.7	72.65	3.61	0.122	
	<b>Final Model;</b>	<b>Tensor:</b>	<b>Med/Copep</b>	<b>32.6</b>	<b>69.04</b>	<b>0</b>	<b>0.031</b>
		<b>predator/pray</b>					

613

#### 614 4. Discussion

615

616 In order to identify and describe potential spawning and nursery areas of *M.*  
 617 *magellanicus* in Chilean Patagonia, we analyzed ichthyoplankton, hydrographic data  
 618 and zooplankton, obtained from 26 oceanographic cruises conducted in the inshore

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4 619 and offshore zones of Chilean Patagonia in spring and winter in the period 1995 -  
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6 620 2019. We determine if there were associations between interannual, seasonal and  
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8 621 zonal changes in the distribution and abundance of *M. magellanicus* eggs and larvae  
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10 622 and changes in bio-oceanographic conditions (temperature, salinity and potential  
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12 623 predators and prey). The results show that eggs were more abundant in winter than  
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14 624 in spring in the IZ and OZ. Eggs and larval abundance decreased from an historical  
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16 625 maximum reached in all zones (1995 – 1998) until our last sampled year (2019),  
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18 626 except in winter 2003 in the NIM and spring 2011 in the NICH. Eggs were located in  
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20 627 the deepest strata and larvae were heterogeneously distributed throughout the water  
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22 628 column. Potential predators (medusae) and prey (copepods) of *M. magellanicus*  
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24 629 eggs and larvae were more abundant in spring than in winter, and in the outer versus  
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26 630 the inner sea of the Chilean Patagonia. GAM's showed disaggregation in the  
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28 631 horizontal distribution of eggs and larvae, a non-linear effect between larval  
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30 632 abundance and temperature being more abundant between 9 and 10 °C, as well as  
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32 633 between eggs and salinity with maximum abundance at salinities around (34) and  
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34 634 salinity around 30 for larvae. As for potential predators and prey, the GAMs showed  
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36 635 higher larval abundances associated with lower abundance of predators and higher  
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38 636 abundance of prey.

637

#### 638 **4.1 Spatial and seasonal changes in hydrographic conditions**

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640 The temperature and salinity gradients in the IZ and OZ, the higher temperature and  
641 greater variability of salinity in spring than in winter, the interannual variations in  
642 temperature in the IZ and OZ of Chilean Patagonia, as well as the permanent  
643 presence in spring and winter of oceanic water masses within the IZ are consistent  
644 with what has been described by several authors for the area (Linford et al., 2023;  
645 Strub et al., 2019; Narváez et al., 2019; Saldías et al., 2019; Pantoja et al., 2011,  
646 Sievers, 2008; Sievers and Silva, 2008).

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648 Within each zone of the IZ, the temperature and salinity gradients are due to the  
649 local interaction between adjacent oceanic water and fresh continental water from

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4 650 rain, runoff, river discharges, and snow and/or ice melt plus of the presence of  
5  
6 651 microbasins resulting from bathymetric constrictions and sills that limit the entry and  
7  
8 652 influence of adjacent oceanic water (Pantoja et al., 2011; Sievers and Silva 2008;  
9  
10 653 Valdenegro and Silva 2003; Cáceres et al., 2002; Dávila et al., 2002). In the OZ,  
11 654 negative temperature and salinity gradients were obtained towards the south, lower  
12 655 surface salinity due to higher surface freshwater intrusions. These results are in  
13 656 agreement with previous research, which indicates that latitudinal and seasonal  
14 657 variability in continental freshwater input plays a key role in modulating the coastal  
15 658 oceanic surface layer in Chilean Patagonia (Saldias et al., 2019; Dávila et al., 2002).  
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22 660 In this study we found interannual temperature changes in the IZ and OZ, with  
23 661 temperature increases in the NICH, CI (between 47 - 49°S), SI and in the OZ, and  
24 662 decreases in the CI (between 50-53°S) and in the NIM. These changes have been  
25 663 previously reported and have been related to the climatic variability induced by the  
26 664 Pacific Decadal Oscillation, El Niño-Southern Oscillation and Southern Annular  
27 665 Mode, noting that the magnitude of the effect is different between zones. The  
28 666 warmest periods found in the IZ (2003 - 2005) and the coldest (2007 - 2009), as well  
29 667 as the warmest periods found in the OZ (2015 - 2016) agree with what has been  
30 668 described in previous research. Likewise, the warmest period found in the OZ in  
31 669 2015-2016 coincided with a strong El Niño event and the positive phase of the  
32 670 Southern Annular Mode (Strub et al., 2019; León-Muñoz et al., 2018; Lara et al.,  
33 671 2016).  
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46 673 The inflow of oceanic water masses to the Chilean Patagonian IZ has been  
47 674 described previously, finding that the main limitation to the inflow of these waters is  
48 675 the shallow depth and narrowness of the channels, as well as the presence of sills.  
49 676 The absence of the ESSW in the SI is attributed to the shallow depth at the western  
50 677 ends of the oceanic channels (Linford et al., 2023; Sievers, 2008; Sievers and Silva,  
51 678 2008).  
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#### 59 680 **4.2 Spawning areas**

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4 681  
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6 682 The presence and abundance of *M. magellanicus* eggs collected in the IZ and OZ  
7  
8 683 during the period 1995 - 2018 in winter and spring (August - November) confirm the  
9  
10 684 hypothesis that the northern Chilean Patagonia zone is an important spawning area  
11  
12 685 for this species. On the other hand, the decrease in the presence and abundance of  
13  
14 686 eggs in spring vs. winter, and the increase in larval length in spring support the  
15  
16 687 hypothesis that the spawning peak occurs extends at least until November (Gorini  
17  
18 688 et al., 2021; Giussi et al., 2016; Niklitscheck et al., 2014).  
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20 689  
21 690 The highest *M. magellanicus* eggs abundance occurred in winter in the NIM.  
22  
23 691 However, the larger number of mature individuals of this species, spawning and/or  
24  
25 692 spent (spawned), are found in the continental shelf break (OZ) at depths concordant  
26  
27 693 with the presence of SAAW and ESSW (Legua and Vargas 2020; Lillo et al., 2011;  
28  
29 694 Lillo et al., 2004). The latter suggests that the eggs found in the IZ would ingress  
30  
31 695 from the main spawning area on the continental shelf, and/or that the Chilean  
32  
33 696 Patagonian IZ is an alternative or secondary spawning area for this species. Veroes  
34  
35 697 et al. (2023) suggest that eggs of this species could enter from the continental shelf  
36  
37 698 (OZ) into the IZ through subsurface transport of oceanic water towards the coast,  
38  
39 699 which would be supported by the permanent presence of ESSW in the NIM, but they  
40  
41 700 did not rule out a secondary/alternative spawning in the inland sea. Further south,  
42  
43 701 the presence of eggs in the CI and in the SI in spring, areas where the influence of  
44  
45 702 subsurface oceanic water is less (i.e. ESSW is absent in the SI), support also the  
46  
47 703 hypothesis of multiple inshore spawning areas for this species although their  
48  
49 704 contribution is probably lower than that of the offshore zone (Niklitscheck et al., 2014;  
50  
51 705 Ernst et al., 2005).  
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53 706  
54 707 The use of multiple spawning areas appears to be a reproductive strategy commonly  
55  
56 708 used by Merlucciidae and macrurids to improve their chances of survival in the  
57  
58 709 southern hemisphere. This strategy has been described for *M. novaezelandiae*, *M.*  
59  
60 710 *australis* and *M. gayi* (Flores et al., 2019; Landaeta and Castro, 2012; Zeldis et al.,  
61  
62 711 1998). Similarly, this has been described for other species such as *Gadus morhua*  
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4 712 in the northern hemisphere, which would employ two spawning grounds, alternating  
5 713 them according to optimal environmental conditions (Hoffle et al., 2014).

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10 715 **4.3 Nursery areas**

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13 717 The presence of *M. magellanicus* larvae in the IZ and OZ of Chilean Patagonia in  
14  
15 718 spring and winter confirm that both are important nursery areas for this species. The  
16  
17 719 abundance of larvae was higher in the IZ than in the OZ in spring and winter  
18  
19 720 suggesting that the IZ would be the most important larval nursery area for this  
20  
21 721 species. However, the results found by Niklitscheck et al. (2014) shows the opposite.  
22  
23 722 These authors point out that although the IZ of Chilean Patagonia is an important  
24  
25 723 nursery area for *M. magellanicus*, its contribution to recruitment is lower when  
26  
27 724 compared to the OZ nursery areas (22% vs 79%). According to these authors, the  
28  
29 725 bifurcation of the West Wind Drift Current offshore and the overall dynamics of the  
30  
31 726 system in which spawning and growth of this species occurs may alter the  
32  
33 727 percentage contribution of each zone due to potential changes in the transport of  
34  
35 728 eggs and larvae. Regarding larval transport, Veroes et al. (2023) reported a large  
36  
37 729 exportation of larvae from the IZ to the OZ, as well as a larger number of large larvae  
38  
39 730 at the oceanic end of the channels in winter 2003, while in spring larvae would enter  
40  
41 731 or be retained in the IZ. Veroes et al. (2023) results in egg and larval fluxes were  
42  
43 732 also related to the larval feeding conditions inshore suggesting a coupling in between  
44  
45 733 the food particles sizes and larval sizes as a result of the different food webs in the  
46  
47 734 inland sea between winter (microbial-based trophic web) and spring (diatom-based  
48  
49 735 trophic web), which would favor larval growth either offshore (winter) or inshore  
50  
51 736 (spring) (Gonzales et al., 2010, 2011; Castro et al., 2022). The previous studies show  
52  
53 737 the greater importance of the offshore winter spawning zone but also show  
54  
55 738 alternative results regarding the presence and abundance of *M. magellanicus* larvae  
56  
57 739 inshore and offshore in winter and spring. The discordance among these results  
58  
59 740 does not allow to clearly assign a permanent greater or lesser importance of the IZ  
60  
61 741 or OZ as nursery zones. As Niklitscheck et al. (2014) pointed out, the variable  
62  
63 742 oceanographic conditions offshore may be playing a major role, a conclusion that  
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4 743 may be complemented by the extremely low biomass of the resource in the last  
5 744 decade which could be affecting the larval presence and abundance in areas not  
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7 745 necessarily the historic ones.  
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11 747 **4.4 Inter-annual changes in egg and larval abundance and distribution**

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15 749 Results from this study showed interannual changes in the abundance of eggs and  
16  
17 750 larvae at the inner and offshore areas associated with changes in the adult  
18  
19 751 population. The decrease in egg and larval abundance in the inshore zones when  
20  
21 752 comparing cruises prior to 2000 and the most recent ones (except winter 2003 and  
22  
23 753 spring 2011) as well as those conducted in the outer sea in winter 2013-2017 and  
24  
25 754 2019, are consistent with the decrease in biomass of reproductive adults of this  
26  
27 755 species reported in the technical reports of hydroacoustic assessment cruises  
28  
29 756 conducted in the outer sea. These reports show the decrease in the estimate of the  
30  
31 757 total and spawning biomass of *M. magellanicus* in the outer sea after the year 2000.  
32  
33 758 The total biomass decreased from 591,000 tons in 1992 to 204,789 tons in 2019,  
34  
35 759 while the spawning biomass decreased from ~550,000 tons in 2001 to ~125,000 tn  
36  
37 760 in 2019 (Legua and Vargas, 2020; Balbontín et al., 2016; Lillo et al., 2004). A second  
38  
39 761 adult population factor potentially contributing to the observed interannual decrease  
40  
41 762 in egg and larval abundance in winter in the outer sea could be associated to an  
42  
43 763 apparent delay in the onset of spawning season of *M. magellanicus* until the third or  
44  
45 764 fourth week of August in recent years as proposed by Payá (2020), while cruises are  
46  
47 765 historically conducted from the first week of August (Payá, 2020). The gradual  
48  
49 766 decrease in larval lengths measured in spring in our study in recent years tend to  
50  
51 767 support this second statement as well.  
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54 769 **4.5 Influence of environmental conditions on the intraseasonal distribution of**  
55  
56 770 ***M. magellanicus* eggs and larvae**

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58 772 The overall results from this study indicate that environmental conditions such as  
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60 773 hydrographic characteristics as well as the larval food abundance and presence of  
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774 predators may affect the egg and larval horizontal and vertical distributions within  
775 each season.

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777 The increase in egg abundance with salinity showed by the GAM results, with a  
778 maximum abundance at salinities around 34, corresponds to salinity at the spawning  
779 depth of the species in offshore waters and coincides with the trend of higher egg  
780 abundances found in the deep and saltier strata (>50 m) inshore (Giussi et al., 2016;  
781 Queirolo et al., 2008) just as has been observed in *M. novaezelandiae* (Langley,  
782 1993; Zeldis, 1993). In the IZ and OZ salinity increased with depth, and salinity  
783 higher than 34 was found in the OZ at all latitudes and in the IZ only between 43.5°S  
784 to 45°S (NIM) in winter, zone where the highest abundance of eggs was found.

785

786 The results of the GAM's for the larvae showed a non-linear effect within the  
787 temperature range of 6°C to 12°C and higher larval abundance between 8°C and  
788 10°C. These results suggest that a dome-like relationship (optimal environmental  
789 window) may exist in which high and low temperature values may not be favorable  
790 for larval development and survival. However, the temperature range preferred by  
791 the larvae would coincides with the temperatures observed in the strata closest to  
792 the surface, supporting the idea of ontogenetic changes of vertical distribution  
793 considering that eggs and the smaller larvae tended to occur in deeper and colder  
794 water (Veroes et al., 2023). Ontogenetic changes of this type have been observed  
795 in *M. novaezelandiae* suggesting that they may be part of similar life history  
796 strategies in fishes of this genus spawning on the edges of continental shelves in  
797 mid- and high-latitude areas (Murdoch et al., 1990).

798

799 The distribution and abundance of eggs and larval *M. magellanicus* and their  
800 potential prey and predators suggest a relationship between them. GAM's showed  
801 higher larval abundances associated with lower abundance of predators and a  
802 higher abundance of prey. During the main spawning peak of *M. magellanicus* in  
803 winter the abundance of predators (medusae) in the OZ and IZ was lower than in  
804 spring favoring eggs' survival. In spring, when larger larvae occurred, these

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4 805 developed larvae with a greater swimming capacity could avoid predation and also  
5  
6 806 feed easily due to a higher prey abundance (copepods). Predation has been pointed  
7  
8 807 out as the main source of mortality (compared to feeding limitation) in larvae of *M.*  
9  
10 808 *novaezelandiae* larvae (Murdoch and Quigley, 1994). On the other hand, the higher  
11  
12 809 abundance of prey (copepods) found in the OZ vs. IZ in spring, as well as a greater  
13  
14 810 size of copepods in the OZ vs. IZ (Landaeta and Castro, 2006; Contreras et al.,  
15  
16 811 2014) suggest favorable feeding of large larvae in the OZ in spring in the northern  
17  
18 812 Patagonian zone. Thus, the ontogenetic change in the early life stages of *M.*  
19  
20 813 *magellanicus* in the vertical and horizontal distribution between the Patagonian  
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22 814 Estuarine System and the adjacent continental shelf presented in this study suggests  
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24 815 it might confer the offspring higher probabilities of survival, which seems to be part  
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26 816 of a reproductive strategy of this species. These results supports, at the same time,  
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28 817 Niklitscheck et al. (2014) hypothesis of a larger proportion of the recruitment resulting  
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30 818 from the OZ nursery areas.

## 31 819

### 32 820 **5. Conclusions**

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35 822 The distribution of eggs and larvae of *M. magellanicus* between the Patagonian  
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37 823 Estuarine System and the adjacent oceanic zone seems to be part of a reproductive  
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39 824 strategy aimed at providing greater chances of survival to their offspring. The  
40  
41 825 spawning peak in winter decreases the probability of predation of eggs and larvae  
42  
43 826 and favors feeding conditions for larval development. The higher abundance of eggs  
44  
45 827 in the deep strata facilitates the entrance of a fraction of the spawn into IZ in winter,  
46  
47 828 when the abundance of potential predators is lower than in spring. Then, the  
48  
49 829 hatching and presence of small larvae in winter and spring within the Patagonian  
50  
51 830 Estuarine System favors the initial and subsequent larval feeding because the larval  
52  
53 831 prey sizes would be according with the size of the larvae and the lower presence of  
54  
55 832 potential predators than in the OZ. Subsequently, when the larvae reach larger sizes,  
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57 833 they tend to move to outer waters where the food (copepods) are larger. Finally, the  
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59 834 interannual decrease in egg and larval abundance is consistent with the decrease in  
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4 835 adult spawned specimens and also with an apparent delay in the onset of the winter  
5 spawning of *M. magellanicus* stock in the northern Chilean Patagonia.  
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10 838 **Acknowledgments**

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12  
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21 BECAS/DOCTORADO NACIONAL 21200739).  
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4 850 **Appendix**  
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7 852 **Appendix A. Kruskal-Wallis and Dunn's post hoc results of temperature between areas,**  
8 853 **seasons and years.**

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10 855 **A.1 Kruskal-Wallis and Dunn's post hoc results of temperature between seasons/years in the**  
11 856 **NICH.**

12 857  
13 858 Kruskal-Wallis test

14 859  
15 860 H (chi2): 130,2

16 861 Hc (tie corrected): 130,2

17 862 p (same): 2,135E-26

18 863 **There is a significant difference between sample medians**

19 864  
20 865 Dunn's post hoc.

	Spring 1995	Spring 2004	Spring 2005	Winter 2006	Spring 2006	Spring 2011
Spring 1995		<b>2.05E-04</b>	<b>1.17E-03</b>	0,1964	<b>0,0009804</b>	0,819
Spring 2004	<b>2.05E-04</b>		1	<b>1.80E-15</b>	0,3396	0,2169
Spring 2005	<b>1.17E-03</b>	1		<b>5.18E-17</b>	1	0,97
Winter 2006	0,1964	<b>1.80E-15</b>	<b>5.18E-17</b>		<b>6.88E-10</b>	<b>0,001187</b>
Spring 2006	<b>0,0009804</b>	0,3396	1	<b>6.88E-10</b>		1
Spring 2011	0,819	0,2169	0,97	<b>0,001187</b>	1	

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28 866

29 867 **In bold significance difference at p < 0.05 Bonferroni corrected p values.**

30 868  
31 869 **A.2. Kruskal-Wallis and Dunn's post hoc results of temperature between seasons/years in the**  
32 870 **NIM.**

33 871  
34 872 Kruskal-Wallis test

35 873  
36 874 H (chi2): 147,2

37 875 Hc (tie corrected): 147,2

38 876 p (same): 3,034E-29

39 877 **There is a significant difference between sample medians**

40 878  
41 879 Dunn's post hoc.

	Spring 1995	Spring 1998	Winter 2003	Spring 2003	Spring 2002	Winter 2007	Spring 2007
Spring 1995		1	<b>8.15E-02</b>	1	<b>0,008897</b>	<b>3.01E-11</b>	<b>0,01778</b>
Spring 1998	1		<b>0,0001115</b>	1	0,9862	<b>5.96E-09</b>	<b>0,0128</b>
Winter 2003	<b>8.15E-02</b>	<b>0,0001115</b>		<b>3.68E-03</b>	<b>3.35E-08</b>	0,07128	1
Spring 2003	1	1	<b>3.68E-03</b>		1	<b>8.76E-11</b>	<b>0,0005449</b>
Spring 2002	<b>0,008897</b>	0,9862	<b>3.35E-08</b>	1		<b>2.20E-19</b>	<b>9,64E-09</b>
Winter 2007	<b>3.01E-11</b>	<b>5.96E-09</b>	0,07128	<b>8.76E-11</b>	<b>2.20E-19</b>		<b>8.62E-03</b>
Spring 2007	<b>0,01778</b>	<b>0,0128</b>	1	<b>0,0005449</b>	<b>9,64E-09</b>	<b>8.62E-03</b>	

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51 881 **In bold significance difference at p < 0.05 Bonferroni corrected p values.**

52 882  
53 883 **A.3. Kruskal-Wallis and Dunn's post hoc results of temperature between seasons/years in the**  
54 884 **OZ.**

55 885  
56 886 Kruskal-Wallis test

57 887  
58 888 H (chi2): 101,4

59 889 Hc (tie corrected): 101,4

60 890 p (same): 1,291E-19

61 891 **There is a significant difference between sample medians**  
62  
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892  
893**Dunn's post hoc.**

	Winter 2013	Winter 2014	Winter 2015	Winter 2016	Winter 2017	Spring 2018	Winter 2019
Winter 2013		0,639	1	<b>2.30E-04</b>	0,4231	<b>2.42E-13</b>	0,4555
Winter 2014	0,639		1	<b>0,0004233</b>	1	<b>9.12E-09</b>	1
Winter 2015	1	1		<b>0,002723</b>	1	<b>1.42E-04</b>	1
Winter 2016	<b>2.30E-04</b>	<b>0,0004233</b>	<b>0,002723</b>		1	1	0,1348
Winter 2017	0,4231	1	1	1		<b>0,04217</b>	1
Spring 2018	<b>2.42E-13</b>	<b>9.12E-09</b>	<b>1.42E-04</b>	1	<b>0,04217</b>		<b>0,0001012</b>
Winter 2019	0,4555	1	1	0,1348	1	<b>0,0001012</b>	

In bold significance difference at  $p < 0.05$  Bonferroni corrected p values.

## Appendix B. Kruskal-Wallis and Dunn's post hoc results of salinity between areas, seasons and years.

### B.1 Kruskal-Wallis and Dunn's post hoc results of salinity between seasons/years in the NICH.

#### Kruskal-Wallis test

H (chi2): 31,86

Hc (tie corrected): 31,86

p (same): **6,322E-06**

**There is a significant difference between sample medians**

#### Dunn's post hoc

	Spring 1995	Spring 2004	Spring 2005	Winter 2006	Spring 2006	Spring 2011
Spring 1995		1	1	<b>0,04921</b>	1	1
Spring 2004	1		1	<b>0,002807</b>	0,3647	1
Spring 2005	1	1		<b>5.15E-03</b>	<b>0,01032</b>	1
Winter 2006	<b>0,04921</b>	<b>0,002807</b>	<b>5.15E-03</b>		1	1
Spring 2006	1	0,3647	<b>0,01032</b>	1		1
Spring 2011	1	1	1	1	1	

In bold significance difference at  $p < 0.05$  Bonferroni corrected p values.

### B.2. Kruskal-Wallis and Dunn's post hoc results of salinity between seasons/years in the NIM

#### Kruskal-Wallis test

H (chi2): 40,13

Hc (tie corrected): 40,13

p (same): **4,297E-07**

**There is a significant difference between sample medians**

#### Dunn's post hoc

	Spring 1995	Spring 1998	Winter 2003	Spring 2003	Spring 2002	Winter 2007	Spring 2007
Spring 1995		1	0,1695	1	0,3706	1	<b>0,01881</b>
Spring 1998	1		1	1	1	1	<b>0,02293</b>
Winter 2003	0,1695	1		1	1	0,5668	<b>3,1E-06</b>
Spring 2003	1	1	1		1	1	<b>0,03257</b>
Spring 2002	0,3706	1	1	1		1	<b>7,06E-03</b>
Winter 2007	1	1	0,5668	1	1		0,1404
Spring 2007	<b>0,01881</b>	<b>0,02293</b>	<b>3,1E-06</b>	<b>0,03257</b>	<b>7,06E-03</b>	0,1404	

923

924 In bold significance difference at  $p < 0.05$  Bonferroni corrected  $p$  values.

925

### 926 B.3. Kruskal-Wallis and Dunn's post hoc results of salinity between seasons/years in the OZ

927

928 Kruskal-Wallis test

929

930 H (chi2): 29,42

931 Hc (tie corrected): 29,42

932 p (same): 5,072E-05

933 There is a significant difference between sample medians

934

935 Dunn's post hoc

	Winter 2013	Winter 2014	Winter 2015	Winter 2016	Winter 2017	Spring 2018	Winter 2019
Winter 2013		1	1	<b>0,0002552</b>	1	1	1
Winter 2014	1		1	<b>0,00038</b>	1	1	1
Winter 2015	1	1		<b>0,007977</b>	1	1	1
Winter 2016	<b>0,0002552</b>	<b>0,00038</b>	<b>0,007977</b>		<b>0,0138</b>	<b>1,69E-02</b>	0,156
Winter 2017	1	1	1	<b>0,0138</b>		1	1
Spring 2018	1	1	1	<b>1,69E-02</b>	1		1
Winter 2019	1	1	1	0,156	1	1	

936

937 In bold significance difference at  $p < 0.05$  Bonferroni corrected  $p$  values.

938

### 939 Appendix C. Kruskal-Wallis and Dunn's post hoc results of eggs abundance between areas, seasons and years.

940

#### 942 C.1 Kruskal-Wallis and Dunn's post hoc results of eggs abundance in spring between sampling areas

943

944 Kruskal-Wallis test

945

946 H (chi2): 3,939

947 Hc (tie corrected): 13,44

948 p (same): 0,009313

949 There is a significant difference between sample medians

950

951 Dunn's post hoc

	NIM	CI	SI	NICH	OZ
NIM		0,7538	1	1	0,6348
CI	0,7538		<b>0,02749</b>	1	1
SI	1	<b>0,02749</b>		0,09106	0,06362
NICH	1	1	0,09106		1
OZ	0,6348	1	0,06362	1	

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948 In bold significance difference at  $p < 0.05$  Bonferroni corrected  $p$  values.

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#### 950 C.2. Kruskal-Wallis and Dunn's post hoc results of eggs abundance in winter in the OZ between years

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953 Kruskal-Wallis test

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955 H (chi2): 7,22

956 Hc (tie corrected): 16,61

957 p (same): 0,005291

958 There is a significant difference between sample medians

959

960 Dunn's post hoc

	Hidroa 2015	Hidroa 2016	Hidroa 2017	Hidroa 2019	Hidroa2013	Hidroa2014
Hidroa 2015		1	1	1	1	0,3449
Hidroa 2016	1		1	1	0,1934	<b>0,02228</b>

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Hidroa 2017	1	1		1	1	1
Hidroa 2019	1	1	1		0,3557	0,06723
Hidroa2013	1	0,1934	1	0,3557		1
Hidroa2014	0,3449	<b>0,02228</b>	1	0,06723	1	

In bold significance difference at  $p < 0.05$  Bonferroni corrected p values.

#### Appendix D. Kruskal-Wallis and Dunn's post hoc results of larval abundance between areas, seasons and years.

##### D.1. Kruskal-Wallis and Dunn's post hoc results of larval abundance in spring between sampling areas

Kruskal-Wallis test

H (chi2): 25,76  
Hc (tie corrected): 39,48  
p (same): 5,586E-08

There is a significant difference between sample medians

Dunn's post hoc

	NICH	NIM	CI	SI	OZ
NICH		0,6478	<b>8.31E-03</b>	<b>0,002368</b>	0,09693
NIM	0,6478		<b>6.14E-05</b>	<b>0,0001875</b>	0,05874
CI	<b>8.31E-03</b>	<b>6.14E-05</b>		0,8093	0,5141
SI	<b>0,002368</b>	<b>0,0001875</b>	0,8093		0,7001
OZ	0,09693	0,05874	0,5141	0,7001	

In bold significance difference at  $p < 0.05$  Bonferroni corrected p values.

##### D.2. Kruskal-Wallis and Dunn's post hoc results of larval abundance in spring in the NICH between years

Kruskal-Wallis test

H (chi2): 30,78  
Hc (tie corrected): 40,18  
p (same): 3,969E-08

There is a significant difference between sample medians

Dunn's post hoc

	1995	2004	2006	2011	2005
1995		0,08085	<b>5.50E-03</b>	0,7967	<b>1.47E-03</b>
2004	0,08085		1	1	1
2006	<b>5.50E-03</b>	1		0,06193	1
2011	0,7967	1	0,06193		<b>0,03172</b>
2005	<b>1.47E-03</b>	1	1	<b>0,03172</b>	

In bold significance difference at  $p < 0.05$  Bonferroni corrected p values.

##### D.3. Kruskal-Wallis and Dunn's post hoc results of larval abundance in spring in the NIM between years

Kruskal-Wallis test

H (chi2): 21,71  
Hc (tie corrected): 26,04  
p (same): 3,107E-05

There is a significant difference between sample medians

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1005 Dunn's post hoc

	1995	1998	2002	2003	2007
1995		<b>0,009148</b>	1	0,6496	1
1998	<b>0,009148</b>		<b>0,01197</b>	<b>0,0003102</b>	<b>0,0003803</b>
2002	1	<b>0,01197</b>		1	1
2003	0,6496	<b>0,0003102</b>	1		1
2007	1	<b>0,0003803</b>	1	1	

In bold significance difference at  $p < 0.05$  Bonferroni corrected p values.

#### D.4. Kruskal-Wallis and Dunn's post hoc results of larval abundance in spring in the CI between years

Kruskal-Wallis test

H (chi2): 4,197  
Hc (tie corrected): 9,848  
p (same): **0,007272**  
There is a significant difference between sample medians

Dunn's post hoc

	1996	2008	2009
1996		<b>0,01324</b>	0,08555
2008	<b>0,01324</b>		1
2009	0,08555	1	

In bold significance difference at  $p < 0.05$  Bonferroni corrected p values.

#### Apenndix E. Kruskal-Wallis and Dunn's post hoc results of eggs abundance by strata in winter and spring at inner zone.

##### E.1. Kruskal-Wallis and Dunn's post hoc results of eggs abundance by strata in spring at inner zone.

Kruskal-Wallis test

H (chi2): 6,104  
Hc (tie corrected): 10,58  
p (same): **0,005098**  
There is a significant difference between sample medians

Dunn's post hoc (bonferroni corrected p values)

	50-100	25-50	0-25
50-100		1	<b>0,00626</b>
25-50	1		0,06077
0-25	<b>0,00626</b>	0,06077	

In bold significance difference at  $p < 0.05$  Bonferroni corrected p values.

##### E.2. Kruskal-Wallis and Dunn's post hoc results of eggs abundance by strata in winter at inner zone (NIM).

Kruskal-Wallis test

H (chi2): 10,34  
Hc (tie corrected): 10,5  
p (same): **0,01478**  
There is a significant difference between sample medians

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1051 Dunn's post hoc

	>100	50-100	25-50	0-25
>100		1	1	0,4636
50-100	1		0,4634	0,01596
25-50	1	0,4634		1
0-25	0,4636	0,01596	1	

1052 In bold significance difference at  $p < 0.05$  Bonferroni corrected p values.

1054 **Appendix F. Kruskal-Wallis and Dunn's post hoc results of larval length between seasons, years, sampling areas and strata.**

1055 **F.1. Kruskal-Wallis and Dunn's post hoc results of larval length by strata in spring at inner zone**

1056 Kruskal-Wallis test

1057 H (chi2): 14,21  
1058 Hc (tie corrected): 14,24  
1059 p (same): 0,002591

1060 **There is a significant difference between sample medians**

1061 Dunn's post hoc

	25-50	0-25	50-100	>100
25-50		0,01995	0,01181	1
0-25	0,01995		1	1
50-100	0,01181	1		1
>100	1	1	1	

1062 In bold significance difference at  $p < 0.05$  Bonferroni corrected p values.

1063 **F.2. Kruskal-Wallis and Dunn's post hoc results of larval length by strata in winter 2003 at inner zone (NIM)**

1064 Kruskal-Wallis test

1065 H (chi2): 112,8  
1066 Hc (tie corrected): 112,8  
1067 p (same): 2,766E-24

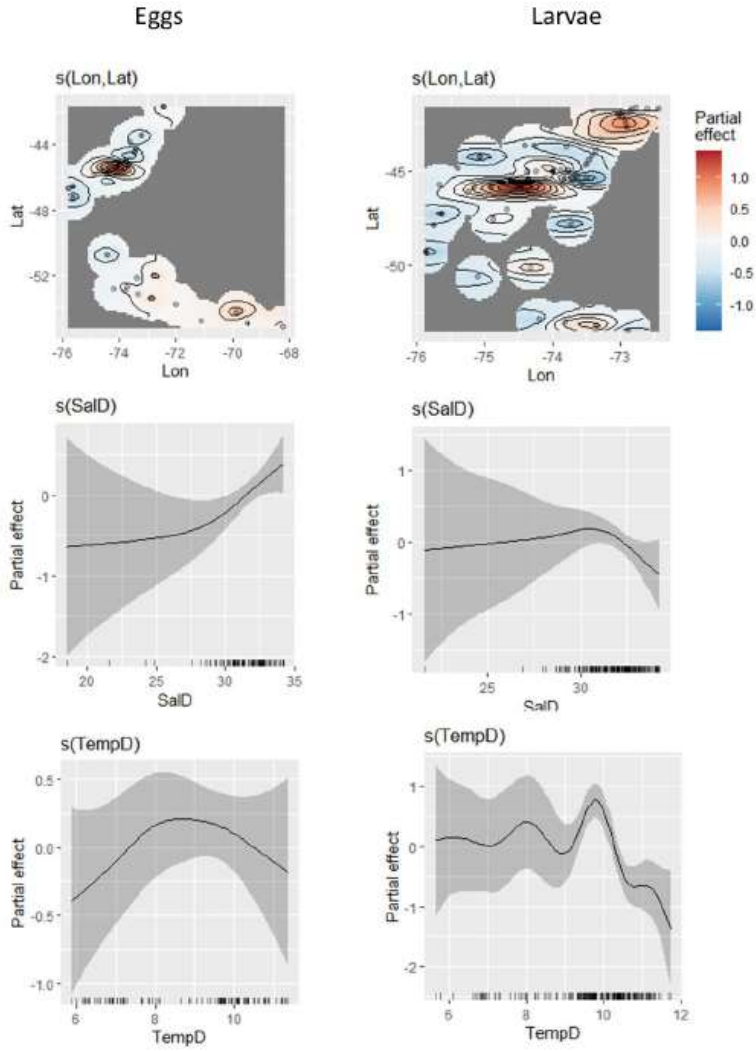
1068 **There is a significant difference between sample medians**

1069 Dunn's post hoc

	0-25	25-50	50-100	>100
0-25		4,54E-17	0,004606	4,28E-15
25-50	4,54E-17		9,80E-08	0,01202
50-100	0,004606	9,80E-08		2,94E-09
>100	4,28E-15	0,01202	2,94E-09	

1070 In bold significance difference at  $p < 0.05$  Bonferroni corrected p values.

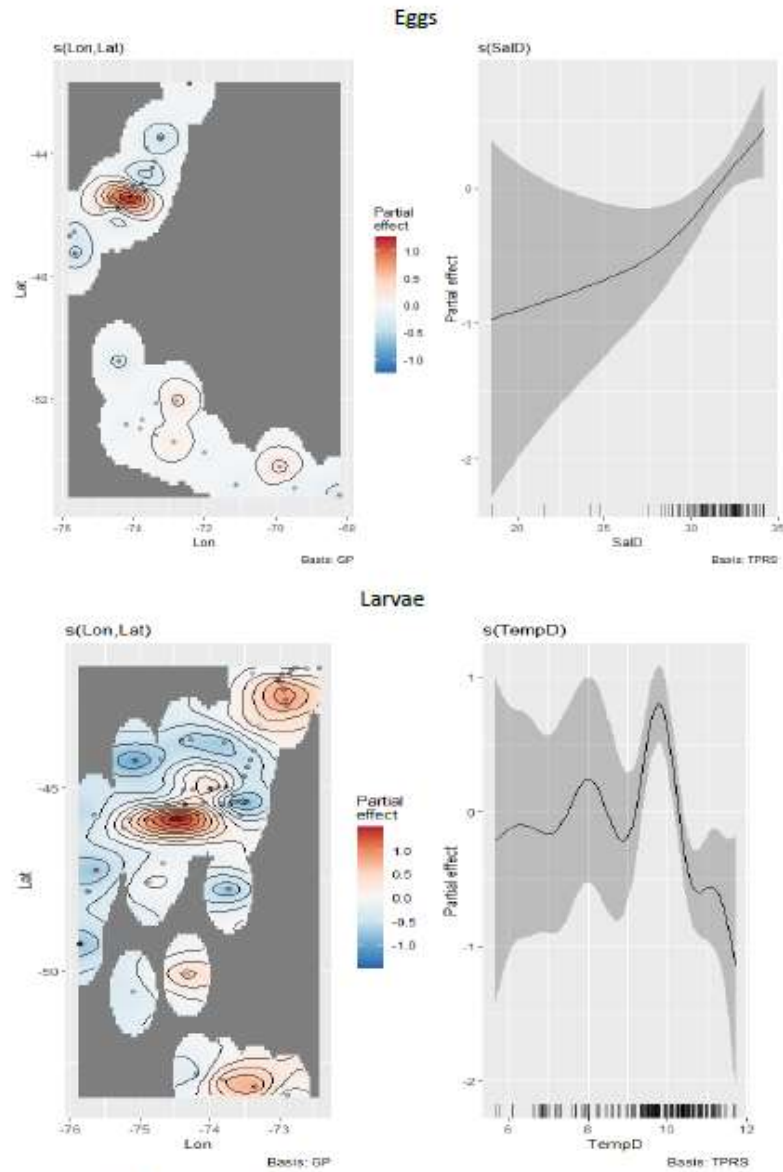
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1089 Appendix G. Full GAM models, showing function smooths with 95% confidence  
1090 bands of the covariates.  
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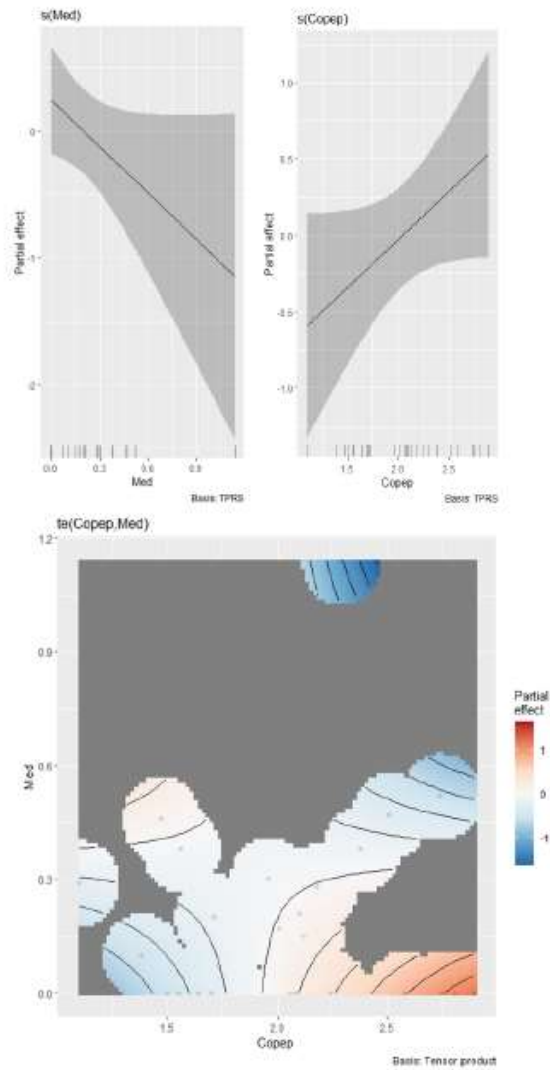


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Appendix H. Final GAM models for eggs and larvae, showing function smooths with 95% confidence bands of the covariates and only significant terms.

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1146 Appendix I. GAM models for larvae, showing function smooths with 95% confidence  
1147 bands of the covariates and tensor product: Copep, Med.

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**3.2 Capítulo 2:** Transporte inferido de estadíos tempranos de vida de merluza de cola (*Macruronus magellanicus*) entre los canales del norte de la Patagonia y la plataforma continental. Artículo científico publicado en la revista “Continental Shelf Research” 252 (2023) 104878. <https://doi.org/10.1016/j.csr.2022.104878>

### **Resumen**

La merluza de cola migra desde el Atlántico suroeste y el Pacífico sureste para reproducirse en la Patagonia norte chilena. El desove ocurre principalmente en invierno en el quiebre de la plataforma continental (CSB), pero también se recolectan huevos y larvas en el Sistema Estuarino Patagónico Chileno (PES) durante invierno y primavera. Con el fin de evaluar si los cambios ontogenéticos en la distribución de los estadios tempranos de vida forman parte de la estrategia reproductiva de la merluza de cola, se analizó la distribución y transporte de huevos y larvas en primavera e invierno en tres canales del PES (Ninualac, Darwin y Pulluche). El muestreo estratificado de ictioplancton mostró la mayor abundancia de huevos en los estratos más profundos, mientras que las larvas se distribuyeron heterogéneamente a lo largo de toda la columna de agua. Las velocidades de las corrientes residuales obtenidas del ADCP indicaron flujos hacia el extremo oceánico (hacia el oeste) en la superficie en todos los canales, excepto en Pulluche en invierno. En profundidad (50-100 m), los flujos se dirigieron hacia el este (costa) en los dos canales del norte, pero hacia el oeste en el canal más al sur. Estas diferencias en las velocidades residuales y en la distribución vertical de huevos y larvas, dieron como resultado diferencias en el flujo de huevos y larvas hacia el mar interior y hacia el océano entre canales y estratos. Los flujos netos estimados en invierno sugirieron que los huevos dentro de los canales ingresarían al PES desde la plataforma continental, principalmente en la capa subsuperficial del canal Darwin, o provendrían de un desove secundario dentro de este mismo canal. Los huevos y las larvas pequeñas se retendrían en el extremo costero del canal Darwin, y larvas desarrolladas serían

exportadas a través del canal Pulluche de regreso a la plataforma continental. La gran abundancia de huevos y larvas de *M. magellanicus* en invierno en el mar interior, junto con la reducción de la producción primaria y la estructura comunitaria del plancton basada en el anillo microbiano sugieren que ingresar a los canales en invierno no sería una parte importante de la estrategia reproductiva de la especie. En cambio, la exportación de larvas desde los canales a la plataforma en invierno podría promover mejores condiciones de alimentación en aguas del mar exterior donde el zooplancton es de mayor tamaño.





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## Inferred transport of early life stages of Patagonian grenadier (*Macrurus magellanicus*) between northern Patagonian channels and the continental shelf

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### ABSTRACT

Patagonian grenadier migrates from the southwest Atlantic and southeast Pacific to reproduce in the northern Chilean Patagonia. Spawning occurs mainly in winter at the continental shelf break (CSB), but eggs and larvae are also collected inshore of the Chilean Patagonian Estuarine System (PES) during winter and spring. In order to evaluate whether the ontogenetic changes in distribution of early life stages was part of the reproductive strategy of Patagonian grenadier, we analyzed the distribution and transport of eggs and larvae in spring and winter in three channels of the PES (Ninualac, Darwin and Pulluche channels). Ichthyoplankton stratified sampling showed the highest abundances of eggs in the deepest strata, whereas larvae were heterogeneously distributed along the entire water column. Residual current velocities obtained from ADCP indicated seaward (westward) fluxes at the surface in all channels, except in Pulluche in winter. At depth (50–100 m) fluxes were eastward (inshore) in the northern 2 channels but seaward in the southernmost channel. These differences in residual velocities, with variations in the distribution of eggs and larvae, resulted in different landward and oceanward flows of eggs and larvae among channels and strata. Estimated net fluxes in winter suggested that eggs within the channels would either enter the PES from the continental shelf, mainly at the subsurface layer of the Darwin channel, or come from a secondary spawning within this same channel. Eggs and small larvae would be retained at the inshore zone of the Darwin channel, and the more advanced developed stages would be exported through the Pulluche channel back to the continental shelf. The inshore high abundance of eggs and larvae of *M. magellanicus* in winter, along with the reduced primary production and microbial-based plankton community previously reported, suggest that entering the channels in winter is not a major part of the reproductive strategy of the species. The exportation of larvae from the channels to the shelf in winter, instead, might promote better feeding conditions in offshore waters where larger zooplankton occurs.

### 1. Introduction

Estuaries are key ecosystems to the reproductive strategies of many marine species, as they can be used as spawning and/or nursery areas due to their suitable conditions, such as higher food availability and protection from predators (Cushing 1975; Blaber 1985; Elliott et al., 2007; Primo et al., 2013; Potter et al., 2015). Similarly, these systems can favor the population connectivity of species through the exportation of individuals when they have reached a less vulnerable stage of development (Rousseau et al., 2017; Guerreiro et al., 2021). Estuaries

are systems that exhibit a typical two-layer vertically averaged circulation pattern known as estuarine circulation. In positive estuaries, a surface layer drives a net volume outflow toward the ocean, below which a second subsurface more saline layer is driven landwards (Valle-Levinson, 2010). Thus, the estuarine circulation can promote the advection or retention in the estuary of zooplankton organisms, such as fish larvae and invertebrates, whose selective migration through these environments is critical to the population dynamics and geographic distribution of many estuarine and marine-benthic species (Boehlert and Mundy 1988; Pietrafesa and Janowitz 1988; Epifanio 1988; Beck et al.,

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2001; Bruno et al., 2014; Meerhoff et al., 2014; Guerreiro et al., 2021).

The Chilean Patagonian Estuarine System (PES) (Niklitschek et al., 2014) extends from the Reloncavi Fjord (41.5°S) to Cape Horn (55.9°S) and is characterized by a complex system of fjords, channels, gulfs, estuaries and bays (Iriarte et al., 2014). It receives freshwater from local rivers, precipitation, surface runoff, groundwater, and glaciers (Pantoja et al., 2011). In the adjacent offshore oceanic area (between 40°S and 50°S), the South Pacific Current (SPC) bifurcates and gives way to the formation of two main currents, one flowing toward the equator called the Humboldt Current and the other flowing southwards called the Cape Horn Current (Strub et al., 2019).

The PES harbors high concentrations of eggs, larvae, and juveniles of some commercially important fish species such as southern hake (*Merluccius australis*) and Patagonian grenadier (*M. magellanicus*), which spawn within or adjacent to it. As a nursery area for Patagonian grenadier, the PES contributes 10–35% of the recruitment of this species in Chilean Patagonia (Niklitschek et al., 2014). It is also an important secondary spawning area in spring for *M. australis* (Flores et al., 2019). The PES, like many estuaries in the world, appears to be used by fish species in a various ways (Potter et al., 2015). However, the processes of connectivity and fluxes of eggs and larvae between the PES and the adjacent continental shelf have received less attention.

Patagonian grenadier (*Macrurus magellanicus* Lönnberg, 1907), also known as long-tail hake and hoki, is a Gadiform and eurybathic species that is distributed on the continental shelf and slope at depths between 20 and 700 m. While juveniles are pelagic, the adults change to a demersal residence (Queirolo et al., 2008). It is distributed in the southeastern Pacific between Valparaíso (33°S) and Cape Horn (55°S) and in the southwestern Atlantic between 33° and 57°S. It is the most abundant demersal fishery resource in Chilean Patagonia and the second of the total annual landings in Argentina. However, the stock of this species has been declining since 1999, and its exploitation status for the Chilean fishery is currently classified as depleted (Castillo-Jordán et al., 2019; Céspedes et al., 2020; Gorini et al., 2021). The spawning and nursery areas of *Macrurus magellanicus* in the south-east Pacific and Atlantic oceans are not clearly identified and studies conducted to understand any migrating behavior during the early life stages are scarce. The only confirmed large spawning area for this species is within the Chilean continental shelf between 41 and 48°S, and it has been proposed that the Atlantic stock would migrate to reproduce in the Pacific since no important spawning areas have been found in the Atlantic (Giusti et al., 2016; Payá, 2020; Gorini et al., 2021). Historically, other potential spawning areas have been proposed for this species based on the occasional presence of eggs, larvae and even some mature adult specimens. These areas include fjords and channels in the north area of the Chilean Patagonia, the continental shelf further south in the same zone (54°–55°S) and the Argentine Patagonia, however, their spatial and temporal persistence have not been confirmed (Machinandiarena and Ehrlich, 1999; Ernst et al., 2005; Landaeta et al., 2011; Giusti et al., 2016).

Except for some recent studies carried out on squat lobster *Munida gregaria* zoea and few fish larvae (León et al., 2008; Flores et al., 2019, 2020; Molina-Valdivia et al., 2021), most research on ichthyoplankton in the northern Chilean Patagonia has focused mainly on studying the composition and abundance of egg and fish larvae either in the fjords and channels of the PES, or in the adjacent continental shelf waters (Balbontin et al., 2004; Balbontin and Bernal, 2005; Landaeta and Castro, 2006b; Landaeta et al., 2009; Bustos et al., 2011; Castillo-Hidalgo et al., 2018; Osorio-Zúñiga et al., 2018). Each area constitutes important spawning and nursery zones for many demersal, midwater or pelagic species, yet most research have not analyzed the distribution of early developmental stages of the species including both areas simultaneously or assessed potential egg and larval fluxes between areas. In this study, we analyzed the vertical and horizontal distribution of eggs and larvae of *M. magellanicus* along three channels of the northern Chilean Patagonia and estimated their net transport to the adjacent main

offshore spawning area during the main winter spawning season and in spring also. The results are then placed into a life history context trying to assess whether the observed ontogenetic changes in distribution along channels form part of a reproductive strategy common for invertebrate and fishes in the northern Chilean Patagonia that connects the species estuarine and shelf residence during the youngest stages of development.

## 2. Material and methods

### 2.1. Study area

The study area covers the Patagonian Estuarine System (PES) in the northern Chilean Patagonia and includes three transverse channels in an east–west direction Ninualac (45.01°S), Darwin (45.44°S), and Pulluche (45.80°S) channels (Fig. 1). The mean depths in the channels are 208 m (Ninualac), 168 m (Darwin) and 90 m (Pulluche), and their extension are 61 km (Ninualac), 70 km (Darwin) and 83 km (Pulluche). Their estimated volumes are  $4.3 \times 10^{10} \text{ m}^3$  (Ninualac),  $4.5 \times 10^{10} \text{ m}^3$  (Darwin) and  $2.9 \times 10^{10} \text{ m}^3$  (Pulluche).

Like many other estuarine systems, hydrodynamics is modulated by the freshwater input, tidal forcing, and wind-driven flows. The primary source of coastal freshwater discharge is the Aysen River, which exhibits a mean annual discharge of about  $620 \text{ m}^3/\text{s}$  (Niemeier and Cereceda, 1994). Many other non-gauged coastal discharges like smaller rivers, precipitation, waterfalls, and glaciers also contribute to the total input of freshwater to this system. The tidal regime is mixed, predominantly semidiurnal, and tidal ranges are about 2.5 m (Cáceres et al., 2002). Southerly and southwesterly winds dominate the wind regime into the inland sea in this area during spring and summer (October–March), and northerly and northwesterly winds during fall and winter

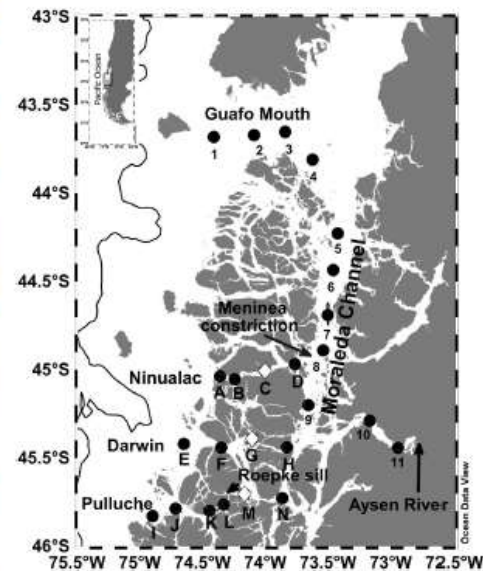


Fig. 1. Study area. Black circles indicate the location of the oceanographic and zooplankton sampling stations. Diamonds are locations of Yo-Yo stations. Stations A to D (Ninualac), E to H (Darwin) and I to N (Pulluche). The solid line on the western side represents the continental shelf break (300 m depth contour).



(April–September). Westerly and southwesterly winds may favor wind-driven, up-estuary surface circulation, decelerating or reversing the direction of the surface layer mean outflow (Cáceres et al., 2002). In this area (Fig. 1), waters of oceanic origin fill the deep inland basins moving eastward through the Guafu mouth area and southward through the Moraleda channel, as evidenced by the observation of Subantarctic Water (SAAW), modified Subantarctic Water (MSAAW), and Equatorial Subsurface Water (ESSW) (Sievers and Silva, 2006). The observations of ESSW show a vertical distribution between 150 m and 400 m, which restricts its distribution to the deeper areas of Moraleda channel northward of Meninea constriction. This bathymetric break seriously limits the deep-water exchange in the meridional orientation, and gives origin to the formation of micro basins (Sievers and Silva, 2006).

## 2.2. Fieldwork and samples collection

Hydrographic data and stratified zooplankton samples were obtained in austral spring 2002 (17–23 November), winter 2003 (9–21 August) and spring 2003 (7–18 November) from CIMAR-Fiorlos 8 and CIMAR-Fiorlos 9 oceanographic cruises carried out onboard the RV Vidal Gormaz (Fig. 1). At each oceanographic station along the cruise track, temperature and salinity profiles were obtained from CTD casts, using a Seabird (SBE-25plus) CTD, equipped with temperature, conductivity and pressure sensors. Mesozooplankton samples were collected with a Tucker trawl net (1-m<sup>2</sup> frame, 300- $\mu$ m mesh size, with flowmeter) from 4 strata (surface: 0–20 m, midwater: 20–50 m, deep: 50–100 m and near bottom: >100 m), depending on the station's maximum depth. All samples were preserved onboard in 10% formalin buffered with sodium borate.

Repeated measurements of water column properties (CTD casts) and stratified zooplankton samples were also obtained over 24-h periods in three Yo-Yo stations located in the center of three channels of the study area (Ninualac, Darwin, Pulluche, depicted by diamonds in Fig. 1) in winter 2003 (August 17, 18 and 20, in each channel, respectively) and in spring 2003 (November 10, 15 and 17, in each channel, respectively). At these same stations, velocity measurements were obtained using a Workhorse Acoustical Doppler Current Profiler (ADCP) RD Instruments of 307.2 kHz over the same 24 h periods in each channel. The ADCP instrument was mounted looking downward in a 3 m in length catamaran attached to the RV Vidal Gormaz side. Data ensembles were averaged every 30 s, and vertical bin size was 4 m.

## 2.3. Laboratory work

In the laboratory, *M. magellanicus* eggs and larvae were identified, sorted and counted following Patchell et al. (1987), Machinandiarena and Ehrlich (1999) and Balbontin et al. (2004). The larvae were measured and classified according to their standard length (SL) as small (<3.7 mm), medium (3.7–4.0 mm), or large (>4.0 mm). The criteria for larval classification were based on the larval lengths and time of absorption of the yolk sac (SL = 4.1 mm, 5 days, Patchell et al., 1987). In all our large larvae (>4.0 mm), the yolk sac was absent (totally absorbed). In small larvae (<3.7 mm) the yolk sac was always present and medium size larvae (3.7–4.0 mm) corresponds with the length range we observed absorption takes place.

## 2.4. Data analysis

Maps of sea surface temperature and salinity, and vertical sections of temperature (°C) and salinity along the three channels were prepared with the data obtained from the oceanographic sampling stations using Ocean Data View (ODV 5.3.0). Horizontal maps of eggs and larvae were prepared using Surfer 13 in which the abundances of eggs and larvae along the water column were expressed in individuals per 10 m<sup>2</sup>.

To visualize potential ontogenetic changes in the horizontal distribution of *M. magellanicus* during the early life stages, mean eggs and

larval (grouped by body length) abundances and their percentage of contribution per station in each of three channels (Ninualac, Darwin, Pulluche), were estimated and diagrammed. These stations were also grouped according to their distance from the Moraleda channel as inshore stations (0–20 km), central stations (20–40 km and 40–60 km) and seaward stations (>60 km).

For diagramming the vertical distribution of eggs and larvae, profiles of mean egg and larval abundance per sampled stratum (expressed as ind./1000 m<sup>3</sup>) at all stations along the 3 channels (Ninualac, Darwin, Pulluche) were obtained for each of the seasonal cruises (Spring 2002; Winter, 2003; Spring 2003).

To visualize potential diel vertical migrations (DVM), mean day and night profiles of larval abundance (grouped by larval length) at Yo-Yo stations were diagrammed. We also calculated the mean weighted depth (MWD, m) per profile and their day vs night displacement (amplitude,  $\Delta$ ). MWD and  $\Delta$ , were obtained following the equations;  $MWD = \frac{\sum (N_i Z_i)}{\sum N_i}$ , where  $N_i$  = organism abundance in stratum  $i$  (ind./1000 m<sup>3</sup>), and  $Z_i$  = mean depth of stratum  $i$ .  $\Delta = MWD_{max} - MWD_{min}$  (is the difference between the maximum and minimum MWD).

The orthogonal components of the water velocity obtained with the ADCP instrument were decomposed into east ( $u$ ) flow and north ( $v$ ) flow components. The data were then rotated counterclockwise to an along- ( $u$ -flow) and an across- ( $v$ -flow) channel coordinate system. This angle was oriented to the direction of greatest variability of the along-channel tidal currents and of weakest across-channel tidal flows, respectively. The corresponding angles of rotation were 35° (Ninualac C.), 0° (Darwin C.), and 65° (Pulluche C.).

The tidal signals represented by the  $M_2$  and  $K_1$  constituents were separated from the subtidal signal of flow components using least-squares sinusoidal regression analysis (Lwiza et al., 1991). The residual flow remaining after this analysis approximated the mean flow during the observation period. Then, the residual  $u$ -velocities were vertically averaged into the three vertical bins defined by the zooplankton sampling strata depth (0–20 m, 20–50 m, and 50–100 m). The stratum velocity >100 m was not used because of the low quality of the data due to the technical limitations of the ADCP used. Negative residual velocities correspond to seaward flows and positive to landward flows.

The net fluxes (number of larvae or eggs per square meter per day) were calculated by multiplying the residual  $u$ -velocity at each stratum by the mean egg or larval density (number of eggs or larvae per cubic meter) at each stratum, according to Meerhoff et al. (2014). Positive net fluxes correspond to organisms coming into the channels, and negative net fluxes out from the channels. In addition, the sum of fluxes at all strata in all the channels was used to estimate seaward or shoreward net fluxes (ind./m<sup>2</sup>/d) per life stages of *M. magellanicus* during winter and spring 2003.

Statistical analyses on egg and larval abundance and oceanographic data included testing for normal distribution (Shapiro-Wilk test), because the high skewness of the data did not allow the use of parametric approaches, we applied Kruskal-Wallis tests or permutational multivariate analysis of variance (PERMANOVA, Bray-Curtis similarity index, 9999 permutations). If significant differences were found, Dunn's post hoc or a similarity percentage analysis (SIMPER, Bray-Curtis similarity measure) was conducted to determine the groups that likely caused the differences.

## 3. Results

### 3.1. Oceanographic conditions in Ninualac, Darwin and Pulluche channels in winter (2003) and spring (2002–2003)

The temperature and salinity vertical sections in spring 2002, winter 2003 and spring 2003 in the Ninualac, Darwin and Pulluche channels showed seasonal differences (Fig. 2). In general, temperature was lower



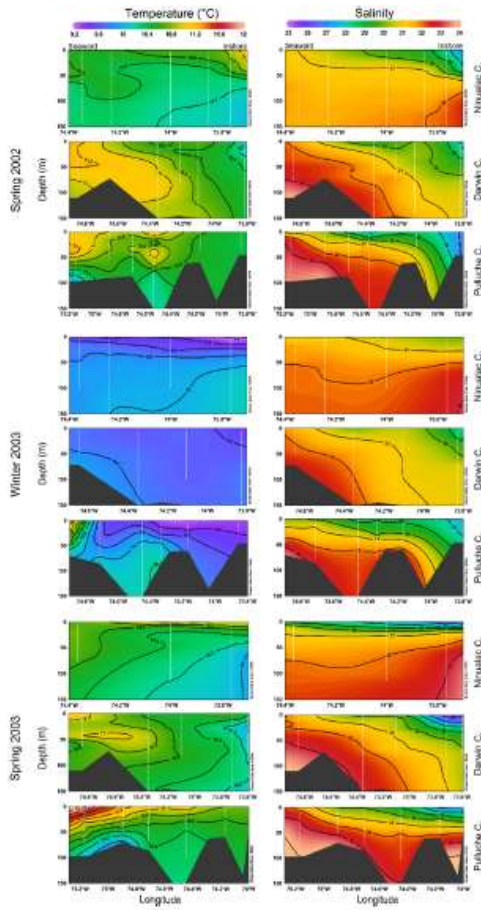


Fig. 2. Temperature (°C) and salinity vertical sections during Spring 2002, Winter and Spring 2003 at the Ninualac, Darwin and Pulluche channels.

in winter compared to spring in the three channels, especially in the shallow strata (Table 1).

In the three channels, a gradual increase in temperature and salinity with depth was observed in winter. There were along-channel differences in the location of the higher salinity water among channels in the deeper strata (>50 m). The most saline water was observed in the inshore stations in the Ninualac channel, while in the Darwin and Pulluche channels it was observed in the seaward stations (Fig. 2). These

differences in the location of high salinity along these channels might be influenced by the deep transport of more saline water of oceanic origin coming from the north through the Moraleda channel. In an horizontal surface view, a surface temperature and salinity latitudinal gradient might be also observed: higher salinity and temperature occurred in the northern area compared with the southern side, suggesting a noticeable influence of freshwater discharges on the southern side (Fig. 3). Similarly, surface temperature and salinity were lower at the inshore stations than the seaward stations (Fig. 3). Statistical differences in temperature and salinity were obtained between inshore and seaward stations and between the shallow and deep strata of the transects along the three channels (Kruskal-Wallis,  $p < 0.05$ ).

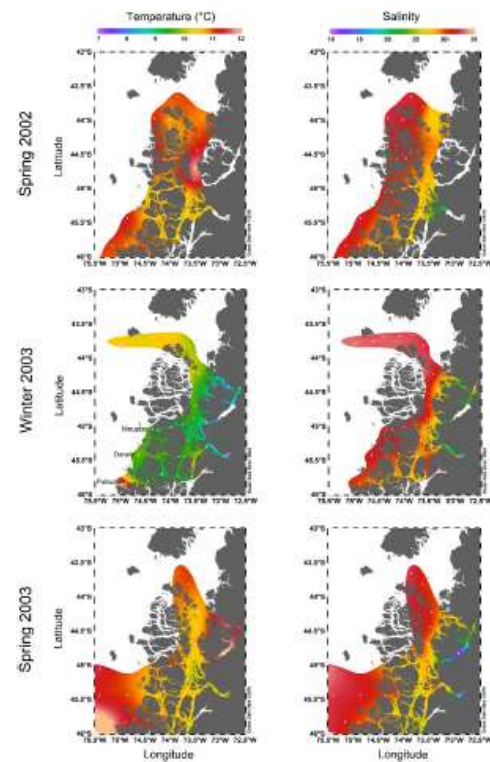


Fig. 3. Sea surface temperature (°C) and sea surface salinity during Spring 2002, Winter and Spring 2003.

Table 1  
Range variation of surface temperature and salinity.

Channel	Temperature (°C)			Salinity		
	Spring 2002	Winter 2003	Spring 2003	Spring 2002	Winter 2003	Spring 2003
Ninualac	10.6-10.9	9.4-9.7	10.7-10.8	28.4-31.0	30.0-31.5	27.0-31.5
Darwin	10.5-10.6	9.6-9.7	10.5-10.6	28.0-31.0	29.0-31.5	26.0-29.8
Pulluche	10.7-11.1	9.4-11.3	10.7-11.8	27.2-30.4	28.0-30.5	27.0-31.6

### 3.2. Residual velocities in the Ninualac, Darwin and Pulluche channels in winter and spring 2003

The vertical residual velocities averaged along the depth ranges of zooplankton strata are shown in Fig. 4 for each channel. The Ninualac and Darwin channels, both in winter and spring 2003 cruises, showed a typical estuarine pattern of two-layer circulation, consistent with an oceanward surface flow (0–20 m) and a shoreward subsurface flow (50–100 m). In the Pulluche channel this pattern was not evident, as a subsurface oceanward flow was present in winter and spring and a surface oceanward flows in spring (Fig. 4).

In the surface stratum (0–20 m) the mean of the magnitudes of residual velocities are higher than deep stratum (50–100 m) in all channels, except in winter in the Ninualac channel, where the opposite occurred. In addition, in the surface stratum in the Ninualac, Darwin and Pulluche channels velocities were higher in spring and lower in winter, while in the midwater and deep strata of the Pulluche channel the opposite occurred (Fig. 4).

The magnitudes of residual velocities in Darwin were stronger than those of Ninualac and Pulluche channels in winter and spring. In winter the median residual velocity were: Darwin = 12.1 cm/s, Pulluche = 5.3 cm/s and Ninualac = 5.1 cm/s, while in spring they were: Darwin = 18.8 cm/s, Ninualac = 10.9 cm/s and Pulluche = 2.8 cm/s. In addition, in Darwin channel in winter and spring the median of magnitudes of residual velocities were higher in the surface stratum than those of the bottom stratum (winter = 36.7 cm/s vs 11.2 cm/s, spring = 45.2 vs 19.7) (Kruskal-Wallis,  $p < 0.05$ ; Dunn's post hoc,  $p < 0.05$ ). No differences in medians of residual velocities were found between the surface and bottom strata of the Ninualac and Pulluche channels (Kruskal-Wallis,  $p > 0.05$ ).

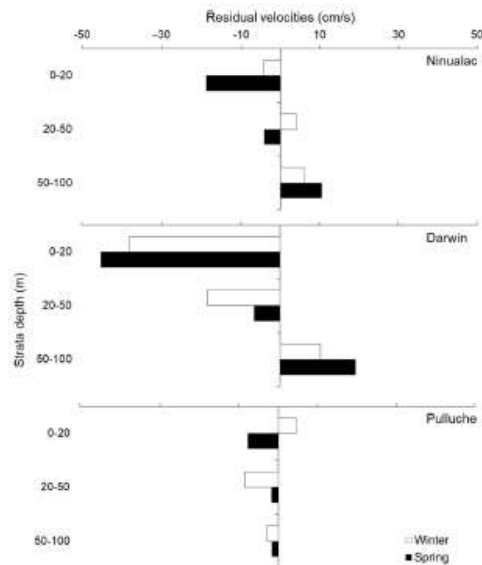


Fig. 4. Horizontal mean residual  $u$ -velocities (cm/s) at the zooplankton sampling strata (0–20 m, 20–50 m and 50–100 m), during winter and spring 2003 in the Ninualac, Darwin and Pulluche channels. The negative values denotes westward (oceanward) flows and positive values denotes eastward (shoreward) flows.

### 3.3. Abundance and horizontal distribution of eggs and larvae

The percentage of stations with eggs and larvae per channel were higher in winter 2003 than springs 2002 and 2003. In spring 2002, no eggs were found at any channel and the percentages of stations with larvae ranged between 40% and 50% per channel. In winter 2003, the three channels contained eggs and larvae. This season the percentage of stations with eggs varied between 25% and 100% per channel, and larvae were present at all stations along the three channels. Finally, in spring 2003, two transects showed presence of eggs and also two transects showed larvae (Table 2).

Difference in egg and larval abundances were observed between seasons (Two-way PERMANOVA, eggs:  $p = 0.0071$ ; larvae:  $p = 0.0001$ ; Appendix A), being winter 2003 when the highest egg and larval abundances occur (Fig. 5). Differences were also detected in egg abundance among channels (Two-way PERMANOVA, eggs:  $p = 0.028$ ; Appendix A) and the channel with larger abundance of eggs varied between seasons (eg. Darwin in winter 2003, Ninualac in spring 2003). However, in terms of larval abundance no differences among channels were detected (Two-way PERMANOVA, larvae:  $p = 0.3258$ ; Appendix A).

The highest egg abundances tended to be located at stations towards the eastward end (inshore stations) at the Darwin (winter 2003) and Ninualac (winter and spring 2003) channels (Fig. 6). However, these different egg distributions along the channels were not statistically significant, similarly, no difference in larval abundances were detected between seaward and inshore stations (Two-way PERMANOVA  $p > 0.05$ , Appendix B).

### 3.4. Larval distribution by size

In winter 2003, 5579 larvae were measured (Ninualac channel = 1504, Darwin channel = 424 and Pulluche channel = 3651). In spring 2002 and 2003 the low abundance of larvae in the channels only allowed us to measure 3 larvae in spring 2002 (Pulluche channel = 2, Ninualac channel = 1) and 2 larvae in spring 2003 (Darwin channel = 2 larvae).

The larval lengths measured in all channels in the spring 2002 and 2003 were larger than those measured in Winter (2003). In spring 2002 the mean larval length in the Pulluche channel was  $18.5 \pm 6.4$  mm and in the Ninualac channel was 12.0 mm (only one larva measured because the others were deteriorated). In spring 2003, the mean larval length in the Darwin channel was  $17.0 \pm 5.7$  mm. Larvae from the Ninualac channel could not be measured because they were damaged and no larvae were found in the Pulluche channel (Table 2). In winter 2003 instead, the mean larval sizes were smaller in all channels ranging from 3.6 to 6.4 mm.

In winter 2003 the shortest larval length occurred in the Darwin channel and the largest in the Ninualac channel (Kruskal – Wallis  $p = 4.67 \times 10^{-5}$ ; Bonferroni corrected  $p$  values  $< 0.05$ , Appendix C). Similarly, comparing inshore vs seaward stations in winter 2003, the larval length at the seaward stations were larger than at inshore stations in all channels (Kruskal – Wallis  $p < 0.05$ , Appendix D).

In winter 2003 we found that medium larvae had the highest proportion throughout all channels, except in the seaward stations of the Pulluche channel where large larvae had the highest proportion. Small larvae had a higher proportion (after medium larvae) towards the center of the Darwin channel, and towards center and inshore of the Pulluche channel. Large larvae had highest proportion in seaward stations while small larvae in the inshore stations (after medium larvae) except in Darwin channel (Fig. 7). The low presence of larvae found in both springs did not allow us to determine if there was a larval size change in the coast-ocean direction along the channels in this season.

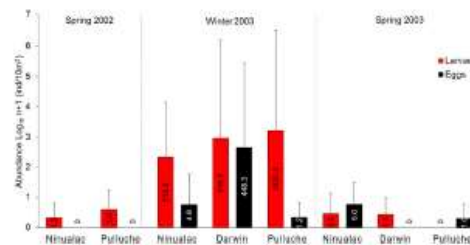
Significant differences were found between offshore distance of the stations (Two-way PERMANOVA,  $p = 0.023$ ) between channels (Two-way PERMANOVA,  $p = 0.0001$ ) and in offshore distance  $\times$  channels (Two-way PERMANOVA,  $p = 0.0054$ ) (Appendix E). According to the



**Table 2**

Egg and larval abundance (ind./10 m<sup>2</sup>) and larval length of all stations in spring 2002, winter and spring 2003 at Ninualac, Darwin and Pulluche channels. *n*: includes Yo-Yo stations; PS: percentage of positive stations; PSA: percentage of positive samples; *p* value: Kruskal-Wallis test, \*: Dunn's post hoc, Bonferroni corrected *p* values; significant at  $\alpha = 0.05$ .

Channel	Number of sampled stations ( <i>n</i> )	% PS Eggs	% PS Larvae	Number of total samples ( <i>n</i> )	% PSA Eggs	% PSA Larvae	Eggs (Ind./10m <sup>2</sup> )		Larvae (Ind./10m <sup>2</sup> )		Larval length		
							Mean ± SD	Median	Mean ± SD	Median	Number of measured larvae	Mean SL (mm)	Median SL (mm)
Spring 2002													
Ninualac	5	0	40	15	0	20	0	0	1.2 ± 2.0	0	1	12.0	12.0
Pulluche	6	0	50	15	0	20	0	0	3.0 ± 3.5	2.1	2	18.5 ± 6.4	18.5
<b>p value (Kruskal-Wallis)</b>							NA		0.486		NA		
Winter 2003													
Ninualac	4	25	100	25	6	100	4.8 ± 9.5	0	215.6 ± 63.5	217.8	1504	4.1 ± 0.2	4.1*
Darwin	4	100	100	29	100	97	448.3 ± 628.4	169*	916.5 ± 1764.5	47.6	424	3.7 ± 0.3	3.7**
Pulluche	6	33	100	25	24	100	1.2 ± 2.0	0	1625.8 ± 1813.0	811	3651	4.0 ± 0.2	4.0***
<b>p value (Kruskal-Wallis)</b>							0.011		0.224		4.7x10 <sup>5</sup>		
Spring 2003													
Ninualac	3	66	33	30	17	7	5.0 ± 4.3	7.1	2.0 ± 3.4	0	0	–	–
Darwin	4	0	50	20	0	5	0	0	1.8 ± 2.4	1	2	17.0 ± 5.7	17.0
Pulluche	4	25	0	24	17	0	1.0 ± 2.1	0	0	0	0	–	–
<b>p value (Kruskal-Wallis)</b>							0.125		0.349		NA		



**Fig. 5.** Mean and standard deviation of egg and larval abundance transformed ( $\text{Log}_{10} n+1$  ind./10 m<sup>2</sup>) in Spring 2002, Winter and Spring 2003 at Ninualac, Darwin and Pulluche channels.

SIMPER analysis, the overall dissimilarity in larvae by size class between inshore stations (0–20 km) and seaward stations (>60 km) was 75.19%. Large larvae explain 36.60% of this dissimilarity, because their abundance was higher in the seaward stations (mean 542 ind./10 m<sup>2</sup>) than in the inshore stations (mean 37.4 ind./10 m<sup>2</sup>). Medium larvae explain 34.5% and small larvae 4.017% of the dissimilarity, both were more abundant in the inshore stations than at seaward stations. Medium larvae mean 582 ind./10 m<sup>2</sup> vs 57.7 ind./10 m<sup>2</sup>, and small larvae 65 ind./10 m<sup>2</sup> vs 0.543 ind./10 m<sup>2</sup>, respectively (Appendix E).

### 3.5. Eggs and larvae vertical distributions

In winter and spring cruises 2003, the vertical distribution from all sampled stations with eggs and larvae presence showed the highest abundances of eggs in the deepest strata (>50 m), while larvae were distributed along the entire water column. In spring 2002 no eggs were found and larvae were found only in the shallowest strata (<50 m) (Fig. 8).

In the three channels in winter 2003, the highest egg abundances

were found in the deepest strata (>50 m), while in spring 2003, in Ninualac and Pulluche channels were found in the midwater stratum 20–50 m. Larvae were present along the entire water column in all channels, except in spring 2002 were found only in the shallowest strata (<50 m) (Fig. 8).

In winter 2003, a Two-way PERMANOVA showed significant differences in eggs and larval abundance between strata, between channels and channels × strata ( $p < 0.05$ , Appendix F). According to the SIMPER analysis, the overall dissimilarity in eggs and larval abundance between strata was 74.84%, being larval abundance higher in the strata >100 m and 0–20 m, and eggs in the strata >100 m and 50–100 m (Appendix F).

In spring 2003, a Two-way PERMANOVA showed significant differences in eggs and larval abundance between strata ( $p = 0.0093$ ), but no between channels ( $p = 0.1391$ ) neither channels × strata ( $p = 0.1063$ ) (Appendix G). According to the SIMPER analysis, the overall dissimilarity in eggs and larval abundance between strata was 47.3%. Similar to winter 2003, egg abundance in spring 2003 were higher in stratum 50–100 m and larvae in stratum >100 m (Appendix G). In spring 2002, no significant differences were found in eggs and larval abundance between strata, channels neither channels × strata ( $p > 0.05$ , Appendix H).

### 3.6. Changes in the horizontal and vertical distribution of eggs and larvae

In winter 2003, the mean weighted depth (MWD) of eggs and larvae along the transects varied among the stations sampled, being deeper at the innermost stations, near the Moraleda channel (inshore), and shallower towards the more oceanic stations (seaward) at the Ninualac and Darwin channels. In the Pulluche channel, instead, MWD of larvae varied between 20 and 40 m along the entire transect, and medium and large larvae ascended to the superficial stratum (0–20 m) at inshore stations (Fig. 9).

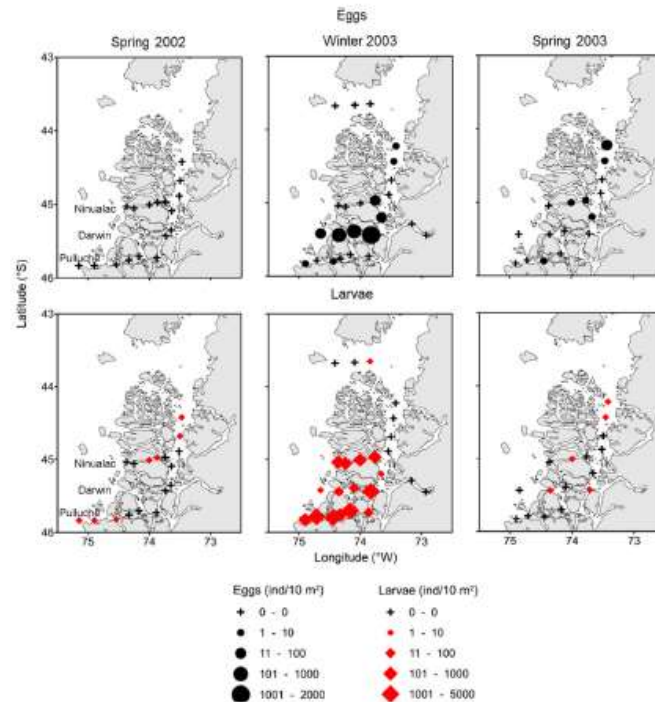


Fig. 6. Distributions of *M. magellanicus* eggs and larvae in spring 2002, winter and spring 2003, along the three sampled channels in the northern Chilean Patagonia.

### 3.7. Diel changes in vertical distribution at Yo-Yo stations

The day-night vertical distribution of each developmental stage varied between channels. In general, small larvae tended to be more abundant during the day and night in the deeper strata, increasing in abundance slightly during the night in shallower strata. Medium-sized larvae in the Ninualac and Pulluche channels had higher abundances at the deepest strata during the day than at night, and higher abundances at surface during the night compared to abundances at surface during the day. However, in the Darwin channel, medium size larvae presented an inverse distribution to that found in Ninualac and Pulluche. Finally, while large larvae in the Ninualac and Pulluche channels were present along the entire water column at night and deeper during the day, in the Darwin channel there were very few large larvae and only during the night (Fig. 10).

In winter 2003, larvae, particularly in the Pulluche channel, showed the clearest MWD changes, being deeper during the day (50–100 m) and shallower at night (20–50 m) (Table 3). The largest difference (A) in the MWD of all size classes-larvae between day and night was found in the Pulluche channel (A = 32 m; Night = 29 m; Day = 61 m), followed by Ninualac (A = 10 m; Night = 48 m; Day = 59 m), and the lowest amplitude was in the Darwin channel (A = 9 m; Night = 53 m; Day = 62 m). Larvae in the Pulluche and Ninualac channels showed differences in their MWD between day and night (Kruskal-Wallis,  $p < 0.05$ , Table 3). The MWD of egg occurred in the deeper strata (>50 m). No differences in MWD of eggs were found between day and night at the Darwin and Pulluche channels Yo-Yo stations (Kruskal-Wallis,  $p > 0.05$ , Table 3).

### 3.8. Eggs and larval net fluxes at each channel

Net egg and larval fluxes by strata were generally higher in winter than in spring (except for net fluxes of eggs in the Ninualac channel and large larvae in the middle stratum of the Pulluche channel, which were higher in spring) and differed in direction and/or magnitude among channels (Fig. 11). While in winter in the Ninualac the net egg flux was zero because no eggs were found, the daily net flux in the Darwin channel showed that eggs entered the channel from the more oceanic zone through the deepest stratum and were exported to the ocean through the middle and surface strata. In contrast, in the Pulluche channel, eggs entered through the shallow stratum (10 ind/m<sup>2</sup>/day) and were exported through the middle (18 ind/m<sup>2</sup>/day) and deep (15 ind/m<sup>2</sup>/day) strata. The larvae in the Ninualac and Darwin entered mainly at depth and were exported at the surface. In Pulluche, on the contrary, the larvae would enter at the surface stratum and would be exported mainly in the intermediate and deepest strata.

Daily net fluxes in spring were very low due to the low abundance of eggs and larvae. By strata, they showed a relatively similar pattern to winter in terms of ingress or exportations from the channels. Eggs and large larvae entered Ninualac through the deepest stratum and eggs were exported from this channel through the middle stratum. In Darwin and Pulluche, eggs and large larvae were exported through the middle and deepest strata (Fig. 11).

Finally, the daily net fluxes of eggs and larvae along the entire water column considering all channels showed that while in winter eggs would enter the channels, larvae of all sizes would be exported from the channels in high abundances. Conversely, in spring eggs and only a few



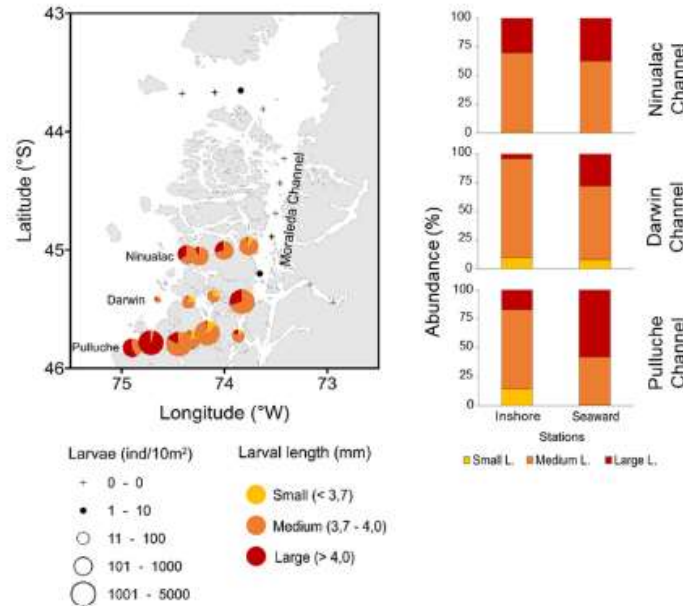


Fig. 7. Proportion (%) of larvae classified by size of *M. magellanicus* in the Ninualac, Darwin and Pulluche channels in winter 2003 and between inshore and seaward stations.

larger larvae would enter the sampled channels (Table 4).

#### 4. Discussion

In order to evaluate whether ontogenetic changes in vertical distribution and inshore-seaward exchange of early life stages were part of the reproductive strategy of Patagonian grenadier, in this study we analyzed the distribution and transport of their eggs and larvae in spring and winter in three channels of the PES adjacent to its main spawning area. Results showed the highest eggs abundance in Darwin channel and the highest larval abundance in Pulluche channel in winter 2003 and very low abundances of both life stages in spring 2002 and 2003. The highest abundances of eggs were found in the deepest stratum of the channels, whereas larvae were heterogeneously distributed along the entire water column. Eggs were more abundant at inshore stations, whereas large larvae were more abundant towards the oceanic end (seaward stations). Oceanographic characteristics and along-channel residual velocities differed between channels. These differences in residual velocities, together with variations in the vertical distribution of eggs and larvae, resulted in different landward and oceanward flows of eggs and larvae among channels and strata.

##### 4.1. Oceanographic conditions

Vertical sections of temperature and salinity, together with vertically averaged along-channel velocities in the Ninualac and Darwin channels during winter (2003) and spring (2002–2003), showed evidence of a typical estuarine circulation pattern. A surface layer of less saline water flowing toward the ocean and a subsurface more saline layer moving landward were consistent with this pattern in both channels (Valle-Levinson, 2010; Castillo et al., 2006). However, in Pulluche channel this pattern was not observed. There was evidence of dominant oceanward

residual velocities at the three strata, except for the surface stratum in winter that moved landward. It is possible that dominant wind forcing blowing eastward during the spring experiment might have influenced the typical landward direction of this first layer. This unusual direction should not be interpreted as a permanent specific direction of the first layer in spring but as a transient condition that might affect eggs and larvae transitory transports. The reversal of the surface layer flow direction by the effect of up-estuary winds is a ubiquitous feature of the Chilean Patagonian fjords (Cáceres et al., 2002, 2007) and it has been well documented in other fjord systems (Farmer, 1976; Svendsen, 1980). It has also been proposed as one of the forcings involved in the generation of a third near-bottom layer of oceanward flow, a vertical pattern of modified estuarine circulation (Valle-Levinson et al., 2014).

The absence of the expected subsurface landward flow in Pulluche channel may be attributed to the influence of bathymetric and coastal morphology effects in the east-west deep connectivity throughout this channel. Cáceres et al. (2002) showed that this channel exhibits a severe restriction to the estuary-shelf deep circulation at the Roepke Sill (Fig. 1), an across-channel moraine of about 20 m depth and 1900 m wide, located into the narrowest and shallowest part of this channel. Long-term ADCP measurements conducted at this sill by Cáceres et al. (2002) revealed that oceanward flows were dominant in the vertical profile of residual velocities into the upper 17 m depths. The salinity field in sections of Pulluche channel (Fig. 2) also suggests evidence of this restriction. In two sections, the deep isohaline of 32 does not enter eastward of 74.2°W, and there is a saline front at about 74°W. This is evidence of a choke point in the two-layer estuarine circulation in the region of Roepke Sill.

##### 4.2. Abundance and distribution of eggs and larvae

The highest abundances of eggs and larvae were found in winter

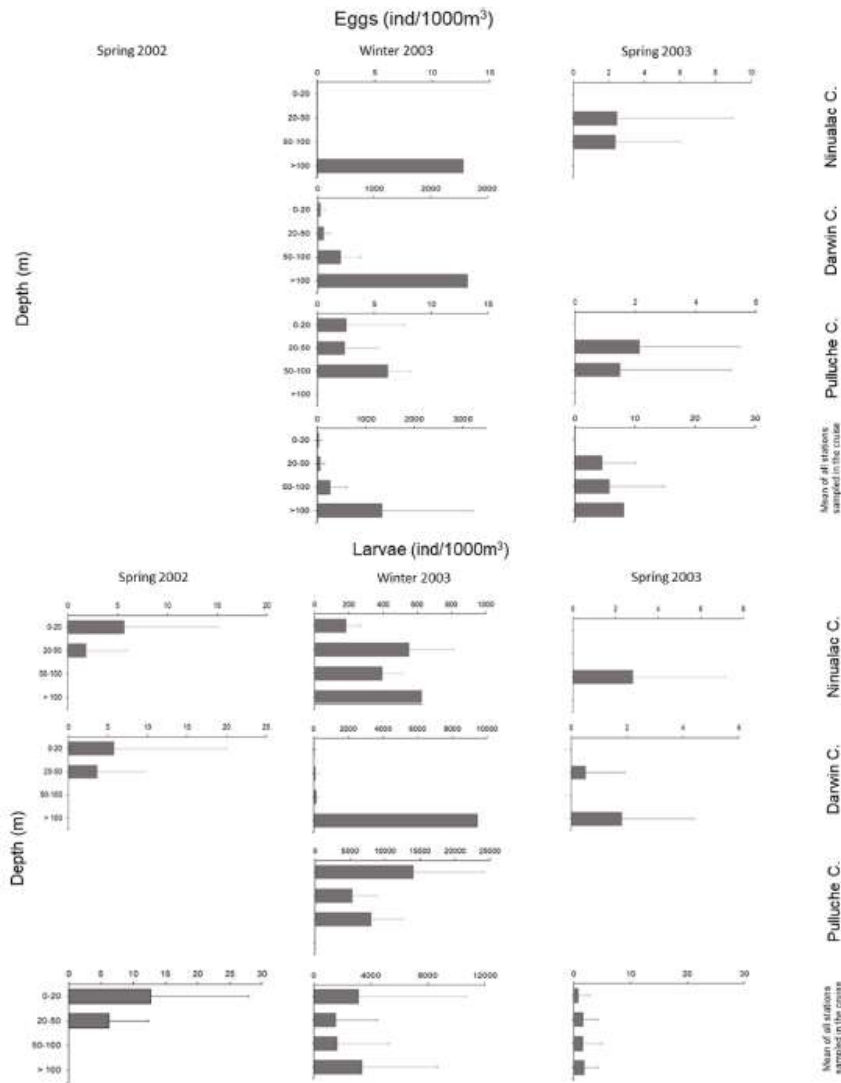


Fig. 8. Mean density and standard deviations per depth strata of eggs and larvae *M. magellanicus* (ind/1000 m<sup>3</sup>) in Spring 2002, Winter and Spring 2003 at Ninualac, Darwin and Pulluche channels. The bottom eggs and larval panels include all stations with presence of eggs and larvae in each season, in all channels including Moraleda and Guafío mouth.

2003 and the lowest in spring 2002–2003, which coincides with the month of massive spawning reported for this species in winter at the continental shelf break in front of our study area (Gorini et al., 2021). The abundances of eggs and larvae of *M. magellanicus* on which the analyses of the present study were conducted (winter, 2003) are the highest reported in the last 26 years (1995–2021) in both inner sea and

continental shelf break (Machinandiarena and Ehrlich, 1999; Ernst et al., 2005; Balbontin and Bernal, 2006; Landaeta et al., 2009; Niklitschek et al., 2014; Osorio-Zúñiga et al., 2018). This reveals the potential importance of the Darwin, Ninualac and Pulluche channels as nursery grounds for this species in some years and constituted a unique opportunity for the analysis of behavior in their early life stages.



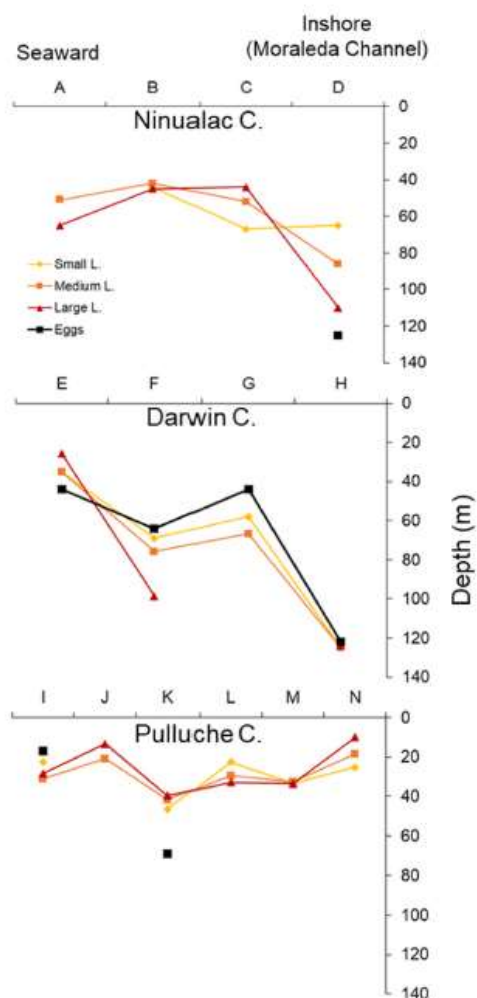


Fig. 9. Mean weighted depth (MWD, m) of the different early life stages (eggs, small, medium and large larvae) of *M. magellanicus* at the Ninualac, Darwin and Pulluche channels. Letters on top of plots indicate the station sampled (see Fig. 1).

#### 4.3. Ingress, retention, and exportation of eggs and larvae between the channels and the continental shelf

The high abundance of eggs and larvae found in the inner sea of northern Chilean Patagonia in winter 2003 could come from two sources: transport by currents from the outer sea to the interior of the channels and/or from mature specimens that entered to spawn in the interior of the channels. *Macruronus magellanicus* eggs were more abundant in the deepest stratum in all channels, which result from mid- and deep-water spawning reported for this species (Giusti et al., 2016;

Queirolo et al., 2005). Spawning at depth would facilitate the ingress of eggs into the channels from the outer sea in the subsurface seawater flow to the coast and channels (Silva et al., 1998; Sievers and Silva, 2006). The eggs would enter mainly through the Darwin and Ninualac channels, considering that in the Pulluche channel the inflow of oceanic water might be limited by the Roeppke sill (Cáceres et al., 2007), which would represent a barrier to the subsurface eggs flux. These results are consistent with the higher egg abundances found in the Ninualac and Darwin channels and the absence of eggs in the inshore stations of the Pulluche channel.

The highest abundances of eggs and small larvae were found in the Darwin Channel, suggesting that the early life stages of this species were retained in this channel. When analyzing the schematic model of horizontal circulation proposed by Silva et al. (1998) and Sievers and Silva (2006), it is observed that at depths of 30 m–150 m towards the coastal (eastern) end of the Darwin Channel there is a "collision" between the outgoing and incoming water masses, which coincides with the highest abundances of eggs and larvae found at this end of the channel.

The hydroacoustic evaluation in the outer sea when we conducted our study in winter 2003 showed a 62% of spawned specimens of *M. Magellanicus* in the outer sea, a great proportion (99%) of specimens >55 cm (juveniles + adults) and a 1% of total length <55 cm (juveniles); in the inner sea in spring 2003 the proportion of juveniles was 93%. This segregation of juveniles and adults has been described for this species, in which the spawners were grouped in the outer sea and the juveniles towards the inner sea (Lillo et al., 2004, 2011), which would decrease the probability of a major spawning in the inner sea in this year.

Accordingly, the concordance between the horizontal circulation patterns, the models, the segregation of juveniles and adults and the abundances of eggs and larvae found in the Ninualac, Darwin and Pulluche channels in winter, suggest that the eggs of Patagonian grenadier would enter the channels from the outer sea. Eggs and small larvae would be retained mainly in the Darwin channel and larvae in more developed stages would be exported to the ocean through the Pulluche channel. This type of physical mechanisms to explain the subsurface transport of early life stages of oceanic spawning species to the coast and channels subsequent transport from the inshore zones to the ocean in more advanced life stages has been proposed for this area before (Landaeta and Castro, 2006a; León et al., 2009; Bustos et al., 2011; Contreras et al., 2014).

#### 4.4. Diel changes in vertical distribution

The depth of mean weighted depth of egg did not show significant changes between day and night. However, larvae tended to show changes between day and night in the Ninualac and Pulluche channels where the largest larvae were found. In this study, the largest larval length in winter 2003 was 6 mm, so the behavioral proposition presented was based on larvae still in preflexion notochordal stage probably with limited swimming abilities.

In other demersal fish species such as Atlantic and Pacific cods, it has also been reported that changes in vertical distribution between day and night begin to be observed in small larvae, and that these changes are clearer and statistically different in larger larvae, being more noticeable in postflexion larvae (Hurt et al., 2009; Lough and Potter, 1993). Landaeta and Castro (2012) reported a similar behavior for *Merluccius gayi*, in which preflexion larvae did not show evidence of diel vertical migrations but larger larvae (>14 mm) did show this behavior, migrating to shallower water during the night. Vertical day-night migrations are likely to be wider in larger larvae due to their greater swimming ability migrating to deeper depths during the day and shallower depths during the night (Castro et al., 2019).

#### 4.5. Reproductive strategies of demersal fishes

The transport of early life stages of fish species from the ocean to the

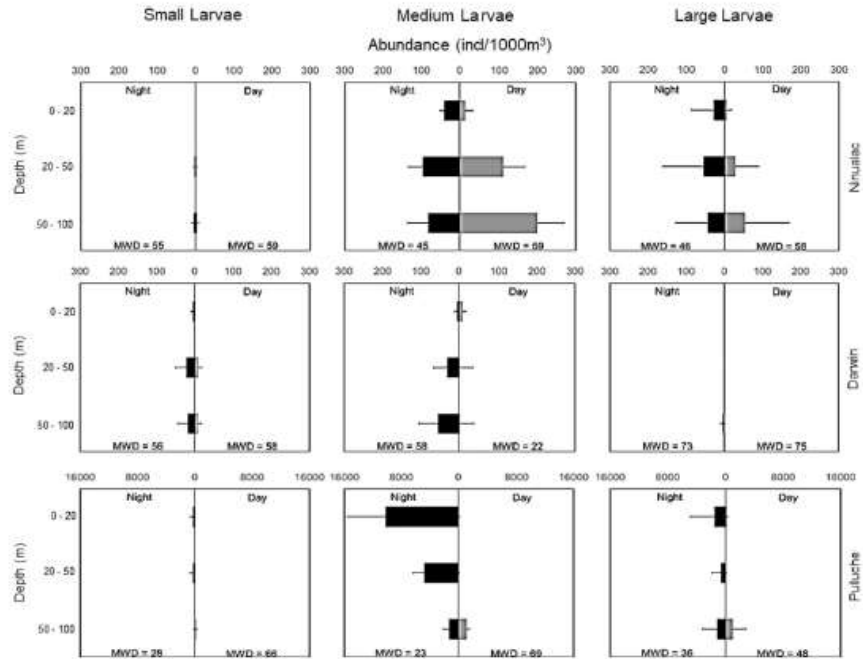


Fig. 10. Mean day and night abundances of larval *M. magellanicus* by size (small, medium and large) at the Ninualac, Darwin and Pulluche channels in winter 2003.

Table 3

Mean Weighted Depth (MWD) and standard deviation ( $\pm$ SD) day/night at 3 channels by life stage (egg, larvae) and larval size classes (small, medium, large).

Channel	Life stage	Mean Weighted Depth (m)					p value
		MWD $\pm$ SD Day	MWD $\pm$ SD Night	Min. Depth	Max. Depth	Amplitud ( $\Delta$ ) Day/Night	
Ninualac	Small L.	59.5	55.0 $\pm$ 20.0	35.0	75.0	4.5	0.655
	Medium L.	58.7 $\pm$ 10.8	44.8 $\pm$ 6.9	39.8	66.3	13.9	0.248
	Large L.	58.2 $\pm$ 3.9	45.5 $\pm$ 7.6	36.8	60.9	12.7	0.083
	Average all larval sizes	58.6 $\pm$ 5.8	48.4 $\pm$ 12.3	37.9	59.4	10.2	0.039*
Darwin	Eggs	73.0 $\pm$ 6.6	65.4 $\pm$ 2.2	63.0	77.6	7.6	0.083
	Small L.	57.7 $\pm$ 6.1	56.1 $\pm$ 13.5	40.5	64.8	1.6	0.564
	Medium L.	22.2	57.9 $\pm$ 16.2	10.0	75.0	47.8	0.180
	Large L.	75.0	72.5 $\pm$ 4.3	67.5	75.0	2.5	0.564
	Average all larval sizes	62.2 $\pm$ 13.3	53.1 $\pm$ 24.5	45.3	74.6	9.1	0.390
Pulluche	Eggs	75.0	65.1 $\pm$ 14.1	55.1	75.0	9.9	
	Small L.	66.4 $\pm$ 6.1	28.0 $\pm$ 4.2	23.2	70.7	38.4	0.083
	Medium L.	68.9 $\pm$ 4.9	23.5 $\pm$ 5.6	17.5	72.4	45.4	0.083
	Large L.	48.3 $\pm$ 29.5	36.3 $\pm$ 10.5	27.4	69.1	12.0	1
	Average all larval sizes	61.0 $\pm$ 17.1	29.2 $\pm$ 8.5	26.5	69.5	31.8	0.001*

coast appears to be a reproductive strategy commonly employed by demersal species (Sundby et al., 2001; Alvarez et al., 2001). This type of transport has also been reported for *Macrurus novaezelandiae* in the two main spawning areas for this species in New Zealand (Zeldis et al., 1990). In the eastern South Pacific Ocean (Central Chile) this has been proposed for *Merluccius gayi* whose spawning occurs at the continental shelf break and their eggs and larvae are transported at the subsurface to the coastal nursery areas (Landaeta and Castro, 2012). In north Patagonia, same area of our study, another demersal species, *Merluccius australis*, the main predator of *M. magellanicus* (Lillo et al., 2004; Neira

et al., 2015), seems to present some similarities but also some differences, in its reproductive strategy compared with that of *M. magellanicus*. This species has also a massive spawning offshore (continental shelf break) in winter, but in contrast to our results, it shows a low inflow of eggs and larvae from offshore into the channels and fjords and vice versa (low connectivity), and, besides, presents a secondary spawning in the inner sea in spring (Flores et al., 2020). Other differences include the vertical distribution of eggs. In our study, *Macrurus magellanicus* eggs in winter and spring 2003 were found in the deepest strata (>50 m), while *M. australis* eggs were found along the



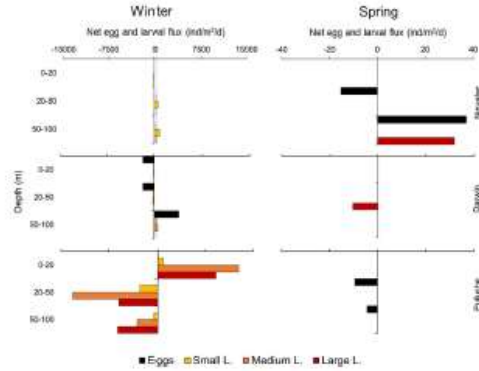


Fig. 11. Net egg and larval fluxes (ind/m<sup>2</sup>/d) along the Ninualac, Darwin and Pulluche channels in Winter and Spring (2003).

Table 4

Net horizontal fluxes (ind/m<sup>2</sup>/d) along the entire water column of each life stage of *M. magellanicus* in Winter and Spring (2003). The negative signal “-” denotes westward (seaward) fluxes.

Life stage	WINTER		SPRING	
	Ingress	Exportation	Ingress	Exportation
Eggs	29	0	8	0
Small L.	0	-2226	0	0
Medium L.	0	-2673	0	0
Large L.	0	-2732	22	0

entire water column, with no differences between strata.

The ingress and/or retention of eggs and small larvae in the channels and subsequent exportation of more developed larvae to the ocean in winter could be beneficial to ensure adequate feeding. This is because the inshore winter pelagic trophic web is based on components of the microbial loop including lower energy dinoflagellates and tintinnids as opposed to the outer sea where larger copepods occur (Landaeta and Castro, 2006a; González et al., 2011). The wide mouth size of hake larvae (>220 μm) (Murdoch, 1990; Landaeta et al., 2019) as well as gastric contents of hake species in general suggest that they are consumers of large zooplankton (70–300 μm, mainly copepods) (Murdoch, 1990; Morote et al., 2011). In the Ninualac and Pulluche channels in spring 2003, it was found that the abundance of large copepods (>500 μm) is greater in the seaward stations than in the inshore (Landaeta and Castro, 2006a). This would be consistent with the hypothesis of exportation to the continental shelf of any larvae that may have entered or developed in inner sea during winter 2003.

Winter spawning in the channels and/or the transport of eggs into

the channels might be part of the reproductive strategy of the species in North Patagonia. However, this could only be confirmed if this behavior was repetitive from year to year and, so far, we do not count with other observations inshore during this season. On the other hand, eggs and larvae of *M. magellanicus* obtained in spring cruises in the same area, show low abundances suggesting scarce spawning in inner sea in spring. This differs from other demersal species such as *M. australis* in the same area whose major spawning is also in winter but with a secondary spawning season inshore in spring (Flores et al., 2019). Accordingly, more intense spawning offshore than inshore in winter and the transport of larger larvae from the channels to the continental shelf in this same season seem to be features shared by several fish species suggesting a common adaptive behavior given that feeding conditions for their larval development in outer waters would be more suitable.

## 5. Conclusions

In this study we evaluated ontogenetic changes in distribution of early life stages to estimate transport of *M. magellanicus* between the Patagonian Estuarine System (PES) and the adjacent continental shelf in northern Chilean Patagonia. Our results suggest that eggs entered the PES from the continental shelf through the Darwin Channel, or that they might have resulted also from a secondary spawning within this channel. Eggs and small larvae would be retained at the inshore zone of the Darwin channel and then, while in more advanced stages, they are exported to the continental shelf through the Pulluche channel. The retention of early life stages within the PES and subsequent export of larger larvae to the ocean would favor the consumption of suitable food for this species. Thus, while small larvae within the estuary could feed on microbial components of the trophic web, larger larvae exported outside the channels to the ocean could consume large copepods, as it has been observed in other Patagonian fishes.

## Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Appendix A. Two-way PERMANOVA results of eggs and larval abundance in Spring 2002, Winter and Spring 2003 at Ninualac, Darwin and Pulluche channels

Source	Sum of sqs	df	Mean square	F	p
Channel	0,881,963	2	0,44,098	2,8712	0,028
Season year	1,27,122	2	0,63,561	4,1385	0,0065
Channel x Season year	1,62,853	4	0,40,713	2,6509	0,0064
Residual	4,14,681	27	0,15,359		
Total	7,9285	35			

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Eggs					
Source	Sum of sqrs	df	Mean square	F	p
Larvae					
Source	Sum of sqrs	df	Mean square	F	p
Channel	0,564,385	2	0,28,219	1,1048	0,3258
Season year	3,94,434	2	1,9722	7,7213	0,0001
Channel x Season year	1,19,224	4	0,29,806	1,1669	0,1172
Residual	6,89,632	27	0,25,542		
Total	12,597	35			

Appendix B. Two-way PERMANOVA results of eggs and larval abundance in Spring 2002), Winter and Spring 2003 at Ninualac, Darwin and Pulluche channels (Offshore distance)

Eggs					
Source	Sum of sqrs	df	Mean square	F	p
Channel	0,881,963	2	0,44,098	2,3152	0,0712
Distance	0,563,406	3	0,1878	0,986	0,4244
Channel x Distance	1,91,178	6	0,31,863	1,6728	0,1059
Residual	4,57,138	24	0,19,047		
Total	7,9285	35			
Larvae					
Source	Sum of sqrs	df	Mean square	F	p
Channel	0,564,385	2	0,28,219	0,7096	0,6475
Distance	0,217,048	3	0,072,349	0,1819	0,9996
Channel x Distance	2,27,207	6	0,37,868	0,9523	0,5139
Residual	9,54,378	24	0,39,766		
Total	12,597	35			

Appendix C. Kruskal-Wallis and Dunn's post hoc results of larval length at Ninualac, Darwin and Pulluche channels in Winter (2003)

Kruskal-Wallis test			
H (chi2):		480,4	
Hc (tie corrected):		480,5	
p (same):		4,67E-105	
There is a significant difference between sample medians.			
Dunn's post hoc.			
	Darwin	Pulluche	Ninualac
Darwin		5,60E-88	1,31E-103
Pulluche	5,60E-88		1,20E-07
Ninualac	1,31E-103	1,20E-07	
In bold significance difference at $p < 0.05$ Bonferroni corrected p values.			

Appendix D. Kruskal-Wallis results of larval length between inshore (0-20 km) - seaward (>60 km) stations at Ninualac, Darwin and Pulluche channels in Winter (2003)

Ninualac	
H (chi2):	5525
Hc (tie corrected):	5527
p (same):	0,01872
There is a significant difference between sample medians.	
Darwin	
H (chi2):	178,1
Hc (tie corrected):	178,1
p (same):	1,26E-40

There is a significant difference between sample mediana.

Pulluche	
H (chi2):	28,06
Hc (tie corrected):	28,07
p (same):	1,17E-07

There is a significant difference between sample mediana.

**Appendix E. Two-way PERMANOVA and SIMPER results of larval abundance by size class at Ninualac, Darwin and Pulluche channels (Offshore distance) in Winter (2003)**

Two-way PERMANOVA:					
Source	Sum of sqrs	df	Mean square	F	p
Offshore distance	1,17,682	3	0,39,227	1,8714	0,023
Channel	2,80,952	2	1,4048	6,7016	0,0001
Offshore distance x Channel	2,34,775	6	0,39,129	1,8067	0,0054
Residual	5,44,997	26	0,20,961		
Total	11,784	37			

SIMPER (Bray-curtis index):

Overall average dissimilarity: 75.19.

Taxon	Av. distim	Contrib. %	Cumulative %	Mean 0-20 km	Mean > 60 km
Large	36,68	48,77	48,77	37,4	5,42E+02
Medium	34,5	45,88	94,66	582	57,7
Small	4017	5342	100	65	0,543

**Appendix F. Two-way PERMANOVA and SIMPER results of eggs and larval abundance by strata at Ninualac, Darwin and Pulluche channels in Winter (2003)**

Two-way PERMANOVA					
Source	Sum of sqrs	df	Mean square	F	p
Channel	8,88,349	2	4,4417	26,463	0,0001
Strata	1,50,763	3	0,50,254	2,9941	0,0001
Channel x strata	2,65,167	6	0,44,194	2633	0,0001
Residual	11,2456	67	0,16,785		
Total	24,288	78			

SIMPER by Strata:

Overall average dissimilarity: 74.84.

Eggs/Larvae	Av. distim	Contrib. %	Cumulative %	Mean 0-20	Mean 20-50	Mean 50-100	Mean > 100
L/1000m3	57,43	76,74	76,74	3,37E+03	1,63E+03	1,75E+03	5,05E+03
E/1000m3	17,41	23,26	100	17,3	35,3	199	1,33E+03

SIMPER by Channels:

Overall average dissimilarity: 82.46.

Eggs/Larvae	Av. distim	Contrib. %	Cumulative %	Mean Ninualac	Mean Darwin	Mean Pulluche
L/1000m3	66,42	80,54	80,54	291	389	6,62E+03
E/1000m3	16,05	19,46	100	0,52	309	1,56

### Appendix G. Two-way PERMANOVA and SIMPER results of eggs and larval abundance by strata at Ninualac, Darwin and Pulluche channels in Spring 2003)

Two-way PERMANOVA					
Source	Sum of sqrs	df	Mean square	F	p
Channel	0,565,251	2	0,28,263	1,7513	0,1391
Strata	1,64,742	3	0,54,914	3,4027	0,0093
Channel x strata	1,12,498	6	0,1875	1,1618	0,1063
Residual	2,9049	18	0,16,138		
Total	6,2425	29			

SIMPER (Bray-Curtis similarity measure):  
Overall average dissimilarity: 47.3.

Eggs/larvae	Av. dissim	Contrib. %	Cumulative %	Mean 20-0	Mean 50-20	Mean 100-50	Mean > 100
E/1000m3	29,75	62,88	62,88	0	2,38	3,94	0
L/1000m3	17,56	37,12	100	0	0,367	1,56	3,65

### Appendix H. Two-way PERMANOVA results of eggs and larval abundance by strata at Ninualac and Pulluche channels in Spring 2002)

Source	Sum of sqrs	df	Mean square	F	P
Channel	0,0664,756	1	0,066,476	0,26,675	0,7524
Strata	1,01879	2	0,5094	2,0441	0,167
Channel x strata	0,519,596	2	0,2598	1,0425	0,3913
Residual	1,99,364	8	0,2492		
Total	3,5985	13			

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## **4. DISCUSIÓN GENERAL**

Con la finalidad de identificar y caracterizar las zonas de desove y crianza de merluza de cola en el Sistema Estuarino Patagónico y la zona oceánica adyacente, así como de inferir conectividad de los estadios tempranos de vida de esta especie entre estas dos zonas, se propuso como objetivo general de la presente tesis evaluar los procesos bio-oceanográficos que influyen en la conectividad de los estadios tempranos de vida de merluza de cola entre el Sistema Estuarino Patagónico y la zona oceánica adyacente en la Patagonia Chilena.

### **4.1. Identificación de las zonas de desove y crianza de *M. magellanicus***

La presencia de huevos y/o larvas de merluza de cola en el 85% de los cruceros oceanográficos analizados en esta tesis, realizados todos en el Sistema Estuarino Patagónico (mar interior) y la plataforma continental adyacente (mar exterior) de la Patagonia chilena en el periodo 1995-2019 (primavera e invierno), muestran la importancia de estas zonas para el desove y crianza de esta especie. Entre las zonas evaluadas, la zona nor-patagónica fue la más importante, ya que presentó la mayor abundancia y persistencia de huevos y larvas. La disminución en la presencia y abundancia de huevos en primavera vs invierno, y el aumento en la longitud larval en primavera sugieren una sola época de desove que iniciaría en invierno, con peak en agosto y se extendería al menos hasta noviembre. La existencia de huevos y larvas en primavera en el mar interior centro y sur de la Patagonia chilena, las proponen como zonas secundarias de desove y crianza de esta especie, debido a su menor intercambio con el agua oceánica adyacente. Los resultados apoyan las hipótesis de concentración de los eventos de desove en la Patagonia norte chilena en invierno (Payá, 2020), un desove sincrónico de invierno (segunda y tercera semana de agosto) a primavera (Payá, 2020; Giussi

et al., 2016), así como múltiples áreas de desove y crianza para esta especie (Niklitscheck et al., 2014; Schuchert et al., 2010).

La disminución en la abundancia de huevos y larvas de *M. magellanicus* el mar interior (1995-2011) y exterior (2013-2019), así como cambios en sus centros de masa en el mar exterior, concuerdan con la disminución y los cambios en los centros de masa del stock desovante reportado en los informes técnicos de los cruceros de evaluación hidroacústica realizados en el mar exterior (Lillo et al., 1997-2016; Lillo y Legua, 2016; Legua y Vargas 2020; Legua, 2023). De igual forma, la menor abundancia de huevos en el mar exterior en agosto y la disminución interanual de las tallas de las larvas en primavera, concuerda con un retraso en el inicio del desove de esta especie reportado por Payá (2020). La concordancia entre los cambios en la distribución y abundancia de huevos y el stock desovante contribuiría a explicar la baja abundancia de huevos y larvas de *M. magellanicus* en el mar interior de la Patagonia norte chilena en años posteriores al 2003.

#### **4.2. El efecto del transporte en la distribución y abundancia de huevos y larvas de *M. magellanicus***

El Sistema Estuarino Patagónico (SEP) y la zona oceánica adyacente están expuestos a un patrón de circulación complejo, que modula el transporte de los estadios tempranos de vida de merluza de cola entre el mar interior y exterior. En este sistema de circulación, en el mar exterior, hacia el norte y en la zona más oceánica se inicia la Corriente de Humboldt cuyo flujo predominante es hacia el norte; acercándose a la costa y debajo de la “capa superficial” se encuentra la corriente sub-superficial Peru-Chile con flujo predominante hacia el sur, y más al sur y en superficie la corriente Cabo de Hornos, cuyo flujo también es hacia el sur. Entre el mar interior y exterior, se encuentra la circulación estuarina, con una

capa superficial que fluye hacia el océano (mar exterior) y una capa profunda que fluye hacia el mar interior (SEP) (Linford et al., 2023; Strub et al., 2019; Sievers y Silva 2006). El análisis de este sistema de circulación en conjunto con la distribución de huevos y larvas de merluza de cola permitió estimar que los huevos encontrados dentro del mar interior de la Patagonia norte chilena, provendrían principalmente de la zona principal de desove en el mar exterior, mientras que los encontrados en el centro y sur serían el resultado de un desove dentro del mar interior.

En invierno de 2003, periodo con la mayor abundancia de huevos y larvas de *M. magellanicus*, el flujo neto de individuos en los canales Ninualac, Darwin y Pulluche, mostró ingreso sub-superficial de huevos hacia el mar interior y posterior exportación de larvas hacia el océano, asociándose a la circulación estuarina y cambios ontogenéticos en la distribución vertical de los primeros estados de desarrollo. Adicionalmente, las mayores abundancias de huevos encontradas en el extremo costero del canal Darwin en invierno de 2003, concuerdan con una zona de retención a profundidades entre ~30 y ~150 m, producto de un “choque” entre las masas de agua oceánica que ingresan a través de la boca del Guafo y las que ingresan por el canal Darwin (Sievers y Silva 2006; Silva et al., 1998). De igual forma, el ingreso de agua oceánica transportada por la PCUC hacia el mar interior a través de la boca del Guafo (Linford et al., 2023), facilitaría el ingreso de huevos de *M. magellanicus*, provenientes de las zonas de desove en el mar exterior. Esto debido a que los huevos se encontraron en el mar exterior sobre el talud continental a profundidades entre 50 y 400 m, concordante con la PCUC (Linford et al., 2023). Estos resultados concuerdan con la hipótesis de que los huevos y larvas encontrados en el mar interior de la Patagonia norte chilena provendrían de la zona principal de desove en la plataforma continental (mar exterior). Por otra parte, los resultados de esta investigación difieren de lo encontrado por Flores et al. (2020) para *M. australis*,

quienes señalan que existe baja conectividad del mar exterior con el interior en los estadios tempranos de vida de esta especie.

Por otro lado, los resultados de este estudio sugieren que los huevos y larvas encontrados hacia el interior de las zonas centro (Golfo de Penas-Canal Concepción) y sur (Cabo Deseado-Cabo de Hornos) de la Patagonia chilena serían el resultado de un desove en el mar interior. Esto se deduce debido a un menor intercambio de agua oceánica con el mar exterior de las zonas centro y sur en comparación a la zona norte (Sievers y Silva 2006), y a la menor abundancia del stock desovante (Legua, 2023) y de huevos en la zona oceánica adyacente a las zonas centro y sur respecto a la norte. Estos resultados fueron particularmente evidentes en el Canal Unión (Zona centro) y la Bahía Parry (Zona sur), cuya ubicación hacia el extremo costero del mar interior limitaría el ingreso de los huevos provenientes del mar exterior, debido a las constricciones batimétricas.

En el mar exterior se observaron cambios latitudinales en la abundancia de huevos de *M. magellanicus* los que concordaron con los cambios latitudinales en la posición de los centroides del stock desovante de esta especie, y, también con los encontrados en el periodo 2013-2015 por Flores et al. (2019) para los huevos de *M. australis* (los que también concordaron con los centroides del stock de los adultos desovantes de esa especie). A pesar de que el patrón general de ubicación de centroides de huevos y reproductores coincide, hay un desplazamiento al norte (2013 y 2015) y al sur (2014 y 2017) de los huevos de *M. magellanicus* respecto a los desovantes. El desplazamiento hacia el norte de los huevos respecto a los desovantes, podría ser el efecto del transporte del impulsado en el inicio de la Corriente de Humboldt hacia el norte (Strub et al., 2019). Un mayor conocimiento de las corrientes en estratos profundos a estas latitudes será necesario para determinar si existe alguna asociación con los

desplazamiento de los huevos hacia el norte. Por otra parte, el desplazamiento hacia el sur de los huevos es atribuible al efecto del inicio de la Corriente del Cabo de Hornos en conjunto con la contracorriente Perú-Chile (PCUC) (Flores et al., 2019). En el presente estudio la mayor abundancia de huevos de *M. magellanicus* se encontró en los estratos más profundos (>50 m), atribuyéndose al desove en media agua y/o profundidad reportado para esta especie (Giussi et al., 2016; Queirolo et al., 2008). El desplazamiento hacia el sur de los huevos comparado con la posición de los adultos desovantes, y de las larvas respecto de los huevos, por lo tanto, es probablemente producto del flujo hacia el sur de la PCUC y la Corriente Cabo de Hornos, más que por el viento u otras corrientes superficiales, a diferencia de lo propuesto por Flores et al. (2019) para *M. australis*, especie en que los huevos se ubicaron a profundidades medias y en superficie.

#### **4.3 Efectos ambientales sobre la distribución y abundancia de huevos y larvas de *M. magellanicus***

Los modelos aditivos generalizados (GAM's) mostraron relación entre la temperatura, salinidad, predadores, presas y abundancia de huevos y larvas de *M. magellanicus*. Estos resultados permitieron, además, apoyar la idea de cambios ontogenéticos en la distribución de los estadios tempranos de vida de esta especie. Las mayores abundancias de huevos se asociaron a salinidades altas (~34), y a temperaturas entre 8 y 9°C, las cuales se encontraron principalmente en los estratos profundos (>50 m), tanto en el mar exterior como interior. Por otro lado, las larvas se asociaron a temperaturas más altas (9 y 10°C) y salinidades más bajas (~32), características de estratos superficiales (<50 m). Estos resultados son consistentes con el desove en profundidad descrito para esta especie (Queirolo et al., 2008; Lillo et al., 2004), mientras que las larvas tendrían la capacidad de distribuirse en toda la columna de agua.



En relación a la distribución horizontal también se presentaron cambios ontogenéticos, entre el mar interior y exterior, particularmente en los canales con orientación este-oeste en la Patagonia norte chilena (en invierno, huevos ingresarían desde el mar exterior al interior y posteriormente las larvas serían exportadas del mar interior al exterior. En el canal Darwin, huevos y larvas pequeñas se encontraron hacia el extremo costero del canal, mientras que larvas más desarrolladas se ubicaron hacia el extremo oceánico). Estos cambios ontogenéticos de distribución horizontal en invierno se asociaron a la distribución de sus potenciales presas (copépodos), encontrándose que la abundancia y talla de los copépodos en el mar exterior fue mayor a la del mar interior lo cual favorecería una alimentación acorde al tamaño de las larvas, concordando con lo que se ha reportado para larvas de otras especies de peces en la Patagonia norte (Landaeta y Castro 2006).

#### **4.4. La estrategia reproductiva de *M. magellanicus***

Los resultados del presente estudio revelan que el peak de desove en invierno de *M. magellanicus* favorece la sobrevivencia de sus estadios tempranos de vida, debido a una menor abundancia de sus potenciales predadores (medusas) en invierno vs primavera, tanto en el mar interior como exterior. El transporte y/o retención de huevos y larvas pequeñas en el mar interior en invierno, facilita la primera alimentación de las larvas, ya que la cadena trófica basada en el anillo microbiano y un menor tamaño de las presas (copépodos) estaría acorde al tamaño de la boca de las larvas. Posteriormente, cuando las larvas están más desarrolladas y se exportan al océano, su principal presa también es de mayor tamaño y además pueden ser energéticamente más beneficiosos (González et al., 2011; Landaeta y Castro 2006). El transporte de estadios de vida temprano de especies de peces desde el océano hacia la costa y posterior exportación de

la costa al océano en etapas de vida más desarrolladas empleado por *M. magellanicus*, parece ser una estrategia reproductiva empleada comúnmente por especies demersales, tales como *Merluccius gayi* y *M. novaezelandiae*, pequeños mesopelágicos como *Maurolicus parvipinnis* y otras especies como *Gadus morhua* (Molina-Valdivia et al., 2021; Höffle et al., 2014; Landaeta y Castro, 2012; Landaeta et al., 2011; Zeldis et al., 1998). Sin embargo, *M. australis*, principal depredador de *M. magellanicus* presenta una estrategia reproductiva diferente a la de *M. magellanicus*, por ejemplo, desova en el mar exterior en invierno, pero, sus estadios tempranos de vida no ingresarían al mar interior, lo cual podría favorecer la sobrevivencia de *M. magellanicus* (Flores et al., 2019; Flores et al., 2020; Neira et al., 2015; Lillo et al., 2004).

Durante los últimos años, sin embargo, ha habido cambios en la fenología de esta especie, particularmente en algunos aspectos de la estacionalidad reproductiva que podrían modificar las posibilidades de sobrevivencia de sus estados tempranos de desarrollo en la zona de aguas interiores, especialmente en primavera. En efecto, se ha estimado un retraso de 10 días en el peak de desove de *M. magellanicus* en la Patagonia norte chilena en el período 1997-2012 (Payá, 2020). El retraso en el inicio del desove de *M. magellanicus* podría conllevar a presentarse estadios de vida menos desarrollados en primavera (p.ej. huevos y larvas pequeñas), lo cual, aumentaría su vulnerabilidad ante la depredación, ya que en primavera la abundancia de sus potenciales depredadores (medusas) aumenta en comparación a invierno. Por otra parte, la disminución de longitud larval en primavera en los últimos años muestreados, disminuiría la capacidad natatoria de las larvas, lo que aunado al incremento en la abundancia de medusas en primavera aumentaría la probabilidad de ser depredadas. Los efectos a largo plazo de estas variaciones en la estacionalidad reproductiva y sus causas (antropogénicas directas (pesca) o indirectas (ambientales como cambio climático) debieran ser materia de estudio en el futuro.

En resumen, en esta investigación se identificaron cambios ontogenéticos de distribución en los estadios tempranos de vida de *M. magellanicus*, que asociados a las condiciones bio-oceanográficas de la zona de estudio sugieren conectividad entre el Sistema Estuarino Patagónico y la zona oceánica adyacente en la Patagonia norte chilena. Hacia el centro y sur de la Patagonia esta conectividad sería menor y los huevos y larvas encontrados provendrían de un desove en el mar interior. Estos cambios ontogenéticos de distribución entre el mar interior y exterior serían parte de la estrategia reproductiva de *M. magellanicus* ya que favorecerían la alimentación de sus estadios iniciales de vida y disminuirían la probabilidad de ser depredados. Sin embargo, los cambios fenológicos descritos en el último tiempo, que incluyen el atraso en el periodo reproductivo con una disminución asociada en la abundancia de huevos y larvas en invierno y de las longitudes larval en primavera en los últimos años muestreados, podría disminuir las probabilidades de sobrevivencia de los estadios de vida más vulnerables de esta especie.

## **5. CONCLUSIONES**

La mayor abundancia de huevos en estratos profundos facilita su ingreso/retención en aguas interiores del Sistema Estuarino Patagónico (SEP) en invierno, mientras que la distribución de las larvas en toda la columna de agua permite la exportación de una fracción de ellas hacia la zona oceánica adyacente. Los resultados sugieren que los huevos ingresaron a la zona norte del PES desde la plataforma continental a través del Canal Darwin donde se retuvieron, y luego, larvas desarrolladas fueron exportadas a la zona oceánica adyacente a través del canal Pulluche. Esto fue resultado de la distribución vertical de huevos y larvas y la circulación estuarina entre el SEP y la zona oceánica adyacente, lo

cual sugiere conectividad de los estadios tempranos de vida de *M. magellanicus* entre estas dos zonas.

En la zona oceánica entre 43-52°S, los cambios latitudinales en la abundancia de huevos respecto a la ubicación de del stock desovante y de larvas respecto de la de los huevos sugieren transporte hacia el sur, probablemente producto de las corrientes CHC y PCUC. Sin embargo, es necesario un estudio más detallado de las características de los flujos de estas corrientes y su variabilidad estacional e interanual, con la finalidad de establecer con mayor precisión su influencia sobre la distribución del ictioplancton hacia el norte y sur en aguas exteriores.

Los modelos aditivos generalizados (GAMs) mostraron un efecto lineal significativo entre los huevos y la salinidad con máxima abundancia en salinidades alrededor de (34), un efecto no lineal entre la abundancia de larvas y la temperatura, siendo más abundantes entre 9-10°C. De igual forma asociaron mayores abundancias larvales a una menor abundancia de depredadores (medusas) y una mayor abundancia de presas (copépodos).

La distribución de huevos y larvas de *M. magellanicus* entre el sistema estuarino patagónico y la zona oceánica adyacente parece ser parte de una estrategia reproductiva tendiente a otorgar mayores posibilidades de sobrevivencia a su descendencia. El peak de desove en invierno disminuye las probabilidades de depredación de huevos y larvas y favorece las condiciones de alimentación acorde al desarrollo larval.

Finalmente, la disminución interanual en la abundancia de huevos y larvas concuerda con la disminución de los ejemplares adultos desovados en los muestreos de invierno. Y por otro lado, los cambios en la fenología (acoplamiento del ciclo de vida con los ciclos naturales del ambiente) de esta especie sugieren

una disminución en probabilidades de sobrevivencia de los estados de desarrollo temprano en el futuro próximo.

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