Universidad de Concepción
Dirección de Postgrado
Facultad de Ciencia Naturales y Oceanográficas- Programa de Magíster en Ciencias mención Oceanografía

Aumento demográfico del erizo de mar *Centrostephanus sylviae* en la isla Robinson Crusoe del archipiélago Juan Fernández: Una aproximación biofísica y ecológica.

Tesis presentada a la facultad de Ciencias Naturales y Oceanográficas de la Universidad de Concepción para optar al grado de Magíster en Ciencias con mención en Oceanografía.

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Julio, 2024

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Universidad de Concepción, dirección de Postgrado

La tesis de Magister con mención en Oceanografía titulada "Aumento demográfico del erizo de mar *Centrostephanus sylviae* en la isla Robinson Crusoe del archipiélago Juan Fernández: Una aproximación biofísica y ecológica" de la Srta. Valentina Paz Nuñez Espinosa y realizada bajo la Facultad de Ciencias Naturales y Oceanográficas de la Universidad de Concepción, ha sido aprobada por la siguiente comisión de evaluación:

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PUBLICACIONES

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DOI: https://doi.org/10.3354/meps12984

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CONGRESOS

Mayo 2024. Valentina Nuñez-Espinosa, Carolina Parada, Braulio Tapia, Billy Ernst, Javier Porobic, David Véliz, Iván Hinojosa. Aumento demográfico del erizo *Centrostephanus sylviae* en la isla Robinson Crusoe del archipiélago Juan Fernández: Una aproximación biofísica y ecológica. XLII Congreso de Ciencias del Mar, Concepción, Chile. 22 al 26 de mayo. /ORAL

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CURSOS Y WORKSHOPS

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Octubre 2016. Lenguaje R, una opción para el análisis de datos. Universidad Católica del Norte, Coquimbo, Chile.

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PREMIOS

Diciembre, 2016. Premio al mejor trabajo de pregrado en III Jornada de Postgrado UCN-ULS. Tema: Influencia de la concentración del oxígeno en el desarrollo embrionario de *Pleuroncodes monodon.* Modalidad Poster. Universidad Católica del Norte, Coquimbo, Chile, diciembre 7 del

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Modelos: Ichthyop, ROMS/CROCO, NEMO

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Agradecimientos

En primer lugar, quisiera agradecer a la Dra. Carolina Parada (Caly) por su apoyo incondicional en todo este largo proceso, por sus consejos, entrega y confianza en mi y en este trabajo. Gracias infinitas por todo lo enseñado Caly, trabajar contigo y aprender de ti han sido una de las experiencias mas valiosas de mi vida, mi gratitud hacia ti es infinita.

A la comisión de este trabajo, Dr. Billy Ernst, Dr. Javier Porobic y Dr. David Véliz por su valioso aporte en la realización de esta investigación, por su siempre buena disposición y paciencia para resolver mis dudas y siempre mejorar el escrito, muchas gracias.

A Guillermo (pupi), por tu confianza inquebrantable en mí y en lo que hago, ¡eres un compañero de lujo!

A Carmen, Norma, Fernanda y Tomás, por su cariño y apoyo incondicional en esta y en todas las decisiones que he tomado, les quiero con toda el alma.

A las amistades nuevas y no tan nuevas que se han ido sumando en el camino, tengo la fortuna de tenerles en mi vida y contar con su afecto y apoyo. Gracias por ayudarme a volver al camino, por contenerme cuando todo se veía oscuro y por celebrar conmigo los pequeños y grandes triunfos. A Sebastián (pelao), Josse, Piero, Consu, Amparo, Su, Fran, Pau, Maca, Cris, y un largo y bonito etc. Gracias por ser mi familia aquí, por hacerme sentir siempre en casa y muy querida, por escuchar, cuestionar, aconsejar y sobre todo reír y compartir los sentires, me siento infinitamente afortunada por haberles conocido y por contar con su amistad.

A les amigues de siempre, que han estado en este y en todos los caminos que he ido tomando en el tiempo, gracias por escucharme, bancarme y acompañarme en todo lo que he vivido, les amo profundamente.

A la comunidad del archipiélago Juan Fernández por su apoyo y colaboración que hacen posible este y muchos trabajos de investigación en el territorio.

Finalmente, todes quienes pasaron conmigo este viaje, a les que siempre estuvieron, les que llegaron y les que se fueron.

Gracias totales.

Resumen

El aumento de la población de erizos de mar de espinas largas (*Centrostephanus sylviae*) ha adquirido una atención significativa en la última década debido al aumento del número de individuos reportados como fauna acompañante en las trampas de langosta de Juan Fernández (*Jasus frontalis*). Además, los riesgos asociados a los cambios en la estructura del ecosistema debido al aumento del blanqueamiento de los arrecifes en el Archipiélago Juan Fernández (JFA) han generado preocupación. En esta investigación se estudió el aumento demográfico de la población de *C. sylviae* en las islas Robinson Crusoe y Santa Clara (RC-SC) a través de cambios en la abundancia relativa de erizos adultos durante los años 2015-2022. Para abordar esta investigación se se estudió la contribución de erizos en sus primeras etapas de vida a la población adulta a través de modelos biofísicos. Se realizaron simulaciones de patrones de dispersión larvaria y conectividad entre las zonas de liberación y reclutamiento para tres años de estudio (2013, 2015 y 2018). Los resultados de las simulaciones de deriva larval combinados con los datos de observación del programa de monitoreo de la pesca de crustáceos ayudaron a identificar las potenciales zonas de reclutamiento (principalmente ubicadas en las áreas este, sureste y suroeste de RC-SC). Además, se estudió la relación entre la abundancia relativa de erizos de mar adultos y los rasgos asociados a la pesquería de las langostas debido a la relación predador-presa evidente en otros ecosistemas semejantes (tal como son el ejemplo del erizo-langosta en Tasmania-Australia y Nueva Zelanda). Se exploró, a través de un modelo lineal generalizado la relación entre la abundancia relativa de erizos adultos y la talla de las langostas capturadas junto a otras variables predictoras (zonas alrededor del AJF, meses de la temporada de la langosta, los años de la series de tiempo, la profundidad de las trampas). Los resultados mostraron que, una vez combinadas todas las zonas, existía una correlación inversa entre la abundancia relativa de erizos de mar y la presencia de langostas de mayor tamaño encontradas en las trampas alrededor de las islas. Este trabajo pone de relieve la compleja dinámica ecológica resultante del aumento de la población de *C. sylviae* en el sistema JFA, subrayando la importancia de abordar esta preguntamediante enfoques ecosistémicos y socioecológicamente integrados.

Palabras Clave: abundancia de erizos, conectividad poblacional, retención, capacidad de dispersión, rasgos ecológico, langosta de Juan Fernández

Abstract

The large increase in the population of long-spined sea urchins (*Centrostephanus sylviae*) has gained significant attention in the past decade due to the rise in the number of individuals reported as bycatch in Juan Fernandez rock lobster traps (*Jasus frontalis*) and the risks associated with changes in the ecosystem structure due to the increase in bleaching of reefs in the Juan Fernandez Archipelago (JFA). We explored the demographic surge of the *C. sylviae* population on Robinson Crusoe and Santa Clara islands (RC-SC) through changes in the relative abundance of adult sea urchins during the years 2015-2022. To seek an explanation for this phenomenon, we explored the potential contributions of early life stages of sea urchins to the adult population via biophysical modeling. We performed simulations of larval dispersal patterns and connectivity between release and recruitment zones for three study years (2013, 2015, and 2018). The results from larval drift simulations combined with observation data from the crustacean fishery monitoring program helped identify recruitment zones (primarily located in the eastern, southeastern, and southwestern areas of RC-SC). Also, we explored the relationship between the relative abundance of adult sea urchins and traits associated with lobsters due to the predator-prey relationship evident in other ecosystems (i.e., in Tasmania and New Zealand). We explored the potential control by lobsters of the sea urchin population size through generalized linear models by analyzing several predictor variables. The results showed that once all zones were combined there was an inverse correlation between the relative abundance of sea urchins and the largest lobsters found in the traps around the islands. This work highlights the complex ecological dynamics resulting from the increase in the *C. sylviae* population in the JFA system, emphasizing the importance of addressing this issue through ecosystemic and socio-ecologically integrated approaches.

Keywords: sea urchins’ abundance, population connectivity, retention, dispersal capacity, ecological traits

INTRODUCCIÓN GENERAL

El archipiélago Juan Fernández (AJF), conformado por las islas Alejandro Selkirk (AS), Robinson Crusoe y Santa Clara (RC-SC), se ubica frente a Chile central a ~700 km de la costa de Chile continental. Se emplaza dentro del sistema de corrientes Chile-Perú (PCCS), que forma parte del sistema de surgencia de borde oriental (EBUS) (Cornejo, 2017). La región donde se localiza AJF se caracteriza por un alto nivel de energía cinética (Eddy Kinetic Energy; EKE) generada por inestabilidades baroclínicas producidas por el cizalle de las corrientes costeras. Estas son el resultado de la estratificación forzada por la surgencia, promovida a su vez por la variación estacional de los vientos (Chelton et al. 2001; Colas et al. 2011; Leth & Shaffer, 2001). El ecosistema de AJF es considerado un '*hot-spot*' de biodiversidad a nivel global, exhibiendo un alto grado de endemismo de especies en su territorio. (Ernst et al. 2010; Friedlander et al. 2016; Vargas et al. 2014). Muchas de estas especies endémicas exhiben características bio-ecológicas contrastantes, entre ellas se destacan: 1) *Jasus frontalis*, invertebrado icónico de este sistema insular y especie endémica del AJF e islas Desventuradas, es una langosta de roca de gran importancia comercial en el archipiélago y cuya pesquería constituye la principal actividad económica (Ernst et al 2013). Su biología se caracteriza por un largo periodo de desarrollo en su fase de vida planctónica (>12 meses). 2) *Centrostephanus sylviae* es otra especie que ha cobrado gran importancia para el sistema AJF el último tiempo. Este equinodermo ha evidenciado un sostenido aumento en su abundancia, siendo encontrado frecuentemente como fauna acompañante dentro de las trampas utilizadas en la pesquería de *J. frontalis* (Ernst et al. 2019). También se ha propuesto que el aumento de esta especie podría estar reflejando un cambio en la estructura del ecosistema del AJF (Porobic et al. 2019). El primer registro de *C. sylviae* en territorio insular chileno fue reportado por Fell (1975), quien comunica la existencia de especímenes en la isla San Félix y en el AJF. Para el género *Centrostephanus,* se ha descrito que el periodo reproductivo inicia a principios del invierno austral, con el desove de la especie produciéndose generalmente a inicios de junio. Luego de la fecundación del huevo y transcurrido un período de ~50 horas (Hudggett et al. 2005) se forma una larva meroplanctónica pluteus, la cual permanece en la columna de agua por aproximadamente cuatro meses. Posteriormente, se desarrollan cinco podios que permitirán la adhesión de este estadio al sustrato para asentarse. Seguido al asentamiento, la larva metamorfosea desarrollándose el estadio juvenil de la especie.

En especies bentónicas con poca movilidad, los atributos y las características biológicas de la fase planctónica son claves para comprender la conectividad entre poblaciones, así como también los diversos procesos biofísicos que modulan aspectos relevantes como el comportamiento larval, la migración y los límites de tolerancia fisiológicos entre otros (Cowen & Sponaugle, 2009). Los patrones de distribución y dispersión larval no siempre están acoplados a los patrones de circulación generales de la zona donde se desarrollan, los procesos dinámicos costeros de menor escala y variables como temperatura, oxígeno disuelto o calidad del hábitat podrían estar jugando un rol protagónico en la liberación larval y reclutamiento (Daly et al. 2020). Otra dimensión crucial para comprender la dinámica de las comunidades de AJF es el contexto ecológico en el que se desarrollan. Para el caso particular de *J. frontalis* y *C. sylviae* no se ha documentado una relación de predador-presa. Sin embargo, existen variados ejemplos de interacciones de especies congenéricas de langostas y erizos donde se evidencia un rol regulador por parte de las langostas (y otras taxa) sobre la población de erizos, disminuyendo así los efectos de la sobrepoblación de erizos en ambientes rocosos (e.g aumento de fondos blanqueados y reconfiguración de nichos espaciales) (Andrew & MacDiarmide, 1991; Dunn et al. 2017; Kawamata & Taino, 2021; Marzloff et al. 2016; Riquelme, 2022).

La dinámica poblacional de las especies anteriormente mencionadas se desarrolla en un sistema altamente complejo que configura relaciones ecológicas que deben abordarse desde múltiples perspectivas y herramientas. Los modelos individuos basado (IBM), constituyen una herramienta útil para estudiar los diversos procesos biofísicos que interactúan y dan forma a las complejas historias de vida temprana de diversas taxa (Swearer et al. 2019). El presente estudio explora el aumento de la abundancia relativa de *C. sylviae* durante la última década (2015-2022) relacionándola con la capacidad de dispersión/retención de la etapa larval en RC-SC utilizando herramientas de modelación biofísica (IBM). Además, se analiza la influencia potencial de *J. frontalis* (y aspectos asociados a su pesquería) sobre la abundancia relativa de los erizos de espina larga a través de modelos lineales generalizados.

Considerando los antecedentes expuestos anteriormente este estudio se abordará de la siguiente manera: 1) Mediante la caracterización de la abundancia relativa de los ejemplares de *Centrostephanus sylviae* se analizan cambios en la presencia de ejemplares provenientes de la fauna acompañante de la pesquería de langostas en AJF durante la serie de tiempo 2015-2022, proveniente del programa de monitoreo biológico pesquero de las pesquerías y del ecosistema asociado al archipiélago de Juan Fernández. 2) A través de la implementación de un modelo biofísico se examinan los patrones de transporte/advección/reclutamiento de zonas delimitadas alrededor de RC-SC con el fin de dilucidar posibles contribuciones de la etapa planctónica de *C. sylviae* a la población de adultos en AJF. 3) Por medio de modelos lineales generalizados (GLM) se exploran relaciones entre la abundancia relativa de los adultos de erizos de espinas largas y rasgos asociados a la pesquería de la langosta de Juan Fernández con el fin de evaluar el control potencial por parte de *J. frontalis* sobre *C. sylviae* en AJF.

Se plantean las siguientes hipótesis de trabajo:

Hipótesis

El aumento progresivo de la población *Centrostephanus sylviae* en las islas Robinson Crusoe y Santa Clara (RC-SC) en el archipiélago Juan Fernández se sustenta en procesos físico/ecológicos que ocurren en distintas fases del desarrollo de *Centrostephanus sylviae*. Así las hipótesis que se plantean corresponden a:

1) La magnitud y dirección de las corrientes locales alrededor de las islas RC-SC modulan el transporte y la advección larval de *C. sylviae* determinando la retención, conectividad y reclutamiento de la especie en la isla.

2) El aumento progresivo del tamaño poblacional de *C. sylviae* responde a la ausencia de controladores naturales en el ecosistema, como *Jasus frontalis*, debido a la extracción selectiva de los individuos (actividad pesquera) sobre la talla comercial (>115 mm). Esto limitaría la capacidad de individuos de talla pequeña para ejercer un control '*topdown*' efectivo sobre la población de erizos alrededor de RC-SC.

Objetivo General

Examinar el aumento en la abundancia relativa de adultos *Centrostephanus sylviae* como pesca incidental en la pesquería de la langosta de Juan Fernández (*Jasus frontalis*) de las islas RC-SC durante los años 2015 a 2022, y evaluar su relación con la dispersión de sus productos reproductivos.

Objetivos específicos

1) Caracterizar la abundancia relativa de *Centrostephanus sylviae* con respecto a distintos años, estratos y zonas alrededor de la isla RC-SC durante el período de estudio (2015-2022).

2) Evaluar los patrones de dispersión/retención y conectividad larval de *C. sylviae* en la isla RC-SC, mediante modelos basados en individuos acoplados a un modelo hidrodinámico.

3) Investigar la posible influencia del tamaño de las langostas, mes/año y estratos/zonas de la distribución de *J. frontalis* en el tamaño poblacional de *C. sylviae*, utilizando modelos lineales generalizados.

“Demographic rise of sea urchin *Centrostephanus sylviae* on Robinson Crusoe Island at the Juan Fernandez Archipelago: A biophysical and ecological approach”

INTRODUCTION

The Chile-Peru current system (CPCS) forms part of the eastern boundary upwelling ecosystem (Cornejo, 2017) characterized by oceanographic processes such as mesoscale eddies, filaments, and meanders that propagate from the South American coast with a high level of kinetic energy (50-110 $cm^2 s^{-2}$) (Hormazábal et al. 2004a, Parada et al. 2021) and interact with oceanic islands. The Juan Fernandez Archipelago (JFA) comprises the Robinson Crusoe and Santa Clara islands (RC-SC) located about 700 km off the coast of Central Chile, and the Alejandro Selkirk Island (AS) situated 162 km to the west (**Fig. 1**). The JFA ecoregion is considered a biodiversity hotspot due to its remote location and high level of endemism (Ernst et al. 2010; Vargas et al. 2014; Friedlander et al. 2016; Cornejo, 2017). UNESCO declared the JFA as a biosphere reserve in 1977 (Ernst et al. 2010), and in 2016, the Mar de Juan Fernandez Marine Park was created with a 2.4-million-hectare surface area.

The lobster *Jasus frontalis* is among the most iconic endemic species within the JFA and represents a keystone species for the artisanal fishing sector, comprising much of the crustacean fishery of the archipelago (Steneck et al. 2017). The distribution of *J. frontalis* occurs from the coastal edge around the islands, up to 200 m in depth (Roman et al. 2018). The lobster is distributed on hard ocean floor habitats such as rocky reefs, with seaweeds and associated fauna (Tepker et al. 2023). Another endemic species of this archipelago is the long-spined urchin *Centrostephanus sylviae*, a species that has gained relevance during the last decade due to the sustained increase in the capture rates of specimens found as bycatch in the lobster traps and the increase of overgrazed and depleted bottoms along the coasts of the islands (Ernst et al., 2019). Ernst et al. (2020) indicated that the increase in the sea urchin population has become relevant among the different stakeholders of the fishery and the Juan Fernandez community. The increase in the presence of *C. sylviae* adults in lobster traps around RC-SC has been substantial, constituting up to 85% of the bycatch and generating significant changes in the rocky subtidal landscape and negatively affecting tourism. Ecosystem modeling of *J. frontalis* at the Juan

Fernández ridge suggests that the high exploitation rate to which lobster of the commercial size are harvested (≥ 115 mm cephalothoracic length -CL-) would have reduced the population control of the urchin, facilitating the population growth of this species (Porobic et al. 2019). Thus, adult lobsters are potentially crucial factors in controlling the sea urchin increase (Ling et al. 2009). In other similar Indo-Pacific ecosystems (i.e., Tasmania; Jhonson et al. 2013), the control of lobsters over sea urchins decreased the effect of overgrazing on macroalgae, and with it, the reduction of the chances of bleaching the rocky substrate, therefore avoiding significant changes in the structure of the ecosystem (Ling et al. 2009). Global evidence suggests that, in general, underwater macroalgae forests are essential for the recruitment, settlement, and survival of the early stages of crustaceans, since they provide food, shelter, and recruitment sites (Hinojosa et al. 2015). Nonetheless, the effect that the increase in overgrazed bottoms may have on the recruitment of *J. frontalis* and the possible increase in urchin larvae in the water column is yet unclear.

The first record of long-spined urchins in these Chilean islands was described by Fell (1975), indicating their presence on San Felix Island and the JFA. Recent studies indicate that even though both island systems are 819 km apart, the populations of *C. sylviae* are highly connected, given the apparent high level of gene flow. The extensive larval period of the species and the meso- and submesoscale structures facilitate larval transport to form a single genetic population (Veliz et al. 2021). For the genus *Centrostephanus,* the distribution has been described around shallow-rocky bottoms with the presence of kelp and coralline algae (Metaxas, 2020). The reproductive period for this genus starts at the beginning of the southern winter, with a peak of spawning at the beginning of June. A meroplanktonic larva is formed, remaining in the water column for approximately four months (Byrne & Andrew, 2013, Cameron & Schroeter, 1980, Huggett et al. 2005). The highest gonadosomatic index of *C. sylviae* occurs from February to May, decreasing during the southern winter (June, July, and August) (Ernst et al. 2020). However, there is no more available information regarding the life history and ecology of the species in the area. It is thought that physical processes could modulate the transport of the reproductive products of C. *sylviae* (Porobic et al. 2019, 2013, 2012; Medel et al. 2018, Veliz et al. 2021). Thus, the dispersion and retention capacity of *C. sylviae* at the larval stage would determine the population distribution of adult sea urchins and hence may show that their spatial niche overlaps with that of adults of *J. frontalis*.

This research explored the increase in the relative abundance of *C. sylviae* around the islands RC-SC during the past decade (2015-2022) and their relationship with the dispersion/connectivity and larval retention within the islands using simulation modeling. In addition, the present work examined the possible influence of several variables on the sea urchin population size, including the size of adult lobsters, by utilizing generalized linear models. The findings of this study will provide valuable insights into the increase in degraded bottoms of rocky substrates and the potential impact on the ecosystem of the archipelago. Stakeholders can use this information to develop effective management and conservation strategies.

DATA AND METHODS

2.1 Data based on the monitoring program.

For the statistical analysis and setup of the biological and ecological components of the model, we used the database recorded by the fisheries biological monitoring program for the JFA ecosystem from 2015 to 2022 for the island subsystem comprising Robinson Crusoe and Santa Clara (RC-SC) (Ernst et al. 2019; Ernst et al. 2022). From this database, information was obtained per lobster trap haul, including cephalothoracic length (CL) of retained (≥115 mm CL) and non-retained lobsters (<115 mm CL) and sea urchin (C. sylviae) bycatch (numbers) in addition to geographic information concerning the areas and depths in which the traps were set.

2.2 Hydrodynamic model

The dynamic representation of the circulation of the study area (JFA) was obtained from the products of two global reanalyses (i.e., CGLOPHY30 and CGLOPHY024) distributed by Copernicus Marine Environment Monitoring Service (CMEMS; http://marine.copernicus.eu/). CGLOPHY030 corresponds to a daily global reanalysis model from which data were used for simulation experiments for 2013, 2015, and 2018 (Fernandez & Lellouche, 2018). GLOPHY024 is a daily global forecast model that has a regular high-resolution grid of 1/12° (~8 km) and 50 levels of depth (0 - 5500 m) (von Schuckmann et al. 2016). The products of both models of the reanalysis were based on the hydrodynamic model Nucleus for European Modelling of the Ocean (NEMO) version 3.1 that assimilates altimetry, satellite data of sea surface temperature, and the salinity of the water column (Gurvan et al. 2019).

2.2.1 Biophysical model, parameters, and indexes

An individual-based model (IBM) coupled to the reanalysis products was implemented using the Ichthyop simulation program (Lett et al. 2008) that allows for the development of spatiotemporal simulation experiments forced by the outputs of the hydrodynamic model, i.e., fields of speed, temperature, and salinity, among others (Lett et al. 2008). We assessed the effects of physical processes on the larval-planktonic stage of *C. sylviae* from the RC-SC insular platform. For the configuration of the IBM, we defined the following biological characteristics of the larval stage of *C. sylviae*: 1) the release date; 2) the release area; 3) the number of larvae released; 4) the place of recruitment. The recruitment was identified from two calculated indices of the statistical values from the IBM model. The first corresponds to the index of connectivity within and between the study areas and is given by the number of larvae released that arrived in an area different from that of their release. The second consists of the retention index calculated from the number of larvae present in the same area in which they were released. The indices were estimated considering 115 days (~4 months) with a window of five days prior and five days after the end of the simulation, since the recruitment takes approximately five days.

2.2.2 Simulation experiments and assessed parameters.

We set up simulation experiments to evaluate connectivity and retention in RC-SC using the years 2013, 2015, and 2018 as case studies. We chose the year 2013 because variation in the time series' abundance was found in cycles lasting two to three years. The year 2015 was selected for being the first year of the time series of the biological monitoring program. Finally, 2018 was the first year with a significant increase in the relative abundance of sea urchins in the time series. The areas of release were defined based on the information recorded by the biological monitoring program of the fisheries and the ecosystem associated with the JFA (Ernst et al., 2022). Six zones were established around RC-SC, and these were used to identify the recruitment of the propagules (**Fig. 1**).

To assess the connectivity between the areas around RC-SC, four months was considered as the duration of the larval period. Each IBM simulation lasted for 122 days (~4-month larval period) following the duration described for *Centrostephanus rodgersii* (Huggett et al., 2005), with a time step of 120 seconds and a recording frequency of 180. Therefore, the model output was recorded every six hours. A daily release of 6000 particles was arranged for 92 consecutive days, in a range of 0 to 80 m depth, considering all the release zones previously defined during the spawning peaks in June, July, and August (Byrne & Andrew,2013). For the IBM l developed in this study, a Lagrangian model was used to simulate the transport of passive larvae, with no vertical migration or active swimming. In addition, larval mortality rate functions associated with temperature were not included (**Table 1**).

2.2.3 Movement equations

The resolution of the position of particles in each time step used in the model was a function of the orthogonal east-west (u) and north south (v) velocity components in addition to the vertical component (w) from the hydrodynamic model output:

$$dx/dt = u,\ dy/dt = v,\ dz/dt = w$$

The integration of the position of the particles in each time step (∂t), was carried out with a fourth order Runge Kutta approximation (Isotani et al. 2012), where y represents the dependent variable, n corresponds to the index of the discrete-time passage and k alludes to the coefficients that represent the approximations of the slope of the function at the different points throughout the time interval:

$$y^{n+1} = y^{n} + (1/6)\ (k^{1} + 2k^{2} + 2k^{3} + k^{4})$$

2.3 The relative abundance of sea urchins and factors that affect their population dynamics.

The relative abundance of sea urchins was estimated based on the frequency of sea urchin catches obtained from lobster trap bycatch. A generalized linear model was implemented (GLM; McCullagh & Nelder, 1983) to determine the factors affecting the bycatch rates of long-spined urchins associated with the eventual control that large lobsters may have on the sea urchin relative abundance. Therefore, five predictor variables were considered, year (*aj*, 2015-2022), month (*mk*, October-May), zone (*zl*, RC_A, RC_B, RC_C, RC_D, RC_E and RC_F), stratum of bathymetric depth (*dm*, 0-50; 50-100; 100-150; and 150-200 m), and two lobster size ranges (*sn*, small, ≤107.5 mm LC and large, >107.5 mm LC). The number of urchins per trap was set to a Poisson random variable (counts), with values equal to or greater than zero (>0). However, many trap hauls had zero urchin bycatch; therefore, the relative abundance of urchins was modeled using different likelihood options: Poisson, zero-inflated Poisson, negative binomial, and zero-inflated negative binomial. Through the Akaike information criterion (AIC; Akaike, 1973) and overdispersion analysis, the GLMs with zero-inflated binomial probability distributions were determined to be the most appropriate. Thus, models with negative binomial distributions allow the relation of the response variable (Y) with the explanatory variables X using a logarithmic link function, where βi are the coefficients of the function estimated from the five predictors $\{aj, mk, zl, dm, sn\}$, while ϵ corresponds to the distribution of the error of the dependent variable belonging to the family of exponential distributions:

$$\log(Y) = X\ \beta i + \epsilon$$

The zero-inflated negative binomial distribution has parameters λ (the mean) and ρ (the scaled variance) and another of form ϕ that represents the dispersion of the error incorporated into the variance. In this case, the distribution was truncated to zero ($y = 0$), meaning that the probability that urchins will not be observed in lobster traps is given by:

$$Y \sim nbinom\ (\lambda, \rho, \phi)$$

The parameters of the linear models were estimated using the glmmTMB function in the R statistical programming environment (Vernazi, 2004; R Development Core Team, 2023). This function allows a wide variety of available probability distribution families, including zero-inflated forms. After the model parameterization, comparisons were made through the AIC using the model's diagnostic values for validation.

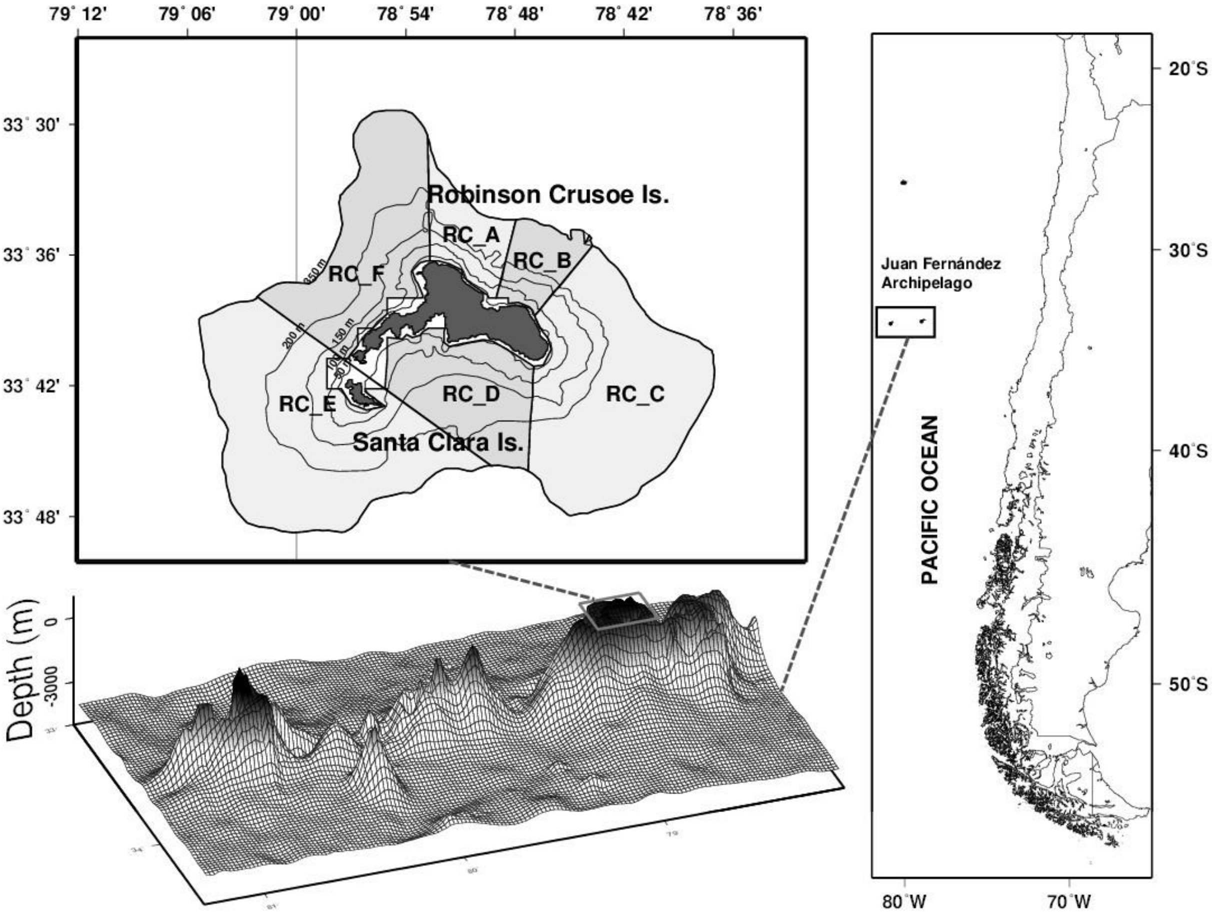

Figure 1. Geographic location of Juan Fernández (JFA) Archipelago on the JF ridge. The upper left panel corresponds to the study area (Robinson Crusoe and Santa Clara Islands) and 6 zones defined for prediction analysis.

Table 1. Configuration of individual-based model simulations (IBM) for *C. sylviae* in the JFA for 2013, 2015 and 2018 case studies.

Case (year)	Model	Beginning-end of simulation	Duration of simulación (days)	N° of batch (nº of daily particles)	Release range depth	Release zone	Recruitment zone
2018	NEMO (CGLOPHY030 - CGLOPHY024)	2018/05/30 (00:30)- 2018/08/29 (00:30)	122	92 (6000 particles per day)	0-80 m	RC (6)	RC (6)
2015	NEMO (CGLOPHY030 - CGLOPHY024)	2015/05/30 (00:30)- 2015/08/29 (00:30)	122	92 (6000 particles per day)	0-80 m	RC (6)	RC (6)
2013	NEMO (CGLOPHY030 - CGLOPHY024)	2013/05/30 (00:30)- 2013/08/29 (00:30)	122	92(6000 particles per day)	0-80 m	RC (6)	RC (6)

RESULTS

3.1 Characterization of relative abundance of sea urchin *Centrostephanus sylviae*.

The time series of relative abundance of sea urchins from the lobster traps spanned from 2015 to 2022. During the first three years of this time series (2015, 2016, and 2017), there was no significant increase in the proportion of *C. sylviae* specimens. From 2018 onwards, there was a significant increment in the relative cumulative proportion, reaching 0.5 overall sea urchin adult bycatch in 2020. Two years later (2022), 0.9 of the overall relative cumulative proportion of sea urchins was observed in RC-SC (**Fig. 2A**). Concerning depth, the relative cumulative proportion reached the value of 0.5 in the first stratum (-50 m), indicating that half of the specimens were found between 0 and 50 m. In contrast, a proportion of 0.9 was reached in the ≤100 m stratum, suggesting that most sea urchins are distributed in the first 100 m. Although individuals were recorded at greater depths (>100 and < 200 m), the proportion was rather marginal (**Fig. 2B**). The northern portion (with greater exposure) of RC-SC corresponding to areas RC_A, RC_B, and RC_F comprised 61% of the individuals captured as bycatch, in contrast to the areas on the southern portion (with less exposure) of the island (RC_C, RC_D and RC_E) that comprised 39% of the individuals. However, the areas with the highest presence of sea urchins were RC_A with 35%, RC_F with 19%, and RC_E with 18% (**Fig. 2C**).

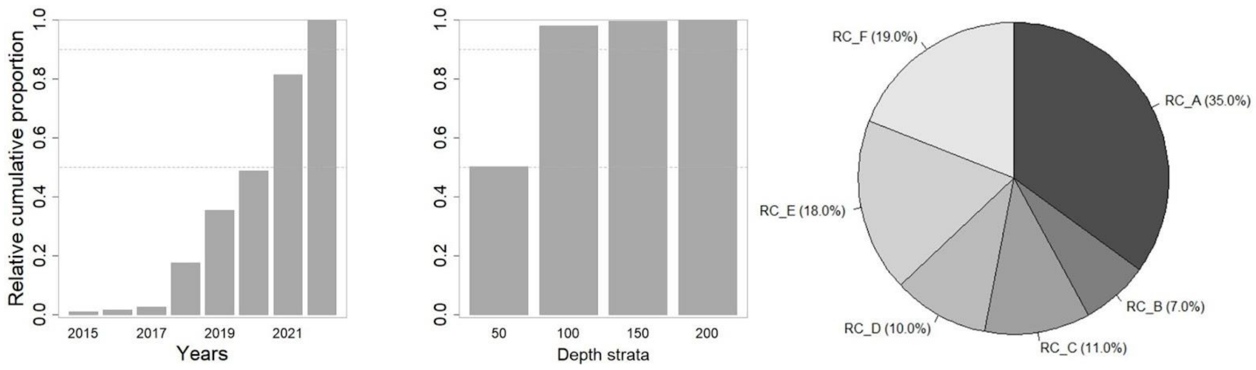

Figure 2. Statistics of sea urchin *Centrostephanus sylviae* captured on lobsters' traps during the 2015-2022 period. A) Relative cumulative proportion per year around RC-SC islands, B) Relative cumulative proportion per depth strata: 0-50m, 50-100m, 100-150m and 150-200 m around RC-SC islands, C) percentage of individuals per zone around RC-SC islands. The grey dotted lines in panels A and B indicate the 0.5 and 0.9 quartiles.

3.2 Predictions of the relative abundance of sea urchin adults

To determine whether elements of the RC-SC system might be influencing the relative abundance of urchins collected as bycatch in the lobster fishery, four predictor variables (year (*aj*), month (*mk*), depth (*dm*), and lobster size (*sn*)) were examined independently. Both simple and multiple linear regression analyses were used to analyze the predictor variables.

The simple linear regression models showed that the temporal factor (*aj*) had a significant influence on the abundance of *C. sylviae* in RC-SC for each of the study zones independent of the others since they were the models with the best-fit value. Once the six zones around RC-SC were integrated and considered as a factor, the year variable remained the parameter that had the greatest influence on the variability of urchin abundance over the given time series (2015-2022) (**Table S1**).

The multiple regression models revealed that the combination of predictors varied among the zones; nevertheless, the AIC value indicated that model M5 that included all relevant predictor variables and considered the six zones surrounding RC-SC as a single factor was the best model (**Table 2**). To quantify the relationship between sea urchin abundance and the predictor variables, we used the values of the estimated coefficients of each level for each variable. Consistent with the simple linear regression analyses, the temporal factor (year) had the most impact on urchin abundance, particularly the year 2021 (3.439955), followed by the year 2022 (3.124251). The lobster size (*sn*) was also a significant component; more specifically small size (0.167113), despite its low coefficient value, helped to explain the fluctuations in *C. sylviae* abundance around RC-SC (**Table S2**).

Table 2. Relative abundance of sea urchin GLM results of the best model fit. Results of models fit a relative abundance response variable (sea urchin volume) using simple (m) and multiple (M) regression models by zone, where the covariables are year factor (*aj*), month (*mk*) depth (*dm*) and rock lobster size (*sn*). AIC corresponds to Akaike information criteria and df to degrees of freedom. Bold and italic indicate best model fit for each level.

	Simple regression				Multiple regression			
All zones	**m1**	$\sim \mathbf{a}_j$	**10**	**12949**	M1	$\sim\mathbf{a}_j$	10	12949
	m2	$\sim m_k$	10	13790	M2	$\sim\mathbf{a}_j + m_k$	17	12825
	m3	$\sim z_l$	8	13699	M3	$\sim\mathbf{a}_j + m_k + d_m$	22	12614
	m4	$\sim d_m$	6	13491	M4	$\sim\mathbf{a}_j + m_k + z_l + d_m$	25	12429
	m5	$\sim s_n$	4	13908	**M5**	$\sim\mathbf{a}_j + \boldsymbol{m}_k + \boldsymbol{z}_l + \boldsymbol{d}_m + \boldsymbol{s}_n$	***26***	***12425***

3.3 Simulation of sea urchin larval transport, connectivity, and density

A significant degree of advection around the RC-SC islands was observed in the larval simulation experiments carried out for the three years (2013, 2015, and 2018) (>90% in each case). Transport via anticyclonic circulation was demonstrated by the simulated larval tracks over the islands. Furthermore, both in the retention region and the offshore area, larval dispersal displayed interannual variation. The year 2018 was the year with the most retention of the three (4.43%), with 2015 being the second highest (2.79%) and 2013 the least (0.38%).

In 2013, the trajectory of the larvae simulated during the first half of their larval stage (-60 days) exhibited a predominant advection towards the northeast region and northwest of the RC-SC islands (RC_A, RB_B, and RC_C), consistent with the mean current (**Fig. S1, S2**). A circulation was observed primarily toward the southwest and southeast regions of the RC-SC islands (RC_D, RC_E, and RC_F) during the period of the second larval stage, close to the recruitment period (>60 days). This circulation aided in larval retention and established connections with the same areas where the *C. sylviae* larvae were first released. The dispersive nature of the surrounding current system notwithstanding, the successful particle trajectories to all zones indicated a distinct pattern of anticyclonic recirculation surrounding the islands. In comparisons of the three years, 2013 had the fewest recruits overall, with a total retention of 2120 larvae (**Fig. 3**). The source region with the largest contribution (32.97%, or 699 larvae) in terms of the number of larvae recruited was the RC_B region, whereas the RC_C zone was the sink zone with the highest proportion (768 larvae or 36%). Regarding the larval accumulation surrounding RC-SC, the year 2013 exhibited particle presence along the island's perimeter, with the northern and northwest portion (in general) of the island having the highest particle number (**Fig. 4**).

In 2015, sub-mesoscale structures that promoted the advection of larvae off the coast were identified. The simulation of the first larval period exhibited predominant advection toward the southwest and southeast regions of the RC-SC islands (**Figs. S3**, **S4**). Larval transit mostly took place in the northern zones second simulation period, exhibiting a link with the eastern sites (RC_E, RC_F) and western areas of the islands (RC_C; **Fig. 5**). The RC_D zone had the highest percentage of contributed larvae (34.51%; 5316 larvae) among the total of released larvae (15403) identified in the time window as a recruitment proxy. However, the RC_F zone was a sink area, with the highest recruitment index reaching 32.95% (5076 larvae) of the larvae recruited. In contrast to 2013, the highest particle accumulation occurred in the eastern area of the islands (**Fig. 6**).

Despite the predominance of the anticyclonic circulation pattern around the RC-SC islands in all years (**Figs. S5**, **S6**), the extension of the transport of larvae out of the coast was limited in 2018 compared to the simulation cases for the years 2013 and 2015 (**Fig. 7**). In this instance, the larval transport's first phase (i.e., the first 60 days of larval dispersion) was primarily centered on the island's northern regions; more than in the other three years. Regarding the six areas around the RC-SC islands, the RC_B zone had the highest contribution of recruited larvae (24%, or 5810 larvae), whereas the RC_C zone had the highest number of recruits (72.38%, or 17,676 larvae). As in 2013, most of the simulated larvae accumulated around the northern zones of the islands (**Fig. 8**).

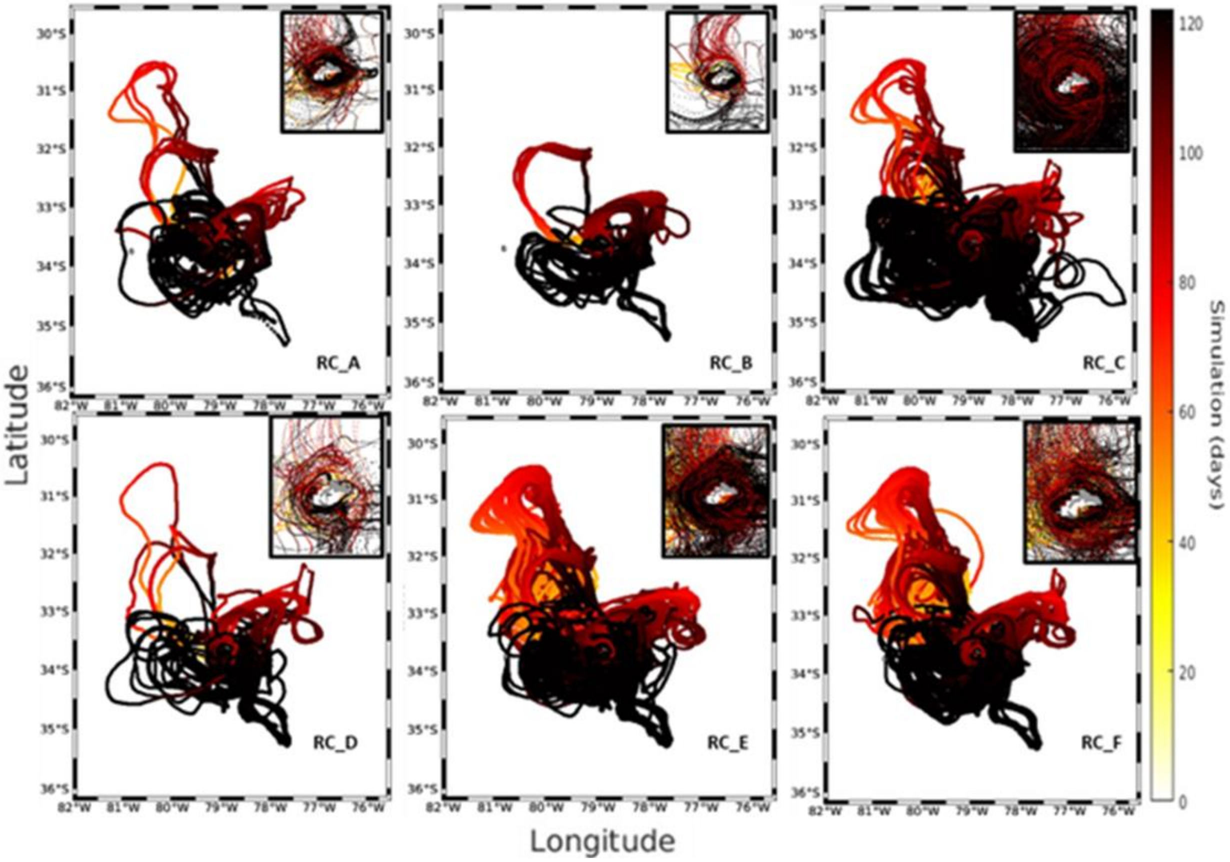

Figure 3. Trajectories of larvae arriving at the RC-SC recruitment zones for the year 2013. Each panel corresponds to the 6 zones used for the predictions, and the small plots show a close-up of the island to more clearly observe the movement patterns followed by the larvae. The color bar represents the days of the IBM simulation.

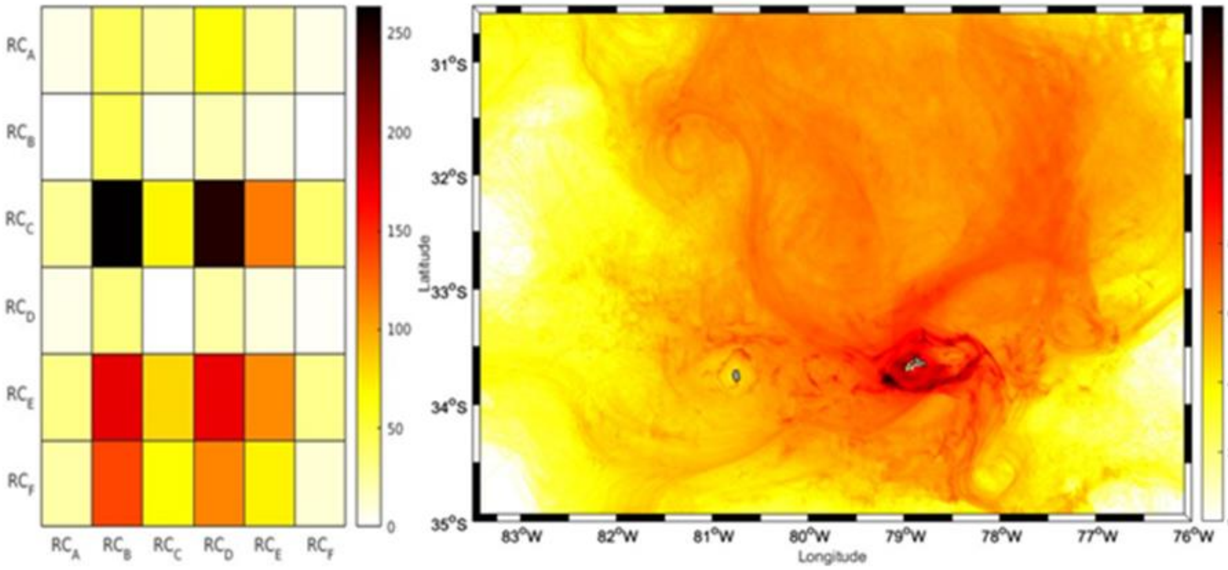

Figure 4. The left panel shows the connectivity matrix of IBM simulation experiments of *C. sylviae* larvae for 2013. On the x-axis the 6 release zones in RC are represented, on the y-axis the recruitment zones for RC are represented (6 zones). The colors represent the concentration of larvae at each site of interaction of the release zones with the recruitment zones. In the left panel of the figure a particle density map is displayed, showing in darker colors the sites with higher larval recurrences, The color bar represents the number of larvae.

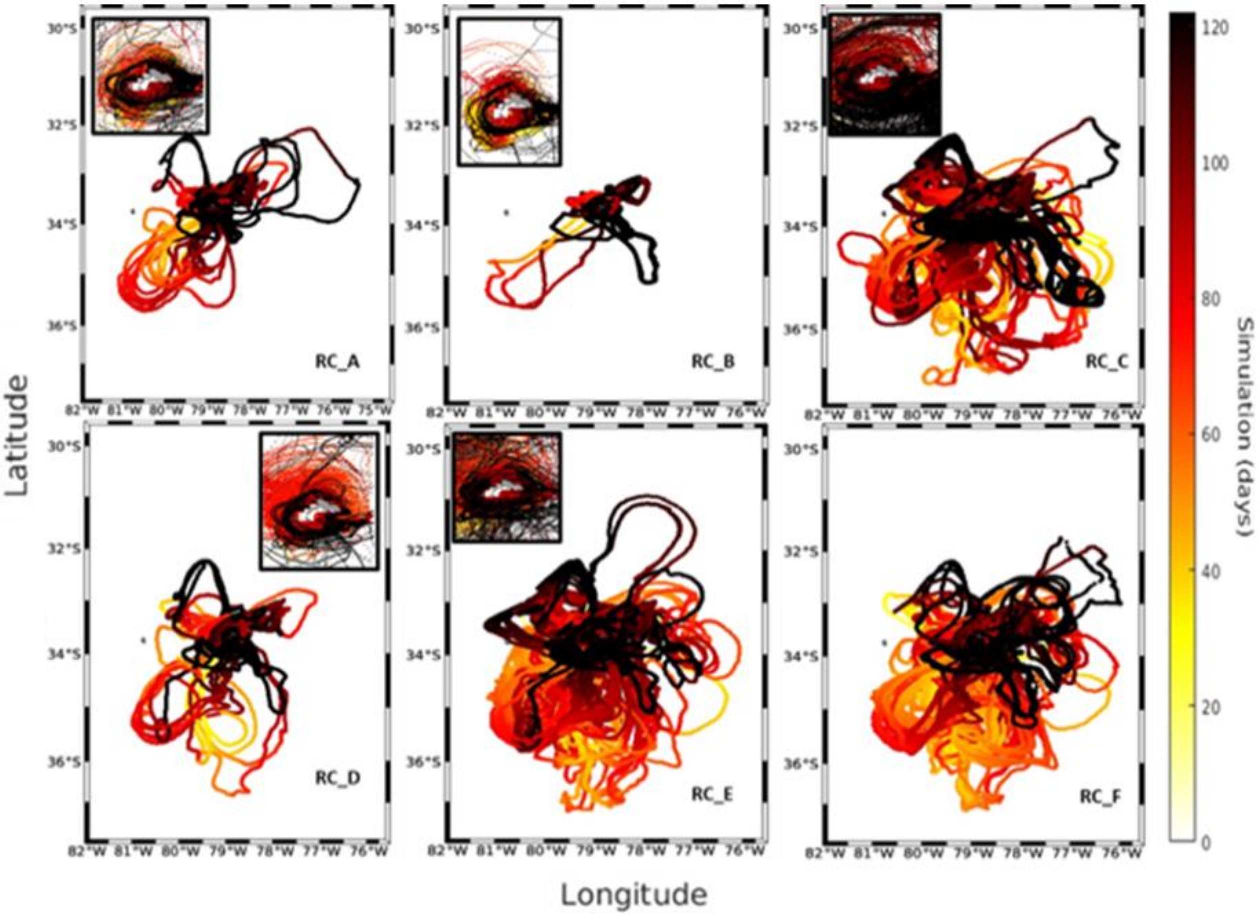

Figure 5: The graph shows the trajectories of larvae arriving at the RC recruitment zones for the year 2015. Each panel is subdivided into each of the 6 zones used for the simulations. The small plots in each figure show a close-up of the island to more clearly observe the movement patterns followed by the larvae as they arrive at the recruitment zone. The color bar represents the days of the IBM simulation.

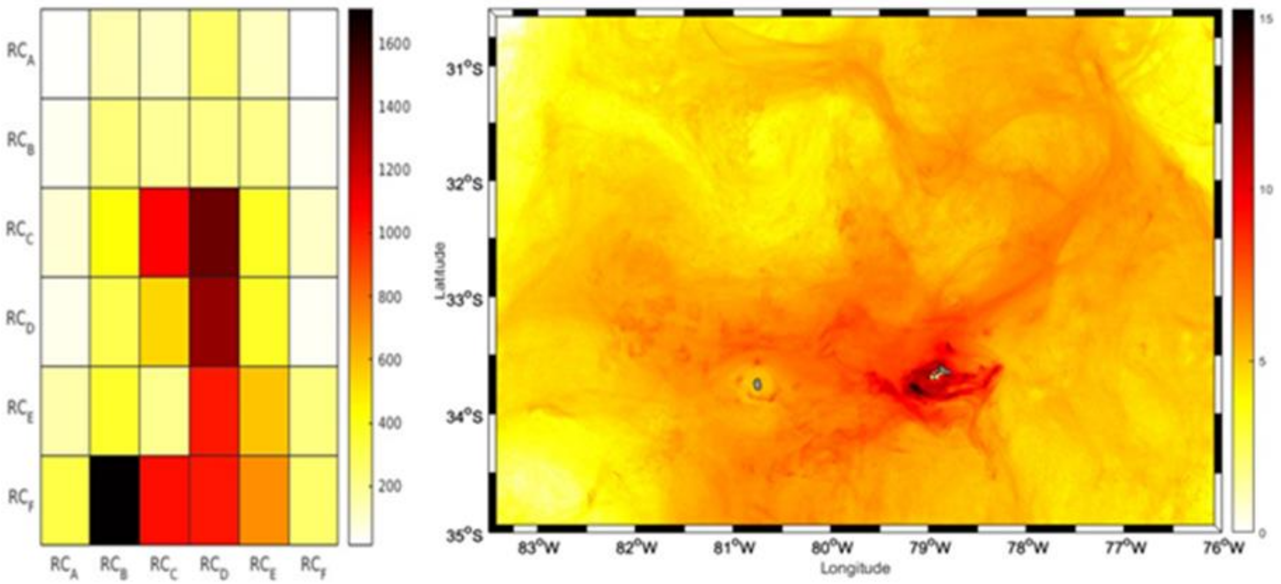

Figure 6. The right panel of the figure shows the connectivity matrix of IBM simulation experiments of *C. sylviae* larvae for 2015. On the x-axis the 6 release zones in RC are represented, on the y-axis the recruitment zones for RC are represented (6 zones). The colors represent the concentration of larvae at each site of interaction of the release zones with the recruitment zones. In the left panel of the figure a particle density map is displayed, showing in darker colors the sites with higher larval recurrences, The color bar represents the number of larvae.

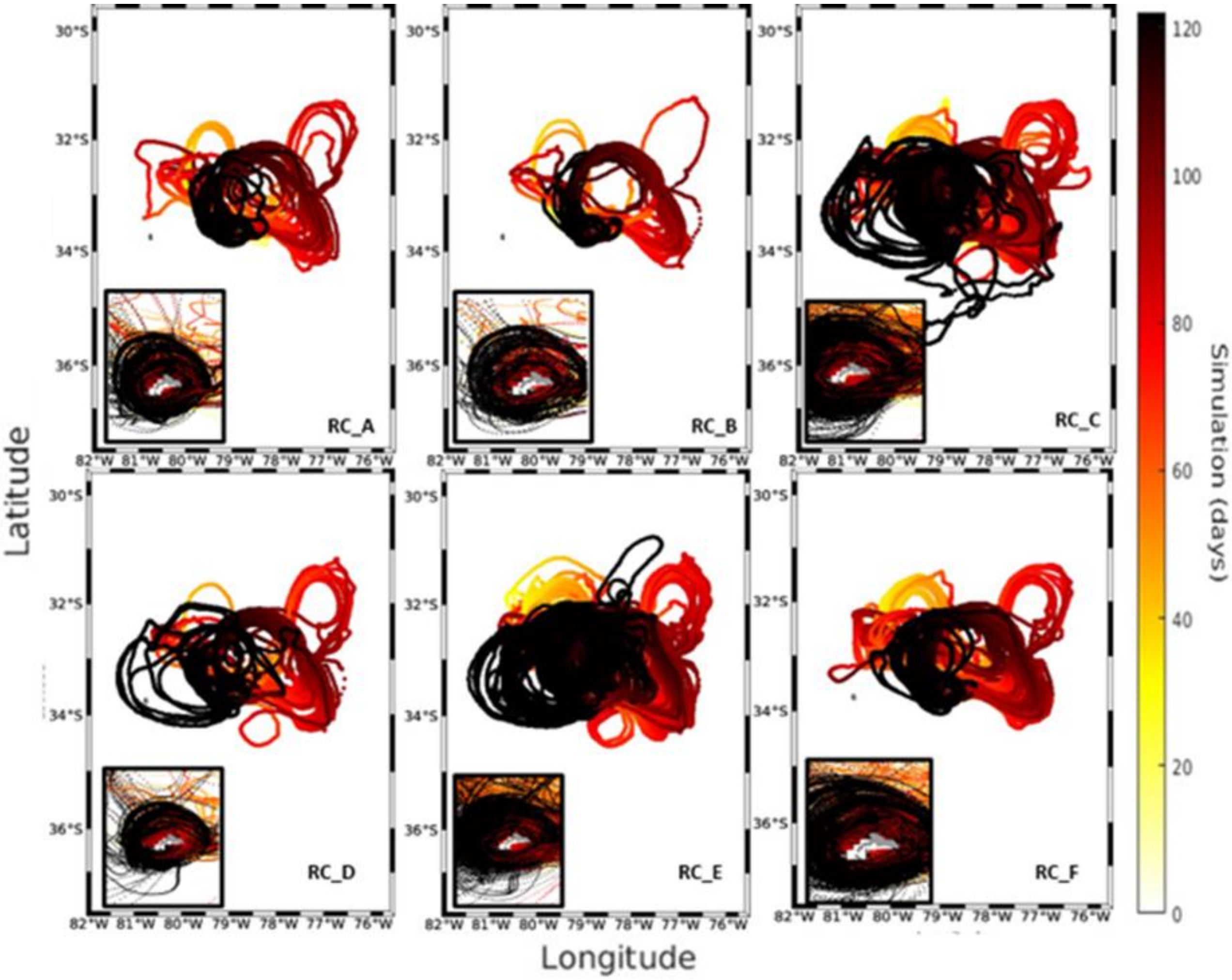

Figure 7. The graph shows the trajectories of larvae arriving at the RC recruitment zones for the year 2018. Each panel is subdivided into each of the 6 zones used for the simulations. The small plots in each figure show a close-up of the island to more clearly observe the movement patterns followed by the larvae as they arrive at the recruitment zone. The color bar represents the days of the IBM simulation.

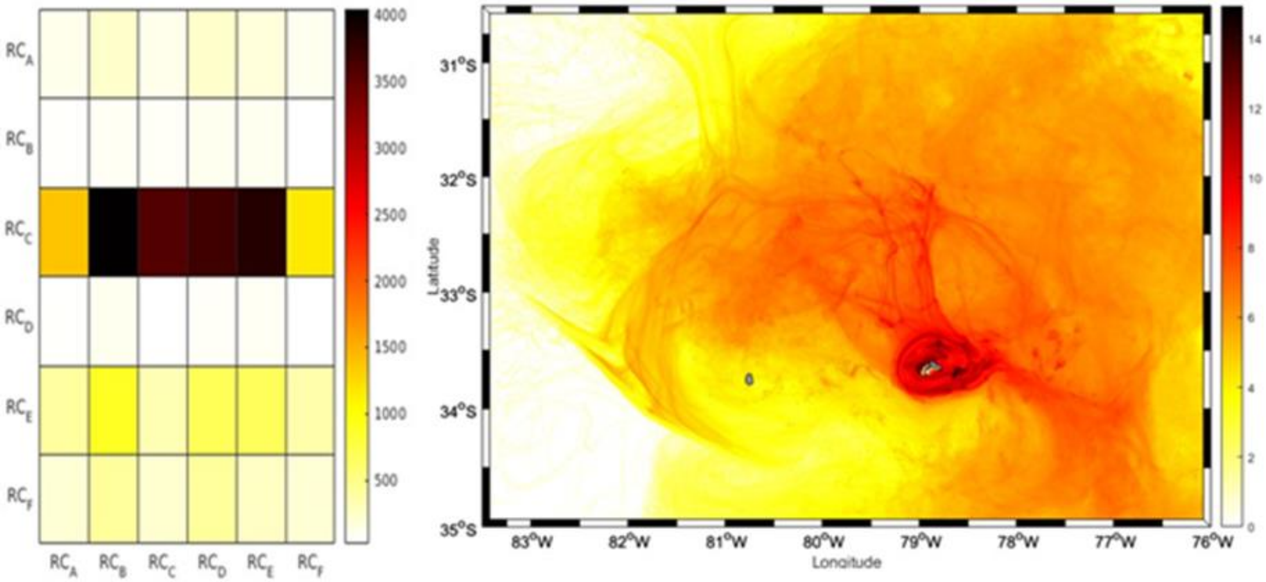

Figure 8. The right panel of the figure shows the connectivity matrix of IBM simulation experiments of *C. sylviae* larvae for 2018. On the x-axis the 6 release zones in RC are represented, on the y-axis the recruitment zones for RC are represented (6 zones). The colors represent the concentration of larvae at each site of interaction of the release zones with the recruitment zones. In the left panel of the figure a particle density map is displayed, showing in darker colors the sites with higher larval recurrences, The color bar represents the quantity of larvae.

DISCUSSION

The results suggest that the demographic increase of *C. sylviae* in the JFA has been gradual and sustained over the last decade, particularly highlighting the period from 2018 onwards that experienced a considerable increase in the number of individuals present as bycatch from the *J. frontalis* fishery. Although individuals are present around the RC-SC island, the results of the biophysical experiments delineated areas that had greater concentrations of particles at the time of recruitment, areas that could potentially be sink zones for this species. The GLM results suggested a slight positive relationship between the presence of urchins present as bycatch and small size of lobsters, consistent with the *C. sylviae* and *J. frontalis* habitat distributions. The predator-prey relationship between species of sea urchins and lobsters has been previously documented, and thus these results may shed light on an interaction that requires further exploration (Smith et al. 2023).

4.1 Spatial and temporal patterns

The distribution of adults of *C. sylviae* around RC-SC exhibited patterns that seemed to be strongly modulated by region-specific environmental and oceanographic factors. The analyses carried out from the fishery biological monitoring program of the lobster fisheries and the ecosystem associated with the JFA (2015-2022, Ernst et al. 2022) indicate that the relative abundance of adult urchins shows two differentiated periods, one of low relative abundance (2015-2017) and a period where the population increased (2018-2022).

A possible cause of the demographic increase in the population of urchins in RC-SC since 2018 is the strong El Niño events registered in the years 2015 and 2016 characterized by an increase of ~2° C in the system (http://www.cpc.ncep.noaa.gov/data/indices/). These climatic fluctuations modulate various factors (i.e., temperature, primary production, advection, and transport) that could affect the recruitment and subsequent distribution of adult urchins (Okamoto et al. 2020, Tong et al. 2000). Currently, there are no records that document the effect of temperature on the distribution of *C. sylviae* adults. However, Hart and Scheibling (1998) reported a decrease in the period of larval development of *S. droebachiensis* urchins at higher temperatures (within tolerance limits). This suggests that the increase in temperature in the water column could potentially have several effects on *C. sylviae:* 1) reduction of the larval period; 2) advancement of adulthood, and 3) advancement of sexual maturity. The above factors may also have influenced the larvae of *J. frontalis* in the archipelago (Tong et al. 2000). Another relevant aspect to consider is that the relative abundance of urchins differs between the areas of the archipelago. This could be related to the presence of preferred microhabitats and more favorable conditions for their development and recruitment. In the northeast and northwest regions of RC-SC, more than 60% of the reefs are located on the island shelf, and most are distributed at depths between 0-150 m a factor that could provide refugia to a large marine community that includes *C. sylviae* (Tapia, 2022). In addition, it has been reported that *C. rodgersii,* a species related to *C. sylviae*, exhibits a preference for irregular substrates that provide shelter, a characteristic that also occurs in species that use reefs as niches (Byrne & Andrew, 2020). The above coincides with the location of the RC_A, and RC_F zones (located in the north and northwest regions of RC-SC, respectively) that exhibited the highest relative abundance of urchins throughout the monitoring period.

The results of the analysis of the relative abundance of adult urchins were consistent with several aspects of the simulations of the dispersion and larval connectivity of the biophysical model for *C. sylviae.* In general, the simulation experiments exhibited significant interannual variability among the three years of study characterized by a high degree of dispersion and advection of the larvae off the coast of RC-SC. The RC_B zone had the greatest relative abundance of adult urchins, and according to the connectivity experiments, this zone retains a low number of particles. However, the area stands out for having the largest contribution of larvae to the other areas of RC-SC. Therefore, the RC_B zone can plausibly be considered as a source, but not as a sink, since it has marginal value as a source of larval recruitment. The RC_E zone is one of three zones with the greatest relative abundance of adults, and this same zone was coincidentally the zone with the greatest particle retention in the simulation experiments for the years 2013 and 2018.

Variation in the degree of larval recruitment can be modulated both by oceanographic aspects and characteristics of the early cycle of the species (duration of the planktonic phase, tolerance limits, or nutritional requirements). However, on average, all of the areas of the island evaluated in this study are connected, and thus support the hypothesis that the resident populations of *C. sylviae* constitute a single genetic population (Veliz et al. 2021). The mechanisms of retention and dispersal of planktonic organisms in the water column are important for understanding the genetics and connectivity of benthic populations in geographically isolated systems (Diaz-Cabrera et. al., 2023). Even though for species of echinoderms the patterns of vertical migration or swimming (Metaxas et al. 2020) have been reported, there are no research data for *C. sylviae*. Thus, future modeling studies should consider other fundamental aspects such as the shape of the pluteus larvae, since the extensions of the arms give it buoyancy as a mechanism to remain at shallower depths. Also, the capacity and swimming dynamics of the larvae, the physiological tolerance limits of both the adults and larvae, and other relevant factors determine not only the distribution patterns of the species but also the rates of mortality. Regarding the hydrodynamic models employed in the present study, it is recommended that future work consider the development of hydrodynamic models with higher spatial resolution to improve the resolution of the islands of the archipelago, the sub-mesoscale structures, and the local circulation patterns.

4.2 Environmental relationship

Another aspect to consider concerning the colonization of the sea urchins in the RC-SC is the impact of the 2010 tsunami. This event generated an uprising of the seabed, causing an increase in the concentration of dissolved organic matter in the water column in addition to the removal of a significant proportion of the fauna of the rocky intertidal zone, thus freeing up space for the potential recruitment of new individuals (Winckler et al. 2010). This could have facilitated the colonization of the subtidal substrates of algae species such as *Ulva spp.* This change in habitat could have provided a new food resource for the urchins, hence the demographic increase and the subsequent contribution to the progressive whitening of the island sea bottoms (Urabe & Nakashizuka, 2016). In contrast, the decrease in starfish by generations of fishermen could have also contributed to decreasing the control of the sea urchin population (J. Chamorro, personal communication). Even though large lobsters could play a role similar to that of starfish, the commercial exploitation of *J. frontalis* has resulted in the extraction of a high percentage of lobsters over the allowed size, thereby decreasing a potential biological control of the urchin population. Together, these elements outline a dynamic and complex panorama that may have contributed to the expansion of *C. sylviae* in the ecosystem (Riquelme, 2022).

4.3 Ecological factors

An important factor to consider is the possible interaction between adult urchins and Juan Fernandez's lobster. The coexistence of these two species raises questions concerning their potential ecological relationships (i.e., predation, resource competition), or the impact they may have on the community structure of the archipelago (Lafferty, 2004; Tegner & Levin, 1983). Changes in lobster fishing restrictions in the short and medium term could eventually contribute to the decrease in the population size of *C. sylviae* in the study area, since a greater biomass of predators (i.e., large lobsters) could increase the consumption of juveniles and small adult urchins (DiFiore & Stier, 2023). However, an increase in natural predators could result in a migration (both in depth and latitudinally) of adults to avoid predation in the long term (Farina et al. 2022). It is also important to note that although there are documented cases of predation of sea urchins by lobsters (i.e., *Jasus edwardsii* and *Centrostephanus rodgersii*) in Tasmania (Johnson et al. 2005), this does not imply that lobsters prefer urchins over other species. Lobsters that are distributed in sea urchin territory exhibit a greater consumption of urchins, but not at a level where they can control the growth of the urchin population (Smith et al. 2022), although this has not been studied in communities with a high degree of isolation as in the case of J. *frontalis* and *C. sylviae* in JFA. There are reports of decreased populations of sea urchins (*Strongylocentrotus droebachiensis*) due to the presence of starfish (*Pycnopodia*) and lobsters (*Homarus americanus*) (Mann & Breen, 1972), and thus these species could be key to the community structure present in the JFA. This suggests the need to evaluate management strategies based on ecosystem approaches using, for example, Intermediate complexity models (Blamey et al. 2014), end-to-end models such as ecopath with ecosim (Lozano-Montes et al. 2013) or Atlantis (Porobic et al. 2019). This will allow evaluation of the impact at the ecosystem level of strategies such as the removal of the urchins or the implementation of a maximum catch size of lobsters (Ernst et al. 2022). The fishermen have discussed such measures with the management committee (return of specimens >165 mm).

4.4 Toward managements and future work

This work highlights the need to develop models that include the interaction of *J. frontalis* and *C. sylviae*. However, the approach lacks information associated with the communities' structures by size and age. In addition, it is essential to fully understand the life history of this species in the JFA, in particular, that it can be an endemic species that is distributed in a highly isolated area. Laboratory and field experiments are required to evaluate the consumption of urchins by lobsters; genetic analysis of lobster feces can determine whether there is DNA of sea urchins and other types of analysis that clarify the complex dynamics of the *C. sylviae* population. In addition to the above, we emphasize the functionality of biophysical models coupled with ocean/individual-based models as robust and far-reaching approaches to help solve complex and dynamic problems. Finally, this study highlights the importance of generating management plans for species of socio-economic interest that include multi-specific ecological approaches.

Conclusión

A la luz de los antecedentes expuestos anteriormente, este trabajo establece lo siguiente:

Temporalmente a lo largo del período de estudio del programa de monitoreo biológico pesquero de las pesquerías y del ecosistema asociado al archipiélago Juan Fernández se identifican dos periodos claramente demarcados: 2015-2017 donde no se observan aumentos sustanciales en la abundancia relativa de erizos y 2018-2022 en los cuales se evidencia el aumento gradual y sostenido de la población de *C. sylviae* residente en RC-SC. En relación con la distribución espacial el >90% de los individuos se distribuye sobre los 100 m de profundidad. Además, los patrones de distribución espacial de ejemplares adultos de *C. sylviae* exhiben una mayor presencia de erizos en la región norte y noroeste de RC-SC coincidente con la zona menos expuesta.

De forma similar a la población adulta, los patrones espaciales de la distribución de los productos reproductivos de *C. sylviae* alrededor de las islas se concentran principalmente en la región norte y noroeste de RC-SC, pudiendo ser potenciales zonas de reclutamiento de la especie. Estos patrones están estrechamente influenciados por el particular régimen de circulación anticiclónica alrededor de las islas, por lo que la dinámica de las corrientes oceánicas superficiales sustenta la conectividad y retención de los productos reproductivos adultos de erizos de espinas largas que al asentarse darán lugar a la próxima cohorte en AJF.

A la luz de estudios de modelación con GLM se destaca para la dinámica poblacional de *C sylviae* sería explicada tanto por el factor temporal (año) como por la talla de *J. frontalis*. Respecto a esto último, esto implica que existiría una potencial interacción ecosistémica entre *J frontalis* y *C. sylviae* caracterizada por una mayor presencia de erizos asociada a langostas de talla pequeña. Si bien esta relación no prevalece por sobre el factor temporal para explicar los cambios en la población de erizos en RC-SC, podríamos estar percibiendo los remanentes de la señal de una relación predador-presa anterior y con ello histéresis ecosistémica. Es por lo anterior que sugerimos que dicha relación debe seguir explorándose en futuros trabajos, con enfoques de manejo ecológico que consideren la complejidad del ecosistema y la interdependencia entre las especies.

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APENDICE

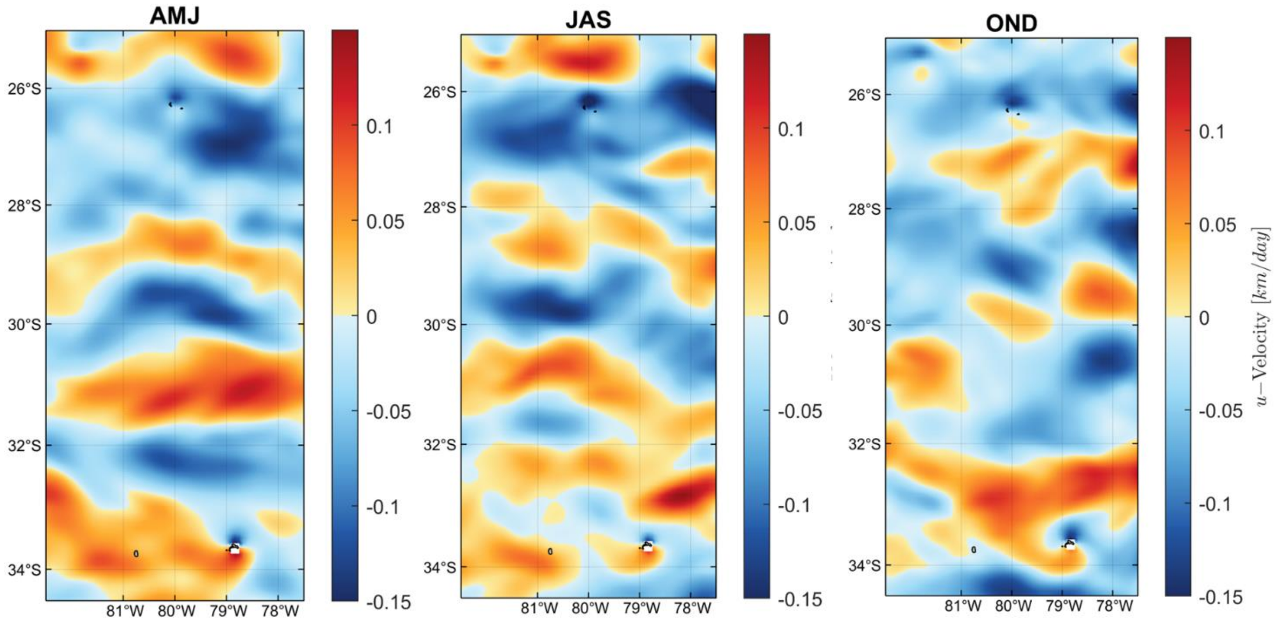

Figure S1. Zonal velocities (positive: east; negative: west) for the larval distribution period of *C. sylviae* (AMJ (autumn): April, May, and June; JAS (winter): July, August, and September; OND (spring): October, November, and December), averaged up to 100 (m) considering the study area (JFA-ID) for the year 2013. Data obtained from the Copernicus model.

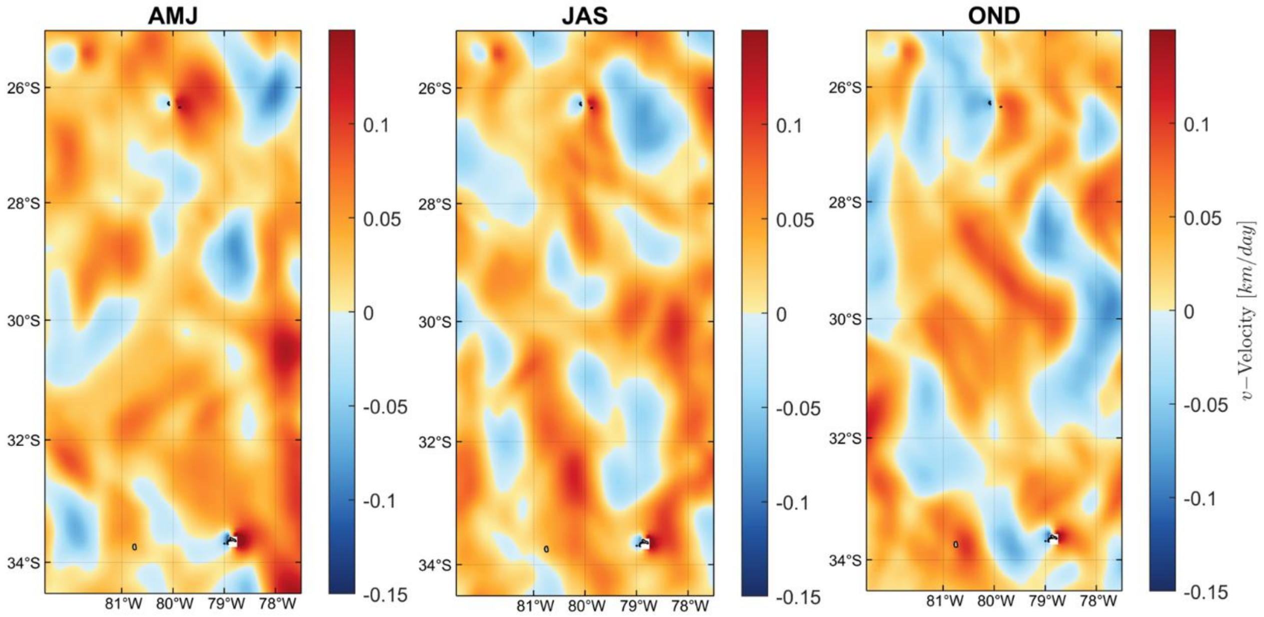

Figure S2. Meridional velocities: (positive: north; negative: south) for the larval distribution period of *C. sylviae* (AMJ (autumn): April, May, and June; JAS (winter): July, August, and September; OND (spring): October, November, and December), averaged up to 100 (m) considering the study area (JFA-ID) for the year 2013. Data obtained from the Copernicus model.

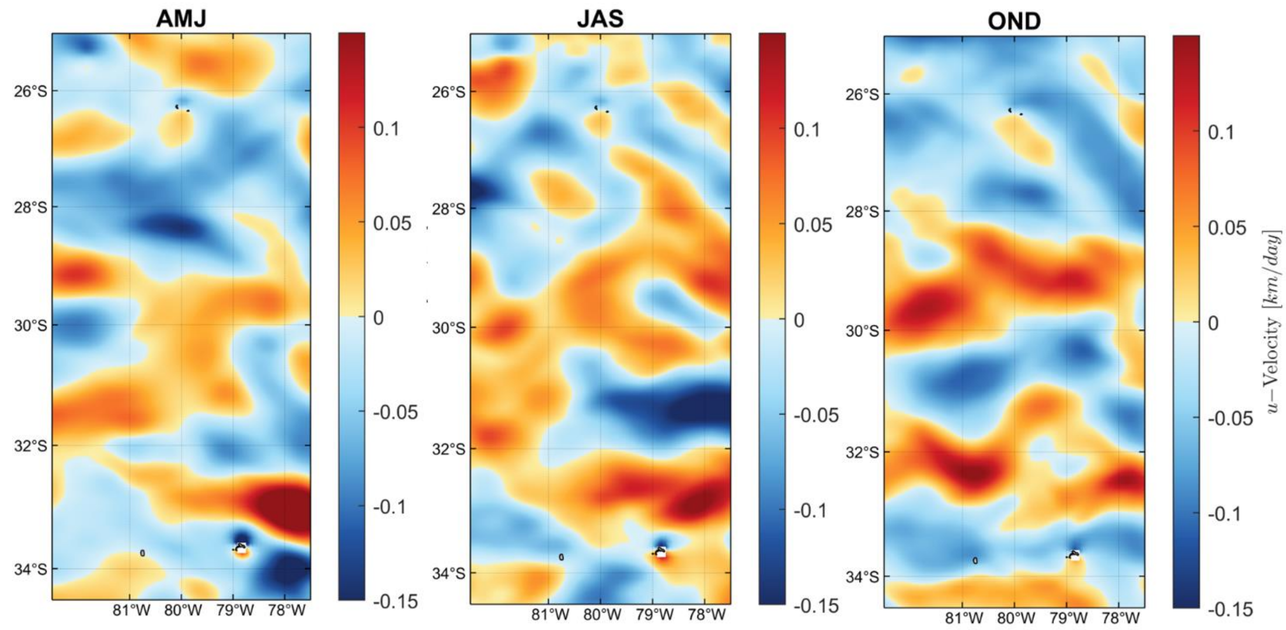

Figure S3. Zonal velocities (positive: east; negative: west) for the larval distribution period of *C. sylviae* (AMJ (autumn): April, May, and June; JAS (winter): July, August, and September; OND (spring): October, November, and December), averaged up to 100 (m) considering the study area (JFA-ID) for the year 2015. Data obtained from the Copernicus model.

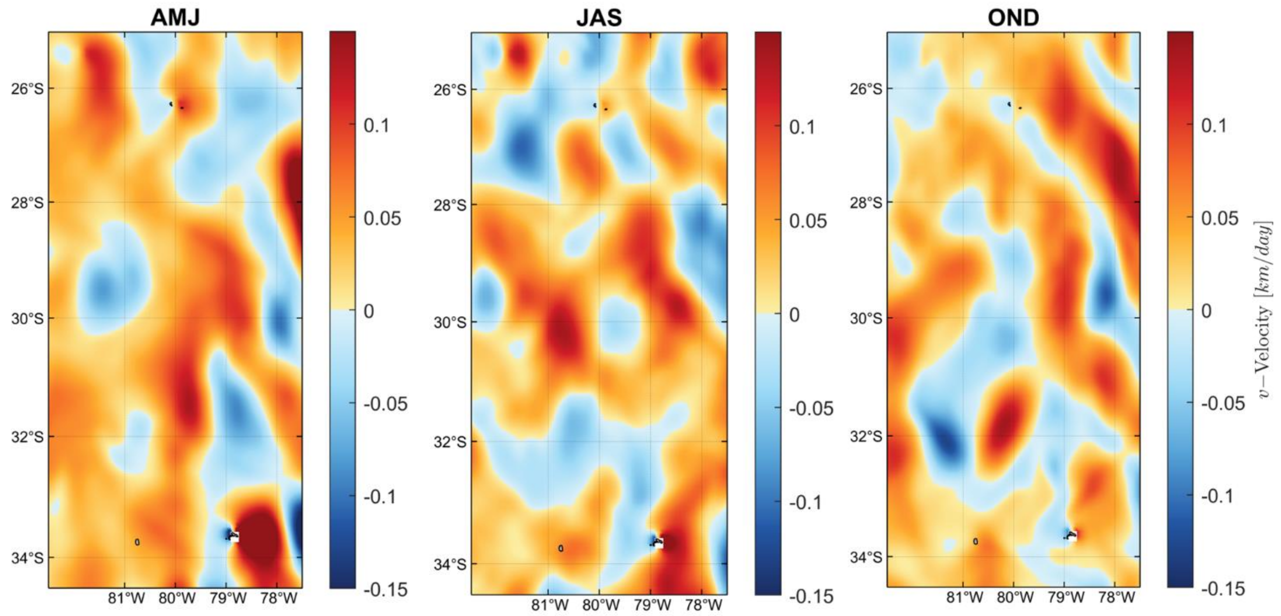

Figure S4. Meridional velocities: (positive: north; negative: south) for the larval distribution period of *C. sylviae* (AMJ (autumn): April, May, and June; JAS (winter): July, August, and September; OND (spring): October, November, and December), averaged up to 100 (m) considering the study area (JFA-ID) for the year 2015. Data obtained from the Copernicus model.

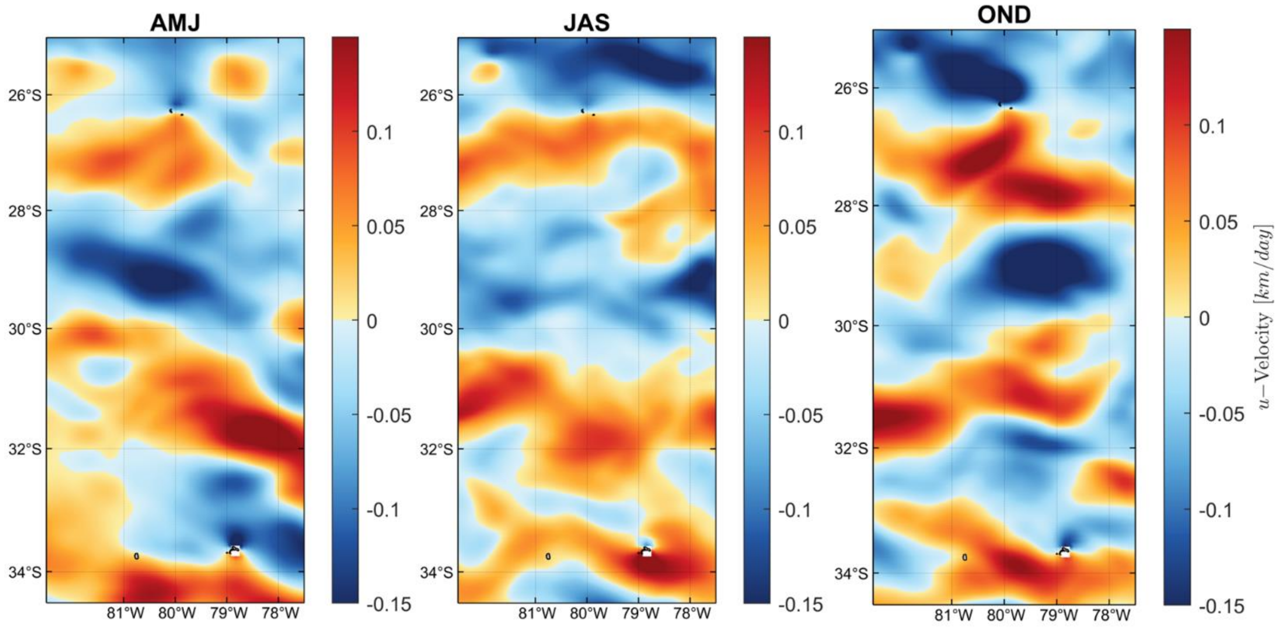

Figure S5. Zonal speeds (positive: east; negative: west) for the larval distribution period of *C. sylviae* (AMJ (autumn): April, May, and June; JAS (winter): July, August, and September; OND (spring): October, November, and December), averaged up to 100 (m) considering the study area (JFA-ID) for the year 2018. Data obtained from the Copernicus model.

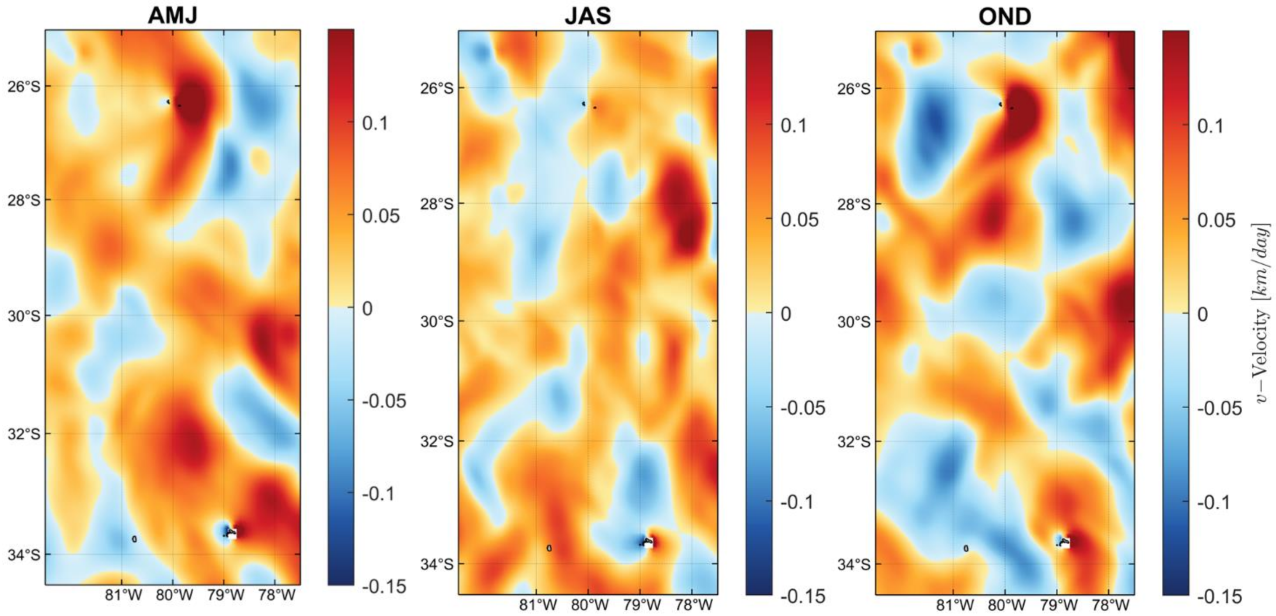

Figure S6. Meridional velocities: (positive: north; negative: south) for the larval distribution period of *C. sylviae* (AMJ (autumn): April, May, and June; JAS (winter): July, August, and September; OND (spring): October, November, and December), averaged up to 100 (m) considering the study area (JFA-ID) for the year 2018. Data obtained from the Copernicus model.

Table S1. Relative abundance of sea urchin GLM results from all zones separately. Results of models fit a relative abundance response variable (sea urchin) using simple (m) and multiple (M) regression models by zone, where the covariables are year factor (*aj*), month (*mk*) depth (*dm*) and rock lobster size (*sn*). AIC corresponds to Akaike information criteria and df to degrees of freedom.

	Simple regression				Multiple regression			
Zone	Model	Covariate	df	AIC	Model	Covariate	df	AIC
RC_A	m0	~1	3	3960	M0	~1	3	3960
	m1	~year	10	3712	M1	a_j	10	3712
	m2	~month	10	3881	M2	~a_j + m_k	17	3616
	m3	~depth	6	3881	M3	~a_j + m_k + d_m	20	3602
	m4	~size	4	3961	M4	~a_j + m_k + d_m+ s_n	21	3603
RC_B	m0	~1	3	743	M0	~1	3	743
	m1	~year	10	687	M1	~a_j	10	687
	m2	~month	10	746	M2	~a_j + m_k	17	690
	m3	~depth	6	748	M3	~a_j + m_k + d_m	20	695
	m4	~size	4	744	M4	~a_j + m_k + d_m+ s_n	21	690
RC_C	m0	~1	3	1122	M0	~1	3	1122
	m1	~year	10	1026	M1	~a_j	10	1026
	m2	~month	10	1093	M2	~a_j + m_k	17	996
	m3	~depth	6	1063	M3	~a_j + m_k + d_m	20	973
	m4	~size	4	1123	M4	~a_j + m_k + d_m + s_n	21	974
RC_D	m0	~1	3	1998	M0	~1	3	1998
	m1	~year	10	1881	M1	~a_j	10	1881
	m2	~month	10	1965	M2	~a_j + m_k	17	1856
	m3	~depth	6	1964	M3	~a_j + m_k + d_m	20	1842
	m4	~size	4	1997	M4	~a_j + m_k + d_m+ s_n	21	1842

RC_E	m0	~1	3	3203	M0	~1	3	3203
	m1	~year	10	2968	M1	$\sim a_j$	10	2968
	m2	~month	10	3181	M2	$\sim a_j + m_k$	17	2951
	m3	~depth	6	3056	M3	$\sim a_j + m_k + d_m$	20	2869
	m4	~size	4	3193	M4	$\sim a_j + m_k + d_m + s_n$	21	2865
RC_F	m0	~1	3	2648	M0	~1	3	2648
	m1	~year	10	2437	M1	$\sim a_j$	10	2437
	m2	~month	10	2628	M2	$\sim a_j + m_k$	17	2418
	m3	~depth	6	2516	M3	$\sim a_j + m_k + d_m$	20	2332
	m4	~size	4	2639	M4	$\sim a_j + m_k + d_m + s_n$	21	2332

Table S2. Summary table of generalized linear model results of the best fit model (M5). Results of the best model fit a relative abundance response variable (sea urchin) using multiple (M) regression models, where the covariables are year factor (*aj*), month (*mk*) depth (*dm*) and rock lobster size (*sn*). Bold and italic indicate the value of the estimate coefficients.

	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	-2.749585	0.337866	-8.138	4.02e-16 ***
Year2016	-0.480882	0.435621	-1.104	0.269636
Year2017	-0.307527	0.496053	-0.620	0.535291
Year2018	2.611183	0.300150	8.700	< 2e-16 ***
Year2019	2.385065	0.296267	8.050	8.25e-16 ***
Year2020	2.977225	0.292650	10.173	< 2e-16 ***
Year2021	***3.439955***	***0.288816***	***11.911***	***< 2e-16 ****
Year2022	3.124251	0.290086	10.770	< 2e-16 ***
Month11	-0.036285	0.123607	-0.294	0.769099
Month12	0.307601	0.117259	2.623	0.008709 **
Month1	0.399968	0.121214	3.300	0.000968 ***
Month2	0.154941	0.141579	1.094	0.273790
Month3	-0.365606	0.167649	-2.181	0.029199 *
Month4	-0.542347	0.193492	-2.803	0.005064 **
Month5	0.086300	0.278837	0.310	0.756941
RC_B	0.291956	0.164416	1.776	0.075780 .
RC_C	-0.384474	0.145698	-2.639	0.008319 **
RC_D	-1.193924	0.114742	-10.405	< 2e-16 ***
RC_E	-0.441501	0.098009	-4.505	6.65e-06 ***
RC_F	-0.928297	0.102084	-9.093	< 2e-16 ***

-100 (m)	0.004437	0.083299	0.053	< 2e-16 ***
-150 (m)	-2.178958	0.226464	-9.622	< 2e-16 ***
-200 (m)	-0.906151	0.602049	-1.505	0.132295
Size.small	0.167127	0.070002	2.387	0.016965 *

p value: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1